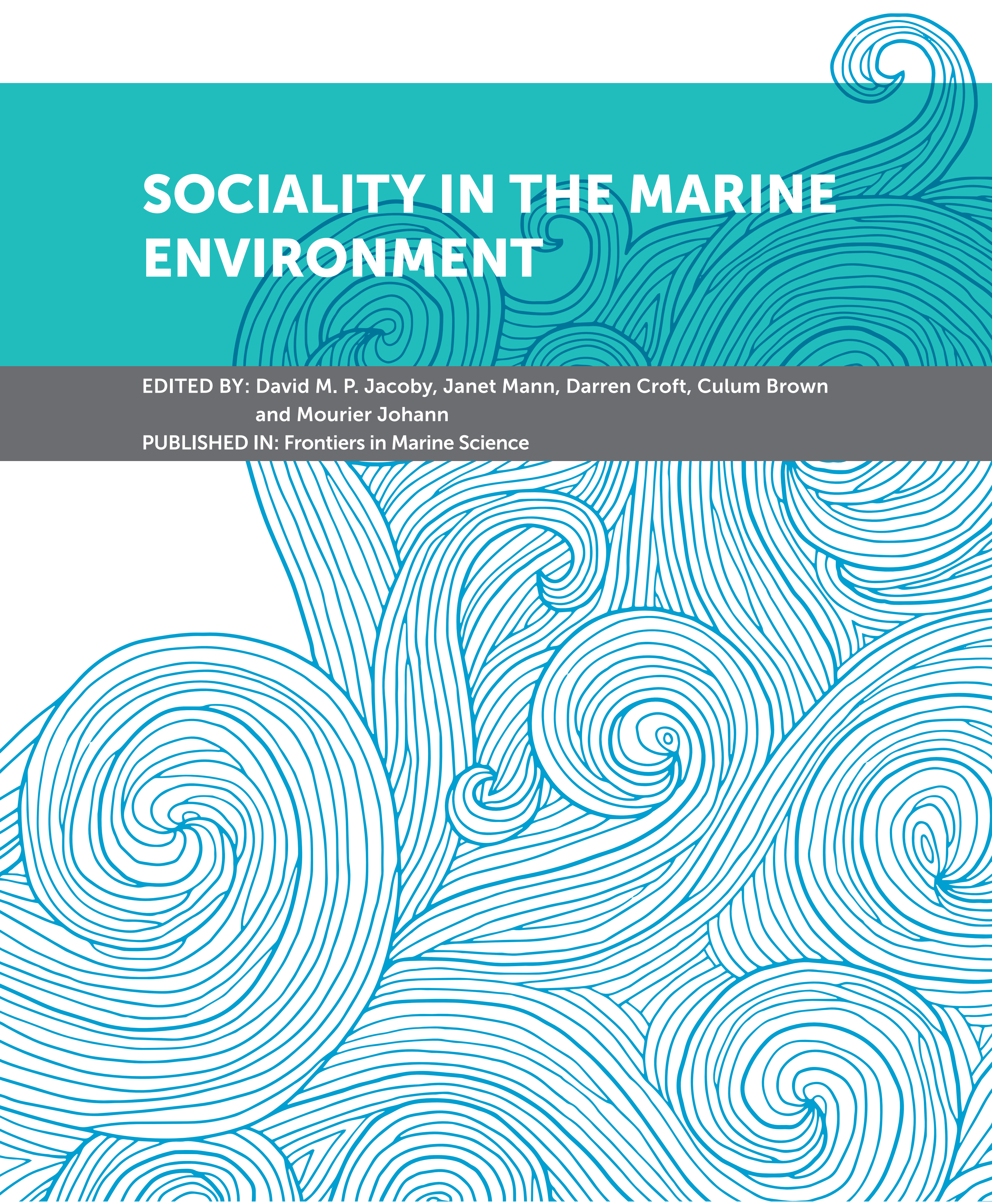


SOCIALITY IN THE MARINE ENVIRONMENT

EDITED BY: David M. P. Jacoby, Janet Mann, Darren Croft, Culum Brown
and Mourier Johann

PUBLISHED IN: Frontiers in Marine Science

frontiers Research Topics

ISSN 1664-8714
ISBN 978-2-88974-723-8
DOI 10.3389/978-2-88974-723-8

About Frontiers

Frontiers is more than just an open-access publisher of scholarly articles: it is a pioneering approach to the world of academia, radically improving the way scholarly research is managed. The grand vision of Frontiers is a world where all people have an equal opportunity to seek, share and generate knowledge. Frontiers provides immediate and permanent online open access to all its publications, but this alone is not enough to realize our grand goals.

Frontiers Journal Series

The Frontiers Journal Series is a multi-tier and interdisciplinary set of open-access, online journals, promising a paradigm shift from the current review, selection and dissemination processes in academic publishing. All Frontiers journals are driven by researchers for researchers; therefore, they constitute a service to the scholarly community. At the same time, the Frontiers Journal Series operates on a revolutionary invention, the tiered publishing system, initially addressing specific communities of scholars, and gradually climbing up to broader public understanding, thus serving the interests of the lay society, too.

Dedication to Quality

Each Frontiers article is a landmark of the highest quality, thanks to genuinely collaborative interactions between authors and review editors, who include some of the world's best academicians. Research must be certified by peers before entering a stream of knowledge that may eventually reach the public - and shape society; therefore, Frontiers only applies the most rigorous and unbiased reviews.
Frontiers revolutionizes research publishing by freely delivering the most outstanding research, evaluated with no bias from both the academic and social point of view. By applying the most advanced information technologies, Frontiers is catapulting scholarly publishing into a new generation.

What are Frontiers Research Topics?

Frontiers Research Topics are very popular trademarks of the Frontiers Journals Series: they are collections of at least ten articles, all centered on a particular subject. With their unique mix of varied contributions from Original Research to Review Articles, Frontiers Research Topics unify the most influential researchers, the latest key findings and historical advances in a hot research area! Find out more on how to host your own Frontiers Research Topic or contribute to one as an author by contacting the Frontiers Editorial Office: frontiersin.org/about/contact

SOCIALITY IN THE MARINE ENVIRONMENT

Topic Editors:
David M. P. Jacoby, University of Lancaster, United Kingdom
Janet Mann, Georgetown University, United States
Darren Croft, University of Exeter, United Kingdom
Culum Brown, Macquarie University, Australia
Mourier Johann, Institut de Recherche Pour le Développement (IRD), France

Citation: Jacoby, D. M. P., Mann, J., Croft, D., Brown, C., Johann, M., eds. (2022). Sociality in the Marine Environment. Lausanne: Frontiers Media SA.
doi: 10.3389/978-2-88974-723-8

Table of Contents

05 ***Editorial: Sociality in the Marine Environment***
David M. P. Jacoby, Culum Brown, Darren P. Croft, Janet Mann and Johann Mourier

09 ***Heterarchy Reveals Social Organization of a Smooth Stingray (*****Bathytoshia brevicaudata*****) Population in a Provisioned Food Context***
Joni Pini-Fitzsimmons, Nathan A. Knott and Culum Brown

19 ***The Next Frontier in Understanding the Evolution of Coral Reef Fish Societies***
Theresa Rueger, Rebecca Branconi, Catheline Y. M. Froehlich, Siobhan J. Heatwole, Marian Y. L. Wong and Peter M. Buston

37 ***Intra-Population Variability in Group Size of Indo-Pacific Humpback Dolphins (*****Sousa chinensis*****)***
Mingming Liu, Mingli Lin, David Lusseau and Songhai Li

47 ***High-Throughput Tracking of Social Networks in Marine Fish Populations***
Eneko Aspillaga, Robert Arlinghaus, Martina Martorell-Barceló, Margarida Barcelo-Serra and Josep Alós

59 ***Companions and Casual Acquaintances: The Nature of Associations Among Bull Sharks at a Shark Feeding Site in Fiji***
Thibaut Bouveroux, Nicolas Loiseau, Adam Barnett, Natasha D. Marosi and Juerg M. Brunnschweiler

70 ***Dynamics of Cetacean Mixed-Species Groups: A Review and Conceptual Framework for Assessing Their Functional Significance***
Jonathan Syme, Jeremy J. Kiszka and Guido J. Parra

89 ***Diversity and Consequences of Social Network Structure in Toothed Whales***
Michael N. Weiss, Samuel Ellis and Darren P. Croft

104 ***Environmental Reconstruction and Tracking as Methods to Explore Social Interactions in Marine Environments: A Test Case With the Mediterranean Rainbow Wrasse*** **Coris julis**
Zoë Goverts, Paul Nührenberg and Alex Jordan

114 ***Social Network Analysis Reveals the Subtle Impacts of Tourist Provisioning on the Social Behavior of a Generalist Marine Apex Predator***
David M. P. Jacoby, Bethany S. Fairbairn, Bryan S. Frazier, Austin J. Gallagher, Michael R. Heithaus, Steven J. Cooke and Neil Hammerschlag

126 ***Non-random Co-occurrence of Juvenile White Sharks (*****Carcharodon carcharias*****) at Seasonal Aggregation Sites in Southern California***
James M. Anderson, Alyssa J. Clevenstine, Brian S. Stirling, Echelle S. Burns, Emily N. Meese, Connor F. White, Ryan K. Logan, John O'Sullivan, Patrick T. Rex, Jack May (III), Kady Lyons, Chuck Winkler, Emiliano García-Rodríguez, Oscar Sosa-Nishizaki and Christopher G. Lowe

140 ***Group Size of Indo-Pacific Humpback Dolphins (*****Sousa chinensis*****): An Examination of Methodological and Biogeographical Variances***
Mingming Liu, Mingli Lin, Xiaoming Tang, Lijun Dong, Peijun Zhang, David Lusseau and Songhai Li

152 ***Social Behaviour of Humpback Whales (*****Megaptera novaeangliae*****) in Hervey Bay, Eastern Australia, a Preferential Female Stopover During the Southern Migration***
Trish Franklin, Wally Franklin, Lyndon Brooks, Peter Harrison, Adam A. Pack and Phillip J. Clapham

169 ***Socially Complex Breeding Interactions in Humpback Whales are Mediated Using a Complex Acoustic Repertoire***
Dana A. Cusano, David Paton, Michael J. Noad and Rebecca A. Dunlop

frontiers in Marine Science

EDITORIAL
published: 28 February 2022
doi: 10.3389/fmars.2022.863595

Editorial: Sociality in the Marine Environment

David M. P. Jacoby[1,2*†], **Culum Brown**[3†], **Darren P. Croft**[4†], **Janet Mann**[5†] and **Johann Mourier**[6†]

[1] Lancaster Environment Centre, Lancaster University, Lancaster, United Kingdom, [2] Institute of Zoology, Zoological Society of London, London, United Kingdom, [3] Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia, [4] Centre for Research in Animal Behaviour, College of Life and Environmental Sciences, University of Exeter, Exeter, United Kingdom, [5] Department of Biology, Georgetown University, Washington, DC, United States, [6] UMS 3514 Plateforme Marine Stella Mare, Université de Corse Pasquale Paoli, Biguglia, France

Keywords: grouping, social organization, network structure, interactions, marine societies, tracking

Edited and reviewed by:
Angel Borja,
Technological Center Expert in Marine and Food Innovation (AZTI), Spain

***Correspondence:**
David M. P. Jacoby
d.jacoby@lancaster.ac.uk

†ORCID:
David M. P. Jacoby
orcid.org/0000-0003-2729-3811
Culum Brown
orcid.org/0000-0002-0210-1820
Darren P. Croft
orcid.org/0000-0001-6869-5097
Janet Mann
orcid.org/0000-0003-0664-175X
Johann Mourier
orcid.org/0000-0001-9019-1717

Specialty section:
This article was submitted to Marine Ecosystem Ecology, a section of the journal Frontiers in Marine Science

Received: *27 January 2022*
Accepted: *07 February 2022*
Published: *28 February 2022*

Citation:
Jacoby DMP, Brown C, Croft DP, Mann J and Mourier J (2022) Editorial: Sociality in the Marine Environment. Front. Mar. Sci. 9:863595. doi: 10.3389/fmars.2022.863595

Editorial on the Research Topic

Sociality in the Marine Environment

INTRODUCTION

Sociality is ubiquitous within the animal kingdom (Krause and Ruxton, 2002). It is well-established that social behavior serves a range of important evolutionary and ecological functions, from coordinating collective behaviors, maintaining group cohesion, and reducing predation risk to facilitating cooperation, reproduction, and establishing dominance hierarchies (Krause et al., 2007; Croft et al., 2008; Schürch et al., 2010; Shizuka and McDonald, 2012). Despite this, our current understanding of the structure, function, and mechanisms underpinning animal societies is disproportionately biased toward terrestrial species. Sociality however, occurs broadly across a diversity of marine taxa, some of which may hold the key to revealing the evolutionary origins of tetrapod social behavior.

But how do marine societies establish themselves, how do animals find and communicate with one another and how are long-lasting social bonds formed and maintained in such a dynamic environment? For example, sound travels efficiently over long distances in the marine environment, but visual signaling tends to be limited to very short distances. The basic physical properties of the marine environment hamper our ability to accurately estimate the size and structure of aggregations in marine animals, let alone determine how bonds are formed, maintained, and disrupted. Considering recent technological and analytical developments, this Research Topic (RT) is intended to showcase the very latest progress in revealing the complex social lives of marine organisms, from large-bodied migratory cetaceans to small territorial reef fishes. Bringing together 69 researchers from 55 institutions/organizations and 13 countries, the RT explores in 13 manuscripts the challenge of measuring meaningful associations in different species, while considering the biological, reproductive, and environmental drivers that structure marine animal groups. Contributions to this RT also reflect on anthropogenic effects that may impact how animals socialize underwater. While the indelible footprint of human activities on our marine ecosystems remains far from fully understood (Halpern et al., 2019; Elliott et al., 2020), these studies complement the wider literature facilitating a better understanding of population-scale processes that structure marine assemblages, an endeavor crucial to marine and species conservation moving forwards (Villegas-Ríos et al., 2022).

MEASURING ASSOCIATIONS

In many instances, associations between organisms are defined based on the proximity between pairs of individuals and the longevity or frequency of this proximity (Franks et al., 2010; Haddadi et al., 2011). For large, migratory species like some cetaceans however, associations can be mediated over considerably greater distances via complex acoustic repertoires that underpin sophisticated social communities and even cultures (Rendell and Whitehead, 2001). While previous work on humpback whales (*Megaptera novaeangliae*) for example, focuses almost exclusively on the feeding (e.g., Allen et al., 2013) or breeding grounds (e.g., Pack et al., 2009), Franklin et al. offer insights into the apparent "black box" of humpback social behavior during their southern migration. Non-agonistic social behaviors associated with resting, gestation, and parental care, appear more prevalent than agonistic competitive social behaviors, reflecting largely the demography (i.e., few mature males) of the groups that form there (Franklin et al.). Cusano et al. however, undertake acoustic recordings at breeding grounds to shed light on how complex repertoires of acoustic signaling in *M. novaeangliae* mediate conflict and aggression when mature males are in direct competition for mates. They report that vocal repertoire and visual displays increased in complexity within "high intensity" groups with frequent turnover.

Clearly defined associations, that consider both the ecological and environmental context in which these associations occur, are at the core of any study into animal social behavior (Farine and Whitehead, 2015; He et al., 2019; Seebacher and Krause, 2019; Sosa et al., 2021). Consequently, this RT was intended to sit at the interface between methodological and ecological developments (**Figure 1**). Aspillaga et al. track the trajectories of 232 pearly razorfish (*Xyrichtys novacula*) using a state-of-the-art, high-resolution acoustic telemetry system to demonstrate harem-like social structure within this small coastal wrasse. Measuring associations from paired proximities down to a scale of 1 m, social organization was hypothesized to be underpinned by male agonistic behaviors (Aspillaga et al.). Further emphasizing the link between movement and social behavior, a study on the Mediterranean Rainbow Wrasse (*Coris julis*) used *in situ* displacement experiments, focal follows, and stereo-videography to measure female aggression toward displaced neighboring (low aggression) and non-neighboring (high aggression) female conspecifics routing back toward their own territories (Goverts et al.).

GROUP SIZE, STRUCTURE, AND COMPOSITION

The size of animal groups can have far-reaching implications for individual social behavior, as well as population-level social structure; in fact, it is often controlled for, both experimentally and analytically, in studies of animal social networks (Croft et al., 2011). Determining group size underwater however can be difficult. When studying the surface behavior of marine cetaceans, photo ID, and observer-based counts are frequently used to quantify groups. Yet a comparative study by Liu, Lin, Tang, et al. demonstrates that group size estimates using both approaches, can be biased by a combination of methodological and biogeographical variances. From data on Indo-Pacific humpback dolphins (*Sousa chinensis*), Liu, Lin, Lusseau, et al. document how variable group size can be within a population displaying fission-fusion behavior. Group size appeared to vary both seasonally and inter-annually, as well as in response to the number of mother-calf pairs present (Liu, Lin, Lusseau, et al.), reiterating behavioral segregation in some cetacean species groups (Galezo et al., 2018). Given the degree of both intra-species and intra-population group size variability and composition, it remains challenging to establish the functional significance and mechanistic drivers of sociality in many species. The link between this variation itself and other ecological variables however, might also help reveal social mechanisms in future studies.

Sociality can extend beyond one's species. For example, birds (Sridhar et al., 2009) and a range of mammals (Goodale et al., 2017) are often in mixed species groups (MSG). In reviewing 203 studies on the functional significance of cetacean MSG, Syme et al. thus argue for better standardization of methods, and put forward a conceptual framework that outlines more distinct, shared terminology across studies of MSGs. This is vital as mixed-species associations will impact the costs and benefits of group living.

Given the difficulties in tracking wide-ranging marine organisms, other species, such as coral reef fishes, can shed light on the evolutionary foundations of marine sociality. Rueger et al. offer a comprehensive journey through the past two decades of developments in this area; their review explores ways in which some reef fishes have become model species with which to test fundamental theories of social evolution including kin selection, cooperative breeding, and sociality with mutualistic partner species (Rueger et al.).

Throughout this RT, social network analyses (SNA) have played a prominent role in better understanding marine sociality. An extensive systematic review of social network structure in toothed whales (Odontoceti), reveals the unifying feature of this group as having relatively densely connected, population-level social networks, with fairly rapid fission-fusion dynamics. Based on a subset of species within this group that have been well-studied (pilot whales, killer whales, sperm whales, and bottlenose dolphins), networks were typically mixed sex units of maternal kin (Weiss et al.). In another well-studied marine predator, Anderson et al. utilize acoustic telemetry and SNA to demonstrate non-random and non-resource-driven, co-occurrences, and community structuring amongst juvenile white sharks (*Carcharodon carcharias*), suggesting that even in wide-ranging, fission-fusion apex predators, group membership during early ontogeny may serve important ecological functions in later life.

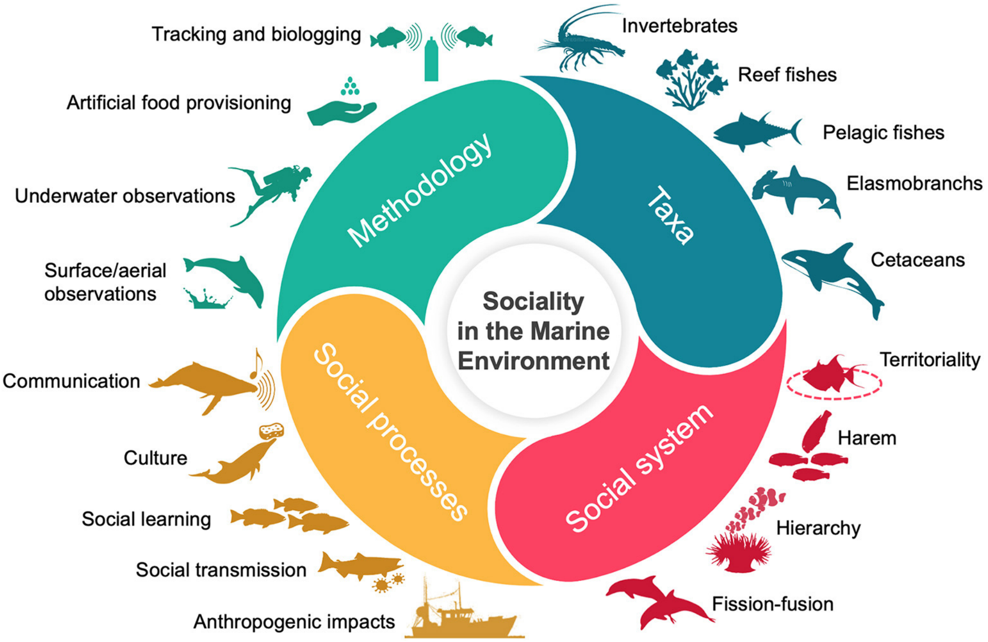


FIGURE 1 | The diversity of sociality in marine species. This RT collates papers from a broad range of species, with different social systems that occupy diverse habitat types. There is an emphasis on the technological and analytical developments required to explore the implications of sociality in the context of ecology, evolution, and conservation within an environment that is increasingly impacted by human activities.

ANTHROPOGENIC INFLUENCES ON SOCIALITY

Undeniably, humans are altering the marine environment, from ocean chemistry (Andersson et al., 2005) and reef habitat complexity (Perry and Alvarez-Filip, 2019), to marine soundscapes (Duarte et al., 2021). In an attempt to better connect people with some of the many threats facing the marine environment and its fauna, diving, and boat-based ecotourism has exploded in recent decades. This RT pulls together three studies that reflect on both the opportunities offered and potential consequences of tourism on the structure and behavior of elasmobranchs provisioned with food for tourists. Jacoby et al. explore aggregation behavior and the distinct social preferences of wide-ranging tiger sharks (*Galeocerdo cuvier*) gathering at a tourism provisioning site. Aggregations were longer lasting and more frequent, and gregariousness more variable at tourist sites, although non-random social preferences occurred outside of the tourism season and were highly variable between individuals potentially mitigating any long-lasting impacts of tourism (Jacoby et al.). Two further studies took advantage of tourism activities to quantify inter-individual interactions and hierarchies in species that would be difficult under "normal" wild conditions. From 13 years of dive observation and photo ID data, Bouveroux et al. show preferred, long-term companionships in another apex predatory elasmobranch, the bull shark (*Carcharhinus leucas*), also measured using SNA that control for potential non-social drivers of aggregation. Avoidance behavior was also observed in this species, suggestive of a potential dominance hierarchy when food is made available. The question of social dominance is explicitly tested by Pini-Fitzsimmons et al., who combine social network theory and hierarchy (heterarchy) to explore the agonistic social interactions of smooth stingrays (*Bathytoshia brevicaudata*) competing for food provisioned at a shallow, coastal location. Heterarchy reveals a relatively stable, linear dominance hierarchy in this species, with social network structure centered around one particularly dominant individual, interestingly not the largest.

CONCLUSION

The diversity of methods and study species presented within this RT is testament to burgeoning interest within marine ecology, to understand how population dynamics can be mediated by social behavior (**Figure 1**). A number of these papers call for more standardized terminology and procedure to better facilitate comparative analyses that explore the evolutionary mechanisms underpinning such widespread social function in marine organisms. Technological developments and associated analyses will continue to assist with the remote measurement of associations and interactions between individuals and at the appropriate scale. This will be key, as we attempt to understand and mitigate the potential impacts of widespread climate-related change to most marine habitats in the near future.

AUTHOR CONTRIBUTIONS

DJ conceived the idea for the RT and provided the first draft of the manuscript. JMourier created **Figure 1**. All authors contributed to the final version.

ACKNOWLEDGMENTS

We thank all the authors that have contributed to this RT, as well as the Frontiers in Marine Science editorial staff for their support. DJ was funded by the Bertarelli Foundation through the Bertarelli Programme in Marine Science.

REFERENCES

Allen, J., Weinrich, M., Hoppitt, W., and Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science* 340, 485–488. doi: 10.1126/science.1231976

Andersson, A. J., MacKenzie, F. T., and Lerman, A. (2005). Coastal ocean and carbonate systems in the high CO_2 world of the anthropocene. *Am. J. Sci.* 305, 875–918. doi: 10.2475/ajs.305.9.875

Croft, D. P., James, R., and Krause, J. (2008). *Exploring Animal Social Networks*. Princeton, NJ; Oxford: Princeton University Press.

Croft, D. P., Madden, J. R., Franks, D. W., and James, R. (2011). Hypothesis testing in animal social networks. *Trends Ecol. Evol.* 26, 502–507. doi: 10.1016/j.tree.2011.05.012

Duarte, C. M., Chapuis, L., Collin, S. P., Costa, D. P., Devassy, R. P., Eguiluz, V. M., et al. (2021). The soundscape of the Anthropocene ocean. *Science* 371, eaba4658. doi: 10.1126/science.aba4658

Elliott, M., Borja, A., and Cormier, R. (2020). Activity-footprints, pressures-footprints and effects-footprints – walking the pathway to determining and managing human impacts in the sea. *Mar. Pollut. Bull.* 155, 111201. doi: 10.1016/j.marpolbul.2020.111201

Farine, D. R., and Whitehead, H. (2015). Constructing, conducting, and interpreting animal social network analysis. *J. Anim. Ecol.* 84, 1144–1163. doi: 10.1111/1365-2656.12418

Franks, D. W., Ruxton, G. D., and James, R. (2010). Sampling animal association networks with the gambit of the group. *Behav. Ecol. Sociobiol.* 64, 493–503. doi: 10.1007/s00265-009-0865-8

Galezo, A. A., Krzyszczyk, E., and Mann, J. (2018). Sexual segregation in Indo-Pacific bottlenose dolphins is driven by female avoidance of males. *Behav. Ecol.* 29, 377–386. doi: 10.1093/beheco/arx177

Goodale, E., Beauchamp, G., and Ruxton, G. D. (2017). *Mixed-Species Groups of Animals: Behavior, Community Structure, and Conservation*. London: Academic Press.

Haddadi, H., King, A. J., Wills, A. P., Fay, D., Lowe, J., Morton, A. J., et al. (2011). Determining association networks in social animals: choosing spatial-temporal criteria and sampling rates. *Behav. Ecol. Sociobiol.* 65, 1659–1668. doi: 10.1007/s00265-011-1193-3

Halpern, B. S., Frazier, M., Afflerbach, J., Lowndes, J. S., Micheli, F., O'Hara, C., et al. (2019). Recent pace of change in human impact on the world's ocean. *Sci. Rep.* 9, 11609. doi: 10.1038/s41598-019-47201-9.

He, P., Maldonado-Chaparro, A. A., and Farine, D. R. (2019). The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. *Behav. Ecol. Sociobiol.* 73, 9. doi: 10.1007/s00265-018-2602-7

Krause, J., Croft, D. P., and James, R. (2007). Social network theory in the behavioural sciences: potential applications. *Behav. Ecol. Sociobiol.* 62, 15–27. doi: 10.1007/s00265-007-0445-8

Krause, J., and Ruxton, G. D. (2002). *Living in Groups*. Oxford: Oxford University Press.

Pack, A. A., Herman, L. M., Spitz, S. S., Hakala, S., Deakos, M. H., and Herman, E. Y. K. (2009). Male humpback whales in the Hawaiian breeding grounds preferentially associate with larger females. *Anim. Behav.* 77, 653–662. doi: 10.1016/j.anbehav.2008.11.015

Perry, C. T., and Alvarez-Filip, L. (2019). Changing geo-ecological functions of coral reefs in the anthropocene. *Funct. Ecol.* 33, 976–988. doi: 10.1111/1365-2435.13247

Rendell, L., and Whitehead, H. (2001). Culture in whales and dolphins. *Behav. Brain Sci.* 24, 309–382. doi: 10.1016/B978-0-12-373553-9.00068-7

Schürch, R., Rothenberger, S., and Heg, D. (2010). The building-up of social relationships: behavioural types, social networks and cooperative breeding in a cichlid. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 4089–4098. doi: 10.1098/rstb.2010.0177

Seebacher, F., and Krause, J. (2019). Epigenetics of social behaviour. *Trends Ecol. Evol.* 34, 818–830. doi: 10.1016/j.tree.2019.04.017

Shizuka, D., and McDonald, D. B. (2012). A social network perspective on measurements of dominance hierarchies. *Anim. Behav.* 83, 925–934. doi: 10.1016/j.anbehav.2012.01.011

Sosa, S., Jacoby, D. M. P., Lihoreau, M., and Sueur, C. (2021). Animal social networks : towards an integrative framework embedding social interactions, space and time. *Methods Ecol. Evol.* 2021, 4–9. doi: 10.1111/2041-210X.13539

Sridhar, H., Beauchamp, G., and Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim. Behav.* 78, 337–347. doi: 10.1016/j.anbehav.2009.05.008

Villegas-Ríos, D., Jacoby, D. M. P., and Mourier, J. (2022). Social networks and the conservation of fish. *Commun. Biol* (In press). doi: 10.1038/s42003-022-03138-w

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 29 April 2021
doi: 10.3389/fmars.2021.641761

Heterarchy Reveals Social Organization of a Smooth Stingray (*Bathytoshia brevicaudata*) Population in a Provisioned Food Context

Joni Pini-Fitzsimmons[1]*, Nathan A. Knott[2] and Culum Brown[1]

[1] Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia, [2] Marine Ecosystems Unit, New South Wales Department of Primary Industries, Huskisson, NSW, Australia

Edited by:
Yannis Peter Papastamatiou,
Florida International University,
United States

Reviewed by:
Guillaume Rieucau,
Louisiana Universities Marine Consortium, United States
Allison Johnson,
University of Nebraska-Lincoln,
United States

****Correspondence:***
Joni Pini-Fitzsimmons
joni.fitzsimmons@gmail.com

Specialty section:
This article was submitted to Marine Megafauna, a section of the journal Frontiers in Marine Science

Received: *14 December 2020*
Accepted: *08 April 2021*
Published: *29 April 2021*

Citation:
Pini-Fitzsimmons J, Knott NA and Brown C (2021) Heterarchy Reveals Social Organization of a Smooth Stingray (Bathytoshia brevicaudata) Population in a Provisioned Food Context. Front. Mar. Sci. 8:641761. doi: 10.3389/fmars.2021.641761

The advent of new technologies and statistical analyses has provided valuable insights into chondrichthyan social behavior. It has become apparent that sharks and rays lead more complex social lives than previously believed. Heterarchy combines hierarchy and social network theory and although it is not a new concept, it is rarely applied to animal social interactions. Here, we applied heterarchy to a case study involving smooth stingrays foraging for fish scraps at boat ramp in Jervis Bay, NSW Australia. We took advantage of their attraction to this site to examine their social behavior during agonistic interactions over the provisioned resource. We observed a stable, relatively linear but shallow dominance hierarchy that was highly transitive dominated by a single individual. Social network analysis revealed a non-random social network centered on the dominant individual. Contrary to previous research, size did not predict dominance, but it was correlated with network centrality. The factors determining dominance of lower ranks were difficult to discern, which is characteristic of despotic societies. This study provides the first heterarchical assessment of stingray sociality, and suggests this species is capable of complex social behavior. Given higher dominance and centrality relate to greater access to the provisioned resource, the observed social structure likely has fitness implications.

Keywords: social network analysis, social organization, dominance, heterarchy, batoidea

INTRODUCTION

The nature of social relationships is dynamic across time and space, and can be altered by individual experience, position within the group, group composition, and context (Sih et al., 2009). The complexity of how these factors interact makes the quantitative assessment of social behavior challenging. Historically, there have been two approaches to disentangle complex social relationships. The first views social interactions through examination of hierarchy structure, which views the world as partially ordered by bottom-up and top-down (i.e., vertical) control mechanisms. The second is a network perspective which identifies nodes (individuals) and the interactions between them as links between nodes (i.e., horizontal peer-to-peer interactions). Both have a long history of use in a wide range of fields (Cumming, 2016). Examining social interactions through the hierarchy lens, for example, has been particularly valuable in understanding social behavior in chickens who can readily recognize dominant individuals and avoid them in future encounters (Gottier, 1968). Recent improvements in social network theory and analysis, in contrast, have substantially broadened our understanding of the transfer of information or disease through populations (e.g., in sharks: Papastamatiou et al., 2020; e.g., in fruit flies: Pasquaretta et al. (2016); see also Farine and Whitehead, 2015; Farine, 2017). While these two approaches are equally valid, there is value in combining both in a unified theory that brings together top-down, bottom-up and peer-to-peer interactions. The combined use of hierarchy and network assessment is known as "heterarchy" (Cumming, 2016), and even though it has only recently been adopted to understand biological systems, heterarchy has already provided novel insights into many aspects of animal behavior, including mating tactics, competition, cooperation, social learning, and information transfer (Sih et al., 2009).

Pairwise interactions are the fundamental building blocks of social structures (Whitehead et al., 2005). Agonistic interactions over limited resources, such as mates, shelter, or food, are of particular interest because access to these resources is key to individual fitness. The primary method of quantifying social interactions in these agonistic contexts is to generate a dominance hierarchy by ranking individuals based on the proportion of their successes (dominant individual or interactions won), failures (subordinate individual or lost interactions) and drawn (neutral) interactions. Dominance structures in social species fall along the "egalitarian" – "despotic" spectrum. These terms describe the degree to which dyadic agonistic interactions are asymmetrical (a clear dominant and subordinate) (Vehrencamp, 1983). Within egalitarian societies, dominant individuals are more tolerant of other individuals, subordinates exhibit more retaliation, and post-conflict reconciliation is more common (Flack and de Waal, 2004), and therefore the dominance structure has weak linearity and a shallow gradient (de Vries et al., 2006). By contrast, despotic societies are characterized by higher levels of aggression, minimal counter-aggression, and are ruled by a single dominant individual (alpha). Despotic societies can take two forms: (i) high levels of aggression between each individual and their immediate subordinate, characterized by strong linearity and a steep dominance gradient (de Vries et al., 2006); or (ii) high levels of aggression between the alpha and all subordinates, with subordinates exhibiting similar dominance ranks (Beaugrand et al., 1984). The latter is characterized by weak linearity and low dominance gradients, making it difficult to distinguish from egalitarian societies. It is here that the addition of social network analysis, using the heterarchical framework, can be of particular value by distinguishing the two. Social networks represent the peer-to-peer relationships between individuals and various metrics can be calculated to characterize individuals or the network as a whole (Farine and Whitehead, 2015). In despotic societies, high values for egocentric metrics such as eigenvector centrality (individuals' influence over the entire network) and strength (number of interactions with other individuals) are expected for the most dominant individual, while low values are expected for all others.

The social behavior of sharks and rays is rarely studied and they have historically been considered solitary animals. It is becoming evident, however, that grouping in many species of elasmobranchs is common (e.g., Bass et al., 2016), as are complex social behaviors (e.g., Sims et al., 2000; Furst, 2011; Mourier et al., 2017a; Papastamatiou et al., 2020). Elasmobranch species that group often exhibit both social congregation (i.e., for reproduction, e.g., Port Jackson sharks (*Heterondontus portusjacksonii*), Bass et al., 2016) and non-social aggregation (i.e., attraction to limited resources; e.g., white (*Carcharodon carcharias*) and tiger sharks (*Galeocardo cuvier*), Clua et al., 2013). In some cases, non-social grouping may also be a condition under which social grouping later develops [e.g., basking sharks (*Cetorhinus maximus*) Sims et al., 2000]. Consistent social interactions can facilitate social learning (Guttridge et al., 2013), which in turn influences social cohesion and robustness to perturbations such as fishing pressure (Mourier et al., 2017b). Formal assessment of elasmobranch social behavior, however, is still in its infancy (Jacoby et al., 2011). Research is further hindered by sharks and rays being inherently elusive, precluding the use of classical study approaches to examine their social behavior using direct observation (Brena et al., 2018), resulting in a lack of information about their behavior. Temporary aggregations competing over limited resources (e.g., food), however, provide unique opportunities to gain insights into their inter- and intra-specific interactions (Dudley et al., 2000; Dicken, 2008; Clua et al., 2013), which can be characterized through a heterarchical framework (e.g., Brena et al., 2018). The provisioning of sharks and rays by humans, which is common in elasmobranch "eco-tourism," has afforded tractable avenues to study sociality in these species (Newsome et al., 2004; Sperone et al., 2010; Maljković and Côté, 2011). For example, Furst (2011) showed that provisioned pink whiprays (*Pateobatis fai,* former: *Himantura* sp.) in Mo'orea, French Polynesia exhibited a strong dominance hierarchy based on size, sex, and color. Similarly, Brena et al. (2018) used heterarchy to examine social behavior in sicklefin lemon sharks (*Negaprion acutidens*) when competing for food and found that morphology seemed to have little influence on shark social structure; instead, pairs of sharks frequently encountered at the same site had fewer agonistic actions. This latter study in particular, highlights the value of using a heterarchical assessment to build our understanding of sociality in these poorly studied species.

Here, we took advantage a population of smooth stingrays (*Bathytoshia brevicaudata*) that is incidentally provisioned with fish scraps discarded by local fishers to conduct as a case study for the use of heterarchical assessment of elasmobranch social behavior in a wild setting. We developed an ethogram of agonistic behaviors, which was used to examine their dominance hierarchy and social network. We then assessed the factors influencing individuals' dominance and network position. The heterarchical approach allowed us to test the hypothesis that this population exhibited a despotic social structure characterized by (i) a highly linear and steep dominance hierarchy, and (ii) a non-random social network, with the most dominant individuals being central. The heterarchy approach also allowed us to distinguish this from the alternate hypothesis that the population exhibited non-social spatial proximity over a food resource characterized by a (i) horizontal dominance relationship and (ii) a random social network. Dominance in elasmobranchs is often dependent on body size (Allee and Dickinson, 1954; Myrberg and Gruber, 1974, Clua et al., 2010) providing an obvious cue to conspecifics about an individual's fighting ability; therefore, we also hypothesized that larger individuals would be dominant and adopt central positions in the social network.

MATERIALS AND METHODS

Study System

The smooth stingray is a large demersal marine stingray with a broad distribution (Last et al., 2016), but despite being common, little is known about their behavior and ecology (Le Port et al., 2012). It is reported that this species forms large breeding aggregations (Le Port et al., 2012) and are often encountered in groups at food provisioning sites (e.g., Newsome et al., 2004; Rizzari et al., 2017), which suggests there may well be complex social interactions occurring in this species. However, the social behavior of smooth stingrays has yet to be formally assessed.

The Woollamia boat ramp (35° 1′ 32″ S, 150° 39′ 59″ E) is located in the lower Currambene Creek in the northwest of Jervis Bay, Australia. Anecdotal evidence suggests smooth stingrays have been incidentally provisioned with fish scraps by recreational fishers here since the installation of fish cleaning facilities in 1985 (R. Simpson, personal communication). Fish scraps are discarded into the shallow water adjacent to the main wharf via a pipe that runs from the center of a fish cleaning table used by recreational fishers. For a detailed map of the study location see **Supplementary Figure 1**.

The population of smooth stingrays at this site is dominated by large adult and sub-adult females that repeatedly visit this location over long time periods (>5 years based on our observations to date) to eat fish scraps discarded by recreational fishers (Pini-Fitzsimmons et al., 2018). Males seldom enter the creek, are very rarely observed and not considered members of the observed population.

Visual Tagging

In August 2016, smooth stingrays were baited into the immediate vicinity of the discard pipe using fish scraps and tagged to allow individual identification. The tags were 316S marine grade stainless steel dart (SSD) heads (Hallprint Pty. Ltd., Hindmarsh Valley, South Australia) with 200 mm long two-color coded vinyl streamers. Passive Integrated Transponders (PIT) were affixed to the distal end to allow secondary identification in case of biofouling. Tags were inserted into the musculature where the pectoral fin meets the body of free-swimming stingrays, following the procedure provided by the tag manufacturer (Hall, 2015), using a 3 m hand-held tagging pole. The tag colors, time of tagging and side of tag insertion were recorded, and each individual was given a name. Sex was determined by the presence (male) or absence (female) of claspers. Disc width was measured from pectoral fin tip to fin tip (*sensu* Last et al., 2016) to the nearest 5 cm using a marked 2 m length of dowel. A total of 15 female smooth stingrays were observed during the tagging period and ultimately tagged. Following size-class estimates (see Le Port et al., 2012) we considered 7 to be adults (>150 cm disc width or gravid) and 8 to be sub-adults (70–150 cm disc width). Five individuals appeared to be in advanced stages of pregnancy (see **Supplementary Table 1** for more information). As expected, no males were observed during tagging, which was unsurprising given that males are rarely seen at the site.

Social Interactions

Dominance measures and social network construction were based on dyadic agonistic interactions. An ethogram of dyadic agonistic interactions (**Figure 2**) was compiled based on prior observations of the sampled population and ethograms available for ray (Furst, 2011) and shark species (Clua et al., 2010, 2013; Sperone et al., 2010). We tested the ethogram over 2 days of observation prior to the study to ensure it was comprehensive. Dyadic interactions we readily observed at the site were divided into four categories: (i) aggressive interactions, for example "chase," "nose shove," and "bite," where a clear dominant and subordinate individual could be identified; (ii) semi-aggressive interactions, where a subordinate individual would "approach and abort" or "charge and abort" an interaction with a dominant individual; (iii) submissive interactions, where a subordinate individual would "avoid" an interaction with or "give way" to a dominant individual; and (iv) neutral interactions where two individuals would "pass," "circle," swim parallel ("parallel swimming") or both avoid ("double avoid") each other, hence both being identified as submissive (see detailed descriptions in **Supplementary Table 2**).

To estimate dominance measures and for constructing the social network, dyadic agonistic interactions were recorded during simulated provisioning events observed between 25th August and 2nd September 2016. Thirteen of the 15 tagged rays showed up reliably during these observations. Provisioning events were simulated using a bait box filled with locally sourced fish frames, to allow olfactory cues to disperse but not allow stingrays to access the bait (*sensu* Laroche et al., 2007; Sperone et al., 2010; Findlay et al., 2016). The bait box was placed into the center of the interaction zone, defined as a 2 m radius around the bait box (**Figure 1**). The location of the interaction zone and positioning of the bait box remained constant throughout the study.

Sixty-one half hour observation sessions were recorded over 8 days, for which stingrays were observed in 41 observation sessions, equating to 20.5 h of behavioral observations. A total of 688 dyadic interactions were recorded and 65% exhibited clear dominant and subordinate individuals (aggressive, semi-aggressive, and submissive interactions; asymmetrical), and the

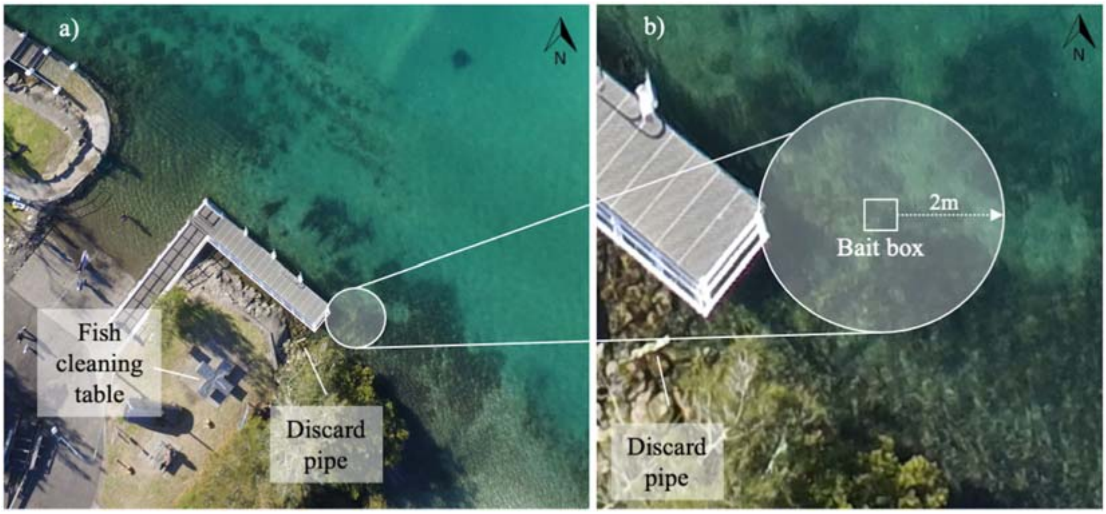


FIGURE 1 | Location of the social interaction zone relative to the cleaning facilities **(a)** and schematic for the social interaction zone around the bait box **(b)**.

remainder were neutral or drawn (symmetrical) interactions. This represents a comprehensive data set of wild elasmobranch behavior within a competitive context. The time of stingray arrivals to the observation area was recorded, and the time of each interaction and the individuals involved were recorded and classified following the ethogram (**Figure 2** and **Supplementary Table 1**). Every observation session was filmed using a GoPro Hero4 positioned above the interaction zone to create an archive and to facilitate clarification of instances when interactions could not be clearly defined in the field.

Data Analysis

All statistical analyses were conducted using R (V.4.0.2; R Core Team, 2020) with the R Studio interface (V.1.3.1093; RStudio Team, 2020). The datasets and associated code are provided in the **Supplementary Material**.

Dominance Measures

The dominance relationships between individuals were quantified using *David's scores* (DS; David, 1987) and *Elo Ratings* (ER; Elo, 1978). DS are a dominance ranking system that takes into account the overall success of individuals across all observed dyadic interactions (Gammell et al., 2003; Bayly et al., 2006). ER account for the sequence of interactions, showing temporal influence on individual dominance (Neumann et al., 2011). DS have been used extensively in social mammals (Koren et al., 2008; Yeater et al., 2013), especially primates (de Vries et al., 2006; Jaeggi et al., 2010; Balasubramaniam et al., 2013), whereas the utility of ER in ethology has only recently been realized (Neumann et al., 2011).

For estimating DS, an asymmetrical interaction matrix was generated from the observed dyadic interactions, where the dominant individual for each interaction was given a value of 1 and the subordinate was given a value of 0. For neutral, or drawn, interactions both individuals were given a value of 0.5 (Neumann and Kulik, 2020). DS and normalized DS (normDS) matrices were generated using the *Dij* method (de Vries, 1998), from which individual normDS scores were generated as an estimate of rank. For estimating ER, a time-stamped dataset of all dyadic interactions, with both dominant-submissive (asymmetrical) and neutral (symmetrical) interactions was used (*sensu* Neumann and Kulik, 2020), and final ER for each individual were extracted as estimates of rank. Kendall's coefficient of concordance (W) was used to determine agreement between normDS and final ER. As the estimated ranks were in high agreement (see section "Dominance"), normDS values were retained for further analysis of the dominance hierarchy.

The steepness (slope or "dominance gradient") of the dominance hierarchy was assessed based on the interaction matrix used to generate normDS and assessed against 1,000 permutations (de Vries et al., 2006). Linearity of the dominance hierarchy was then calculated using the *modified Landau's h'* (*sensu* de Vries, 1995) and tested against 1,000 permutations of the interaction matrix (de Vries et al., 2006). The transitivity, or overall consistency of the dominance hierarchy was also calculated using triangle transitivity (*Ttri*; Shizuka and McDonald, 2012) and tested against 1,000 permutations. Triangle transitivity estimates the degree to which, if individual A is dominant over B and B is dominant over C, A is also dominant over C (Shizuka and McDonald, 2012) and has been shown to perform better than h' when dominance relationships between all dyads are not known (Shizuka and McDonald, 2012).

Social Network Analysis

A directed social network was constructed from the dyadic interaction dataset described above, with the omission of drawn interactions. Drawn interactions were omitted because we were specifically interested in the aggressive/submission interactions. Four node-level (i.e., individual) metrics were calculated using this network: (i) out-degree, measured as the number of

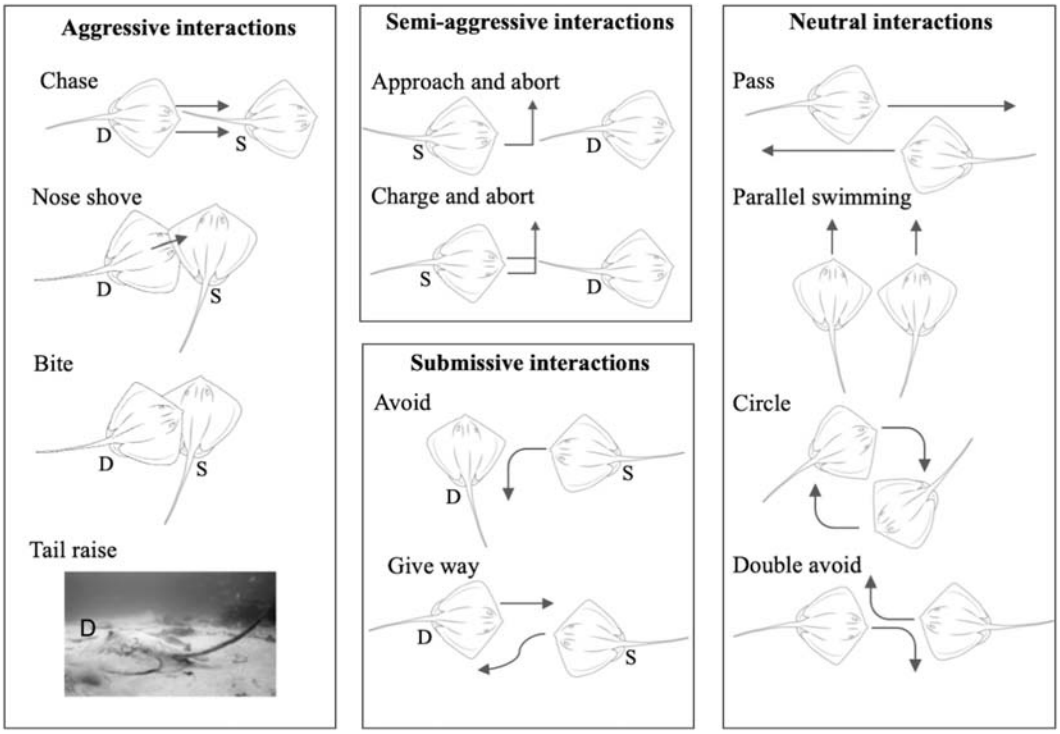


FIGURE 2 | Visual ethogram of dyadic interactions exhibited over simulated provisioning. Dominant individuals are marked "D" and submissive individuals are marked "S" for asymmetrical interactions. Full descriptions of interaction types are given in **Supplementary Table 2**.

aggressive interactions instigated by an individual; (ii) in-degree, measured as the number of submissive interactions by an individual; (iii) weighted degree (or strength), measured as the total number of interactions for an individual; and (iv) eigenvector centrality as a measure of individuals' influence or overall centrality in the network. To confirm the observed social network contained more preferred/avoided interactions than expected at random, the coefficient of variance (standard deviation/mean) of the observed social network was calculated and tested against the coefficients of variance of 1,000 network permutations (Farine and Whitehead, 2015). The permutation method consisted of swaps of dominant and submissive individuals within the dyadic interaction dataset while not allowing an individual to compete against itself (see **Supplementary Materials**).

Factors Influencing Dominance and Network Centrality

As dominance hierarchies are typically size-dependent in sharks (Allee and Dickinson, 1954; Myrberg and Gruber, 1974, Clua et al., 2010) and speculated for rays (Newsome et al., 2004), we expected the observed dominance hierarchy to be determined by disc width. In addition, we expected central individuals in the observed social network to be more dominant, and therefore for eigenvector centrality and weighted degree to be correlated with disc width. A Spearman rank correlation was used to compare normDS with disc width. Similarly, Spearman rank correlations were used to compare eigenvector centrality with normDS and disc width, respectively. To determine if the observed correlation coefficients differed from those expected by chance, eigenvector centrality was calculated for networks produced from 1,000 data-stream permutations and Spearman rank correlations were conducted between the eigenvector centrality values for each permutation and normDS and disc width, respectively, and compared with the correlation coefficients of the observed eigenvector centrality values. Permutations were conducted in the same manner described above. Spearman rank correlations were used as we were only concerned with comparing the rank of individuals rather than their discrete values.

RESULTS

Overall group composition remained relatively constant throughout the study period. That is, no new individuals were observed, and, with the exception of two tagged individuals not being observed during the observation period, there was no obvious trend of group size decreasing over time as would be expected if individuals were leaving the system. The ratio of interactions to individuals was 52.9, which is higher than the suggested ratio of 10–20 (Sánchez-Tójar et al., 2017). Further, the observed proportion of known dyads was moderate (0.69) and within what we would expect under a Poisson process (mean = 0.64, 2.5 and 97.5% quantiles = 0.43 and 0.86). This indicates sufficient sampling for estimating dominance and the social network.

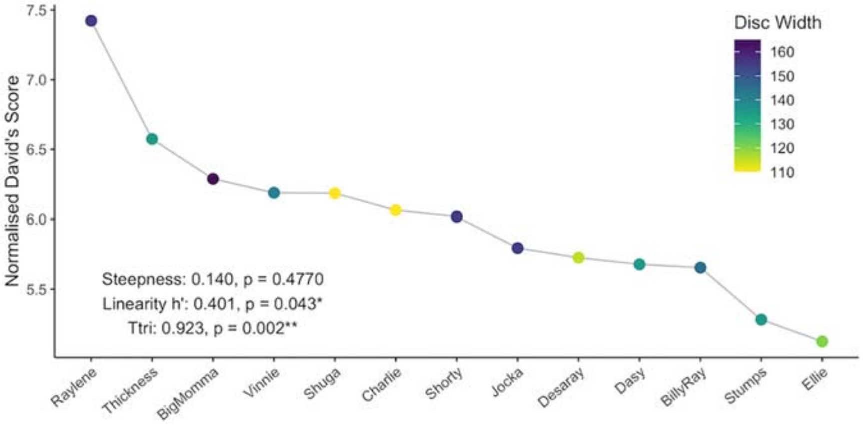


FIGURE 3 | Individual normalized David's scores and associated steepness, linearity, and triangle transitivity (Ttri) of the dominance hierarchy. Nodes are colored by disc width (cm).

Dominance

NormDS and final ER differed for all individuals and were highly concordant (Kendall's coefficient of concordance: $N = 13$, $W = 0.82$), indicating the presence of a dominance hierarchy (**Figure 3**). The observed dominance hierarchy was not very steep (steepness = 0.140) and was not significantly different from random ($p = 0.477$). The linearity was only moderate ($h' = 0.401$; Martin and Bateson, 1993; Lehner, 1996) but was significantly different from random (right-tailed $p = 0.043$). The observed dominance hierarchy was highly transitive (Ttri = 0.923) and significantly different from random ($p = 0.002$), and thus estimates of dominance are reasonably certain. The difference in normDS between the highest and second highest ranking individuals (Raylene and Thickness, respectively; see **Figure 3**) was 0.849, while the average difference between all other neighboring subordinates was only 0.132 (IQR = 0.047 – 0.144).

Social Network Analysis

The Coefficient of Variance of the observed social network was 3.240 and was significantly higher than expected by chance (mean $CV_{\text{random}} = 2.916$; $p < 0.001$; **Figure 4B**), indicating that the observed network (**Figure 4B**) was not random.

Factors Influencing Dominance and Network Centrality

The mean disc width of tagged smoothed stingrays was 137 cm (±5 SE) (range 110–165 cm; $n = 15$). NormDS was not significantly correlated with disc width (Spearman's rank correlation: $N = 13$, $R = 0.287$, $p = 0.343$), indicating that the largest individuals were not the most dominant. NormDS was not significantly correlated with eigenvector centrality either (Spearman's rank correlation: $N = 13$, $R = 0.055$, $p = 0.859$), indicating that the most central individuals in the network were not the most dominant. However, eigenvector centrality was significantly positively correlated with disc width (Spearman's rank correlation: $N = 13$, $R = 0.723$, $p = 0.005$), and the observed R was significantly higher than expected by chance ($R_{\text{random}} = 0.403$), indicating that larger individuals were most central in the network. Moreover, the most central individual (highest eigenvector centrality), Raylene, exhibited the highest egocentric metrics and dominance (**Table 1**). Correlation plots are provided in **Supplementary Figure 2**.

DISCUSSION

Here, we made use of a population of female smooth rays that frequently gather to forage on scraps provided by recreational fishers at a boat ramp (Pini-Fitzsimmons et al., 2018) to observe social interactions in an agonistic context in the wild. We used this observation as a case study for the application of heterarchy which combines aspects of dominance and social network approaches to understand complex social interactions. The observed dominance hierarchy was moderately linear but quite shallow, with a single alpha individual (Raylene). Network analysis revealed a non-random social network with Raylene at the center (**Figure 4A**). Collectively these results support the hypothesis that this population exhibits a social structure indicative of a despotic society and not merely a random assortment of individuals attracted to a food source. It is important to note that the observed dominance hierarchy and social network may only be specific to this or similar contexts, where individuals are competing over a limited food resource. Although our observations were made at a long-standing food provisioning site, similar interactions likely take place in nature at high quality feeding patches. It is likely not indicative of their broader social behavior of which we currently know very little. It is well documented that priority access to food through dominance has fitness benefits (Koenig, 2002). Contrary to observations for provisioned (Clua et al., 2010) and free-living (Allee and Dickinson, 1954; Myrberg and Gruber, 1974) shark populations, body size (here disc width) was not a determining factor for dominance, however it was positively correlated with network centrality.

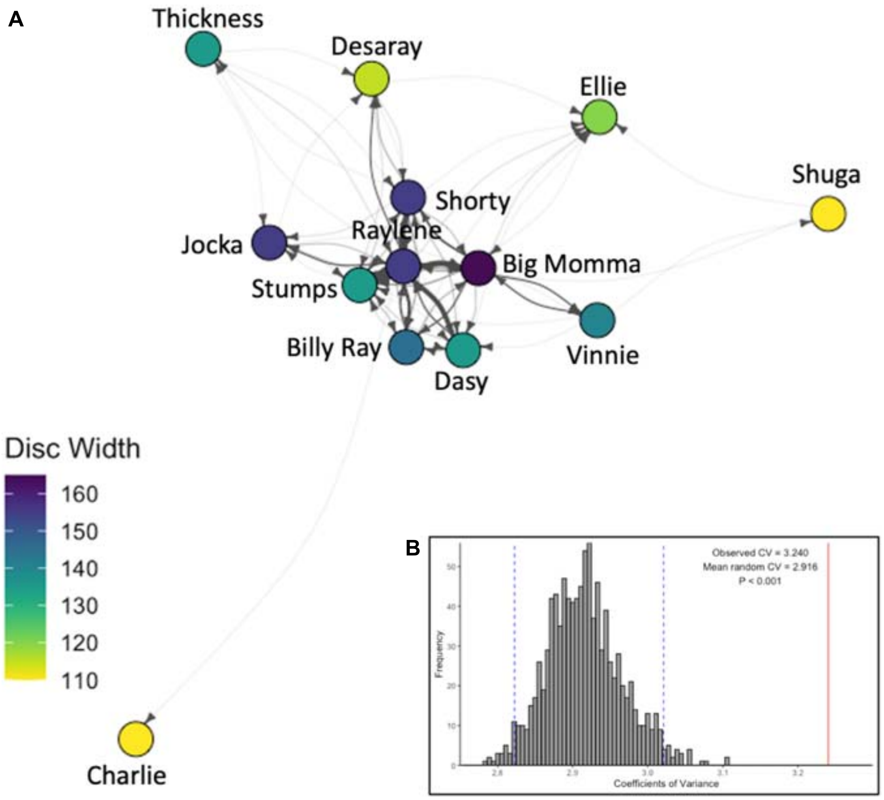


FIGURE 4 | The observed social network. **(A)** Weighted and directed social network, where arrows show direction of interactions, line thickness indicates total number of interactions between individuals in the given direction (divided by 10 for clarity), nodes are colored by disc width (cm). **(B)** Histogram of the Coefficients of Variation of 1,000 network permutations and 95% confidence intervals (vertical dashed blue lines) compared to that of the observed social network (vertical solid red line).

In the present study, asymmetrical interactions accounted for the majority of observed dyadic interactions. In addition, while dominance was not correlated with eigenvector centrality, a single individual (Raylene) had the highest weighted degree, dominance rank and eigenvector centrality (**Table 1**). These data indicate the dominance structure observed in this population is reflective of a despotic social structure with Raylene as the alpha (**Figure 3**). Some may argue that the shallow dominance hierarchy observed here is indicative of an egalitarian society (van Schaik, 1989 cited in de Vries et al., 2006); however, a despotic social system can be characterized by the most and second most dominant individuals having a difference in normDS that is greater than that between all other neighboring subordinates (Beaugrand et al., 1984). Here, the difference between the normDS of Raylene and the next subordinate (Thickness) was 6.5-fold higher than the average difference between all other neighboring subordinates (**Figure 3** and **Table 1**). Despotic systems are also characterized by low counter aggression from subordinates to dominants (Thierry, 2007). It is clear from the edges in the social network (**Figure 4A**) and in-degrees (**Table 1**), that Raylene received little counter aggression. Thus, we can be confident that the social hierarchy observed here is reflective of a society at the despotic end of the spectrum.

Despotism is typically described for highly social species such as wolves (*Canis lupus lupus*; Cordoni and Palagi, 2008), spotted hyenas (*Crocuta crocuta*; Wahaj et al., 2001) and a number of non-human primates (see Palagi and Norscia, 2015), that live in social groups at all times. Individuals continually reinforce and reconcile relationships to maintain social unity (Palagi and Norscia, 2015). It is unknown whether grouping of smooth stingrays observed here extends outside of the observed context (competing over food). Our ongoing acoustic tagging will provide important new insights into this species broader social behavior. Nevertheless, observation of such a highly social system having developed over the repeated provisioning of a limited food resource within smooth stingrays is rather extraordinary and reinforces the suggestion that this species is capable of complex social behaviors. Although the observation period was somewhat limited (8 days), our data is based on an intense sampling regime (30.5 h of observation capturing 688 social interactions) which is exceptional for wild elasmobranchs that are notoriously difficult to study. Furthermore, our long-term observations at this location suggest that these thirteen individuals comprise the bulk of the animals that make regular appearance at the provisioning site. All of these individuals have been repeatedly observed at this location over multiple years and eight of them in particular are consistently observed.

TABLE 1 | Summary of individual size, dominance (Normalized David's score) and egocentric metrics calculated for the social network.

Individual	Disc width (cm)	Normalized David's score	In-degree	Out-degree	Weighted degree	Eigenvector centrality
Raylene	155	7.423	53	251	304	0.879
Thickness	135	6.574	2	5	7	0.034
Big Momma	165	6.288	67	57	124	0.207
Vinnie	140	6.188	12	14	26	0.048
Shuga	110	6.185	1	2	3	0.015
Charlie	110	6.064	1	0	1	0.000
Shorty	155	6.018	65	30	95	0.121
Jocka	155	5.795	17	8	25	0.075
Desaray	115	5.726	17	6	23	0.029
Dasy	135	5.678	44	21	65	0.203
Billy Ray	145	5.655	48	25	73	0.210
Stumps	135	5.282	113	29	142	0.273
Ellie	120	5.125	9	1	10	0.004

Moreover, these animals are long lived, so it is likely that they repeatedly interact with other individuals over very long timeframes. Thus, we have reason to be confident that structured social interactions we observed in this population in this context are likely real. Future research will address social organization of this and other populations in similar contexts, for example, where provisioning occurs as part of unstructured wildlife tourism.

An individuals' success in agonistic interactions carries with it direct and indirect fitness implications. Successful individuals usually have greater access to better quality resources, such as mates, shelter, and food (Dugatkin, 2009). The restriction of access to limited resources by dominant individuals resulting in the reduced reproductive success of subordinates is well documented (Lomnicki, 1988; Koenig, 2002), particularly among highly social primates (Fedigan, 1983; Ellis, 1995). In the present study, observations were made for a population of smooth stingrays that are competing over limited provisioned food resources, and more dominant and central individuals gained access to the bait more often, which likely reflects access to provisioned food during normal provisioning events (fish scraps discarded by fishers). Further, we believe that Currambene Creek, within which the Woollamia Boat Ramp is situated, may have reproductive significance for female stingrays. Five of our subjects were heavily gravid individuals entering agonistic interactions with the most dominant (Raylene) exhibiting the most advanced stages of pregnancy. We suggest that dominance increases net gain from the provisioned resource, which in turn aids in meeting the nutritional demands of pups during gestation and reduces the energetic costs associated with foraging naturally. These observations may have clear implications for reproduction and movement patterns in this species.

Dominance hierarchies in provisioned shark aggregations are thought to be size-dependent (Newsome et al., 2004; Clua et al., 2010; Maljković and Côté, 2011), which is supported by previous studies on free-living shark social behavior (Allee and Dickinson, 1954; Myrberg and Gruber, 1974). Newsome et al. (2004) stated that larger female smooth stingrays chased smaller individuals away from provisioned food in Hamelin Bay, Western Australia. It is of some note that neither males nor juveniles were ever observed at this location in the present study. While the influence of individual disc width on dominance was not significant, disc width did predict eigenvector centrality, suggesting larger individuals are more central to the network. More central individuals have greater influence within social networks, and we have shown that size clearly impacts social interactions in this context. Given the relatively similar dominance scores of all subordinate individuals, we might not expect to see a global influence of disc width on dominance rank. Further, Raylene was not the biggest female within the group. However, it may be that disc width is not the most suitable measure of body size in this species, rather body weight may be a better metric. Alternatively, there might be an effect of personality in smooth stingray dominance and centrality (Byrnes and Brown, 2016).

To conclude, in their review of social capacity in elasmobranchs, Jacoby et al. (2011) highlighted a need for fine-scale analysis of shark and ray groups in the form of social network analysis in order to better inform shark and ray conservation. Here, we combine dominance and social network analysis (heterarchy) of a provisioned population of stingrays, which indicated that smooth stingrays are not only capable of exhibiting social behaviors, but also display a highly complex despotic social structure. A better understanding the structure of animal communities enables us to elucidate their ecological function, as well as that of the groups and specific individuals within them (Cumming, 2016). For example, the selective removal of individuals from a network may provide insights into the robustness of the society to selective pressures (e.g., Mourier et al., 2017b). Removal of specific individuals may lead to population fragmentation. Similarly, subgroups within a community may occupy specific locations or habitats that are exceptionally exposed to anthropogenic change, which can have clear implications for population genetics, fisheries management, and conservation. While our case-study is limited in scope, understanding of the heterarchical structure of societies will add to our capacity to understand the structure-function relationships within ecological systems (Cumming, 2016).

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

Tagging of smooth stingrays and behavioral observations were carried out under approval from the Macquarie University Animal Ethics Committee under ARA2014/015-7 and NSW DPI Fisheries Scientific Collection Permit P08/0010-4.4.

AUTHOR CONTRIBUTIONS

JP-F designed and coordinated the study, collected field data, carried out the statistical analysis, and drafted the manuscript. CB and NK assisted in project design and coordination, and assisted in drafting the manuscript. All authors gave final approval for publication.

FUNDING

The project benefited greatly from funding provided by the Macquarie University and the New South Wales Department of Primary Industries. JP-F was supported by the Macquarie University RTP Scholarship.

ACKNOWLEDGMENTS

We would like to thank Macquarie University's Behavior, Ecology and Evolution of Fishes laboratory for the assistance of its members and the large number of volunteers who assisted with fieldwork for this project. Special thanks also goes to Johann Mourier for his assistance in statistical analysis and modeling of the data presented here. We would also like to thank the World Famous Fish and Chip Shop, Huskisson for their donation of fish frames and offal and the local fishers at the Woollamia Boat Ramp, also known as the Table of Knowledge, who shared their vast local knowledge of fishing, boating and the "local" stingrays, for keeping us entertained on slow field days. JP-F was supported by the Macquarie University RTP Scholarship. The content of this manuscript has appeared previously online in JP-F's Master of Research Thesis (Pini-Fitzsimmons, 2017).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.641761/full#supplementary-material

REFERENCES

Allee, W. C., and Dickinson, J. C. J. (1954). Dominance and subordination in the smooth dogfish *Mustelus canis* (Mitchill). *Physiol. Zool.* 27, 356–364. doi: 10.1086/physzool.27.4.30152372

Balasubramaniam, K. N., Berman, C. M., de Marco, A., Dittmar, K., Majolo, B., Ogawa, H., et al. (2013). Consistency of dominance rank order: a comparison of David's scores with I&SI and bayesian methods in macaques. *Am. J. Primatol.* 75, 959–971. doi: 10.1002/ajp.22160

Bass, N. C., Mourier, J., Knott, N. A., Day, J., Brown, C., and Guttridge, T. (2016). Long-term migration patterns and bisexual philopatry in a benthic shark species. *Mar.Freshw. Res.* 68, 1414–1421. doi: 10.1071/MF16122

Bayly, K.l, Evans, C. S., and Taylor, A. (2006). Measuring social structure: a comparison of eight dominance indices. *Behav. Process.* 73, 1–12. doi: 10.1016/j.beproc.2006.01.011

Beaugrand, J. P., Caron, J., and Comeau, L. (1984). Social organization of small heterosexual groups of Green swordtails (*Xiphophorus helleri*, Pisces, Poeciliidae) under conditions of captivity. *Behaviour* 91, 24–60. doi: 10.1163/156853984X00209

Brena, P. F., Mourier, J., Planes, S., and Clua, E. E. (2018). Concede or clash? solitary sharks competing for food assess rivals to decide. *Proc. R. Soc. Lon. B Biol. Sci.* 285:9. doi: 10.1098/rspb.2018.0006

Byrnes, E. E., and Brown, C. (2016). Individual personality differences in port Jackson sharks Heterodontus portusjacksoni. *J. Fish. Biol.* 89, 1142–1157. doi: 10.1111/jfb.1299

Clua, E., Buray, N., Legendre, P., Mourier, J., and Planes, S. (2010). Behavioural response of sicklefin lemon sharks *Negaprion acutidens* to underwater feeding for ecotourism purposes. *Mar. Ecol. Prog. Ser.* 414, 257–266. doi: 10.3354/meps0874

Clua, E., Chauvet, C., Read, T., Werry, J., and Lee, S. Y. (2013). Behavioural patterns of a Tiger shark (*Galeocerdo cuvier*) feeding aggregation at a blue whale carcass in Prony Bay, New Caledonia. *Mar. Freshwat. Behav. Physiol.* 46, 1–20. doi: 10.1080/10236244.2013.773127

Cordoni, G., and Palagi, E. (2008). Reconciliation in wolves (*Canis lupus*): new evidence for a comparative perspective. *Ethology* 114, 289–308. doi: 10.1111/j.1439-0310.2008.01474.x

Cumming, G. S. (2016). Heterarchies: reconciling networks and hierarchies. *Trends Ecol. Evol.* 31, 622–632. doi: 10.1016/j.tree.2016.04.009

David, H. A. (1987). Ranking from unbalanced paired-comparison data. *Biometrika* 74, 432–436. doi: 10.2307/233616

de Vries, H. (1995). An improved test of linearity in hierarchies containing unknown or tied relationships. *Anim. Behav.* 50, 1375–1389. doi: 10.1016/0003-3472(95)80053-0

de Vries, H. (1998). Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Anim. Behav.* 55, 827–843. doi: 10.1006/anbe.1997.0708

de Vries, H., Stevens, J. M. G., and Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Anim. Behav.* 71, 585–592. doi: 10.1016/j.anbehav.2005.05.015

Dicken, M. L. (2008). First observations of young of the year and juvenile great white sharks (*Carcharodon carcharias*) scavenging from a whale carcass. *Mar. Freshw. Res.* 59, 596–602. doi: 10.1071/MF07223

Dudley, S. F. J., Anderson-Reade, M. D., Thompson, G. S., and McMullen, P. B. (2000). Concurrent scavenging off a whale carcass by great white sharks, *Carcharodon carcharias*, and tiger sharks, *Galeocerdo cuvier*. *Fish. Bull.* 98, 646–649.

Dugatkin, L. A. (2009). *Principles of Animal Behaviour*. 2nd Edn. London: W. W. Norton & Company.

Ellis, L. (1995). Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Ethol. Sociobiol.* 16, 257–333. doi: 10.1016/0162-3095(95)00050-U

Elo, A. E. (1978). *The Rating of Chess Players, Past and Present*. New York, NY: Arco.

Farine, D. R. (2017). When to choose dynamic vs. static social network analysis. *J. Anim. Ecol.* 87, 128–138. doi: 10.1111/1365-2656.12764

Farine, D. R., and Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *J. Anim. Ecol.* 84, 20. doi: 10.1111/1365-2656.12418

Fedigan, L. M. (1983). Dominance and reproductive success in primates. *Am. J. Phys. Anthropol* 26(Suppl. S1), 91–129. doi: 10.1002/ajpa.1330260506

Findlay, R., Gennari, E., Cantor, M., and Tittensor, D. P. (2016). How solitary are white sharks: social interactions or just spatial proximity? *Behav. Ecol. Sociobiol.* 70, 1735–1744. doi: 10.1007/s00265-016-2179-y

Flack, J. C., and de Waal, F. B. M. (2004). "Dominance style, social power and conflict management: a conceptual framework," in *Macaque Socieities: A Model for the Study of Social Organisation*, eds B. Thierry, M. Singh, and W. Kaumanns (New York, NY: Cambridge University Press), 157–182.

Furst, E. A. (2011). *Network Analysis of the Tahitian Ray (Himantura fai): Is There Social Structure to the Feeding Frenzy?*. Berkeley, CA: University of California.

Gammell, M. P., de Vries, H., Jennings, D. J., Carlin, C. M., and Hayden, T. J. (2003). David's score: a more appropriate dominance ranking method than

Clutton-Brock et al.'s index. *Anim. Behav.* 66, 601–605. doi: 10.1006/anbe.2003.2226

Gottier, R. F. (1968). The dominance-submission heirarchy in the social behaviour of the domestic chicken. *J. Genet. Psychol.* 112, 205–226.

Guttridge, T., van Dijk, S., Stamhuis, E. J., Krause, J., Gruber, S. H., and Brown, C. (2013). Social learning in juvenile lemon sharks, *Negaprion brevirostris*. *Anim. Cogn.* 16, 55–64. doi: 10.1007/s10071-012-0550-6

Hall, D. (2015). *Hallprint Fish Tags*. Available online at: https://www.hallprint.com/ (accessed June 2015).

Jacoby, D. M. P., Croft, D. P., and Sims, D. W. (2011). Social behaviour in sharks and rays: analysis, patterns and implications for conservation. *Fish Fish.* 13, 399–417. doi: 10.1111/j.1467-2979.2011.00436.x

Jaeggi, A. V., Stevens, J. M. G., and Van Schaik, C. P. (2010). Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees. *Am. J. Phys. Anthropol.* 143, 41–51. doi: 10.1002/ajpa.21288

Koenig, A. (2002). Competition for resources and its behavioral consequences among female primates. *Int. J. Primatol.* 23, 759–783. doi: 10.1023/A:1015524931226

Koren, L., Mokady, O., and Geffen, E. (2008). Social status and cortisol levels in singing rock hyraxes. *Horm. Behav.* 54, 212–216. doi: 10.1016/j.yhbeh.2008.02.020

Laroche, R. K., Kock, A. A., Dill, L. M., and Oosthuizen, W. H. (2007). Effects of provisioning ecotourism activity on the behaviour of white sharks *Carcharodon carcharias*. *Mar. Ecol. Prog. Ser.* 338, 199–209. doi: 10.3354/meps338199

Last, P. R., White, W. T., de Carvalho, M. R., Seret, B., Stehmann, M. F. W., and Naylor, G. J. P. (2016). *Rays of the World*. Clayton, Vic: CSIRO Publishing.

Le Port, A., Lavery, S., and Montgomery, J. C. (2012). Conservation of coastal stingrays: seasonal abundance and population structure of the short-tailed stingray dasyatis brevicaudata at a marine protected area. *ICES J. Mar. Sci.* 69, 1427–1435. doi: 10.1093/icesjms/fss120

Lehner, P. N. (1996). *Handbook of Ethological Methods*, 2nd Edn. Cambridge: Cambridge University Press.

Lomnicki, A. (1988). *Population Ecology of Individuals*. Princeton: Princeton University Press.

Maljković, A., and Côté, I. M. (2011). Effects of tourism-related provisioning on the trophic signatures and movement patterns of an apex predator, the Caribbean reef shark. *Biol. Conserv.* 144, 859–865. doi: 10.1016/j.biocon.2010.11.019

Martin, P., and Bateson, P. (1993). *Measuring Behaviour: An Introductory Guide*, 2nd Edn Cambridge: Cambridge University Press.

Mourier, J., Bass, N. C., Guttridge, T., Day, J., and Brown, C. (2017a). Does detection range matter for inferring social networks in a benthic shark using acoustic telemetry? *R. Soc. Open Sci.* 4:170485. doi: 10.1098/rsos.170485

Mourier, J., Brown, C., and Planes, S. (2017b). Learning and robustness to catch-and- release fishing in a shark social network. *Biol. Lett.* 13:20160824. doi: 10.1098/rsbl.2016.0824

Myrberg, A. A., and Gruber, S. H. (1974). The behavior of the bonnethead shark, *Sphyrna tiburo*. *Copeia* 1974, 358–374. doi: 10.2307/1442530

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., et al. (2011). Assessing dominance heirarchies: validation and advantages of progressive evaluation with Elo-rating. *Anim. Behav.* 82, 911–921. doi: 10.1016/j.anbehav.2011.07.016

Neumann, C., and Kulik, L. (2020). *EloRating – a Brief Tutorial. Version 0.46.11* (accessed October 2020).

Newsome, D., Lewis, A., and Moncrieff, D. (2004). Impacts and risks associated with developing, but unsupervised, stingray tourism at Hamelin Bay, Western Australia. *Int. J. Tour. Res.* 6, 305–323. doi: 10.1002/jtr.491

Palagi, E., and Norscia, I. (2015). The season for peace: reconciliation in a despotic species (*Lemur catta*). *PLoS One* 10:e0142150. doi: 10.1371/journal.pone.0142150

Papastamatiou, Y. P., Bodey, T. W., Caselle, J. E., Bradley, D., Freeman, R., Friedlander, A. M., et al. (2020). Multiyear social stability and social information use in reef sharks with diel fission–fusion dynamics. *Proc. R. Soc. B Biol. Sci.* 287:20201063. doi: 10.1098/rspb.2020.1063

Pasquaretta, C., Battesti, M., Klenschi, E., Bousquet, C. A. H., Sueur, C., and Mery, F. (2016). How social network structure affects decision-making in *Drosophila melanogaster*. *Proc. R. Soc. B Biol. Sci.* 283:20152954. doi: 10.1098/rspb.2015.2954

Pini-Fitzsimmons, J. (2017). *Top Shelf Bottom Feeders: Food Provisioning in Stingrays*. Master of Research Thesis. Sydney, NSW: Department of Biological Sciences, Macquarie University.

Pini-Fitzsimmons, J., Knott, N. A., and Brown, C. (2018). Effects of food provisioning on site use in the short-tail stingray, *Bathytoshia brevicaudata*. *Mar. Ecol. Prog. Series* 600, 99–110. doi: 10.3354/meps12661

R Core Team. (2020). *R: A Language and Environment for Statistical Computing. Verson 4.0.2*. Vienna: R Foundation for Statistical Computing.

Rizzari, J. R., Semmens, J. M., Fox, A., and Huveneers, C. (2017). Observations of marine wildlife tourism effects on a non-focal species. *J. Fish Biol.* 91, 981–988. doi: 10.1111/jfb.13389

RStudio Team. (2020). *RStudio: Integrated Development for R. Version 1.3.1093*. Boston, MA: PBC.

Sánchez-Tójar, A., Schroeder, J., and Farine, D. R. (2017). A practical guide for inferring reliable dominance hierarchies and estimating their uncertainty. *J. Anim. Ecol.* 87, 594–608. doi: 10.1111/1365-2656.12776

Shizuka, D., and McDonald, D. B. (2012). A social network perspective on measurements of dominance hierarchies. *Anim. Behav.* 83, 925–934. doi: 10.1016/j.anbehav.2012.01.011

Sih, A., Hanser, S. F., and McHugh, K. A. (2009). Social network theory: new insights and issues for behavioral ecologists. *Behav. Ecol. Sociobiol.* 63, 975–988. doi: 10.1007/s00265-009-0725-6

Sims, D. W., Southall, E. J., Quayle, V. A., and Fox, A. M. (2000). Annual social behaviour of basking sharks associated with coastal front areas. *Proc. R. Soc. B Biol. Sci.* 267, 1897–1904. doi: 10.1098/rspb.2000.1227

Sperone, E., Micarwlli, P., Andreotti, S., Spinetti, S., Andreani, A., Serena, F., et al. (2010). Social interactions among bait-attracted white sharks at Dyer Island (South Africa). *Mar. Biol. Res.* 6, 408–414. doi: 10.1080/17451000903078648

Thierry, B. (2007). Unity in diversity: lessons from Macaque societies. *Evol. Anthropol.* 16, 224–238. doi: 10.1002/evan.20147

van Schaik, C. P. (1989). "The ecology of social relationships amongst female primates," in *Comparative Socioecology of Mammals and Man*, eds V. Standen, and R. Foley (Oxford: Blackwell Scientific), 195–218.

Vehrencamp, S. L. (1983). A model for the evolution of despotic versus egalitarian societies. *Anim. Behav.* 31, 667–682. doi: 10.1016/S0003-3472(83)80222-X

Wahaj, S. A., Guse, K. R., and Holekamp, K. E. (2001). Reconciliation in spotted hyena (*Crocuta crocuta*). *Ethology* 107, 1057–1074. doi: 10.1046/j.1439-0310.2001.00717.x

Whitehead, H., Bejder, L., and Ottensmeyer, C. A. (2005). Testing association patterns: issues arising and extensions. *Anim. Behav.* 69, e1–e6. doi: 10.1016/j.anbehav.2004.11.004

Yeater, D. B., Miller, L. E., Caffery, K. A., and Kuczaj, S. A. II (2013). Effects of an increase in group size on the social behavior of a group of rough-Toothed Dolphins (*Steno bredanensis*). *Aquat. Mamm.* 39, 344–355. doi: 10.1578/AM.39.4.2013.344

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Marine Science

REVIEW
published: 05 May 2021
doi: 10.3389/fmars.2021.665780

The Next Frontier in Understanding the Evolution of Coral Reef Fish Societies

Theresa Rueger[1,2]*, Rebecca Branconi[1], Catheline Y. M. Froehlich[3], Siobhan J. Heatwole[3], Marian Y. L. Wong[3] and Peter M. Buston[1]

[1] Department of Biology and Marine Program, Boston University, Boston, MA, United States, [2] College of Life and Environmental Sciences, University of Exeter, Penryn, United Kingdom, [3] Centre for Sustainable Ecosystem Solutions, School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, NSW, Australia

Research on sociality in marine fishes is a vibrant field that is providing new insights into social evolution more generally. Here, we review the past two decades of research, identifying knowledge gaps and new directions. Two coral reef fishes, with social systems similar to other cooperative breeders, have emerged as models: the clown anemonefish *Amphiprion percula* and the emerald goby *Paragobiodon xanthosoma*. In these systems, non-breeders do not forgo their own reproduction to gain indirect genetic benefits. Rather, they do so because they stand to inherit the territory in the future and there are strong ecological and social constraints. The reasons why breeders tolerate non-breeders remain obscure, though it is plausibly a combination of weak kin selection, bet-hedging, and benefits mediated via mutualistic interactions with cnidarian hosts. The latter is particularly interesting, given the parallels with other social animals with mutualistic partners, such as acacia ants. Looking beyond the two model species, our attention is turning to species with more complex social organization, such as the damselfish *Dascyllus aruanus*. Here, variable group stability, conflict intensity, and reproductive skew provide opportunities to test theories of social evolution that have only been tested in a few taxa. New methods like social network analysis are enabling us to uncover more subtle effects of ecology on social interactions. More recently, comparative methods have yielded insights into the correlates of interspecific variation in sociality in the genera to which our model species belong. Phylogenetically controlled contrasts within the genus *Gobiodon*, have revealed the role of ecology, life history traits, and their interaction in sociality: smaller bodied species are more social than larger bodied species, which are only social on large corals. As climate change affects coral reefs, there is a pressing need to understand the many ways in which environmental disturbance influences these unique social systems. In sum, coral reef fishes have enabled us to test the robustness of current theories of social evolution in new taxa and environments, and they have generated new insights into social evolution that are applicable to a wider variety of taxa.

Keywords: social evolution, eusociality, sociality, cooperative breeding, reproductive skew, coral reef fishes

Edited by:
David M. P. Jacoby,
Zoological Society of London,
United Kingdom

Reviewed by:
Michael Gil,
University of California, Davis,
United States
Kátia de Meirelles Felizola Freire,
Universidade Federal de Sergipe,
Brazil

***Correspondence:**
Theresa Rueger
theresa.rueger@gmail.com

Specialty section:
This article was submitted to
Marine Biology,
a section of the journal
Frontiers in Marine Science

Received: *08 February 2021*
Accepted: *01 April 2021*
Published: *05 May 2021*

Citation:
Rueger T, Branconi R, Froehlich CYM, Heatwole SJ, Wong MYL and Buston PM (2021) The Next Frontier in Understanding the Evolution of Coral Reef Fish Societies. Front. Mar. Sci. 8:665780. doi: 10.3389/fmars.2021.665780

INTRODUCTION

A major transition in the evolution of life was animals beginning to live in groups (Szathmáry and Smith, 1995). Animal groups represent some of the most complex forms of life, and they exist on a continuum, from simple gatherings, which dilute the risk of predation, to complex societies with division of labor and reproduction (Sherman et al., 1995; Bourke, 2011). Complex societies, where some individuals forgo reproduction, have been a focus of evolutionary ecology ever since Darwin pointed out that such societies pose difficulties for his theory of natural selection (Darwin, 1859). Since Hamilton's pivotal insight about kin selection (Hamilton, 1964), the field of social evolution has made significant advances in explaining eusocial societies in insects, and cooperative breeding in birds and mammals (e.g., Woolfenden and Fitzpatrick, 1984; Emlen and Wrege, 1988; Keller and Reeve, 1994; Kokko et al., 2002; Clutton-Brock, 2002; Griffin and West, 2003; Shen et al., 2017). Relatively few studies have attempted to explain similar societies in fishes, and marine fishes in particular have been overlooked (Buston and Balshine, 2007; Taborsky and Wong, 2017). This is likely because of the challenges of working in marine environments and because some criteria considered to be prerequisites for the evolution of complex societies are (presumably) unmet in most marine fishes. However, studying these taxa and their societies has the potential to test the robustness of current theories, generate new insights, and advance the field of social evolution.

Using Marine Systems to Test the Robustness of Current Theories in Social Evolution

The complex groups in which some marine fishes are organized bear many similarities with cooperatively breeding societies in mammals, birds, freshwater fishes and invertebrates (Taborsky and Limberger, 1981; Emlen, 1991; Sherman et al., 1995; Duffy et al., 2000; Bourke, 2011), but there are two key differences. First, alloparental care, where group members care for offspring other than their own, which is a feature of cooperative breeding in birds, mammals and freshwater fishes (Riedman, 1982; Wong and Balshine, 2011), has only very rarely been observed in marine fishes (see review in Wisenden, 1999; Phillips et al., 2020). However, cooperation in marine fishes may take other forms, such as subordinates modifying their growth to remain small and reduce conflict (Buston, 2003a; Wong et al., 2007), or defending and maintaining the territory (Mariscal, 1966; Iwata and Manbo, 2013). Second, the organization in family groups, which characterizes the social systems of most terrestrial species (Emlen, 1995), is lacking in marine systems. The vast majority of marine fishes have a dispersive larval phase, which was long presumed to prevent the formation of kin groups (Victor, 1984; Leis, 1991; Shanks, 2009). However, recent studies have shown that limited dispersal and other mechanisms may lead to subtle relatedness patterns in marine fishes (D'Aloia and Neubert, 2018; D'Aloia et al., 2018; Rueger et al., 2020, 2021), indicating that there is a possibility for weak kin selection to play a role in their social evolution.

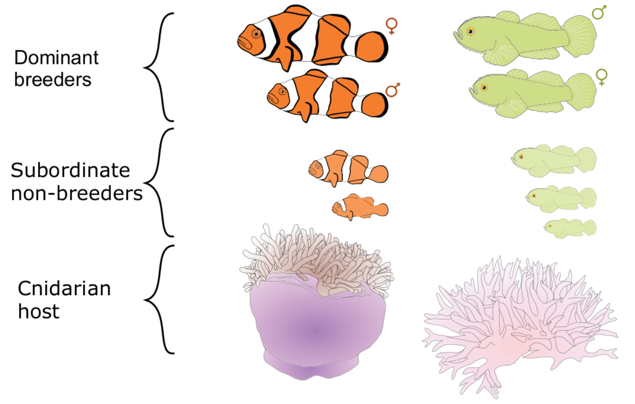


FIGURE 1 | Schematic of the social organization of *Amphiprion percula* **(left)** and *Paragobiodon xanthosoma* **(right)**.

Regardless of whether kin selection is operating or alloparental care is occurring in marine fishes, if we dismiss these species from the study of sociality on the grounds that they are different from other social vertebrates, then a great opportunity for expanding and transforming the field is missed. It has been argued that sociality should be viewed as a continuum, rather than falling in narrow categories (Sherman et al., 1995). Therefore, it is more useful for the field overall to study the remarkable behavioral convergence and distinctions between different taxa, rather than exclude large groups of animals from consideration on account of them not meeting specific criteria (Sherman et al., 1995; Hing et al., 2017).

Established Study Systems

The first two decades of social evolution research in marine fishes have focused on two coral reef fish species found in the Indo-Pacific: the clown anemonefish *Amphiprion percula* (Pomacentridae) and the emerald coral goby *Paragobiodon xanthosoma* (Gobiidae). The aim of using these fishes was to test the robustness of our current understanding of social evolution and generate new insights. These two fishes were chosen because they bear a striking resemblance to the simple eusocial societies of cooperatively breeding birds and mammals (Emlen, 1991; Sherman et al., 1995; Buston, 2002; Wong, 2007; Wong and Buston, 2013). In both *A. percula* and *P. xanthosoma*, groups of individuals are found in close association with cnidarian hosts (anemones or corals) that provide the fish with protection from predators, food and a place to lay their eggs (Lassig, 1976; Fautin, 1992). Each host contains one group of fish, which is typically composed of a breeding pair and a small number of subordinate non-breeders (**Figure 1**). Within each group there is a size-based dominance hierarchy: the largest two individuals are the breeders, and the non-breeders get progressively smaller (Buston, 2003a; Wong et al., 2007). These fishes, like many coral reef fishes, are hermaphroditic: clown anemonefish can change sex from male to female (Fricke and Fricke, 1977; Moyer and Nakazono, 1978); coral-dwelling gobies can change sex in both directions (Lassig, 1977; Kuwamura et al., 1994; Nakashima et al., 1996; Munday,

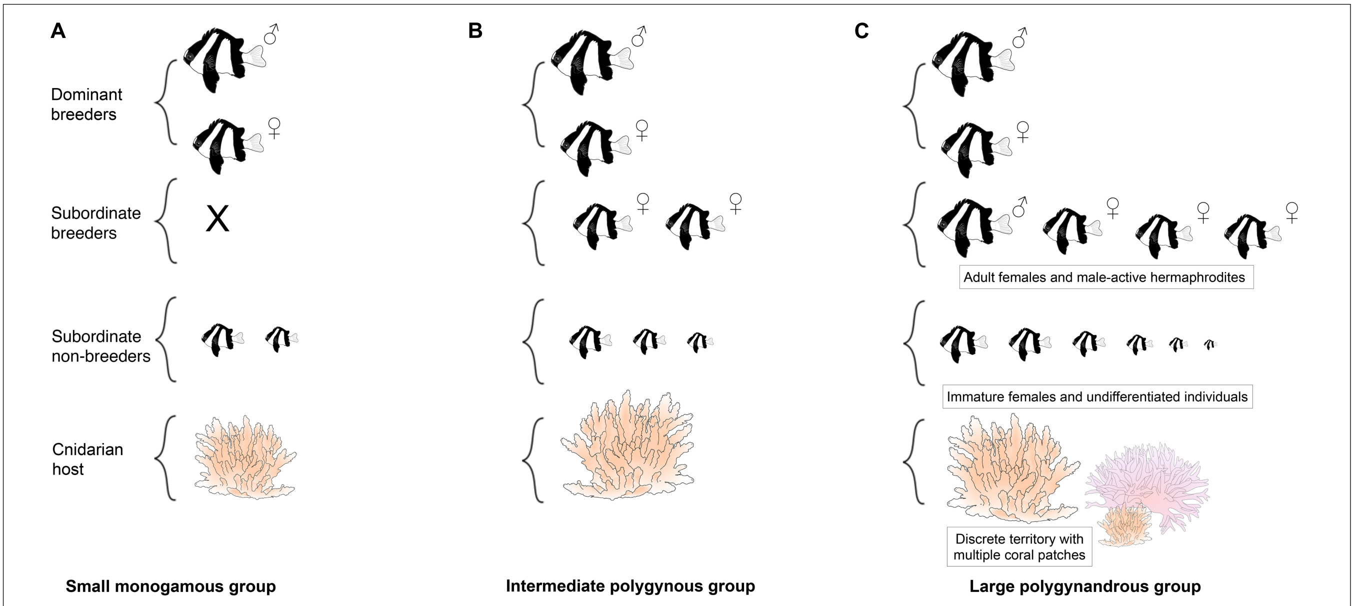


FIGURE 2 | Schematic of the variable social organization **(A–C)** of *Dascyllus aruanus*. X denotes no individuals present at that rank.

2002). Breeding occurs year-round and generally on a lunar cycle; for each egg clutch, the female lays several hundred eggs, which the male fertilizes and then takes care of until they hatch 1 week later (Buston, 2004b; Wong et al., 2008b).

While they have greatly improved our understanding of sociality in the marine realm, focusing solely on *A. percula* and *P. xanthosoma* presents some limitations. To broaden our understanding of social evolution, it is crucial to encompass model species with more variable social systems, reproductive skew, and individual mobility. Such species allow us to test the predictions of theoretical models by manipulating genetic, ecological, and social variables (Buston et al., 2007b).

Extending Research From Simple to Complex Social Systems

One good candidate that provides such opportunities is the humbug damselfish, *Dascyllus aruanus* (Pomacentridae). It is another coral reef fish that is widespread throughout the Indo-Pacific and lives in social groups in close association with branching corals (Sale, 1971; Forrester, 1991; Holbrook et al., 2000). Unlike *A. percula* and *P. xanthosoma*, *D. aruanus* sometimes have multiple coral hosts within their territories, and fish move between them, both on their own and in groups (Mann et al., 2014). Residents of each territory actively repel unfamiliar conspecifics (Schmitt and Holbrook, 1999; Jordan et al., 2010), limiting movement of individuals between territories (Forrester, 1991). Within each territory there is a single group of fish (Sale, 1971; Coates, 1980a; Forrester, 1991), composed of 1–2 breeding males, 3–4 breeding females and 2–4 subordinate non-breeders (**Figure 2**; Sale, 1972; Holbrook et al., 2000; Wong et al., 2012). A striking feature of humbug damselfish societies is that the mating system is plastic, shifting from monogamy to polygyny to polygynandry as group and coral size increases (**Figure 2**; Wong et al., 2012). The groups have weakly defined size-based dominance hierarchies: males tend to be the largest dominant individuals, females tend to be intermediate in size, and subordinate non-breeders tend to be the smallest individuals (**Figure 2**; Coates, 1980a; Cole, 2002; Asoh, 2003; Wong et al., 2012). These fish are generally protogynous hermaphrodites (Sale, 1970; Cole, 2002; Asoh, 2003): if the male of a focal group disappears, then a large female from the focal group or a nearby group changes sex and takes his place (Fricke and Holzberg, 1974; Coates, 1982); if the dominant female disappears, the next ranking male can revert back to being a female if no immigration occurs (Kuwamura et al., 2016). This species breeds on a lunar or semi-lunar cycle: females deposit eggs in a nest and males fertilize the eggs and care for them for 2–5 days until they hatch (Sale, 1970; Mizushima et al., 2000).

In this review we synthesize the existing literature on *A. percula*, *P. xanthosoma,* and *D. aruanus*, highlighting how they have contributed to our understanding of sociality in the marine environment. We show that studying these and other marine fishes provides new insights into the evolution of sociality, and we uncover knowledge gaps and suggest future directions in the field.

PART 1: WHY DO NON-BREEDERS FORGO REPRODUCTION?

Most of the major hypotheses of social evolution that pertain to why subordinate non-breeders forgo their own reproduction have been tested in marine fishes using long-term monitoring, experimental manipulations, molecular tools and mathematical modeling throughout the past two decades (**Table 1**).

Present Direct Genetic Benefits: Current Reproduction

The first question to address is whether subordinates in our model systems truly are non-breeders. Subordinates in *A. percula*

TABLE 1 | Major hypotheses for why non-breeders forgo their own reproduction in three tractable systems within coral reefs: the clown anemonefish, the emerald coral goby and the Humbug damselfish.

Hypothesis	Clown anemonefish (*Amphiprion percula*)	Emerald coral goby (*Paragobiodon xanthosoma*)	Humbug damselfish (*Dascyllus aruanus*)
(1) Present direct genetic benefits: current reproduction	Fricke and Fricke, 1977; Rueger et al., 2018 🟦	Lassig, 1976; Wong et al., 2008a 🟦	Wong et al., 2012 🟨
(2) Present indirect genetic benefits: kin selection	Buston, 2004b; Buston et al., 2007a 🟦	Wong, 2007; Rueger et al., 2021 🟦	Buston et al., 2009 🟦
(3) Future direct genetic benefits: inheritance	Buston, 2004a 🟨	Wong et al., 2007 🟨	Coates, 1982 ▤
(4) Poor inside options: social constraints	Buston, 2003a,b; Branconi et al., 2020 🟨	Wong et al., 2007, 2008a 🟨	TBD ⬜
(5) Poor outside options: ecological constraints	Buston, 2003a, 2004a; Branconi et al., 2020 🟨	Wong, 2010 🟨	TBD ⬜

References included directly test the given hypothesis; Blue: hypothesis has been falsified; gold: hypothesis has been supported; blue-gold lines: condition-dependent; gray: there is work to be done (TBD).

and *P. xanthosoma* do not have functional gonads (Lassig, 1976; Fricke and Fricke, 1977; Moyer and Nakazono, 1978), and they do not develop functional gonads due to the threat of eviction (Wong et al., 2008a; Rueger et al., 2018). This confirms that the subordinates truly are non-breeders, and it demands further investigation as to why they choose to forgo reproduction and cooperate in social groups.

In contrast, for *D. aruanus* early evidence indicated that subordinates do have functional gonads (Asoh, 2003; Cole, 2002). A study combining field observations with genetic parentage analysis showed that high ranking and large individuals (dominants and high-ranking subordinates), from within the group as well as extra-group individuals, are more likely to breed and attain large reproductive shares than low-ranking and small individuals (Wong et al., 2012). However, low-ranking and small *D. aruanus* do reproduce, and reproductive skew is very variable compared to *A. percula* or *P. xanthosoma*.

Present Indirect Genetic Benefits: Kin Selection

The kin selection hypothesis makes two critical predictions: first, non-breeders enhance the fitness of breeders; second, non-breeders are closely related to breeders (Hamilton, 1964; Emlen and Wrege, 1988; Griffin and West, 2003). Both predictions have been tested using *A. percula* and *P. xanthosoma*. In *A. percula*, a removal experiment revealed that non-breeders had no direct effect on the survival or reproduction of breeders during a year-long study (Buston, 2004b). Similarly, there was no evidence that *P. xanthosoma* non-breeders engaged in behaviors that might enhance survival or reproduction of the breeders (Wong, 2007). Genetic analysis showed that subordinate non-breeders were not closely related to the breeders in *A. percula* (Buston et al., 2007a) or *P. xanthosoma* (Rueger et al., 2021).

Although the first prediction that non-breeders enhance the fitness of breeders has not been tested experimentally for *D. aruanus*, it seems likely to be supported in small groups where the subordinates are females, since the fitness of the dominant male is enhanced by having more potential mates. However, the answer may be more nuanced in large groups where some of the subordinates are males, since it is not clear how they impact the fitness of dominant breeders (Wong et al., 2012). The second prediction that non-breeders are closely related to breeders has been tested directly. The mean coefficient of relatedness among group members was close to zero, and any pairs of close relatives were small and similar in size, suggesting that siblings may recruit together but that kin associations break-up post recruitment (Buston et al., 2009).

Taken together, the results from all three species suggest that kin selection does not play a role in explaining why non-breeders tolerate their position in coral reef fishes. The limited role of kin selection in all three model species is interesting given that kin selection is thought to be the major driver of these types of social systems in other taxa.

Future Direct Genetic Benefits: Territory Inheritance

The territory inheritance hypothesis makes two critical predictions: first, non-breeders have the capacity to reproduce in the future; second, the probability of territory inheritance is high (Williams, 1966; Kokko and Johnstone, 1999). Both predictions were tested using *A. percula* and *P. xanthosoma*. In both species subordinate non-breeders have the capacity to reproduce in the future, as they filled breeding vacancies when dominant breeders were removed (Buston, 2004a; Wong et al., 2007). In all cases it was the highest ranked non-breeder (rank three in the group hierarchy) that inherited the breeding vacancy; in no cases did a smaller non-breeder from a lower rank in the same coral/anemone or a non-breeder from elsewhere usurp the breeding vacancy (Buston, 2004a; Wong et al., 2007). Taken together, these results are some of the clearest demonstrations (not confounded by kin selection) that individuals will adopt non-breeding positions because of the potential to reproduce in the future. These studies indicate that territory inheritance is a driving force behind the evolution of non-breeding strategies in coral reef fishes.

In *D. aruanus,* the first prediction that non-breeders have the capacity to reproduce in the future is likely less crucial, because parentage analyses indicate that subordinates gain some current reproduction (Wong et al., 2012). Regarding the second prediction that the probability of territory inheritance is high, dominant male-removal experiments showed that when the experimental corals were caged, it was the largest female of the group that changed sex and took his place (Coates, 1982). However, sexually mature individuals also have the potential to move from one territory to another (**Figure 3**; Sale, 1971; Asoh, 2003; Wong et al., 2012), which would reduce the probability of territory inheritance relative to *A. percula* and *P. xanthosoma,* because resident individuals can be usurped in some contexts.

Poor Inside Options: Social Constraints

The social constraints hypothesis makes two predictions: first, individuals will remain in groups and engage in cooperative actions when there is some social constraint; second, critically, the likelihood of individuals contesting to breed will increase when the social constraint is relaxed (Muthoo, 2000; Buston and Zink, 2009). In *A. percula* and *P. xanthosoma*, well-defined size differences are maintained between individuals adjacent in rank by precise regulation of subordinate growth (Buston, 2003b; Buston and Cant, 2006; Wong et al., 2007). In *A. percula*, higher ranked individuals evict or occasionally kill subordinates that are similar in size to themselves (Allen, 1972; Buston, 2003a). In both species, the likelihood of a subordinate winning a contest is zero when the pair's size ratio matches that found under natural conditions (Wong et al., 2007, 2016), indicating that the size ratio represents a social constraint. In experimental settings, subordinates were more likely to contest and sometimes won a fight when the social constraints were relaxed (Wong et al., 2007; Branconi et al., 2020). These results demonstrate that strong social constraints are a driving force behind the evolution of non-breeding strategies in coral reef fishes.

To date, no experimental studies have been conducted to test the social constraints hypothesis in *D. aruanus*. However, multiple features of humbug damselfish societies point toward less social constraints operating than in other systems. In *D. aruanus* groups, there is no well-defined size ratio (*sensu* Buston and Cant, 2006) between individuals of different ranks. This suggests that social constraints over rank and reproduction may be more relaxed in this species, as shown by the frequent occurrence of reproduction by subordinates (Wong et al., 2012). Alternatively, other factors may influence subordinate reproduction. For example, the size of prey taken by individuals is not correlated with their absolute size but with their rank (Coates, 1980b); this could affect the amount of time spent by subordinates foraging for food, their energy budgets and, in turn, their fitness. Future research with experimental manipulation of inside options analogous to Branconi et al. (2020) is needed in *D. aruanus*.

Poor Outside Options: Ecological Constraints

The ecological constraints hypothesis makes two predictions: first, individuals will remain in groups and engage in cooperative actions when there is some ecological constraint; second, critically, the likelihood of individuals leaving to breed will increase when the ecological constraint is relaxed (Emlen, 1982; Cant and Johnstone, 2009). Both predictions have been tested using *A. percula* and *P. xanthosoma*. In both species, there are two types of ecological constraints: (i) it is risky to move between patches of habitat (Mariscal, 1970; Lassig, 1981; Elliott et al., 1995) and (ii) the alternative habitat is saturated (Lassig, 1977; Fautin, 1992; Elliott and Mariscal, 2001). In *A. percula,* non-breeders did not leave to breed elsewhere when habitat vacancies were created, showing that habitat saturation alone does not prevent them from dispersing (Buston, 2003a, 2004a). In both species, cross-factored experiments showed that the likelihood of dispersal increased as alternative habitats became less saturated and as risks of movement decreased (Wong, 2010; Branconi et al., 2020). These results demonstrate that individuals will adopt non-breeding positions because of the combination of habitat saturation and risks of movement, indicating that strong ecological constraints are a driving force behind the evolution of non-breeding strategies in coral reef fishes.

Observational evidence suggests that ecological constraints will also play a role in *D. aruanus* but may be condition-dependent. Small immature juveniles move more frequently between coral heads on continuous reef habitats (lower risk of movement) than in patchy reef habitats (higher risk of movement) (Nanami and Nishira, 2001). In addition, the survival rate was 3.3 times higher on continuous habitat than on patchy habitat, suggesting that there are real risks associated with living in patchy habitats (Nanami and Nishira, 2001). Large sexually mature individuals are known to move between groups to breed (**Figure 3**; Sale, 1971; Asoh, 2003). The reasons that large

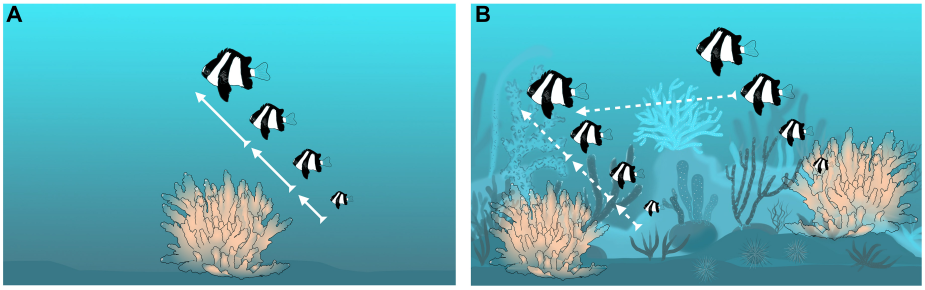


FIGURE 3 | Relationship between ecological constraints and territory inheritance within groups of *Dascyllus aruanus*; arrows represent changes in rank via inheritance or movement (bold continuous arrows show high probability of territory inheritance in the group; dashed arrows show some lower probability of territory inheritance in the group and some probability of inheritance via movement from the neighboring group). **(A)** Patchy habitat with strong ecological constraints, little movement and high probability of territory inheritance; **(B)** More continuous habitat, with weak ecological constraints, lots of movement, and lower probability of territory inheritance.

individuals might move more than small individuals are twofold: (i) large individuals are less likely to move forward in their resident queue than small individuals, because there are fewer individuals ahead of them to die; and, (ii) large individuals are less likely to be preyed upon while moving between groups than small individuals, because they are faster and exceed the gape limitation of more predators. To tease apart the relative effects of these factors and assess the validity of the ecological constraints hypothesis in *D. aruanus*, more experimental work analogous to Wong (2010) and Branconi et al. (2020) is needed.

PART 2: WHY DO BREEDERS TOLERATE NON-BREEDERS?

The major hypotheses looking at why dominant breeders would tolerate non-breeders that share their territories have received much less attention in marine fishes (**Table 2**).

Reproductive Control via Threat of Eviction

The reproductive control hypothesis makes two predictions: reproduction is resource-limited; and reproduction in subordinates is suppressed via the threat of eviction (Clutton-Brock et al., 2010). Both predictions have been tested using *P. xanthosoma* and *A. percula*. In both species, a feeding experiment revealed that reproduction by the dominant female is resource limited, providing an incentive for dominants to evict subordinates (Wong et al., 2008a; Rueger et al., 2018). Such evictions do indeed occur if subordinates are sexually mature (Wong et al., 2008a; Rueger et al., 2018). Overall, these studies provide clear evidence that dominants use the threat of eviction to keep subordinates from reproducing. The fact that dominants have the ability to evict subordinates suggests that subordinates are tolerated either because they are inconsequential or because they provide some benefit to dominant breeders.

In contrast, *D. aruanus* subordinate males and females can obtain large shares of total reproduction within their groups (Wong et al., 2012). While reproduction by males is limited by the number of females and eggs produced, no studies have tested whether dominants try to suppress the reproduction of same-sex subordinates or whether reproduction is resource-limited for females. Investigating how reproductive shares of both sexes are negotiated will be an interesting avenue of future research.

Present Direct Genetic Benefits: Current Reproduction

The present direct genetic benefits hypothesis predicts that the dominant breeders will accrue some immediate fitness advantages from the presence of non-breeders (Woolfenden and Fitzpatrick, 1984; Emlen and Wrege, 1988). In *A. percula*, this was tested using year-long observations of survival, growth and reproduction of 71 groups together with an experimental manipulation of 14 groups where subordinates were removed from breeding pairs (Buston, 2004b). Non-breeders had no effect on the survival, growth or reproduction of breeders, which rules out the possibility that present direct genetic benefits motivate breeders to tolerate non-breeders in their groups (Buston, 2004b; Buston and Elith, 2011). The generality of these findings has yet to be tested using *P. xanthosoma*.

For the dominant male in *D. aruanus* groups, having multiple breeding females may increase the number and genetic diversity of offspring he can sire, as long as he can provide sufficient parental care (Forsgren et al., 1996; Mizushima et al., 2000; Wong et al., 2012). For the dominant female, it is possible that the presence of subordinates enables her to feed more and produce more eggs because of the increased vigilance of the group and/or have higher survival due to predator dilution effects in larger groups (Rubenstein, 1978; Beauchamp, 2015). Future work is needed to experimentally test these hypotheses.

Present Indirect Genetic Benefits: Kin Selection

The kin selection hypothesis predicts that the dominants benefit from the presence of non-breeders because they are relatives that inherit the breeding territory. For such kin selection to operate, relatedness within groups does not need to be high but it

TABLE 2 | Major hypotheses for why breeders tolerate non-breeders in their territories in three tractable systems within coral reefs: the clown anemonefish, the emerald coral goby and the Humbug damselfish.

Hypothesis	**Clown anemonefish (*Amphiprion percula*)**	**Emerald coral goby (*Paragobiodon xanthosoma*)**	**Humbug damselfish (*Dascyllus aruanus*)**
(1) Reproductive control via threat of eviction	Rueger et al., 2018 🟨	Wong et al., 2008a 🟨	Wong et al., 2012 🟦
(2) Present direct genetic benefits: current reproduction	Buston, 2004b; Buston and Elith, 2011 🟦	TBD ⬜	TBD ⬜
(3) Present indirect genetic benefits: kin selection	Buston et al., 2007a; Salles et al., 2016; TBD ⬜	Rueger et al., 2021 🟨	Buston et al., 2009 🟦
(4a) Future direct genetic benefits: Mate-replacement benefits	Buston, 2004b; TBD ⬜	Wong et al., 2007; TBD ⬜	Coates, 1982; Kuwamura et al., 2016 ▤
(4b) Future direct genetic benefits: Mutualist mediated benefits	TBD ⬜	TBD ⬜	TBD ⬜

References included directly test the given hypothesis; Blue: hypothesis has been falsified; gold: hypothesis has been supported; blue-gold stripes: condition-dependent; gray: so far there is only observational evidence, and there is work to be done (TBD).

does need to be higher than the population average (Hamilton, 1963, 1964; West-Eberhard, 1975). In *A. percula*, in a study using seven microsatellite markers to assess relatedness within nine groups, there was no evidence that these groups were on average composed of close relatives ($r < 0.001$; Buston et al., 2007a). However, low numbers of markers and samples may be insufficient to detect subtle relatedness patterns. A complete genealogy revealed that *A. percula* offspring often settle close to their parents and close relatives are sometimes found in the same group (Salles et al., 2016), suggesting there may be potential for weak kin selection. Recent research on *P. xanthosoma*, using a larger microsatellite panel and greater sample size (20 microsatellite markers and 16 groups), found evidence that groups are composed of distant relatives ($r = 0.026$; Rueger et al., 2021). This suggests that weak kin selection might tip the balance, motivating the dominants to tolerate subordinates within their territories even if they provide no other benefits. This and other recent examples of fine-scale relatedness patterns in marine fishes [likely caused by limited dispersal (Rueger et al., 2020)] underline the necessity to assess genetic relatedness when studying marine fishes, so that the potential for weak kin selection is not prematurely dismissed.

For *D. aruanus,* kin selection plays a role only for the early life stages, since siblings may be recruiting together but kin associations break up after settlement (see section "Present indirect genetic benefits: kin selection", Buston et al., 2009). Accordingly, there are no present indirect genetic benefits conferred to the dominants by tolerating subordinates in *D. aruanus*.

Future Direct Genetic Benefits

Rapid Mate-Replacement Benefits

The mate-replacement hypothesis predicts that the dominants benefit from the presence of non-breeders because they serve as rapid mate replacements should one of the breeders perish (Fricke, 1979). This hypothesis was tested in *A. percula,* and the mean time taken for a widowed female to recommence breeding was only 2.3 lunar months less in the presence of non-breeders versus in their absence; this suggests that females who tolerated at least one subordinate non-breeder had just a 2% gain in relative fitness (Buston, 2004b). It is possible that instead, the major benefit comes in the form of reducing the variance rather than the mean in the time taken to recommence breeding (Rubenstein, 2011; Koenig and Walters, 2015), though this has not been tested in *A. percula*. When breeding females were removed from *P. xanthosoma* groups, non-breeders took their place within days and none of the breeding vacancies were taken over by an individual from another group (Wong et al., 2007). Mate-replacement benefits may be more important in *P. xanthosoma* than *A. percula,* because *P. xanthosoma* are estimated to have shorter breeding tenures than *A. percula*

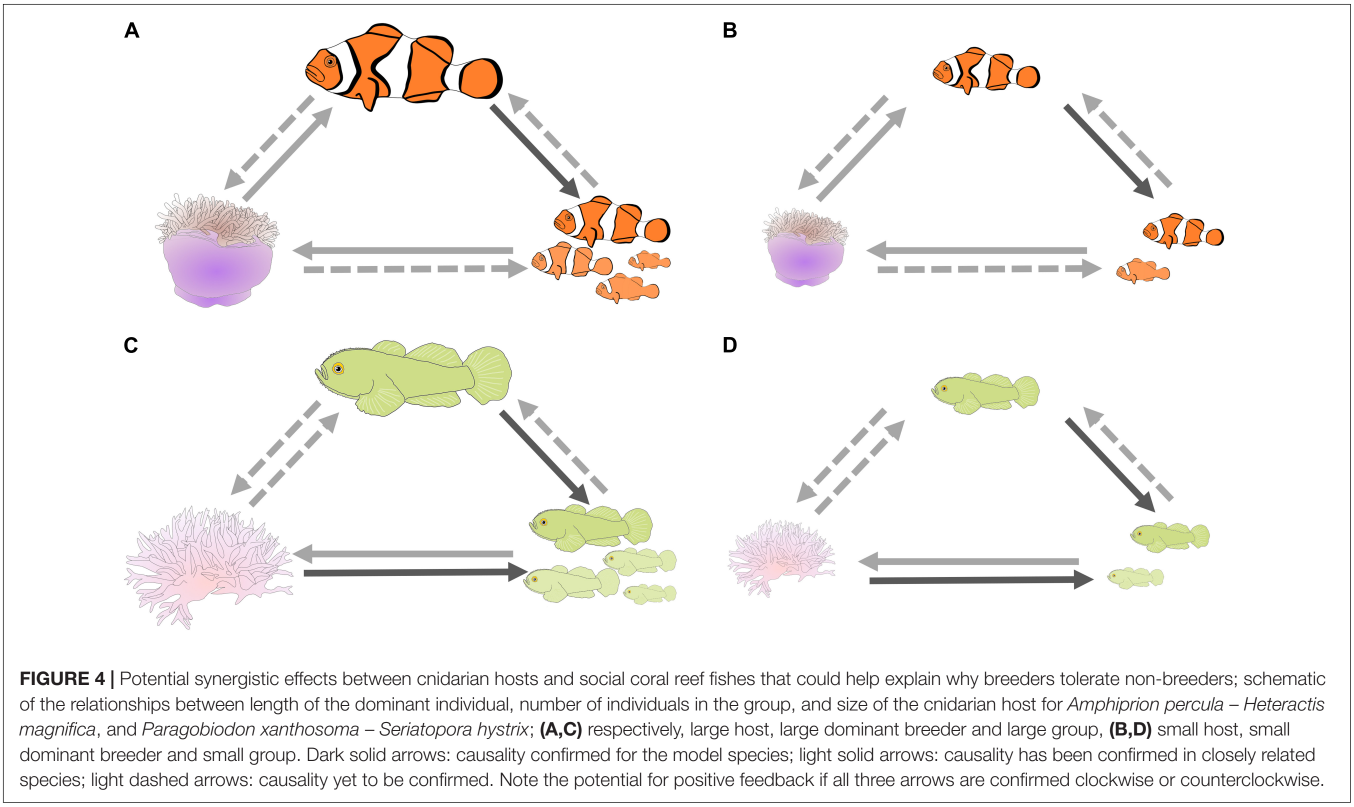


FIGURE 4 | Potential synergistic effects between cnidarian hosts and social coral reef fishes that could help explain why breeders tolerate non-breeders; schematic of the relationships between length of the dominant individual, number of individuals in the group, and size of the cnidarian host for *Amphiprion percula – Heteractis magnifica*, and *Paragobiodon xanthosoma – Seriatopora hystrix*; **(A,C)** respectively, large host, large dominant breeder and large group, **(B,D)** small host, small dominant breeder and small group. Dark solid arrows: causality confirmed for the model species; light solid arrows: causality has been confirmed in closely related species; light dashed arrows: causality yet to be confirmed. Note the potential for positive feedback if all three arrows are confirmed clockwise or counterclockwise.

(Kuwamura et al., 1996; Buston and García, 2007) so that a single month of lost reproduction is a greater fraction of their total reproduction. The magnitude of rapid mate-replacement benefits and the generality of these findings are yet to be determined.

In *D. aruanus,* no studies have directly tested if subordinate non-breeders act as rapid mate replacements. However, the frequent occurrence of immigration by extra-group individuals (Fricke and Holzberg, 1974; Coates, 1982; Wong et al., 2012) suggests that sexually maturing subordinates may not represent the fastest mate-replacement option in this species, at least on continuous reef where ecological constraints are relaxed. Dominant male-removal experiments showed that another male or a large female (that can change sex to male) will frequently immigrate from another group to fill breeding vacancies (Coates, 1982). On the other hand, dominant female-removal experiments showed that small males can change sex back to female when no females or juveniles immigrate to their group (Kuwamura et al., 2016). The latter study suggests that, in isolated groups, subordinates may act as rapid mate replacements. Evidently, mate-replacement benefits will be context-dependent.

Mutualist Mediated Benefits

The mutualist mediated benefits hypothesis predicts that dominant breeders benefit from the presence of subordinate non-breeders because (i) non-breeders enhance the survival, growth, and size of the cnidarian hosts, and (ii) large cnidarian hosts enhance the survival, growth, and reproduction of the breeders. These synergistic effects, whereby the group achieves things that the breeders alone cannot (Bourke, 2011), have not been tested directly in any of the three focal species, but a range of evidence points toward the plausibility of the hypothesis.

There are positive correlations between the length of the dominant, the number of individuals in the group, and the size of the cnidarian host in *A. percula* and *P. xanthosoma* (**Figure 4**; Fautin, 1992; Elliott and Mariscal, 2001; Buston, 2003a; Wong, 2011; Chausson et al., 2018; Barbasch et al., 2020). These correlates could be caused by extrinsic factors, e.g., dominants, groups, and cnidarians may all flourish at good sites on the reef (the null hypothesis), or they could be caused by intrinsic factors, e.g., the number of fish in a group influencing host size. Indeed, the causality of some of these relationships has been determined: female size influences the number of fish in a group, due to the rules of the size hierarchy in both species (*A. percula – Heteractis magnifica*, Buston, 2003b; Buston and Cant, 2006; Branconi et al., 2020; *P. xanthosoma – Seriatopora hystrix*, Wong et al., 2007; Wong, 2011); and, at least in *A. percula*, anemone size is positively correlated with the growth of the fish, explaining why larger anemones are associated with larger females (Buston, 2002), and larger females lay more eggs, resulting in more parental care and higher embryo survival (Buston and Elith, 2011; Barbasch et al., 2020). Thereby larger anemones might have a positive influence on fish reproductive output. The latter results are likely explained by larger anemones providing greater foraging area, because foraging is confined to the anemone (Barbasch et al., 2020), and/or larger anemones providing more egesta, which may provide important nutrition (Verde et al., 2015). The critical experiment, manipulating cnidarian size and examining the effect on the breeders remains to be done.

For both model species, we are also missing experimental tests of the first prediction, that non-breeders enhance the fitness of the cnidarian host. However, several mechanisms are plausible, and they have been experimentally demonstrated in other anemone-anemonefish interactions. The number of individuals in a group influences anemone size, due to effects on anemone growth and expansion behavior (*A. bicinctus* – *Entacmaea quadricolor*, Porat and Chadwick-Furman, 2004; *A. chrysopterus* – *H. magnifica*, Holbrook and Schmitt, 2005; and, *A. melanopus* – *E. quadricolor*, Frisch et al., 2016), and the presence of anemonefish facilitates recovery of anemones after bleaching events (*A. akindynos* – *E. quadricolor*, Pryor et al., 2020). A suite of cooperative behaviors directed toward the anemone have been observed in *A. percula*, including defensive behaviors toward anemone predators, and cleaning (Mariscal, 1966; Iwata and Manbo, 2013). It is plausible that similar behaviors beneficial to the host also occur in *P. xanthosoma*, because they have been found in closely related gobies. For example, *Gobiodon histrio* and *P. echinocephalus* trim competing seaweed and reduce coral damage in *Acropora* spp. (Dixson and Hay, 2012). In *P. xanthosoma*, the coral size has been shown to influence the number of individuals in a group in a manipulative experiment (Thompson et al., 2007).

In *D. aruanus*, there is also a correlation between fish group size and coral host size (Wong et al., 2012). Several studies suggest that the presence of fish might enhance the survival and growth of their coral hosts by: (i) providing aeration to the corals (Goldshmid et al., 2004); (ii) defending the coral from predation by corallivorous fish (Chase et al., 2014); (iii) enhancing coral bleaching resilience and recovery (Chase et al., 2018); and (iv) alleviating the impact of sediments on corals (Chase et al., 2020). Potentially, all of these mechanisms may be more pronounced and effective when groups are larger with multiple subordinates. While the effect of subordinate behaviors on the cnidarian hosts has yet to be measured directly, their occurrence in the group as a whole increases the plausibility of the hypothesis that non-breeders may have a positive effect on the host which, in turn, positively impacts breeders and provides incentives for breeders to tolerate non-breeders.

Conclusion of Parts 1 and 2

Why subordinates in coral reef fish societies forgo their own reproduction has been thoroughly investigated. Unlike cooperatively breeding birds and mammals, subordinates do not gain indirect genetic benefits. Rather, subordinates gain direct genetic benefits in the future, because they stand to inherit the breeding territory. They behave peacefully instead of contesting for a breeding position due to social constraints; they remain in the group instead of dispersing to breed elsewhere due to ecological constraints. This solves the paradox of why individuals forgo their own reproduction in marine fishes. More generally, it shows that non-breeding strategies can evolve, and complex groups can form, in the absence of kin selection.

Subordinate non-breeders in groups of *A. percula* and *P. xanthosoma* are tolerated, despite resource-limited reproduction and the demonstrated ability of dominant breeders to evict them. Why dominants tolerate subordinates may be explained by the effects of several factors that each confer small fitness advantages to the breeders. First, dominants might accrue some indirect genetic benefits from tolerating their distant relatives who go on to inherit the territory (Rueger et al., 2021). Second, dominants might accrue some future genetic benefits by tolerating subordinates who serve as rapid mate replacements (Buston, 2004b). Third, dominants might accrue some future genetic benefits by tolerating subordinates who contribute to the growth of the mutualistic host, which in turn helps breeders grow and reproduce more. The latter has yet to be tested directly in either model species, but some evidence indicates it may be a fruitful topic for future investigations.

Dascyllus aruanus has a much more variable social system and consequently their social group formation is more challenging to understand. In *D. aruanus*, present direct genetic benefits exist; subordinate males and females gain benefits by reproducing for themselves, and the dominants benefit either by reproducing with subordinates or gaining other fitness benefits due to the presence of subordinates. However, how their reproductive shares are determined remains to be seen. Kin selection only plays a limited role. The magnitude of future genetic benefits, in terms of territory inheritance for the subordinates and rapid mate replacement for the dominants, are dependent on the ecological context: individuals move readily between groups in continuous habitats when ecological constraints are weaker; individuals move less between groups in patchy habitats when ecological constraints are stronger. Future investigations, direct experiments, and the application of more innovative methods such as social network analysis (SNA), are essential to better understand why these fish live in such complex social groups (**Box 1**). The use of *D. aruanus* as a complex model system for the research of social evolution has the potential to generate new insights into the origin and maintenance of social systems in coral reef fishes and other marine taxa.

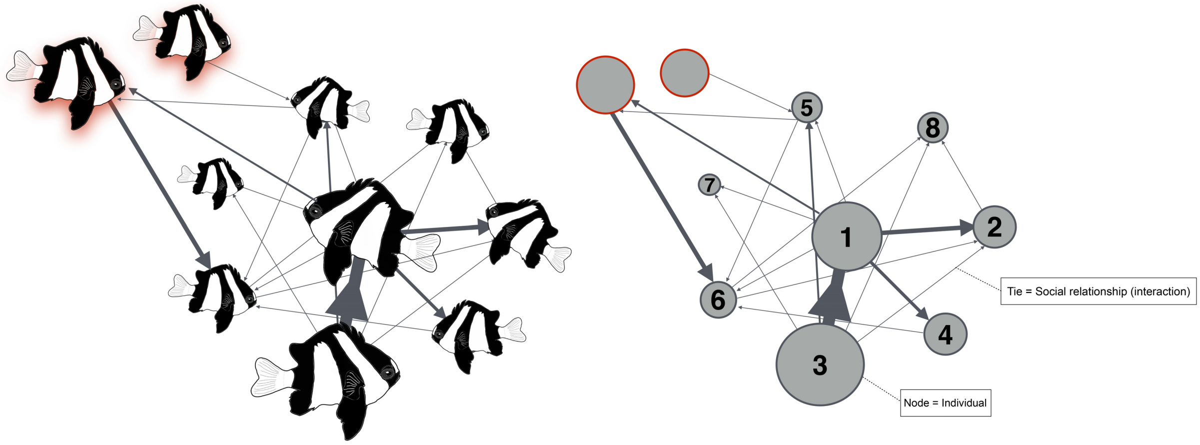
PART 3: FROM MODEL SPECIES TO MODEL GENERA

Amphiprion percula, *P. xanthosoma,* and *D. aruanus* have provided valuable insights into sociality in marine fishes. Moving beyond the investigation of these model species to comparative studies among congeners is an important next step, marking a transition from trying to understand what drives sociality within a species, to what drives variation in sociality among species. This next step is crucial for determining the extent to which variation in social systems across closely related species is explained by variation in key drivers of social evolution. In turn, this assists in discerning the conditions that likely gave rise to sociality (Brown, 1974; Kocher and Paxton, 2014; Hing et al., 2017).

The most important step in explaining drivers of interspecific social variation is to conduct phylogenetically controlled comparisons. Such a study has been conducted using the coral-dwelling gobies from the genus *Gobiodon* whose phylogeny is relatively well resolved (e.g., Harold et al., 2008; Herler et al., 2009; Duchene et al., 2013; Hing et al., 2019). Recent research on *Gobiodon* has investigated social variability by adopting an

BOX 1 | Complex methods for more complex groups.

While experimental approaches can help us understand some of the mechanisms involved in the origin and maintenance of social systems in coral reef fishes, the application of social network analysis (SNA) offers an opportunity to understand sociality on a finer scale. This is particularly crucial for species such as *D. aruanus*, that have larger groups and more variable dominance structures. SNA is one of the most powerful and effective methods used in evolutionary biology to characterize the temporary internal structure of social groups and their stability over time (Croft et al., 2008; Sueur et al., 2019; Romano et al., 2020; Sosa et al., 2021). In SNA, social entities (individuals) are considered nodes and their social relationships (interactions) are considered ties (**Box Figure 1**). This reveals the group network as a web of direct and indirect inter-relationships that provide a holistic perspective for the study of sociality and group dynamics (Croft et al., 2008; Wey et al., 2008). With the ability to depict different levels of interactions within groups (dominant vs. subordinate individuals) and between groups (intra- vs. extra-group individuals), SNA could help us solve many open questions relating to *D. aruanus* sociality. In *D. aruanus* individuals show clearly defined aggressive and submissive interactions (Branconi et al., 2019a), making it possible to characterize social networks. For example, SNA, together with new tagging methods (Branconi et al., 2019b), may help evaluate group structure and stability across time, according to habitat quality and different degrees of social and ecological constraints.



BOX FIGURE 1 | Hypothetical weighted and directed social network of a small group of *Dascyllus aruanus*. The thickness of the ties (interactions) is proportional to the strength of the connection between the individuals, and the size of the nodes (individuals) is proportional to their respective number of social interactions. Numbers denote individual ID. Red shaded individuals/nodes denote extra-group individuals.

integrative approach that examines ecological factors and life-history traits together with phylogenetically controlled contrasts. Hing et al. (2019) used 15 *Gobiodon* species to measure the diversity and frequency of group sizes and calculated a sociality index for each species. The sociality index (outlined in Avilés and Harwood, 2012) accounts for the proportion of groups within the population, proportion of subordinates within groups (indicating propensity to join a group and be tolerated by dominants), and proportion of the life cycle spent in groups (indicating propensity for delayed dispersal). The sociality index for each *Gobiodon* species was used to determine the phylogenetic signal of sociality, and its link to factors previously identified as influencing fitness (ecological factors: host coral size and host coral generalization; and life-history trait: body size; Wong, 2011; Hing et al., 2018). While there was some evidence of a weak phylogenetic signal (i.e., ancestral basis) in the evolution of sociality in *Gobiodon*, ecological and life history factors were found to play more important roles (Hing et al., 2019). Larger-bodied species tended to be less social than smaller-bodied species (Hing et al., 2019). Furthermore, sociality depended more on coral size for larger species, likely due to the requirement for larger hosts in order for larger individuals to form groups (**Figure 5**; Hing et al., 2019). Interestingly, one of the few other comparative studies examining relationships between evolutionary history, ecological factors and life-history traits in marine fishes found that there was a strong ancestral basis for sociality (pair-forming versus solitary living) in *Chaetodon* butterflyfishes (Nowicki et al., 2018). Further, Hodge et al. (2018) identified the trade-off between morphological defense strategies and social organization as a crucial driver of butterflyfish evolution, highlighting the importance of employing broad phylogenetically informed approaches in studying reef fish sociality.

In anemonefishes, there has been no formal investigation of interspecific variation in their social behavior using phylogenetically controlled comparisons, even though their phylogenetic relationships have been well resolved (e.g., Elliott et al., 1999; Santini and Polacco, 2006; Litsios et al., 2012; Litsios and Salamin, 2014; Li et al., 2015; Rolland et al., 2018). However, there is some observed social variation between species that are ecologically similar, which indicates that *Amphiprion* species are good candidates for comparative studies. *Amphiprion ocellaris* societies associated with the anemone *Stichodactyla gigantea* in Indonesia seem to function quite similarly to the *A. percula* societies associated with the anemone *Heteractis magnifica* in Papua New Guinea described above (Mitchell, 2003, 2005). In contrast, *A. perideraion* societies associated with *H. magnifica* in the same lagoons and bays as *A. percula* in Papua New Guinea seem to be subtly different (Allen, 1972; Fautin and Allen, 1992; Elliott and Mariscal, 2001; Buston and Cant, 2006; Rueger et al., 2018).The number of individuals in a group, the structure of the size hierarchy, aggression, and cooperative behaviors are traits that seem to vary across the genus (Allen, 1972; Moyer and Nakazono, 1978; Hattori, 1994; Srinivasan et al., 1999; Mitchell and Dill, 2005), raising the question: what causes this variation?

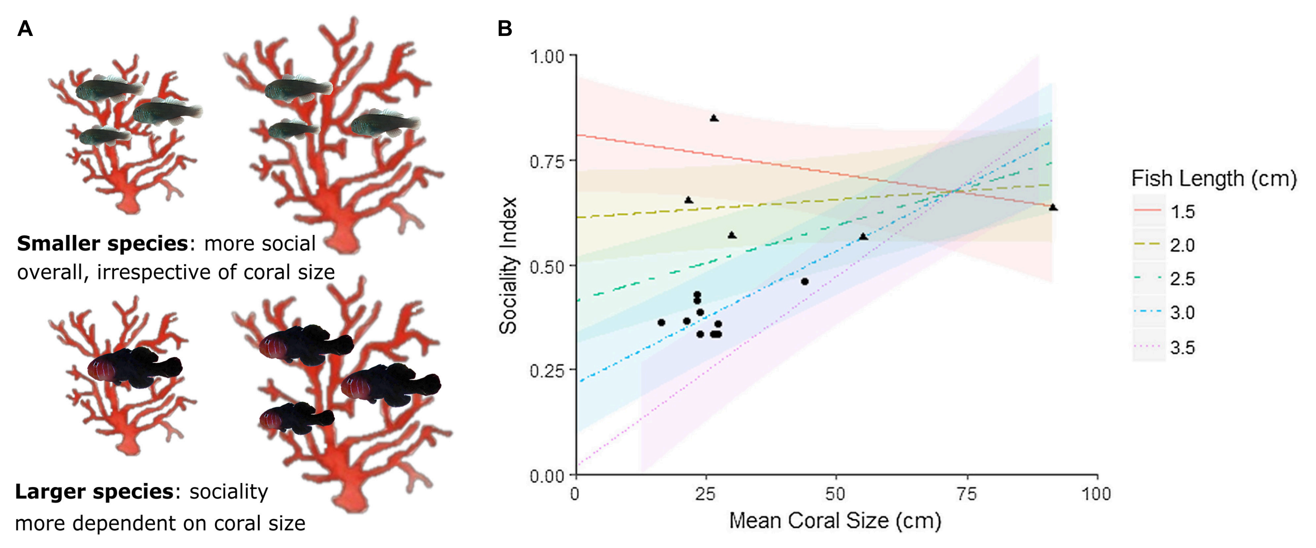


FIGURE 5 | Relationships between social group size, host *Acropora* coral size, and body size for species in the genus *Gobiodon*. **(A)** Schematic depicting variation in group sizes between small and large species in relation to coral size; **(B)** modeled predictions for interactions between coral size and body size (fish length) and their effects on the sociality index (encompassing the proportion of groups within the population, proportion of subordinates within groups, and proportion of the life cycle spent in groups; see Avilés and Harwood, 2012) for *Gobiodon* species. Raw data are the black symbols where pair-forming species are represented by circles and group-forming species are represented with triangles. Modeled body sizes are represented by the colored lines shown in the legend (Figure modified from Hing et al., 2019). The figure is reproduced with permission from Elsevier.

The strength of kin selection seems unlikely to vary greatly across the *Amphiprion* genus, because in all studies to date, their larvae have been shown to disperse from their natal anemone (*A. polymnus,* Jones et al., 2005; Saenz-Agudelo et al., 2011; *A. percula*, Almany et al., 2007; Planes et al., 2009; Buston et al., 2012; Almany et al., 2017; *A. omanensis*, Simpson et al., 2014; *A. bicinctus*, Nanninga et al., 2015; *A. clarkii,* Catalano et al., 2020). The strength of ecological constraints might vary across the genus, causing differences in movement analogous to the differences seen in *D. aruanus* in patchy and continuous habitats (see section "Poor inside options: social constraints" above; **Figure 3**). Ecological constraints can vary among species either because the ecology varies, e.g., *A. clarkii* moves more in sub-tropical waters than tropical waters perhaps due to reduced risks of predation and/or reduced habitat saturation (Hattori, 1994), or because the species traits vary while the ecology is constant, e.g., *A. perideraion* moves more than *A. percula* in the same waters (Rueger et al., 2018), perhaps due to being a better swimmer. A small reduction in the strength of ecological constraints is likely to have effects on territory inheritance because it creates the potential for individuals to have their position usurped (**Figures 3**, **6**). This, in turn, could have knock-on effects for the size hierarchy, conflict, and aggression, as the incentives for subordinates to remain small are reduced (**Figure 6**). More work needs to be done to test these hypotheses and to understand the causes of interspecific variation in social behavior among closely related species of marine fishes.

Conclusion of Part 3

Extending our investigations from model species to model genera is allowing us to gain new insights into social evolution in the marine realm. In *Gobiodon/Paragobiodon* (Gobiidae) and *Amphiprion/Premnas* (Pomacentridae), there is social variation among species that is unlikely to be explained by variation in the strength of kin selection across the genus. Instead, variation in life history traits might interact with the ecology (habitat patch size and risks of movement) to cause these differences. Comparative research on coral-dwelling gobies has highlighted the nuanced and complex nature of sociality within the taxon. Such integrative and quantitative approaches to the study of sociality can be applied to any taxa and provide a robust framework for future comparative work. Interestingly, whether or not there is a strong ancestral basis for sociality appears to differ depending on which reef fish family is examined. Thus, there may be different key drivers of social variation between different taxa. Further comparative studies in other marine fishes, using integrative approaches that incorporate sociality indices, will allow comparisons across diverse taxa to enhance our understanding of social evolution.

PART 4: SOCIALITY AND ENVIRONMENTAL CHANGE

It has long been recognized that environmental variation may alter the state of sociality within and amongst species (Rubenstein and Lovette, 2007; Duffy and Macdonald, 2009; Rubenstein, 2011; Shen et al., 2017). As environmental disturbances affect marine ecosystems with more frequency and intensity and environmental variability in these ecosystems increases (Turner, 2010; Hughes et al., 2018), a key question is: how will the sociality

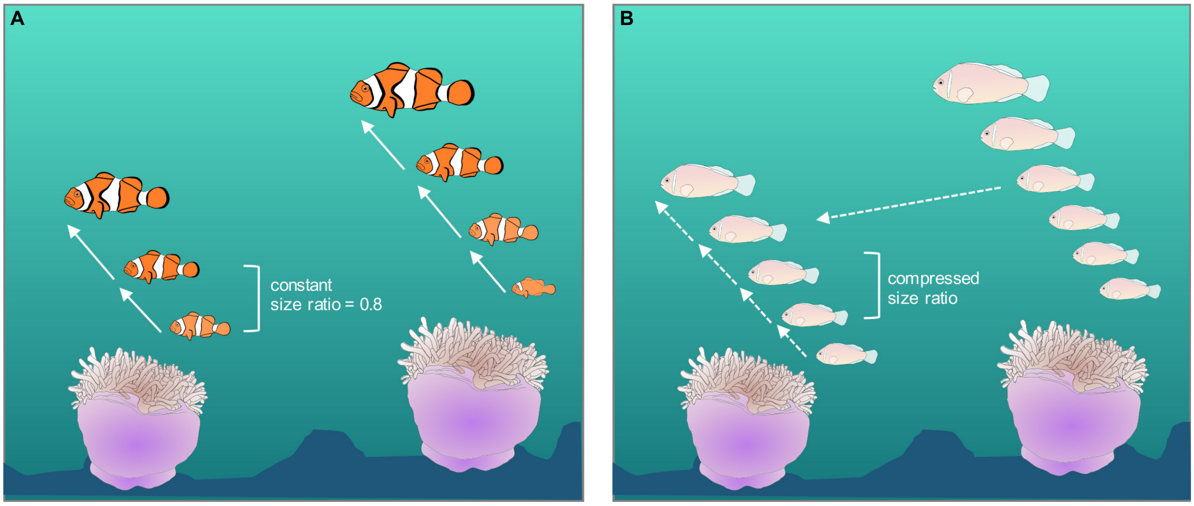


FIGURE 6 | Possible relationship between ecological constraints, territory inheritance, and social organization and behaviors; **(A)** schematic of social organization in *Amphiprion percula*, where ecological constraints are high, movement between anemones does not occur, the probability of territory inheritance is high and the size hierarchy is strict with exact ratios; **(B)** social organization of *Amphiprion perideraion* where ecological constraints are relaxed, movement between anemones does occur, groups are less stable and the size hierarchy is more variable.

of coral reef fishes be influenced? Environmental disturbances can impact sociality in at least four distinct ways: (i) by influencing the relative population size and structure of the fish and their cnidarian hosts; (ii) by influencing the subordinate non-breeders' payoffs associated with staying in or leaving groups; (iii) by influencing the dominant breeders' payoffs associated with tolerating subordinates; and (iv) by negatively impacting the mechanisms that individuals use to engage in social interactions.

Environmental Disturbances Can Change Population Structure and Habitat Saturation

A recent study investigated the impacts of environmental disturbances using before and after disturbance data for populations of social and pair-forming *Gobiodon* species. Thirteen *Gobiodon* species and their mutually beneficial *Acropora* host coral species were monitored throughout two category 4 tropical storms in consecutive years to determine multi-species responses (Hing et al., 2018). After the two storms, the group size of group-forming species ($n = 5$) declined, while the group size of pair-forming species ($n = 8$) showed little variation. Group-forming species occupied larger corals than pair-forming species both before and after the storms, but as coral size decreased, so did the number of group members overall (**Figures 7A,B**). Interestingly, although the number of vacant corals did not change after disturbances, smaller corals became more saturated after disturbances and gobies occupied smaller corals. Thus, it appears that the benefits of group-living in this genus are affected by habitat size rather than habitat availability – both factors which can be strongly influenced by environmental disturbances (Hing et al., 2018).

Environmental Disturbance Can Change Relative Payoffs Associated With Staying or Leaving

Some insights into how environmental conditions are driving sociality in marine fishes may be gained by studying the social consequences of recent disturbances (Hing et al., 2018). Climatic events and crown-of-thorns outbreaks are especially pertinent since they increase the frequency of bleaching and mortality of cnidarians (Cheal et al., 2017; Hughes et al., 2017, 2018, 2019; Pratchett et al., 2017), and social coral reef fishes such as gobies, damselfishes, and anemonefishes depend on live cnidarian hosts (Bonin et al., 2009; Saenz-Agudelo et al., 2011; Pratchett et al., 2020). Although there is a clear preference for healthy hosts, both gobies and anemonefishes are willing to settle and use bleached hosts as long as the hosts are alive (Bonin et al., 2009; Saenz-Agudelo et al., 2011). Individuals are however unwilling to remain in dead hosts (Bonin et al., 2009).

If cnidarian hosts die as a result of environmental disturbances, then dispersal of those occupying them to other habitats will be increasingly difficult (**Figures 7C,D**). After corals were heavily disturbed by crown-of-thorns starfish, *D. aruanus* and two other damselfish species declined substantially, but there was size-specific success in dispersing (Pratchett et al., 2020). Smaller and intermediate-sized individuals were more successful at relocating to a new group than larger individuals, likely because they represented less of a threat to bigger resident breeders (Coker et al., 2013; Pratchett et al., 2020). Dispersing individuals also risk finding uninhabited hosts, which are unattractive to damselfishes (Pratchett et al., 2020), gobies (Wong, 2010), and anemonefishes (Branconi et al., 2020). As the relative payoffs associated with staying and leaving shift under

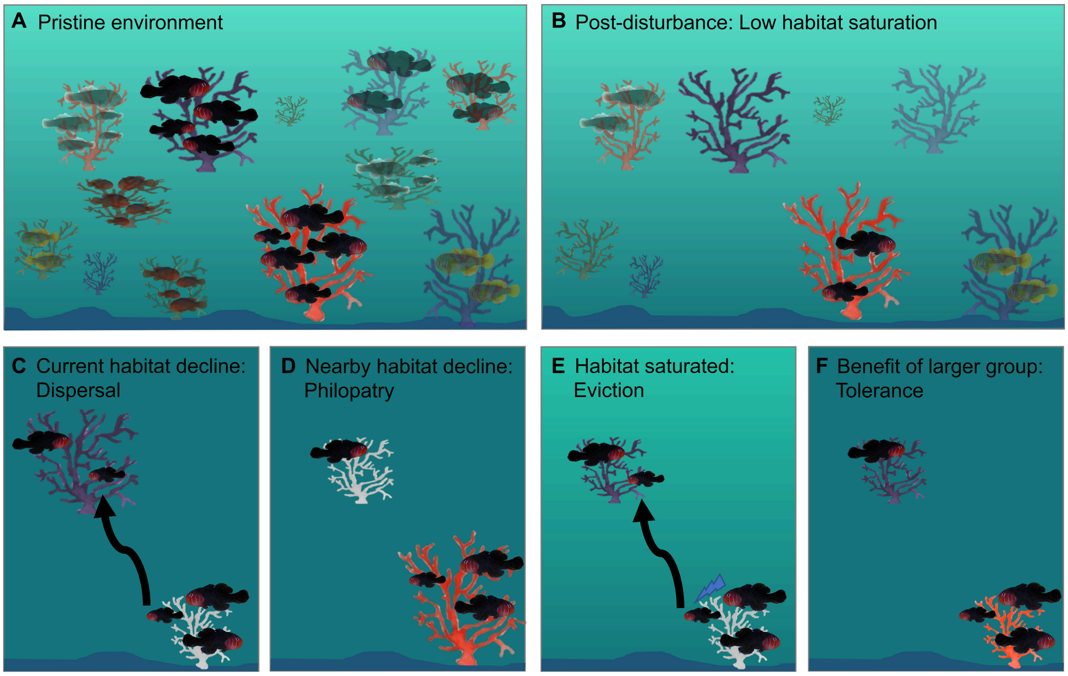


FIGURE 7 | Possible effects of environmental disturbances on the sociality of reef fishes, using *Gobiodon* with *Acropora* coral hosts as examples. After disturbances, a pristine environment **(A)** can become less saturated if fish populations decline more than their habitat **(B)**. If habitat declines (i.e., smaller and unhealthy corals) influence subordinates' payoffs to stay or leave, then current coral patch quality **(C)** and nearby coral patch quality **(D)** will affect the subordinates' decisions to stay or leave. If habitat declines influence payoffs of dominants tolerating subordinates, then subordinates in smaller patches will either be evicted **(E)** or be tolerated because of synergistic effects **(F)**.

environmental disturbances, we anticipate they will continue to play a major role in governing sociality.

Environmental Disturbances Can Change the Payoffs Associated With Tolerating Subordinates

From the dominants' perspectives, environmental disturbances might alter the payoffs associated with tolerating subordinates (**Figures 7E,F**). For example, larger-bodied goby species are typically only group-living when corals are large in size (Hing et al., 2019). Within our model species, group sizes tend to be larger when the cnidarians and the dominant breeders are larger (Buston and Cant, 2006; Wong, 2011). Thus, maintaining sociality may no longer be an option when the cnidarian hosts become smaller due to climate change (Pisapia et al., 2020), perhaps because there are simply not enough resources within a single host to support multiple individuals (Wong et al., 2008a; Rueger et al., 2018).

However, remaining in social groups may instead be especially important throughout disturbances, due to synergistic benefits of sociality. It is now known that fish inhabitants provide important services to their cnidarian hosts (Goldshmid et al., 2004; Chong-Seng et al., 2011; Dixson and Hay, 2012; Dirnwoeber and Herler, 2013; Garcia-Herrera et al., 2017), including the moderation of bleaching susceptibility and the promotion of host recovery through increasing water movement and nutrient cycling (Chase et al., 2018; Pryor et al., 2020). Larger group sizes could therefore lead to quicker recovery from bleaching. From a synergistic effects perspective, remaining social might then be beneficial for breeders and non-breeders alike.

Environmental Disturbances May Interfere With Proximate Mechanisms Essential for Sociality

Social group formation is not just dependent on the benefits associated with different social strategies, but it also depends on the ability of the fish to recognize these benefits (e.g., kin recognition), and to enact strategies that confer these benefits (e.g., growth regulation). If reef fishes lose important sensory and physiological abilities with environmental disturbances, as they seem to do (e.g., Munday et al., 2009, 2010; Dixson et al., 2010; Pankhurst and Munday, 2011; Donelson et al., 2016), then group formation and maintenance may be affected long-term. For example, ocean acidification can reduce the ability of coral reef fishes to detect predators, kin, and habitat (Munday et al., 2009, 2010; Dixson et al., 2010) and as a consequence, non-breeders may change their decisions to remain philopatric or disperse (Dixson et al., 2010). Additionally, new recruits may lose the ability to detect kin and habitat, which could result in changed levels of relatedness within groups and reduced fish replenishment, respectively (Munday et al., 2009, 2010). Finally, the stress levels of fish increase when their hosts bleach

(Beldade et al., 2017), and juvenile fishes' metabolism and behavior changes (Cortese et al., 2020), all of which could alter social decisions and group cohesion. Combined, there are several sensory and physiological effects of environmental disturbances that may impact the maintenance of sociality in coral reef fishes.

Conclusion of Part 4

As climate change causes disturbances on coral reefs, the decisions of non-breeders to forgo reproduction and breeders to tolerate non-breeders may be altered. From the point of view of the non-breeder, if habitat becomes less saturated as a result of disturbance, then leaving to breed elsewhere may become a better strategy to gain breeding status more quickly (Wong, 2010). If habitats are declining in quality, the decision to stay or leave will depend on how the current habitat is faring relative to the habitats around it. From the point of view of the breeder, if habitats become smaller as a result of continued disturbances (Pisapia et al., 2020), then tolerating non-breeders may not be a good strategy due to resource limitations (Wong et al., 2008a,b; Rueger et al., 2018; Hing et al., 2019). On the other hand, tolerating non-breeders might become more strongly favored because the synergistic benefits of sociality might enable the habitat to recover and grow quicker post-disturbance. Furthermore, environmental disturbances may negatively influence the proximate mechanisms that individuals require to engage in efficient social interactions. As we uncover more links between environmental effects and sociality, we will be able to assess whether sociality within species of coral reef fishes is stable or plastic in response to environmental change.

GENERAL CONCLUSION

In reviewing the past two decades of sociality research in coral reef fishes, we show that work on marine fishes can provide important insights into the evolution of sociality. Many of these insights are not just applicable to our model species, but to a wider range of taxa. First, even in taxa with dispersive larval phases, subtle relatedness patterns may help explain patterns of sociality (Buston et al., 2009; Rueger et al., 2021). However, in contrast to most terrestrial social animals, kin selection alone does not explain social evolution in marine fishes and does not play a central role in most cases. As we have laid out, relatedness may be only one of many factors working together to motivate dominant breeders to accept non-breeders, even if they provide no alloparental care. Second, we have come to understand that while alloparental care is absent, other forms of cooperative actions can be taken by subordinate group members, such as regulating their growth (Buston, 2003a; Buston and Cant, 2006; Wong et al., 2008a). The active regulation of subordinate growth is one of the most remarkable findings emerging from social evolution research in coral reef fishes and has since informed studies of growth regulation in other social vertebrates (Bender et al., 2005; Huchard et al., 2016). Third, coral reef fish studies have provided some of the only direct support for well-known social evolution hypotheses such as the mate-replacement hypothesis (Buston, 2004a) and the reproductive control hypothesis of reproductive skew (Rueger et al., 2018).

Future Directions

Recently recurring goals in the field of marine sociality research include expanding our focus from a few model species with simple social systems to fishes with more complex social systems and expanding to whole taxonomic groups to assess the variation of sociality. These goals will require the application of methods new to the field of marine fish research, such as social network analysis and the use of sociality indices and phylogenetically controlled models. Another crucial future research direction is what role the cnidarian host plays in the sociality of coral reef fish species. This is because (i) synergistic effects may be an important factor in motivating dominant breeders to tolerate subordinates that are not close relatives, and (ii) the host's susceptibility to environmental disturbances may have severe consequences for the social organization of many marine species in the future, especially as we move further into the Anthropocene. Climate change and related stressors have the potential to alter sociality by influencing the physiology and behavior of animals directly or by altering their habitat and mutualistic partners. The applicability of these future studies will go well beyond coral reef fishes and extend to any social animal that lives in a mutualistic relationship with another organism.

AUTHOR CONTRIBUTIONS

TR, MW, and PB conceived of the manuscript. TR, RB, CF, SH, MW, and PB reviewed the literature, contributed critical discussion, and wrote the manuscript. All the authors contributed to the article and approved the submitted version.

FUNDING

This project received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement No. 841263. TR was supported by a Marie Sklodowska-Curie Individual Global Fellowship (H2020-MSCA-IF-2018, Grant No. 841263). RB was supported by a Warren McLeod Fellowship from Boston University. CF was supported by a University Postgraduate Award. SH was supported by an Australian Government Research Training Program Scholarship, both administered through the University of Wollongong.

ACKNOWLEDGMENTS

We would like to thank two reviewers who helped us improve this manuscript.

REFERENCES

Allen, G. R. (1972). *The Anemonefishes: Their Classification and Biology*. Neptune City, NJ: TFH Publ., Inc.

Almany, G. R., Berumen, M. L., Thorrold, S. R., Planes, S., and Jones, G. P. (2007). Local replenishment of coral reef fish populations in a marine reserve. *Science* 316, 742–744. doi: 10.1126/science.1140597

Almany, G. R., Planes, S., Thorrold, S. R., Berumen, M. L., Bode, M., Saenz-Agudelo, P., et al. (2017). Larval fish dispersal in a coral-reef seascape. *Nat. Ecol. Evol.* 1:148.

Asoh, K. (2003). Gonadal development and infrequent sex change in a population of the humbug damselfish, Dascyllus aruanus in continuous coral-cover habitat. *Mar. Biol.* 142, 1207–1218. doi: 10.1007/s00227-003-1051-6

Avilés, L., and Harwood, G. (2012). A quantitative index of sociality and its application to group-living spiders and other social organisms. *Ethology* 118, 1219–1229. doi: 10.1111/eth.12028

Barbasch, T. A., Rueger, T., Srinivasan, M., Wong, M. Y., Jones, G. P., and Buston, P. M. (2020). Substantial plasticity of reproduction and parental care in response to local resource availability in a wild clownfish population. *Oikos* 129, 1844–1855. doi: 10.1111/oik.07674

Beauchamp, G. (2015). *Animal Vigilance: Monitoring Predators and Competitors*. Cambridge, MA: Academic Press.

Beldade, R., Blandin, A., O'Donnell, R., and Mills, S. C. (2017). Cascading effects of thermally-induced anemone bleaching on associated anemonefish hormonal stress response and reproduction. *Nat. Commun.* 8:716. doi: 10.1038/s41467-017-00565-w

Bender, N., Hamilton, I. M., and Heg, D. (2005). Size differences within a dominance hierarchy influence conflict and help in a cooperatively breeding cichlid. *Behaviour* 142, 1591–1613. doi: 10.1163/156853905774831846

Bonin, M. C., Munday, P. L., McCormick, M. I., Srinivasan, M., and Jones, G. P. (2009). Coral-dwelling fishes resistant to bleaching but not to mortality of host corals. *Mar. Ecol. Prog. Ser.* 394, 215–222. doi: 10.3354/meps08294

Bourke, A. F. (2011). *Principles of Social Evolution*. Oxford: Oxford University Press.

Branconi, R., Barbasch, T. A., Francis, R. K., Srinivasan, M., Jones, G. P., and Buston, P. M. (2020). Ecological and social constraints combine to promote evolution of non-breeding strategies in clownfish. *Commun. Biol.* 3:649.

Branconi, R., Garner, J., Buston, P. M., and Wong, M. Y. (2019a). A new non-invasive technique for temporarily tagging reef fishes. *Copeia* 1, 85–91. doi: 10.1643/ot-18-057

Branconi, R., Wong, M. Y., and Buston, P. M. (2019b). Comparison of video and SCUBA diver observations for measuring coral reef fish behavior: a case study using the humbug damselfish *Dascyllus aruanus*. *J. Fish Biol.* 94, 490–498.

Brown, J. L. (1974). Alternate routes to sociality in jays – with a theory for the evolution of altruism and communal breeding. *Am. Zool.* 14, 63–80. doi: 10.1093/icb/14.1.63

Buston, P. M. (2002). *Group Structure of the Clown Anemonefish, Amphiprion Percula*. PhD thesis, Ithaca, N.Y: Cornell University.

Buston, P. M. (2003a). Forcible eviction and prevention of recruitment in the clown anemonefish. *Behav. Ecol.* 14, 576–582. doi: 10.1093/beheco/arg036

Buston, P. M. (2003b). Size and growth modification in clownfish. *Nature* 424, 145–146. doi: 10.1038/424145a

Buston, P. (2004a). Does the presence of non-breeders enhance the fitness of breeders? an experimental analysis in the clown anemonefish *Amphiprion percula*. *Behav. Ecol. Sociob.* 57, 23–31. doi: 10.1007/s00265-004-0833-2

Buston, P. M. (2004b). Territory inheritance in the clown anemonefish. *Proc. R. Soc. B.* 271, S252–S254.

Buston, P. M., and Balshine, S. (2007). Cooperating in the face of uncertainty: a consistent framework for understanding the evolution of cooperation. *Behav. Process.* 76, 152–159. doi: 10.1016/j.beproc.2007.01.020

Buston, P. M., Bogdanowicz, S. M., Wong, M. Y., and Harrison, R. G. (2007a). Are clownfish groups composed of close relatives? an analysis of microsatellite DNA variation in *Amphiprion percula*. *Mol. Ecol.* 16, 3671–3678. doi: 10.1111/j.1365-294x.2007.03421.x

Buston, P. M., Reeve, H. K., Cant, M. A., Vehrencamp, S. L., and Emlen, S. T. (2007b). Reproductive skew and the evolution of group dissolution tactics: a synthesis of concession and restraint models. *Anim. Behav.* 74, 1643–1654. doi: 10.1016/j.anbehav.2007.03.003

Buston, P. M., and Cant, M. A. (2006). A new perspective on size hierarchies in nature: patterns, causes, and consequences. *Oecologia.* 149, 362–372. doi: 10.1007/s00442-006-0442-z

Buston, P. M., and Elith, J. (2011). Determinants of reproductive success in dominant pairs of clownfish: a boosted regression tree analysis. *J. Anim. Ecol.* 80, 528–538. doi: 10.1111/j.1365-2656.2011.01803.x

Buston, P. M., Fauvelot, C., Wong, M. Y., and Planes, S. (2009). Genetic relatedness in groups of the humbug damselfish *Dascyllus aruanus*: small, similar-sized individuals may be close kin. *Mol. Ecol.* 18, 4707–4715. doi: 10.1111/j.1365-294X.2009.04383.x

Buston, P. M., and García, M. B. (2007). An extraordinary life span estimate for the clown anemonefish Amphiprion percula. *J. Fish Biol.* 70, 1710–1719. doi: 10.1111/j.1095-8649.2007.01445.x

Buston, P. M., Jones, G. P., Planes, S., and Thorrold, S. R. (2012). Probability of successful larval dispersal declines fivefold over 1 km in a coral reef fish. *Proc. Biol. Sci.* 279, 1883–1888. doi: 10.1098/rspb.2011.2041

Buston, P. M., and Zink, A. G. (2009). Reproductive skew and the evolution of conflict resolution: a synthesis of transactional and tug-of-war models. *Behav. Ecol.* 20, 672–684. doi: 10.1093/beheco/arp050

Cant, M. A., and Johnstone, R. A. (2009). How threats influence the evolutionary resolution of within-group conflict. *Am. Nat.* 173, 759–771. doi: 10.1086/598489

Catalano, K. A., Dedrick, A. G., Stuart, M. R., Puritz, J. B., Montes, H. R. Jr., and Pinsky, M. L. (2020). Quantifying dispersal variability among nearshore marine populations. *Mol. Ecol.* doi: 10.1111/mec.15732

Chase, T. J., Pratchett, M. S., Frank, G. E., and Hoogenboom, M. O. (2018). Coral-dwelling fish moderate bleaching susceptibility of coral hosts. *PLoS One* 13:e0208545. doi: 10.1371/journal.pone.0208545

Chase, T. J., Pratchett, M. S., McWilliam, M. J., Tebbett, S. B., and Hoogenboom, M. O. (2020). Damselfishes alleviate the impacts of sediments on host corals. *R. Soc. Open Sci.* 7:7192074.

Chase, T. J., Pratchett, M. S., Walker, S. P. W., and Hoogenboom, M. O. (2014). Small-scale environmental variation influences whether coral-dwelling fish promote or impede coral growth. *Oecologia* 176, 1009–1022. doi: 10.1007/s00442-014-3065-9

Chausson, J., Srinivasan, M., and Jones, G. P. (2018). Host anemone size as a determinant of social group size and structure in the orange clownfish (*Amphiprion percula*). *PeerJ* 6:e5841. doi: 10.7717/peerj.5841

Cheal, A. J., MacNeil, M. A., Emslie, M. J., and Sweatman, H. (2017). The threat to coral reefs from more intense cyclones under climate change. *Glob. Change Biol.* 23, 1511–1524. doi: 10.1111/gcb.13593

Chong-Seng, K. M., Cole, A. J., Pratchett, M. S., and Willis, B. L. (2011). Selective feeding by coral reef fishes on coral lesions associated with brown band and black band disease. *Cor. Reef.* 30, 473–481. doi: 10.1007/s00338-010-0707-1

Clutton-Brock, T. (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296, 69–72. doi: 10.1126/science.296.5565.69

Clutton-Brock, T. H., Hodge, S. J., Flower, T. P., Spong, G. F., and Young, A. J. (2010). Adaptive suppression of subordinate reproduction in cooperative mammals. *Am. Nat.* 176, 664–673. doi: 10.1086/656492

Coates, D. (1980a). Prey-size intake in humbug *Dacyllus aruanus* (Pisces: Pomacentridae) living within social groups. *J. Anim. Ecol.* 49, 335–340. doi: 10.2307/4292

Coates, D. (1980b). The discrimination of and reactions towards predatory and non-predatory species of fish by humbug damselfish. *Dascyllus aruanus* (Pisces, Pomacentridae). *Zeitschr. Tierpsy.* 52, 347–354. doi: 10.1111/j.1439-0310.1980.tb00722.x

Coates, D. (1982). Some observations on the sexuality of the humbug damselfish *Dascyllus aruanus* (Pisces. Pomacentridae) in the field. *Zeitschr. Tierpsy.* 59, 7–18. doi: 10.1111/j.1439-0310.1982.tb00328.x

Coker, D. J., Walker, S. P. W., Munday, P. L., and Pratchett, M. S. (2013). Social group entry rules may limit population resilience to patchy habitat disturbance. *Mar. Ecol. Prog. Ser.* 493, 237–242. doi: 10.3354/meps10493

Cole, K. S. (2002). Gonad morphology, sexual development, and colony composition in the obligate coral-dwelling damselfish *Dascyllus aruanus*. *Mar. Biol.* 140, 151–163. doi: 10.1007/s002270100681

Cortese, D., Norin, T., Beldade, R., Crespel, A., Killen, S. S., and Mills, S. C. (2020). Physiological and behavioural effects of anemone bleaching on symbiont anemonefish in the wild. *Funct. Ecol.* 35, 663–674. doi: 10.1111/1365-2435.13729

Croft, D. P., James, R., and Krause, J. (2008). *Exploring Animal Social Networks*. Princeton, NJ: Princeton University Press.

D'Aloia, C. C., and Neubert, M. G. (2018). The formation of marine kin structure: effects of dispersal, larval cohesion, and variable reproductive success. *Ecology* 99, 2374–2384. doi: 10.1002/ecy.2480

D'Aloia, C. C., Xuereb, A., Fortin, M. J., Bogdanowicz, S. M., and Buston, P. M. (2018). Limited dispersal explains the spatial distribution of siblings in a reef fish population. *Mar. Ecol. Prog. Ser.* 607, 143–154. doi: 10.3354/meps12792

Darwin, C. (1859). *The Origin of Species*, 6th Edn. London: John Murray.

Dirnwoeber, M., and Herler, J. (2013). Toxic coral gobies reduce the feeding rate of a corallivorous butterflyfish on *Acropora corals*. *Coral Reefs* 32, 91–100. doi: 10.1007/s00338-012-0947-3

Dixson, D. L., and Hay, M. E. (2012). Corals chemically cue mutualistic fishes to remove competing seaweeds. *Science* 338, 804–807. doi: 10.1126/science.1225748

Dixson, D. L., Munday, P. L., and Jones, G. P. (2010). Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecol. Lett.* 13, 68–75. doi: 10.1111/j.1461-0248.2009.01400.x

Donelson, J. M., Wong, M., Booth, D. J., and Munday, P. L. (2016). Transgenerational plasticity of reproduction depends on rate of warming across generations. *Evol. Appl.* 9, 1072–1081. doi: 10.1111/eva.12386

Duchene, D., Klanten, S. O., Munday, P. L., Herler, J., and van Herwerden, L. (2013). Phylogenetic evidence for recent diversification of obligate coral-dwelling gobies compared with their host corals. *Mol. Phylog. Evol.* 69, 123–132. doi: 10.1016/j.ympev.2013.04.033

Duffy, J. E., and Macdonald, K. S. (2009). Kin structure, ecology and the evolution of social organization in shrimp: a comparative analysis. *Proc. R. Soc. B.* 277, 575–84. doi: 10.1098/rspb.2009.1483

Duffy, J. E., Morrison, C. L., and Ríos, R. N. (2000). Multiple origins of eusociality among sponge-dwelling shrimps (Synalpheus). *Evolution* 54, 503–516. doi: 10.1554/0014-3820(2000)054[0503:mooeas]2.0.co;2

Elliott, J. K., Elliott, J. M., and Mariscal, R. N. (1995). Host selection, location, and association behaviors of anemonefishes in field settlement experiments. *Mar. Biol.* 122, 377–389. doi: 10.1007/bf00350870

Elliott, J. K., Lougheed, S. C., Bateman, B., McPhee, L. K., and Boag, P. T. (1999). Molecular phylogenetic evidence for the evolution of specialization in anemonefishes. *Proc. R. Soc. B.* 266, 677–685. doi: 10.1098/rspb.1999.0689

Elliott, J. K., and Mariscal, R. N. (2001). Coexistence of nine anemonefish species: differential host and habitat utilization, size and recruitment. *Mar. Biol.* 138, 23–36. doi: 10.1007/s002270000441

Emlen, S. T. (1982). The evolution of helping. I. an ecological constraints model. *Am. Nat.* 119, 29–39. doi: 10.1086/283888

Emlen, S. T. (1991). "Evolution of cooperative breeding in birds and mammals," in *Behavioural Ecology: An Evolutionary Approach*, 3rd Edn, eds J. R. Krebs and N. B. Davies (Oxford: Blackwell), 301–337.

Emlen, S. T. (1995). An evolutionary theory of the family. *PNAS* 92, 8092–8099.

Emlen, S. T., and Wrege, P. H. (1988). The role of kinship in helping decisions among white-fronted bee-eaters. *Behav. Ecol. Sociob.* 23, 305–315. doi: 10.1007/bf00300577

Fautin, D. G. (1992). Anemonefish recruitment: the roles of order and chance. *Symbiosis* 14, 143–160.

Fautin, D. G., and Allen, G. R. (1992). *Field Guide to Anemonefishes and their Host Sea Anemones*. Perth, WA: Western Australian Museum, 165.

Forrester, G. E. (1991). Social rank, individual size and group composition as determinants of food-consumption by humbug damselfish. *Dascyllus aruanus*. *Anim. Behav.* 42, 701–711. doi: 10.1016/s0003-3472(05)80116-2

Forsgren, E., Karlsson, A., and Kvarnemo, C. (1996). Female sand gobies gain direct benefits by choosing males with eggs in their nests. *Behav. Ecol. Sociob.* 39, 91–96. doi: 10.1007/s002650050270

Fricke, H., and Fricke, S. (1977). Monogamy and sex change by aggressive dominance in coral reef fish. *Nature* 266, 830–832. doi: 10.1038/266830a0

Fricke, H. W. (1979). Mating system, resource defence and sex change in the anemonefish *Amphiprion akallopisos*. *Zeit. Tierpsychol.* 50, 313–326. doi: 10.1111/j.1439-0310.1979.tb01034.x

Fricke, H. W., and Holzberg, S. (1974). Social units and hermaphroditism in a pomacentrid fish. *Naturwissenschaften* 61, 367–368. doi: 10.1007/bf00600312

Frisch, A. J., Rizzari, J. R., Munkres, K. P., and Hobbs, J. P. A. (2016). Anemonefish depletion reduces survival, growth, reproduction and fishery productivity of mutualistic anemone–anemonefish colonies. *Coral Reefs* 35, 375–386. doi: 10.1007/s00338-016-1401-8

Garcia-Herrera, N., Ferse, S. C. A., Kunzmann, A., and Genin, A. (2017). Mutualistic damselfish induce higher photosynthetic rates in their host coral. *J. Exp. Biol.* 220, 1803–1811. doi: 10.1242/jeb.152462

Goldshmid, R., Holzman, R., Weihs, D., and Genin, A. (2004). Aeration of corals by sleep-swimming fish. *Limnol. Oceanogr.* 49, 1832–1839. doi: 10.4319/lo.2004.49.5.1832

Griffin, A. S., and West, S. A. (2003). Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. *Science* 302, 634–636. doi: 10.1126/science.1089402

Hamilton, W. D. (1963). The evolution of altruistic behavior. *Am. Nat.* 97, 354–356.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *J. Theor. Biol.* 7, 17–52. doi: 10.1016/0022-5193(64)90039-6

Harold, A. S., Winterbottom, R., Munday, P. L., and Chapman, R. W. (2008). Phylogenetic relationships of Indo-Pacific coral gobies of the genus Gobiodon (Teleostei: Gobiidae), based on morphological and molecular data. *Bull. Mar. Sci.* 82, 119–136.

Hattori, A. (1994). Inter-group movement and mate acquisition tactics of the protandrous anemonefish *Amphiprion clarkii*, on a coral reef. Okinawa. *Jap. J. Ichthy.* 41, 159–165.

Herler, J., Koblmüller, S., and Sturmbauer, C. (2009). Phylogenetic relationships of coral-associated gobies (Teleostei, Gobiidae) from the Red Sea based on mitochondrial DNA data. *Mar. Biol.* 156, 725–739. doi: 10.1007/s00227-008-1124-7

Hing, M. L., Klanten, O. S., Dowton, M., Brown, K. R., and Wong, M. Y. (2018). Repeated cyclone events reveal potential causes of sociality in coral-dwelling Gobiodon fishes. *PLoS One* 13:e0202407. doi: 10.1371/journal.pone.0202407

Hing, M. L., Klanten, O. S., Dowton, M., and Wong, M. Y. (2017). The right tools for the job: cooperative breeding theory and an evaluation of the methodological approaches to understanding the evolution and maintenance of sociality. *Front. Ecol. Evol.* 5:100. doi: 10.3389/fevo.2017.00100

Hing, M. L., Klanten, O. S., Wong, M. Y., and Dowton, M. (2019). Drivers of sociality in *Gobiodon fishes*: an assessment of phylogeny, ecology and life-history. *Mol. Phylo. Evol.* 137, 263–273. doi: 10.1016/j.ympev.2019.05.020

Hodge, J. R., Alim, C., Bertrand, N. G., Lee, W., Price, S. A., Tran, B., et al. (2018). Ecology shapes the evolutionary trade-off between predator avoidance and defence in coral reef butterflyfishes. *Ecol. Let.* 21, 1033–1042. doi: 10.1111/ele.12969

Holbrook, S. J., Forrester, G. E., and Schmitt, R. J. (2000). Spatial patterns in abundance of damselfish reflects availability of suitable habitat. *Oecologia* 122, 109–120. doi: 10.1007/pl00008826

Holbrook, S. J., and Schmitt, R. J. (2005). Growth, reproduction and survival of a tropical sea anemone (Actiniaria): benefits of hosting anemonefish. *Coral Reefs.* 24, 67–73. doi: 10.1007/s00338-004-0432-8

Huchard, E., English, S., Bell, M. B., Thavarajah, N., and Clutton-Brock, T. (2016). Competitive growth in a cooperative mammal. *Nature* 533, 532–534. doi: 10.1038/nature17986

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., et al. (2018). Spatial and temporal patterns of mass bleaching of corals in the *Anthropocene*. *Science* 359, 80–83. doi: 10.1126/science.aan8048

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., et al. (2017). Global warming and recurrent mass bleaching of corals. *Nature* 543, 373–377.

Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Chase, T. J., Dietzel, A., et al. (2019). Global warming impairs stock–recruitment dynamics of corals. *Nature* 568, 387–390. doi: 10.1038/s41586-019-1081-y

Iwata, E., and Manbo, J. (2013). Territorial behaviour reflects sexual status in groups of false clown anemonefish (*Amphiprion ocellaris*) under laboratory conditions. *Acta Ethol.* 16, 97–103. doi: 10.1007/s10211-012-0142-0

Jones, G. P., Planes, S., and Thorrold, S. R. (2005). Coral reef fish larvae settle close to home. *Curr. Biol.* 15, 1314–1318. doi: 10.1016/j.cub.2005.06.061

Jordan, L. A., Avolio, C., Herbert-Read, J. E., Krause, J., Rubenstein, D. I., and Ward, A. J. W. (2010). Group structure in a restricted entry system is mediated by both resident and joiner preferences. *Behav. Ecol. Sociob.* 64, 1099–1106. doi: 10.1007/s00265-010-0924-1

Keller, L., and Reeve, H. K. (1994). Partitioning of reproduction in animal societies. *Tree* 9, 98–102. doi: 10.1016/0169-5347(94)90204-6

Kocher, S. D., and Paxton, R. J. (2014). Comparative methods offer powerful insights into social evolution in bees. *Apidologie* 45, 289–305. doi: 10.1007/s13592-014-0268-3

Koenig, W. D., and Walters, E. L. (2015). Temporal variability and cooperative breeding: testing the bet-hedging hypothesis in the acorn woodpecker. *Proc. Biol. Sci. B* 282:20151742. doi: 10.1098/rspb.2015.1742

Kokko, H., Brooks, R., McNamara, J. M., and Houston, A. I. (2002). The sexual selection continuum. *Proc. Biol. Sci. B.* 269, 1331–1340.

Kokko, H., and Johnstone, R. A. (1999). Social queuing in animal societies: a dynamic model of reproductive skew. *Proc. Biol. Sci. B.* 266, 571–578. doi: 10.1098/rspb.1999.0674

Kuwamura, T., Nakashima, Y., and Yogo, Y. (1996). Plasticity in size and age at maturity in a monogamous fish: effect of host coral size and frequency dependence. *Behav. Ecol. Sociobiol.* 38, 365–370. doi: 10.1007/s002650050253

Kuwamura, T., Nakashimn, Y., and Yogo, Y. (1994). Sex change in either direction by growth-rate advantage in the monogamous coral goby, *Paragobiodon echinocephalus*. *Behav. Ecol.* 5, 434–438. doi: 10.1093/beheco/5.4.434

Kuwamura, T., Suzuki, S., and Kadota, T. (2016). Male-to-female sex change in widowed males of the protogynous damselfish *Dascyllus aruanus*. *J. Ethol.* 34, 85–88. doi: 10.1007/s10164-015-0450-8

Lassig, B. R. (1976). Field observations on the reproductive behaviour of *Paragobiodon spp*. (Osteichthyes: Gobiidae) at heron island great barrier reef. *Mar. Freshw. Behav. Phy.* 3, 283–293. doi: 10.1080/10236247609378517

Lassig, B. R. (1977). Socioecological strategies adopted by obligate coral dwelling fishes. *Proc. 3rd Int. Symp. Coral Reefs.* 1, 565–570.

Lassig, B. R. (1981). Significance of the epidermal ichthyotoxic secretion of coral-dwelling gobies. *Toxicon* 19, 729–735. doi: 10.1016/0041-0101(81)90068-4

Leis, J. M. (1991). "The pelagic stage of reef fishes: the larval biology of coral reef fishes," in *The Ecology of Fishes on Coral Reefs*, ed. P. F. Sale (Cambridge, MA: Academic Press), 183–230. doi: 10.1016/b978-0-08-092551-6.50013-1

Li, J., Chen, X., Kang, B., and Liu, M. (2015). Mitochondrial DNA genomes organization and phylogenetic relationships analysis of eight anemonefishes (Pomacentridae: Amphiprioninae). *PLoS One* 10:e0123894. doi: 10.1371/journal.pone.0123894

Litsios, G., and Salamin, N. (2014). Hybridisation and diversification in the adaptive radiation of clownfishes. *BMC Evol. Biol.* 14:245. doi: 10.1186/s12862-014-0245-5

Litsios, G., Sims, C. A., Wüest, R. O., Pearman, P. B., Zimmermann, N. E., and Salamin, N. (2012). Mutualism with sea anemones triggered the adaptive radiation of clownfishes. *BMC Evol. Biol.* 12:212. doi: 10.1186/1471-2148-12-212

Mann, R. P., Herbert-Read, J. E., Ma, Q., Jordan, L. A., Sumpter, D. J. T., and Ward, A. J. W. (2014). A model comparison reveals dynamic social information drives the movements of humbug damselfish (*Dascyllus aruanus*). *J. R. Soc. Interface* 11:20130794. doi: 10.1098/rsif.2013.0794

Mariscal, R. N. (1966). "20 the symbiosis between tropical sea anemones and fishes: a review," in *Proceedings of the Galapagos: Proceedings of the Symposia of Galapagos International Scientific Project*, (Berkeley, CA: Univ of California Press), 157.

Mariscal, R. N. (1970). The nature of the symbiosis between Indo-Pacific anemone fishes and sea anemones. *Mar. Biol.* 6, 58–65. doi: 10.1007/bf00352608

Mitchell, J. S. (2003). Mobility of *Stichodactyla gigantea* sea anemones and implications for resident false clown anemonefish. *Amphiprion ocellaris*. *Environ. Biol. Fishes.* 66, 85–90. doi: 10.1023/a:1023286009054

Mitchell, J. S. (2005). Queue selection and switching by false clown anemonefish. *Amphiprion ocellaris*. *Anim. Behav.* 69, 643–652. doi: 10.1016/j.anbehav.2004.05.017

Mitchell, J. S., and Dill, L. M. (2005). Why is group size correlated with the size of the host sea anemone in the false clown anemone fish? *Canad. J. Zool.* 83, 372–376. doi: 10.1139/z05-014

Mizushima, N., Nakashima, Y., and Kuwamura, T. (2000). Semilunar spawning cycle of the humbug damselfish *Dascyllus aruanus*. *J. Ethol.* 18, 105–108. doi: 10.1007/s101640070008

Moyer, J. T., and Nakazono, A. (1978). *Protandrous hermaphroditism* in six species of the anemonefish genus Amphiprion in Japan. *Jap. J. Ichthyol.* 25, 101–106.

Munday, P. L. (2002). Bi-directional sex change: testing the growth-rate advantage model. *Behav. Ecol. Sociob.* 52, 247–254. doi: 10.1007/s00265-002-0517-8

Munday, P. L., Dixson, D. L., Donelson, J. M., Jones, G. P., Pratchett, M. S., Devitsina, G. V., et al. (2009). Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *PNAS* 106, 1848–1852. doi: 10.1073/pnas.0809996106

Munday, P. L., Dixson, D. L., McCormick, M. I., Meekan, M., Ferrari, M. C. O., and Chivers, D. P. (2010). Replenishment of fish populations is threatened by ocean acidification. *PNAS* 107, 12930–12934. doi: 10.1073/pnas.1004519107

Muthoo, A. (2000). A non-technical introduction to bargaining theory. *World Econ.* 1, 145–166.

Nakashima, Y., Kuwamura, T., and Yogo, Y. (1996). Both-ways sex change in monogamous coral gobies, *Gobiodon spp*. *Environ. Biol. Fish.* 46, 281–288. doi: 10.1007/bf00005004

Nanami, A., and Nishira, M. (2001). Survival rates of juvenile coral reef fishes differ between patchy and continuous habitats. *Bull. Mar. Sci.* 69, 1209–1221.

Nanninga, G. B., Saenz-Agudelo, P., Zhan, P., Hoteit, I., and Berumen, M. L. (2015). Not finding Nemo: limited reef-scale retention in a coral reef fish. *Coral Reefs* 34, 383–392. doi: 10.1007/s00338-015-1266-2

Nowicki, J. P., O'Connell, L. A., Cowman, P. F., Walker, S. P. W., Coker, D. J., and Pratchett, M. S. (2018). Variation in social systems within *Chaetodon butterflyfishes*, with special reference to pair bonding. *PLoS One* 13:e0194465. doi: 10.1371/journal.pone.0194465

Pankhurst, N. W., and Munday, P. L. (2011). Effects of climate change on fish reproduction and early life history stages. *Mar. Freshwater Res.* 62, 1015–1026. doi: 10.1071/mf10269

Phillips, E., DeAngelis, R., Gogola, J. V., and Rhodes, J. S. (2020). Spontaneous alloparental care of unrelated offspring by non-breeding *Amphiprion ocellaris* in absence of the biological parents. *Sci. Rep.* 10:4610.

Pisapia, C., Edmunds, P. J., Moeller, H. V., Riegl, B. M., McWilliam, M., Wells, C. D., et al. (2020). Projected shifts in coral size structure in the Anthropocene. *Adv. Mar. Biol.* 87, 31–60. doi: 10.1016/bs.amb.2020.07.003

Planes, S., Jones, G. P., and Thorrold, S. R. (2009). Larval dispersal connects fish populations in a network of marine protected areas. *PNAS* 106, 5693–5697. doi: 10.1073/pnas.0808007106

Porat, D., and Chadwick-Furman, N. E. (2004). "Effects of anemonefish on giant sea anemones: expansion behavior, growth, and survival," in *Coelenterate Biology 2003*, eds D. G. Fautin, J. A. Westfall, P. Cartwrigh, M. Daly, C. R. Wyttenbach (Dordrecht: Springer), 513–520. doi: 10.1007/978-1-4020-2762-8_58

Pratchett, M. S., Caballes, C. F., Wilmes, J. C., Matthews, S., Mellin, C., Sweatman, H. P. A., et al. (2017). Thirty years of research on crown-of-thorns starfish (1986–2016): scientific advances and emerging opportunities. *Diversity* 9:41. doi: 10.3390/d9040041

Pratchett, M. S., Messmer, V., and Wilson, S. K. (2020). Size-specific recolonization success by coral-dwelling damselfishes moderates resilience to habitat loss. *Sci. Rep.* 10:17016.

Pryor, S. H., Hill, R., Dixson, D. L., Fraser, N. J., Kelaher, B. P., and Scott, A. (2020). Anemonefish facilitate bleaching recovery in a host sea anemone. *Sci. Rep.* 10:18586.

Riedman, M. L. (1982). The evolution of alloparental care and adoption in mammals and birds. *Quart. Rev Biol.* 57, 405–435. doi: 10.1086/412936

Rolland, J., Silvestro, D., Litsios, G., Faye, L., and Salamin, N. (2018). Clownfishes evolution below and above the species level. *Proc. R. Soc. B.* 285:20171796. doi: 10.1098/rspb.2017.1796

Romano, V., Macintosh, A. J., and Sueur, C. (2020). Stemming the flow: information, infection, and social evolution. *Tree* 35, 849–853. doi: 10.1016/j.tree.2020.07.004

Rubenstein, D. I. (1978). “On predation, competition, and the advantages of group living,” in *Social Behavior*, eds P. P. G. Bateson, and P. H. Klopfer (Boston, MA: Springer), 205–231. doi: 10.1007/978-1-4684-2901-5_9

Rubenstein, D. R. (2011). Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. *PNAS* 108, 10816–10822. doi: 10.1073/pnas.1100303108

Rubenstein, D. R., and Lovette, I. J. (2007). Temporal environmental variability drives the evolution of cooperative breeding in birds. *Curr. Biol.* 17, 1414–1419. doi: 10.1016/j.cub.2007.07.032

Rueger, T., Barbasch, T. A., Wong, M. Y., Srinivasan, M., Jones, G. P., and Buston, P. M. (2018). Reproductive control via the threat of eviction in the clown anemonefish. *Proc. Biol. Sci. B.* 285:20181295. doi: 10.1098/rspb.2018.1295

Rueger, T., Bogdanowicz, S. M., Buston, P. M., and Wong, M. Y. (2021). Potential for kin selection in groups of a social coral reef fish. *Mol. Ecol.* 18, 4707–4715.

Rueger, T., Harrison, H. B., Buston, P. M., Gardiner, N. M., Berumen, M. L., and Jones, G. P. (2020). Natal philopatry increases relatedness within groups of coral reef cardinalfish. *Proc. Biol. Sci. B.* 287:20201133. doi: 10.1098/rspb.2020.1133

Saenz-Agudelo, P., Jones, G. P., Thorrold, S. R., and Planes, S. (2011). Detrimental effects of host anemone bleaching on anemonefish populations. *Coral Reefs* 30, 497–506. doi: 10.1007/s00338-010-0716-0

Sale, P. F. (1970). Behaviour of the humbug fish. *Austr. Nat. Hist.* 16, 362–366.

Sale, P. F. (1971). Extremely limited home range in a coral reef fish. *Dascyllus aruanus* (Pisces, Pomacentridae). *Copeia.* 1971, 325–327.

Sale, P. F. (1972). Influence of corals on dispersion of the pomacentrid fish, *Dascyllus aruanus*. *Ecology* 53, 741–744. doi: 10.2307/1934795

Salles, O. C., Pujol, B., Maynard, J. A., Almany, G. R., Berumen, M. L., Jones, G. P., et al. (2016). First genealogy for a wild marine fish population reveals multigenerational philopatry. *PNAS* 113, 13245–13250. doi: 10.1073/pnas.1611797113

Santini, S., and Polacco, G. (2006). Finding nemo: molecular phylogeny and evolution of the unusual life style of anemonefish. *Gene* 385, 19–27. doi: 10.1016/j.gene.2006.03.028

Schmitt, R. J., and Holbrook, S. J. (1999). Mortality of juvenile damselfish: implications for assessing processes that determine abundance. *Ecology* 80, 35–50. doi: 10.1890/0012-9658(1999)080[0035:mojdif]2.0.co;2

Shanks, A. L. (2009). Pelagic larval duration and dispersal distance revisited. *Biol. Bull.* 216, 373–385. doi: 10.1086/bblv216n3p373

Shen, S. F., Emlen, S. T., Koenig, W. D., and Rubenstein, D. R. (2017). The ecology of cooperative breeding behaviour. *Ecol. Lett.* 20, 708–720.

Sherman, P. W., Lacey, E. A., Reeve, H. K., and Keller, L. (1995). Forum: the eusociality continuum. *Behav. Ecol.* 6, 102–108. doi: 10.1093/beheco/6.1.102

Simpson, S. D., Harrison, H. B., Claereboudt, M. R., and Planes, S. (2014). Long-distance dispersal via ocean currents connects *Omani clownfish* populations throughout entire species range. *PLoS One* 9:e107610. doi: 10.1371/journal.pone.0107610

Sosa, S., Jacoby, D. M. P., Lihoreau, M., and Sueur, C. (2021). Animal social networks: towards an integrative framework embedding social interactions, space and time. *Meth. Ecol. Evol.* 12, 4–9. doi: 10.1111/2041-210x.13539

Srinivasan, M., Jones, G. P., and Caley, M. J. (1999). Experimental evaluation of the roles of habitat selection and interspecific competition in determining patterns of host use by two anemonefishes. *Mar. Ecol. Prog. Ser.* 186, 283–292. doi: 10.3354/meps186283

Sueur, C., Romano, V., Sosa, S., and Puga-Gonzalez, I. (2019). Mechanisms of network evolution: a focus on socioecological factors, intermediary mechanisms, and selection pressures. *Primat* 60, 167–181. doi: 10.1007/s10329-018-0682-7

Szathmáry, E., and Smith, J. M. (1995). The major evolutionary transitions. *Nature* 374, 227–232.

Taborsky, M., and Limberger, D. (1981). Helpers in fish. *Behav. Ecol. Sociob.* 8, 143–145. doi: 10.1007/bf00300826

Taborsky, M., and Wong, M. Y. (2017). “Sociality in fishes,” in *Comparative Social Evolution*, eds D. I. Rubenstein and P. Abbot (Cambridge: Cambridge University Press), 354. doi: 10.1017/9781107338319.013

Thompson, V. J., Munday, P. L., and Jones, G. P. (2007). Habitat patch size and mating system as determinants of social group size in coral-dwelling fishes. *Coral Reefs* 26, 165–174. doi: 10.1007/s00338-006-0181-y

Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology* 91, 2833–2849. doi: 10.1890/10-0097.1

Verde, E. A., Cleveland, A., and Lee, R. W. (2015). Nutritional exchange in a tropical tripartite symbiosis II: direct evidence for the transfer of nutrients from host anemone and zooxanthellae to anemonefish. *Mar. Biol.* 162, 2409–2429. doi: 10.1007/s00227-015-2768-8

Victor, B. C. (1984). Coral reef fish larvae: patch size estimation and mixing in the plankton. *Limnol. Oceanogr.* 29, 1116–1119. doi: 10.4319/lo.1984.29.5.1116

West-Eberhard, M. J. (1975). The evolution of social behavior by kin selection. *Quart. Rev. Biol.* 50, 1–33. doi: 10.1086/408298

Wey, T., Blumstein, D. T., Shen, W., and Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim. Behav.* 75, 333–344. doi: 10.1016/j.anbehav.2007.06.020

Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack’s principle. *Am. Nat.* 100, 687–690. doi: 10.1086/282461

Wisenden, B. D. (1999). Alloparental care in fishes. *Rev. Fish. Biol. Fisher.* 9, 45–70.

Wong, M., and Balshine, S. (2011). The evolution of cooperative breeding in the African cichlid fish, *Neolamprologus pulcher*. *Biol. Rev.* 86, 511–530. doi: 10.1111/j.1469-185x.2010.00158.x

Wong, M. Y. (2010). Ecological constraints and benefits of philopatry promote group-living in a social but non-cooperatively breeding fish. *Proc. R. Soc. B.* 277, 353–358. doi: 10.1098/rspb.2009.1453

Wong, M. Y., and Buston, P. M. (2013). Social systems in habitat-specialist reef fishes: key concepts in evolutionary ecology. *Biosciences* 63, 453–463. doi: 10.1525/bio.2013.63.6.7

Wong, M. Y., Buston, P. M., Munday, P. L., and Jones, G. P. (2007). The threat of punishment enforces peaceful cooperation and stabilizes queues in a coral-reef fish. *Proc. R. Soc. B.* 274, 1093–1099. doi: 10.1098/rspb.2006.0284

Wong, M. Y., Fauvelot, C., Planes, S., and Buston, P. M. (2012). Discrete and continuous reproductive tactics in a hermaphroditic society. *An. Behav.* 84, 897–906. doi: 10.1016/j.anbehav.2012.07.013

Wong, M. Y., Munday, P. L., Buston, P. M., and Jones, G. P. (2008a). Fasting or feasting in a fish social hierarchy. *Curr. Biol.* 18, R372–R373.

Wong, M. Y., Munday, P. L., Buston, P. M., and Jones, G. P. (2008b). Monogamy when there is potential for polygyny: tests of multiple hypotheses in a group-living fish. *Behav. Ecol.* 19, 353–361. doi: 10.1093/beheco/arm141

Wong, M. Y., Uppaluri, C., Medina, A., Seymour, J., and Buston, P. M. (2016). The four elements of within-group conflict in animal societies: an experimental test using the clown anemonefish, *Amphiprion percula*. *Behav. Ecol. Soc.* 70, 1467–1475. doi: 10.1007/s00265-016-2155-6

Wong, M. Y. L. (2011). Group size in animal societies: the potential role of social and ecological limitations in the group-living fish, *Paragobiodon xanthosomus*. *Ethology* 117, 638–644. doi: 10.1111/j.1439-0310.2011.01913.x

Wong, M. Y. (2007). *The Evolution of Animal Societies: Monogamy, Group-living and Conflict in a Coral-dwelling Fish*. PhD thesis, Douglas QLD: James Cook University.

Woolfenden, G. E., and Fitzpatrick, J. W. (1984). *The Florida Scrub Jay: Demography of a Cooperative-breeding Bird*. Princeton, NJ: Princeton University Press.

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Marine Science

ORIGINAL RESEARCH
published: 14 June 2021
doi: 10.3389/fmars.2021.671568

Intra-Population Variability in Group Size of Indo-Pacific Humpback Dolphins (*Sousa chinensis*)

Mingming Liu[1,2,3†], **Mingli Lin**[1†], **David Lusseau**[3,4†] and **Songhai Li**[1,5*†]

[1] Marine Mammal and Marine Bioacoustics Laboratory, Institute of Deep-sea Science and Engineering, Chinese Academy of Sciences, Sanya, China, [2] University of Chinese Academy of Sciences, Beijing, China, [3] School of Biological Sciences, University of Aberdeen, Aberdeen, United Kingdom, [4] National Institute of Aquatic Resources, Technical University of Denmark, Lyngby, Denmark, [5] Tropical Marine Science Institute, National University of Singapore, Singapore, Singapore

Edited by:
Darren Croft,
University of Exeter, United Kingdom

Reviewed by:
Clarissa Teixeira,
Instituto de Pesquisas Cananeia, Brazil
Kerki Jog,
James Cook University, Australia

***Correspondence:**
Songhai Li
lish@idsse.ac.cn

†ORCID:
Mingming Liu
orcid.org/0000-0003-3802-1002
Mingli Lin
orcid.org/0000-0002-9182-0519
David Lusseau
orcid.org/0000-0003-1245-3747
Songhai Li
orcid.org/0000-0003-4977-1722

Specialty section:
This article was submitted to Marine Megafauna, a section of the journal Frontiers in Marine Science

Received: *24 February 2021*
Accepted: *20 May 2021*
Published: *14 June 2021*

Citation:
Liu M, Lin M, Lusseau D and Li S (2021) Intra-Population Variability in Group Size of Indo-Pacific Humpback Dolphins (Sousa chinensis). Front. Mar. Sci. 8:671568. doi: 10.3389/fmars.2021.671568

Group size is a key social trait influencing population dynamics of group-living animals. The Indo-Pacific humpback dolphins (IPHDs), *Sousa chinensis*, a shallow water delphinid species, display a fission-fusion social system. Yet little is known about how social organization of this species vary with temporal scales and behavioral state. In this study, we sampled group size estimates from the world's second largest population of humpback dolphins (*Sousa* spp.), which inhabit the eastern waters of Zhanjiang, China. IPHD group sizes changed seasonally and inter-annually, but not with tidal phases. Group sizes also changed with behavioral state of IPHD groups and with number of mother-calf pairs present. IPHDs formed larger groups in the autumn than in other seasons, which might be related to seasonal changes in food availability and reproductive cycle. Of the groups observed, we recorded the presence of mother-calf pair in 85 groups (i.e., nursery groups: 47 ones with one pair, 25 ones with two pairs, and others with three pairs). Notably, nursery groups were about 2–4 times larger than non-nursery groups. In addition, group sizes greatly increased with the number of mother-calf pairs. Living in relatively large groups, more protection, food, and resources might be available for IPHD mothers and calves, and such social strategy provide higher reproduction efficiency and survival success for this species. During our observations, feeding (45.5%) and traveling (25.2%) represented the majority of IPHD's behavioral budget, while socializing (8.4%) and resting/milling (6.8%) were not frequently observed. Resting/milling groups were approximately 50% smaller than feeding, traveling, or socializing groups, while the latter three types had a similar mean group size. Large groups when IPHDs foraged, traveled, or socialized, might provide more added group benefits. For the first time, our findings clearly revealed intra-population variability in IPHD group sizes across different behavioral and temporal variables, and provided a better understanding of IPHDs' adaptations to various biological processes and ecological constraints.

Keywords: sociality, humpback dolphin, group size, social dynamics, season, mother-calf pairs, behavior

INTRODUCTION

For social animals, group-living is an important behavioral strategy, and their social interactions are usually variable and dynamic (Silk, 2007). Living in a group, social relationships of group members are generally considered a product of trade-offs between energetic costs and benefits (Parrish and Edelstein-Keshet, 1999; Lusseau, 2003). In dolphin societies, the energetic trade-offs are typically associated with food (Heithaus and Dill, 2002), safety (Lima and Dill, 1990), reproduction (Mann et al., 2000), and resources. Consequently, group-living strategy of dolphin species offers a foundation to build more complex social relationships, such as cooperation or competition that have the scope to increase survival and reproduction (Benoit-Bird and Au, 2003; Orbach et al., 2014), and therefore, ultimately affect population dynamics (Lusseau and Newman, 2004).

Almost all dolphins were described with fission-fusion societies (Kent et al., 2008), but there is large intra- and inter-specific variability in social organization depending on ecological landscape in which the dolphin species reside (Gygax, 2002a; Lusseau et al., 2003; Gowans et al., 2007). Group size is among the main characteristics of social organization of dolphin populations (Lusseau et al., 2006; Cantor et al., 2012; Kappeler, 2019). Changes in group size over time and space can reflect fission-fusion dynamics of dolphins, thus are essential to represent the variability of social interactions (Connor, 2000; Gygax, 2002b; Lusseau et al., 2003). Dolphins can vary their group sizes at spatial scales (Bouveroux et al., 2018; Liu et al., 2020b), and at temporal scales (e.g., year, season, month, and day; Koper et al., 2016; Wang et al., 2016; Sarabia et al., 2018).

The Indo-Pacific humpback dolphin (*Sousa chinensis* Osbeck, 1765), hereafter referred as IPHD, is a shallow water delphinid species (Jefferson and Curry, 2015; Jefferson and Smith, 2016). Its habitat preference of shallow and near-shore waters has been widely documented in most of the known IPHD populations, as well as in the other three recognized relative species of *Sousa* spp. (Jefferson and Rosenbaum, 2014). The IPHD was assessed "Vulnerable" by the IUCN Red List of Threatened Species (Jefferson et al., 2017). Our socio-behavioral knowledge on humpback dolphins (*Sousa* spp.) mainly came from studies on IPHDs in the Chinese waters (Chen et al., 2011; Dungan et al., 2012, 2016; Wang et al., 2015), Australian humpback dolphins (*S. sahulensis*) in the Australian waters (Parra et al., 2011; Hunt et al., 2019; Hawkins et al., 2020), and Indian Ocean humpback dolphins (*S. plumbea*) in the South Africa waters (Karczmarski, 1999; Koper et al., 2016; Bouveroux et al., 2019). Some studied populations were documented to display fission-fusion dynamics with some long-lasting social relationships. Typically, the IPHDs live in groups of less than 10 individuals (Parsons, 2004; Chen et al., 2011; Würsig et al., 2016), and their societies include both stable (i.e., preferred companionships) and fluid (i.e., casual acquaintances) social interactions (Dungan et al., 2012, 2016; Wang et al., 2015).

Intra-specific variability in IPHD group sizes is not fully investigated, although some previous studies have basically described social characteristics of humpback dolphins. Previous studies suggested dolphin group sizes and composition may be associated with species characteristics, habitat structure, and social-environmental aspects of populations (Baird and Dill, 1996; Gibson and Mann, 2008b; Degrati et al., 2019). Changes in humpback dolphin group size, such as annual (Koper et al., 2016), seasonal (Chen et al., 2011; Wang et al., 2016), and behavioral variations (Würsig et al., 2016), are often habitat-specific and affected by a series of environmental variables at a regional scale. For instance, the mean group size observed for the Indian Ocean humpback dolphins in the Algoa Bay, South Africa, decreased from 7 individuals in 1990s to only 3 in 2010s (Karczmarski, 1999; Koper et al., 2016), whilst such a sharp decline has not been observed in other regions. In several known humpback dolphin populations, it has been reported that feeding groups, especially those groups following fishing trawlers (Parsons, 2004; Würsig et al., 2016), and breeding groups (Baldwin et al., 2004; Liu et al., 2020b), were much larger than those groups engaged in other behaviors, indicating a potential influence of behavioral states on group size.

A few studies have reported group size variations in the IPHDs. For example, the IPHDs in the Xiamen Bay, China, showed seasonal variations in their group sizes, with larger groups formed during the winter and spring when compared to summer and autumn (Wang et al., 2016). In the eastern Taiwan Strait, Dungan et al. (2016) revealed that IPHD groups were larger when contained calves, suggesting the importance of nursery behavior on IPHDs' sociality. However, we still lack an understanding of temporal and behavioral factors associated with intra-population variability in the IPHD group sizes. Thus, we know little about how the IPHDs vary their group sizes to adapt to various habitats.

In this study, we showed the variability in IPHD group sizes recorded in the eastern waters of Zhanjiang, China. We assessed whether IPHD group sizes varied at three temporal scales (year, season, and tide) and across two behavioral domains (number of mother-calf pairs, and behavioral state). We expect that IPHD group sizes vary with some of the above factors. This study aims to provide a better understanding of social characteristics of IPHDs at a population level, and to reveal potential factors important for the social dynamics of this population specifically, and IPHDs more generally.

MATERIALS AND METHODS

Study Area

Our survey area is the near-shore, eastern waters of Zhanjiang, China (**Figure 1**), covering an area of approximately 1,000 km^2. This area is a shallow-water embayment (water depth range: 2–40 m) with a sandy/muddy seafloor (Zhou et al., 2007; Xu et al., 2015; Liu et al., 2017a). The population of IPHDs residing in this area was first reported by Zhou et al. (2007). To provide protection for this population, the local Zhanjiang government established a protected area i.e., Zhanjiang Leizhou Bay Municipal Humpback Dolphin Nature Reserve (110° 26′−110° 29′ E, 20° 44′ −20° 46′ N; Area: 21-km^2; **Figure1**) in 2007 (Xu et al., 2015; Liu et al., 2020a). Based on local rainfalls and climate characteristics, we defined four season phases for the study

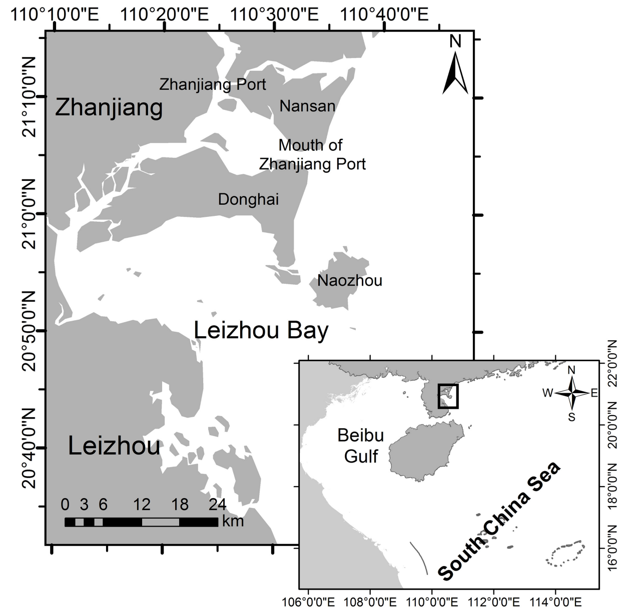


FIGURE 1 | Map of the study area: the eastern waters of Zhanjiang, China.

area: spring (March–May), summer (June–August), autumn (September–November), and winter (December–February) (Liu et al., 2017b). We divided tidal condition of a day into four consecutive phases: high, ebb, low, and flood (Liu et al., 2021).

Data Collection

To conduct field surveys, we used either a 12-m-length wooden fishing boat (60 HP outboard engine) or a 7-m-length fiberglass speed boat (75 HP outboard engine). We carried out surveys during October-November of 2013, and quarterly from January 2015 to May 2018. During our surveys, at least two experienced observers scanned the front 180° of sea surface, and searched IPHDs with the naked eyes and/or 7 × 50 binoculars (Li et al., 2016; Liu et al., 2020a). We performed the surveys only during the daytime and good visual conditions without rain or fog, and only under satisfied sea states of Beaufort scale ≤ 3.

In this study, we used the term "group" to define one or more dolphins observed with spatial co-occurrence (each member within 200 m of any other members) or social associations (all individuals within a unit in a similar behavioral state) (Wang et al., 2016; Liu et al., 2020b, 2021). Once a IPHD group was sighted, we approached and observed the group with 10−50 m between our boat and the group, unless the group actively approach us. During each observation, we recorded date, time, GPS location, group size, group composition based on age classes, number of mother-calf pairs (absence as 0), and primary behavioral state.

We used a hand-held Garmin 78 s GPS receiver (Garmin, Taiwan, China) to obtain information on date, time, and GPS location. For each group, we used the method of multiple-counts (minimum/best/maximum) to generate observer-based group size estimates (Gerrodette et al., 2002). We determined the group composition based on IPHD coloration patterns along with age classes (Jefferson et al., 2012). We determined the presence/absence of mother-calf pair and number of mother-calf pairs by observing and counting how many individuals are poorly marked, obviously dark-gray, small (i.e., ∼1m length, less than half of adult body length), and at consistent echelon positions with an adult. We determined the behaviors of IPHDs using five recognizable behavioral states: feeding, traveling, socializing, resting, and milling (Parsons, 2004; Stockin et al., 2009; Würsig et al., 2016). See behavioral definitions in **Table 1**. Raw group size data (observer-based best estimates) were later verified with photographs taken during each sighting: if the observer-based best count was smaller than the number of individuals photographically identified for a group, the group size was modified as the latter (López et al., 2018).

Data Analysis

To test whether variability in IPHD group sizes was associated with temporal and/or behavioral variables, we constructed univariate generalized linear models (GLMs) with multivariate analysis of variance. We included five factors into our models, including three temporal factors i.e., year (2013, 2015, 2016, 2017, and 2018), season (spring, summer, autumn, and winter), and tide (high, ebb, low, and flood), and two behavioral factors i.e., number of mother-calf pairs (0, 1, 2, and 3) and behavioral state (feeding, traveling, socializing, and resting/milling) (**Table 2**). Not only resting and milling represented a small percentage in the behavioral budget of the dolphins, but these behavioral states are also similar in low activity rate (**Table 1**). Thus, we integrated resting and milling into one single behavioral state for analysis.

In total, we built five main effects and ten pairwise interaction terms into the GLMs. Our null hypothesis was that there was no difference in the IPHD group sizes across different years, seasons, tidal phases, number of mother-calf pairs, and behavioral states. Once a significant effect was found for either main factor, we performed the Kruskal-Wallis tests to make *post hoc* pair-wise multiple comparisons using Tukey's HSD (equal variances, $p > 0.05$) or Tamhane's T2 method (unequal variances, $p < 0.05$). We also built and pruned a classification and regression tree (CART), in order to determine which variable is predominant in affecting the IPHD group sizes (De'ath and Fabricius, 2000; Liu et al., 2019). Results on IPHD group sizes are reported as mean ± standard deviation (SD) unless otherwise stated. We conducted all statistical analyses in the IBM SPSS 19.0 (SPSS Inc., Chicago, Illinois), and defined a significance level of $P < 0.05$.

RESULTS

Over 5 years (2013 and 2015–2018), we carried out 174-day boat-based surveys in the study area (**Table 2**). In total, we achieved 11,676 km survey effort (**Figure 2A**) and sighted 253 IPHD groups (**Figure 2B**). Throughout the survey period, group encounter rate was 2.17 sightings per 100 km (**Table 2**). Of the 253 groups, we sampled 229 (90.5%) with available group size estimates, generating a mean group size of 10.9 ± 8.8 individuals (range: 1–48). Of the 229 sampled groups, 227 (99.1%), 225

TABLE 1 | Summary of behavioral definitions and observations of Indo-Pacific humpback dolphins in the eastern waters of Zhanjiang, China.

Behavioral state	Behavioral characteristics	Number of groups (% out of the total groups)
Feeding	• Move in various directions without an obvious pattern, dive frequently and steeply downwards (often preceded by fluke up or peduncle arches), with extended submersion times. • Rapid accelerations and erratic movement at the surface, sometimes with indicative behaviors on chasing fish, such as directly pursuing a fish (fish jumping at surface), or with fish in their mouth, or following the fishing boats (especially trawlers), or sea birds in attendance for prey.	76 (30.0%)
Traveling	• Move persistently and directionally with a regular pattern of surfacing and diving, and are not underwater for extended lengths of time. • Dive angles are shallow, and dive intervals are short but relatively consistent.	79 (31.2%)
Socializing	• Dolphins are in close proximity, with showing high levels of interaction (chasing, rolling, rubbing, and other body contacts). • Fins and flukes often break the surface of the water, and aerial or acrobatic behavior occasionally occurs such as leaps or flips. • Dive direction is unpredictable, and dive intervals vary.	38 (15.0%)
Resting	• Almost statically float on the surface. • Dolphins swim in close proximity, but without interaction; Dolphins surface in a synchronized manner and most of the time is spent at the water surface; Dive angles are shallow. • No aerial behavior and activity levels are low.	8 (3.2%)
Milling	• Dolphins circle in a small area at low speed with no apparent direction and net movement. Dive intervals vary, and the activity levels are low. • Milling may indicate a transitory phase between other functional behaviors i.e., feeding, traveling, socializing, and resting.	9 (3.6%)
Undetermined	• Within one encounter, the observers have insufficient observation time window to determine the primary behavioral state. • Undetermined to be any categories above.	43 (17.0%)

TABLE 2 | Annual survey effort, sighting information, and group size of Indo-Pacific humpback dolphins in the eastern waters of Zhanjiang, China, in 2013, and 2015–2018.

Year	No. of survey days	Survey distance (kms)	No. of dolphin sightings	Group encounter rate (No. of groups per 100 kms)	Group size (mean ± SD)
2013	4	220	4	1.82	18.8 ± 11.4
2015	55	3,638	91	2.50	8.2 ± 6.3
2016	59	3,692	66	1.79	10.1 ± 8.1
2017	46	3,546	78	2.20	9.5 ± 8.8
2018	10	580	14	2.41	13.1 ± 11.0
Total	174	11,676	253	2.17	10.9 ± 8.8

(98.3%), 195 (85.2%), and 134 (58.5%) were comprised of less than 40, 30, 20, and 10 individuals, respectively (**Figure 3**). In addition, 24 groups (9.2%) consisted of single individual, and 17 (7.4%) were observed in a pair of individuals.

We recorded the presence of mother-calf pair in 85 groups (33.6%), where 47 had one pair of mother-calf (18.6%), 25 had two pairs (9.9%), and the other 13 had three pairs (5.1%) (**Figure 4A**). Feeding (30.0%) and traveling (31.2%) represented the great majority of behavioral states recorded in the study area (**Figure 4B**). Furthermore, we recorded 38 socializing groups (8.4%), 8 resting groups (3.2%), and 9 milling groups (3.6%), while 43 groups (17.0%) could not be determined with identifiable behavioral state (**Table 1**). IPHD group size was highest in 2013 (18.8 ± 11.4) and lowest in 2015 (8.2 ± 6.3) (**Table 2**). Although mean values of group sizes varied across years, there was no variation in group sizes among different years (Kruskal-Wallis test, $\chi^2 = 8.8$, $P = 0.168$). Our GLMs showed that variations in group sizes were associated with the season ($F = 1.0$, df = 3, $P = 0.002$), number of mother-calf pairs ($F = 9.0$, df = 3, $p < < 0.001$), behavioral state ($F = 0.9$, df = 3, $P = 0.033$), year × season ($F = 4.9$, df = 12, $P = 0.04$), year × number of mother-calf pairs ($F = 5.1$, df = 12, $P = 0.001$), year × behavioral state ($F = 3.3$, df = 12, $P = 0.014$), and season × behavioral state ($F = 2.8$, df = 9, $P = 0.031$), but were not associated with other factors or interaction terms (**Table 3**).

IPHD group sizes varied among seasons (Kruskal-Wallis test, $\chi^2 = 2.6$, $P = 0.045$). Group size in the autumn (14.1 ± 9.4) was larger than those in the spring (9.0 ± 6.9), summer (9.0 ± 6.6) and winter (7.8 ± 6.0) (Tukey's HSD tests, $P_{autumn\ vs\cdot\ spring} = 0.022$, $P_{autumn\ vs\cdot\ summer} = 0.018$, and $P_{autumn\ vs\cdot\ winter} = 0.007$), while there was no variation in group sizes across spring, summer, and winter (**Figure 5A**). In addition, there was no variation in group sizes with tidal phases (Kruskal-Wallis test, $\chi^2 = 1.343$, $P = 0.719$) (**Figure 5B**).

IPHD group sizes varied with the presence of mother-calf pair, as nursery groups (16.8 ± 5.2) were about 2–4

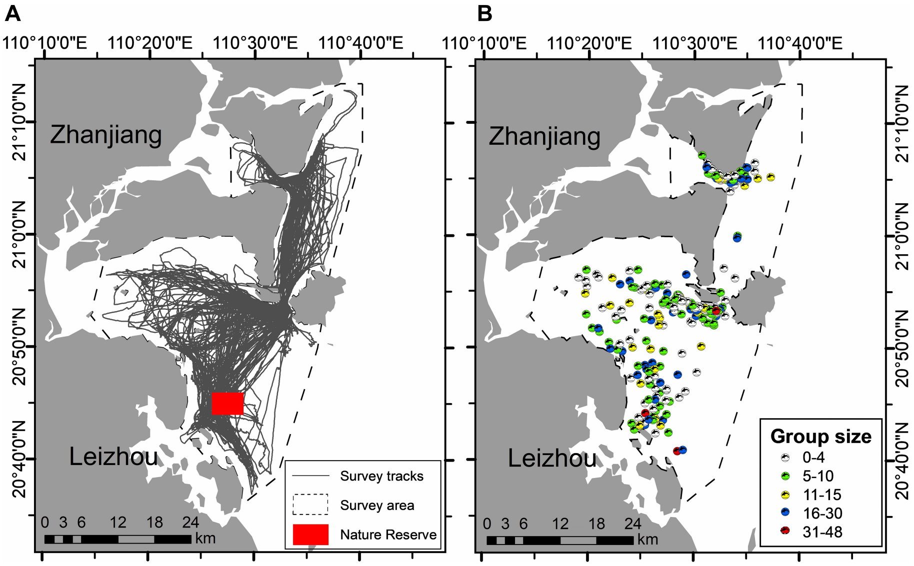


FIGURE 2 | (A) Survey routes and **(B)** 253 sightings of Indo-Pacific humpback dolphins achieved in the eastern waters of Zhanjiang, China in 2013, and 2015–2018.

times larger than non-nursery groups (i.e., groups without mother-calf pair, 6.8 ± 6.3). Group sizes also varied with the number of mother-calf pair (Kruskal-Wallis test, $\chi^2 = 76.417$, $P < 0.001$). We found a positive influence of the number of mother-calf pairs on IPHD group sizes: group sizes with one pair of mother-calf, two pairs, and three pairs were 10.2 ± 6.2, 17.4 ± 5.4, and 24.9 ± 9.6, respectively (**Figure 5C**).

We detected variation in IPHD group sizes across different behavioral states (Kruskal-Wallis test, $\chi^2 = 14.1$, $P = 0.003$). Resting/milling group size (5.5 ± 3.9) was smaller than feeding (12.1 ± 8.7), traveling (10.1 ± 8.1), and socializing group size (12.3 ± 6.5) ($P_{feeding\ vs.\ resting/milling} = 0.002$, $P_{traveling\ vs.\ resting/milling} = 0.012$, and $P_{socializing\ vs.\ resting/milling} = 0.003$; **Figure 5D**). However, group size was similar among feeding, traveling, and socializing behaviors (**Figure 5D**).

We built a CART with six leaves (**Figure 6**), including only three final explanatory variables i.e., number of mother-calf pairs, season, and behavioral state. We excluded the other two variables, i.e., year and tide, because they were insignificant in our GLMs (**Table 3**). In total, 68.1% of the variances in IPHD group sizes could be explained by the CART. The first split of CART was based on the number of mother-calf pairs, with ≤ 1 in the left branch [group size ≤ 10) and > 1 in the right branch (group size > 10)]. Then, these two branches were continuously divided into autumn in the left (group size > 8 or 15), spring, summer, and winter in the right (group size ≤ 8 or 15). The final splitting process was repeated for the two right seasonal branches, separating behavioral states into resting/milling in the next left (group size ≤ 5 or 10), and feeding, traveling, and socializing in the next right (group size > 5 or 10).

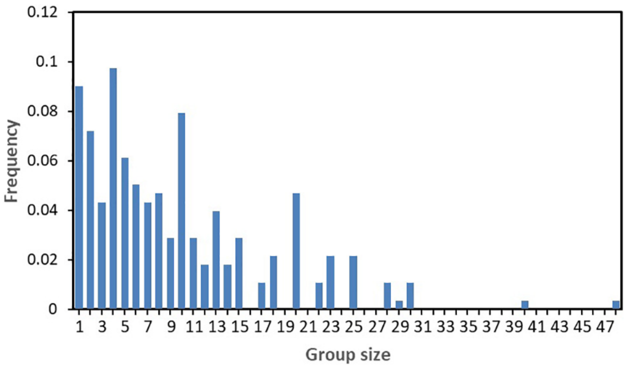


FIGURE 3 | Frequency histogram of 229 group size estimates of Indo-Pacific humpback dolphins in the eastern waters of Zhanjiang, China.

DISCUSSION

Our study yielded several critical findings. First, we demonstrated that IPHD group sizes in the Zhanjiang waters were influenced by the season, number of mother-calf pairs, behavioral state, and the interaction between these factors. Second, our results showed that IPHD group size was larger in the autumn (September-November) compared to the other seasons. Third, we observed a positive relation of nursery behavior in IPHD group sizes, as nursery groups were 2–4 times larger than those non-nursery groups, and group sizes increased with the number of mother-calf pairs. Lastly, we displayed variations in IPHD group sizes across various behavioral states:

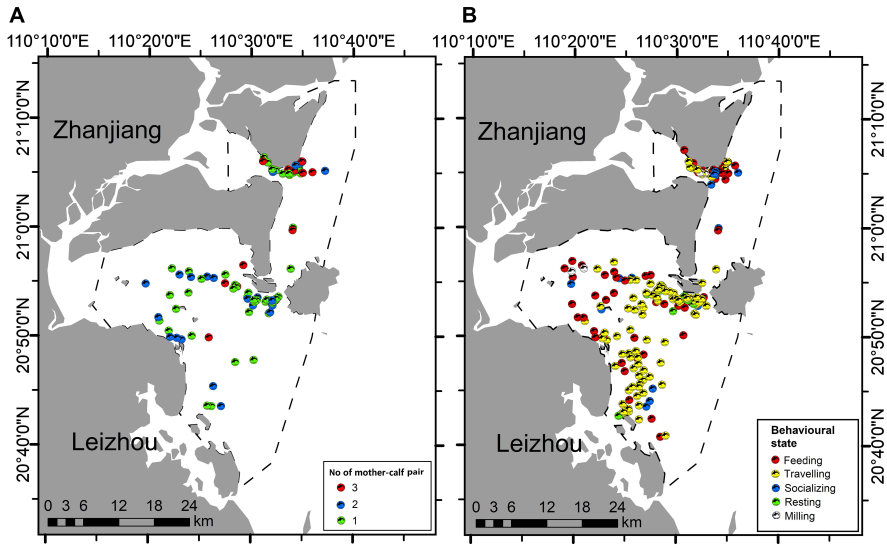


FIGURE 4 | Sighting locations of Indo-Pacific humpback dolphins in the eastern waters of Zhanjiang, China: **(A)** nursery groups (number of mother-calf pairs: 1, 2, and 3), and **(B)** groups engaged in various behavioral states (feeding, traveling, socializing, resting, and milling).

TABLE 3 | Generalized linear models (GLMs) built to determine potential temporal (year, season, and tide) and/or behavioral effects (number of mother-calf pairs, and behavioral state) on group sizes of Indo-Pacific humpback dolphins in the eastern waters of Zhanjiang, China.

Source of variation	Type III sum of squares	df	Mean square	F	*P*
Corrected model	10,287.9	125	82.3	2.3	**<0.001***
Intercept	11,541.3	1	11,541.3	323.6	**<0.001***
Year	374.7	4	124.9	3.5	0.395
Season	107.7	3	35.9	1.0	**0.002***
Tide	334.1	3	111.4	3.1	0.131
Number of mother-calf pairs	964.2	3	321.4	9.0	**<0.001***
Behavioral state	99.0	3	33.0	0.9	**0.033***
Year × Season	693.3	12	173.3	4.9	**0.04***
Year × Tide	579.8	12	96.6	2.7	0.228
Year × Number of mother-calf pairs	729.4	12	182.4	5.1	**0.001***
Year × Behavioral state	477.6	12	119.4	3.3	**0.014***
Season × Tide	270.1	9	30.0	0.8	0.581
Season × Number of mother-calf pairs	184.5	9	36.9	1.0	0.404
Season × Behavioral state	403.3	9	100.8	2.8	**0.031***
Tide × Number of mother-calf pairs	85.3	9	14.2	0.4	0.178
Tide × Behavioral state	412.7	9	68.8	1.9	0.088
Number of mother-calf pairs × Behavioral state	131.8	9	26.4	0.7	0.597
Error	2,532.3	71	35.7		
Total	33,934.8	197			
Corrected total	12,820.2	196			

**Asterisks represent statistical significance level of P < 0.05 (in bold). Five main interactions and ten pairwise interactions were included into the models.*

resting/milling groups were approximately 50% smaller than feeding, traveling, or socializing groups, but the latter three had a similar size.

We observed a mean group size larger for the IPHDs in the Zhanjiang waters when compared to other estimates reported in this are by previous studies, including 8 (median) documented by Zhou et al. (2007), 7.5 ± 5.45 by Xu et al. (2012), and 8.12 ± 5.85 by Xu et al. (2015). These differences among studies can be related to different methodologies, as the previous studies only applied photo-identification technique to estimate the group size, while we used observer-based best counts complemented with photo-identification estimates. Photo-identification approach often generates an underestimated group size for each IPHD group (Liu et al., 2020b), which is based on the natural markings of each identifiable dolphin. However, some individuals within one group might be not photographically captured, and some

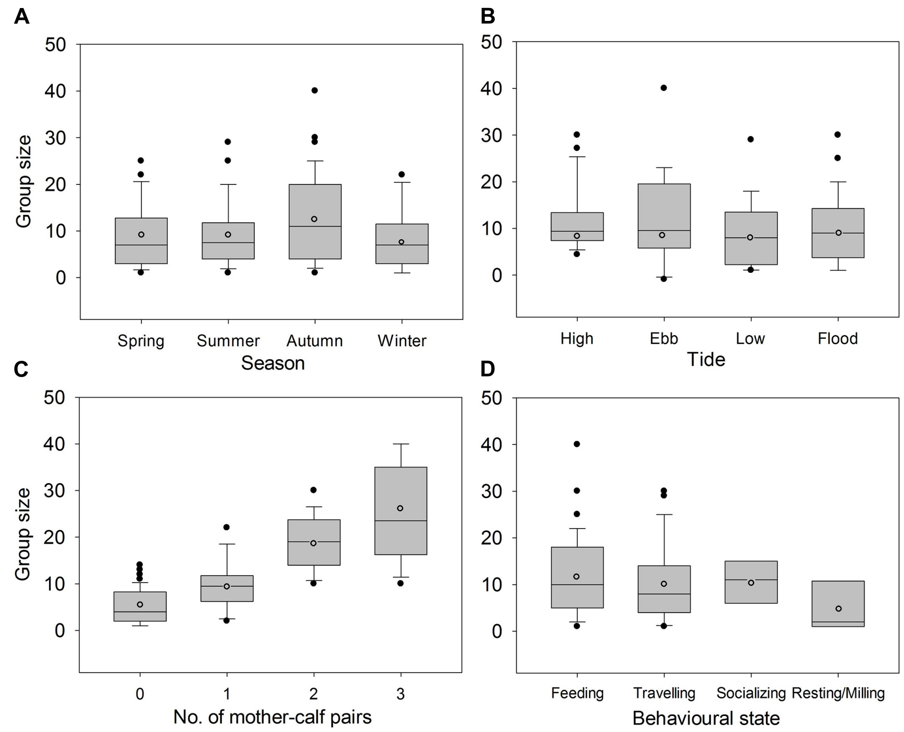


FIGURE 5 | Boxplots of group sizes of Indo-Pacific humpback dolphins in the eastern waters of Zhanjiang, China, categorized by **(A)** season, **(B)** tide, **(C)** number of mother-calf pairs, and **(D)** behavioral state. Mean values (open circles), median values (black horizontal line), lower (25%) and upper (75%) quartiles, and outlier values (black dots) were illustrated.

young individuals and especially claves, are poorly marked or unmarked, both of which would lead to an underestimation of IPHD group size (Gerrodette et al., 2002; López et al., 2018).

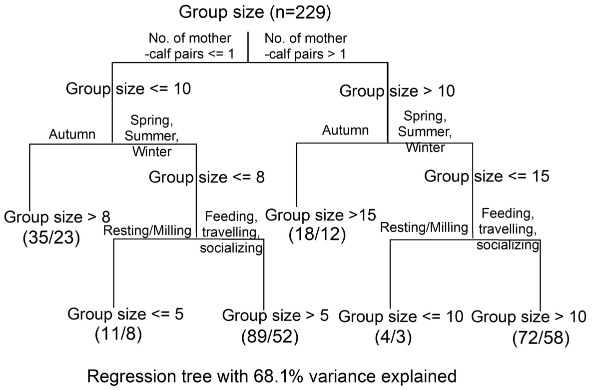


FIGURE 6 | A classification and regression tree (CART) to explain group size variability of Indo-Pacific humpback dolphins in the eastern waters of Zhanjiang, China. Explanatory variables included number of mother-calf pairs (0, 1, 2, and 3), season (spring, summer, autumn, and winter) and behavioral state (feeding, traveling, socializing, and resting/milling). Each split was labeled with a threshold of group size that determined the split. For each of six final leaves, successfully observed values and failure ones were shown, respectively. Each terminal node was labeled with a final threshold of group size.

Thus, IPHD group size data used in this study are more methodologically credible.

We observed annual fluctuations of the IPHD group sizes, while there was no statistical difference in group sizes across different years. The inter-annual fluctuations of group sizes were obvious, with the largest value in 2013 (18.8 ± 11.4) and the smallest in 2015 (8.2 ± 6.3), which might be due to the small sample size in 2013 ($n = 4$). Additionally, we observed that IPHD group sizes were relatively stable with a mean of ∼8–9 individuals across different tidal phases, indicating scant tidal fluctuations of group sizes.

Within a certain population, temporal and behavioral variations in social characteristics were generally attributed to environmental adaptations of dolphins to various biological requirements and ecological constraints, such as food availability (Heithaus and Dill, 2002), mating opportunities (Orbach et al., 2014), predation risk (Kelley et al., 2011), or nurturing offspring (Mann et al., 2000). Compared to oceanic dolphin species, most IPHD populations are subject to relatively low predation risk from sharks or killer whales (Gowans et al., 2007; Würsig et al., 2016). Therefore, the intra-population variability in IPHD group sizes illustrated by our GLMs and CART might be primarily explained by food availability and reproductive processes, which were considered to vary temporally and by behaviors (Wang et al., 2016; Liu et al., 2020b).

Since 1998, the Chinese government designated a mandatory summer-fishing-ban-season (from May 1 to August 16 per year) in the territorial waters of South China Sea, aiming to preserve fisheries resources especially those reproduction-driven fish aggregations. Consequently, fisheries resources during and after the fishing ban season could be more abundant than before the season. Such seasonal variations in IPHD food resources might be a main driver leading to larger feeding groups in the autumn. Besides, previous studies in the study area indicated that the newborn IPHD calves peaked at the period between July and October (Zhou et al., 2007; Xu et al., 2012, 2015). Consequently, seasonal variations in IPHD group sizes can be related to their tendency to form larger breeding/mating aggregation during the autumn to improve mating opportunities and reproductive success (Baldwin et al., 2004; Orbach et al., 2014). However, seasonal variations in IPHD group sizes in the study area was different from that observed in the Xiamen Bay, China, where the mean group size of IPHDs during the winter-spring (7.2 individuals) were larger than those during the summer-autumn (mean: 4.4 individuals) (Wang et al., 2016). Such regional difference suggested that the variability in IPHD group sizes might vary across various habitats, as an adaptation to different ecological constraints in different geographical regions (Liu et al., 2021).

As demonstrated by our data, more mother-calf pairs were recorded in IPHD groups, the group size would be larger. More importantly, our CART clearly indicated that IPHD group sizes were primarily determined by the number of mother-calf pairs. Such positive impact of nursery behavior on enlarging group size has not only been reported for the IPHDs in the eastern Taiwan Strait (Dungan et al., 2016), and also for other dolphin species such as bottlenose dolphins (*Tursiops* spp.) (Gibson and Mann, 2008b), dusky dolphins (*Lagenorhynchus obscurus* Gray, 1828) (Degrati et al., 2019), and Guiana dolphins (*Sotalia guianensis*) (Azevedo et al., 2005; Santos and Rosso, 2007; Emin-Lima et al., 2010). This social strategy i.e., dolphin group became larger when calves were present, could bring a variety of added benefits such as enhanced calf-assistance, cooperative calf-caring, reduced maternal investments, and increased calf-protection (against predators or intraspecific aggression) (Mann et al., 2000; Gibson and Mann, 2008a; Kent et al., 2008).

Our data indicated that IPHD groups were mainly engaged in feeding and traveling behaviors, while socializing and resting/milling were less frequently observed. Such a behavioral budget was consistent with the patterns documented for humpback dolphins in the Hong Kong waters (Parsons, 2004; Würsig et al., 2016), in the Algoa Bay, South Africa (Karczmarski, 1999), and in the Cleveland Bay, Australia (Parra et al., 2011). Our results showed that resting/milling IPHD groups were smaller than feeding, traveling, or socializing groups, while the latter three group types had a similar group size. This increase in feeding, traveling, or socializing group size has been reported for the bottlenose dolphins (Heithaus and Dill, 2002), common dolphins (*Delphinus* spp.) (Neumann, 2001; Stockin et al., 2009), and dusky dolphins (Degrati et al., 2019). IPHDs tended to form large, temporary, and functional gathering of different social units when they were not resting or milling (Würsig et al., 2016), which might help strengthen group added benefits (Baird and Dill, 1996; Neumann, 2001; Yeater et al., 2013).

To conclude, our data are essential to show temporal and behavioral variations in IPHD group sizes in the Zhanjiang waters. Our findings suggested that the intra-population variability of IPHD group sizes was potentially associated with some environmental cycles and behavioral changes, and could be influenced by the food availability and reproductive process of IPHDs. To better protect the IPHDs in the Zhanjiang waters, we highlight the importance of protecting nursery groups/activities of IPHDs. According to our findings, we empathize that breeding season is an important period in the annual cycle of IPHDs, and in the study area, particular conservation effort is required during the autumn. The IPHDs in the study area also tended to form larger groups when they were engaged in feeding behavior and when food resources are more abundant (e.g., summer-fishing-ban-season), which indicated that social dynamics of IPHDs could be greatly influenced food availability. Therefore, protecting food resources from overfishing should be one of the most important actions to maintain social dynamics of IPHDs and to conserve this species. Compared to previous studies, we found that the intra-population variations in IPHD group sizes might vary among different habitats. Therefore, more data on IPHD mating strategies, reproductive fitness, prey resources, fisheries-dolphin conflicts, and how these factors may influence social dynamics of IPHDs are interesting venues of future research.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by IDSSE-SYLL-MMMBL-01.

AUTHOR CONTRIBUTIONS

MLiu and MLin: data collection. MLiu: formal analysis and writing—original draft. SL and MLin: funding acquisition. MLiu, MLin, DL, and SL: methodology. MLin, DL, and SL: writing—review and editing. All authors contributed to the article and approved the submitted version.

FUNDING

This research was financially supported by the National Natural Science Foundation of China (41406182, 41306169, and 41422604), the Biodiversity Investigation, Observation and Assessment Program (2019-2023) of Ministry of Ecology and Environment of China, and the Ocean Park Conservation Foundation of Hong Kong (MM02-1516, AW02-1920). The writing of this paper was supported in part by the China-United Kingdom Newton Fund Ph.D. Placement from China Scholarship Council and British Council.

ACKNOWLEDGMENTS

We express our big thanks to all the colleagues and students at the Marine Mammal and Marine Bioacoustics Laboratory for their logistical support in field work. We thank Peijun Zhang, Lijun Dong, Mingzhong Liu, Kuan Li, and Francesco Caruso for their assistance in field work.

REFERENCES

Azevedo, A. F., Viana, S. C., Oliveira, A. M., and Van Sluys, M. (2005). Group characteristics of marine tucuxis (*Sotalia fluviatilis*) (Cetacea: Delphinidae) in Guanabara Bay, south-eastern Brazil. *J. Mar. Biol. Assoc. U.K.* 85, 209–212. doi: 10.1017/s0025315405011082h

Baird, R. W., and Dill, L. M. (1996). Ecological and social determinants of group size in transient killer whales. *Behav. Ecol.* 7, 408–416. doi: 10.1093/beheco/7.4.408

Baldwin, R. M., Collins, M., Van Waerebeek, K., and Minton, G. (2004). The indo-pacific humpback dolphin of the Arabian region: a status review. *Aquat. Mamm.* 30, 111–124. doi: 10.1578/am.30.1.2004.111

Benoit-Bird, K., and Au, W. (2003). Hawaiian spinner dolphins aggregate midwater food resources through cooperative foraging. *J. Acoust. Soc. Am.* 114, 2300–2300. doi: 10.1121/1.4780872

Bouveroux, T. N., Caputo, M., Froneman, P. W., and Plön, S. (2018). Largest reported groups for the indo-Pacific bottlenose dolphin (*Tursiops aduncus*) found in Algoa Bay, South Africa: trends and potential drivers. *Mar. Mamm. Sci.* 34, 645–665. doi: 10.1111/mms.12471

Bouveroux, T., Kirkman, S. P., Conry, D., Vargas-Fonseca, O. A., and Pistorius, P. A. (2019). The first assessment of social organisation of the indian ocean humpback dolphin (*Sousa plumbea*) along the south coast of South Africa. *Can. J. Zool.* 97, 855–865. doi: 10.1139/cjz-2018-0244

Cantor, M., Wedekin, L. L., Guimaraes, P. R., Daura-Jorge, F. G., Rossi-Santos, M. R., and Simoes-Lopes, P. C. (2012). Disentangling social networks from spatiotemporal dynamics: the temporal structure of a dolphin society. *Anim. Behav.* 84, 641–651. doi: 10.1016/j.anbehav.2012.06.019

Chen, T., Qiu, Y., Jia, X., Hung, S. K., and Liu, W. (2011). Distribution and group dynamics of indo-Pacific humpback dolphins (*Sousa chinensis*) in the western Pearl River Estuary, China. *Mamm. Biol.* 76, 93–96. doi: 10.1016/j.mambio.2010.01.001

Connor, R. C. (2000). "Group living in whales and dolphins," in *Cetacean Societies: Field Studies of Dolphins and Whales*, eds J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead (Chicago: University of Chicago Press), 199–218.

De'ath, G., and Fabricius, K. E. (2000). Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81, 3178–3192. doi: 10.1890/0012-9658(2000)081[3178:cartap]2.0.co;2

Degrati, M., Coscarella, M. A., Crespo, E. A., and Dans, S. L. (2019). Dusky dolphin group dynamics and association patterns in Península Valdés, Argentina. *Mar. Mamm. Sci.* 35, 416–433. doi: 10.1111/mms.12536

Dungan, S. Z., Hung, S. K., Wang, J. Y., and White, B. N. (2012). Two social communities in the Pearl River Estuary population of Indo-Pacific humpback dolphins (*Sousa chinensis*). *Can. J. Zool.* 90, 1031–1043. doi: 10.1139/z2012-071

Dungan, S. Z., Wang, J. Y., Araújo, C. C., Yang, S. C., and White, B. N. (2016). Social structure in a critically endangered Indo-Pacific humpback dolphin (*Sousa chinensis*) population. *Aquat. Conserv.* 26, 517–529. doi: 10.1002/aqc.2562

Emin-Lima, R., Moura, L. N., Rodrigues, A. F., and Silva, M. L. (2010). Note on the group size and behavior of Guiana dolphins (*Sotalia guianensis*) (Cetacea: Delphinidae) in Marapanim Bay, Pará, Brazil. *Lat. Am. J. Aquat. Mamm.* 8, 167–170.

Gerrodette, T., Perryman, W., and Barlow, J. (2002). *Calibrating Group Size Estimates of Dolphins in the Eastern Tropical Pacific Ocean*. Administrative Report LJ-02-08. La Jolla, CA: Southwest Fisheries Science Center, 1–20.

Gibson, Q. A., and Mann, J. (2008a). Early social development in wild bottlenose dolphins: sex differences, individual variation and maternal influence. *Anim. Behav.* 76, 375–387. doi: 10.1016/j.anbehav.2008.01.021

Gibson, Q. A., and Mann, J. (2008b). The size, composition and function of wild bottlenose dolphin (*Tursiops* sp.) mother-calf groups in Shark Bay, Australia. *Anim. Behav.* 76, 389–405. doi: 10.1016/j.anbehav.2008.01.022

Gowans, S., Würsig, B., and Karczmarski, L. (2007). The social structure and strategies of delphinids: predictions based on an ecological framework. *Adv. Mar. Biol.* 53, 195–294. doi: 10.1016/s0065-2881(07)53003-8

Gygax, L. (2002a). Evolution of group size in the dolphins and porpoises: interspecific consistency of intraspecific patterns. *Behav. Ecol.* 13, 583–590. doi: 10.1093/beheco/13.5.583

Gygax, L. (2002b). Evolution of group size in the superfamily Delphinoidea (Delphinidae, Phocoenidae and Monodontidae): a quantitative comparative analysis. *Mamm. Rev.* 32, 295–314. doi: 10.1046/j.1365-2907.2002.00114.x

Hawkins, E. R., Pogson-Manning, L., Jaehnichen, C., and Meager, J. J. (2020). Social dynamics and sexual segregation of Australian humpback dolphins (*Sousa sahulensis*) in Moreton Bay, Queensland. *Mar. Mamm. Sci.* 36, 500–521. doi: 10.1111/mms.12657

Heithaus, M. R., and Dill, L. M. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83, 480–491. doi: 10.1890/0012-9658(2002)083[0480:faatsp]2.0.co;2

Hunt, T. N., Allen, S. J., Bejder, L., and Parra, G. J. (2019). Assortative interactions revealed in a fission-fusion society of Australian humpback dolphins. *Behav. Ecol.* 30, 914–927. doi: 10.1093/beheco/arz029

Jefferson, T. A., and Curry, B. E. (2015). Humpback dolphins: a brief introduction to the genus Sousa. *Adv. Mar. Biol.* 72, 1–16. doi: 10.1016/bs.amb.2015.04.001

Jefferson, T. A., and Rosenbaum, H. C. (2014). Taxonomic revision of the humpback dolphins (*Sousa* spp.), and description of a new species from Australia. *Mar. Mamm. Sci.* 30, 1494–1541. doi: 10.1111/mms.12152

Jefferson, T. A., and Smith, B. D. (2016). Re-assessment of the conservation status of the Indo-Pacific humpback dolphin (*Sousa chinensis*) using the IUCN Red List criteria. *Adv. Mar. Biol.* 73, 1–26. doi: 10.1016/bs.amb.2015.04.002

Jefferson, T. A., Hung, S. K., Robertson, K. M., and Archer, F. I. (2012). Life history of the Indo-Pacific humpback dolphin in the Pearl River Estuary, southern China. *Mar. Mamm. Sci.* 28, 84–104. doi: 10.1111/j.1748-7692.2010.00462.x

Jefferson, T. A., Smith, B. D., Braulik, G. T., and Perrin, W. (2017). *Sousa chinensis*, the IUCN red list of threatened species 2017: e.T82031425A50372332. Available online at: https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T82031425A50372332.en (Accessed on 2 March 2019)

Kappeler, P. M. (2019). A framework for studying social complexity. *Behav. Ecol. Sociobiol.* 73:13.

Karczmarski, L. (1999). Group dynamics of humpback dolphins (*Sousa chinensis*) in the Algoa Bay region, South Africa. *J. Zool.* 249, 283–293. doi: 10.1111/j.1469-7998.1999.tb00765.x

Kelley, J. L., Morrell, L. J., Inskip, C., Krause, J., and Croft, D. P. (2011). Predation risk shapes social networks in fission-fusion populations. *PLoS One* 6:e24280. doi: 10.1371/journal.pone.0024280

Kent, E. E., Mazzoil, M., McCulloch, S. D., and Defran, R. H. (2008). Group characteristics and social affiliation patterns of bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon, Florida. *Florida Sci.* 71, 149–168.

Koper, R. P., Karczmarski, L., du Preez, D., and Plön, S. (2016). Sixteen years later: occurrence, group size, and habitat use of humpback dolphins (*Sousa plumbea*) in Algoa Bay, South Africa. *Mar. Mamm. Sci.* 32, 490–507. doi: 10.1111/mms.12279

Li, S., Lin, M., Xu, X., Xing, L., Zhang, P., Gozlan, R. E., et al. (2016). First record of the Indo-Pacific humpback dolphins (*Sousa chinensis*) southwest of Hainan Island, China. *Mar. Biodivers. Rec.* 9:3.

Lima, S. L., and Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68, 619–640. doi: 10.1139/z90-092

Liu, M., Bejder, L., Lin, M., Zhang, P., Dong, L., and Li, S. (2020a). Determining spatial use of the world's second largest humpback dolphin population: implications for place-based conservation and management. *Aquat. Conserv.* 30, 364–374. doi: 10.1002/aqc.3253

Liu, M., Dong, L., Lin, M., and Li, S. (2017a). Broadband ship noise and its potential impacts on Indo-Pacific humpback dolphins: implications for conservation and management. *J. Acoust. Soc. Am.* 142, 2766–2775. doi: 10.1121/1.5009444

Liu, M., Lin, M., Dong, L., Xue, T., Zhang, P., Tang, X., et al. (2020b). Group sizes of Indo-Pacific humpback dolphins in waters southwest of Hainan Island, China: insights into rare records of large groups. *Aquat. Mamm.* 46, 259–265. doi: 10.1578/am.46.3.2020.259

Liu, M., Lin, M., Dong, L., Zhang, P., and Li, S. (2021). Spatiotemporal variations in fine-scale habitat use of the world's second largest population of humpback dolphins. *J. Mamm.* gyab001. doi: 10.1093/jmammal/gyab001 [Epub ahead of print].

Liu, M., Lin, M., Turvey, S. T., and Li, S. (2017b). Fishers' knowledge as an information source to investigate bycatch of marine mammals in the South China Sea. *Anim. Conserv.* 20, 182–192. doi: 10.1111/acv.12304

Liu, M., Lin, M., Turvey, S. T., and Li, S. (2019). Fishers' experiences and perceptions of marine mammals in the South China Sea: insights for improving community-based conservation. *Aquat. Conserv.* 29, 809–819. doi: 10.1002/aqc.3073

López, B. D., Grandcourt, E., Methion, S., Das, H., Bugla, I., Al Hameli, M., et al. (2018). The distribution, abundance and group dynamics of Indian Ocean humpback dolphins (*Sousa plumbea*) in the Emirate of Abu Dhabi (UAE). *J. Mar. Biol. Assoc. U.K.* 98, 1119–1127. doi: 10.1017/s0025315417001205

Lusseau, D. (2003). The emergent properties of a dolphin social network. *Proc. R. Soc. Lond. B Biol. Sci.* 270, S186–S188.

Lusseau, D., and Newman, M. E. (2004). Identifying the role that animals play in their social networks. *Proc. R. Soc. Lond. B Biol. Sci.* 271, S477–S481.

Lusseau, D., Schneider, K., Boisseau, O. J., Haase, P., Slooten, E., and Dawson, S. M. (2003). The bottlenose dolphin community of doubtful Sound features a large proportion of long-lasting associations. *Behav. Ecol. Sociobiol.* 54, 396–405. doi: 10.1007/s00265-003-0651-y

Lusseau, D., Wilson, B. E. N., Hammond, P. S., Grellier, K., Durban, J. W., Parsons, K. M., et al. (2006). Quantifying the influence of sociality on population structure in bottlenose dolphins. *J. Anim. Ecol.* 75, 14–24. doi: 10.1111/j.1365-2656.2005.01013.x

Mann, J., Connor, R. C., Barre, L. M., and Heithaus, M. R. (2000). Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behav. Ecol.* 11, 210–219. doi: 10.1093/beheco/11.2.210

Neumann, D. R. (2001). Activity budget of free-ranging common dolphins (*Delphinus delphis*) in the northwestern Bay of Plenty, New Zealand. *Aquat. Mamm.* 27, 121–136.

Orbach, D. N., Packard, J. M., and Würsig, B. (2014). Mating group size in dusky dolphins (*Lagenorhynchus obscurus*): costs and benefits of scramble competition. *Ethology* 120, 804–815. doi: 10.1111/eth.12253

Parra, G. J., Corkeron, P. J., and Arnold, P. (2011). Grouping and fission-fusion dynamics in Australian snubfin and Indo-Pacific humpback dolphins. *Anim. Behav.* 82, 1423–1433. doi: 10.1016/j.anbehav.2011.09.027

Parrish, J. K., and Edelstein-Keshet, L. (1999). Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science* 284, 99–101. doi: 10.1126/science.284.5411.99

Parsons, E. C. M. (2004). The behavior and ecology of the Indo-Pacific humpback dolphin (*Sousa chinensis*). *Aquat. Mamm.* 30, 38–55. doi: 10.1578/am.30.1.2004.38

Santos, M. D. O., and Rosso, S. (2007). Ecological aspects of marine tucuxi dolphins (*Sotalia guianensis*) based on group size and composition in the Cananéia estuary, southeastern Brazil. *Lat. Am. J. Aquat. Mamm.* 6, 71–82.

Sarabia, R. E., Heithaus, M. R., and Kiszka, J. J. (2018). Spatial and temporal variation in abundance, group size and behaviour of bottlenose dolphins in the Florida coastal Everglades. *J. Mar. Biol. Assoc. U. K.* 98, 1097–1107. doi: 10.1017/s002531541700090x

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philos. Trans. R. Soc. B Biol. Sci.* 362, 539–559. doi: 10.1098/rstb.2006.1994

Stockin, K. A., Binedell, V., Wiseman, N., Brunton, D. H., and Orams, M. B. (2009). Behavior of free-ranging common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand. *Mar. Mamm. Sci.* 25, 283–301. doi: 10.1111/j.1748-7692.2008.00262.x

Wang, X., Wu, F., Turvey, S. T., Rosso, M., and Zhu, Q. (2016). Seasonal group characteristics and occurrence patterns of Indo-Pacific humpback dolphins (*Sousa chinensis*) in Xiamen Bay, Fujian Province, China. *J. Mamm.* 97, 1026–1032. doi: 10.1093/jmammal/gyw002

Wang, X., Wu, F., Turvey, S. T., Rosso, M., Tao, C., Ding, X., et al. (2015). Social organization and distribution patterns inform conservation management of a threatened Indo-Pacific humpback dolphin population. *J. Mamm.* 96, 964–971. doi: 10.1093/jmammal/gyv097

Würsig, B., Parsons, E. C. M., Piwetz, S., and Porter, L. (2016). The behavioural ecology of Indo-Pacific humpback dolphins in Hong Kong. *Adv. Mar. Biol.* 73, 65–90. doi: 10.1016/bs.amb.2015.08.008

Xu, X., Song, J., Zhang, Z., Li, P., Yang, G., and Zhou, K. (2015). The world's second largest population of humpback dolphins in the waters of Zhanjiang deserves the highest conservation priority. *Sci. Rep.* 5:8147.

Xu, X., Zhang, Z., Ma, L., Li, P., Yang, G., and Zhou, K. (2012). Site fidelity and association patterns of Indo-Pacific humpback dolphins off the east coast of Zhanjiang, China. *Acta Theriol.* 57, 99–109. doi: 10.1007/s13364-011-0058-5

Yeater, D. B., Miller, L. E., Caffery, K. A., and Kuczaj, II S. A. (2013). Effects of an increase in group size on the social behavior of a group of rough-toothed dolphins (*Steno bredanensis*). *Aquat. Mamm.* 39, 344–355. doi: 10.1578/am.39.4.2013.344

Zhou, K., Xu, X., and Tian, C. (2007). Distribution and abundance of Indo-Pacific humpback dolphins in Leizhou Bay, China. *N.Z. J. Zool.* 34, 35–42. doi: 10.1080/03014220709510061

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 23 June 2021
doi: 10.3389/fmars.2021.688010

High-Throughput Tracking of Social Networks in Marine Fish Populations

Eneko Aspillaga[1], Robert Arlinghaus[2,3], Martina Martorell-Barceló[1], Margarida Barcelo-Serra[1] and Josep Alós[1]*

[1] Institut Mediterrani d'Estudis Avançats (IMEDEA, CSIC-UIB), Esporles, Spain, [2] Department of Biology and Ecology of Fishes, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany, [3] Division of Integrative Fisheries Management, Faculty of Life Sciences, Humboldt-Universität zu Berlin, Berlin, Germany

Despite their potential to generate high-quality positioning data, the use of high-resolution acoustic telemetry systems (HRATS) has been neglected in coastal marine areas due to the limitations that these environments pose to the transmission of acoustic signals. In this work, we applied a HRATS and social network analysis (SNA) to study the social interactions of the pearly razorfish (*Xyrichtys novacula*), a small coastal wrasse, in a Mediterranean marine reserve. Our analysis was based on proximity measures estimated from high-resolution trajectories from 232 individuals tracked during 55 days within a marine protected area. Associations were defined as the proportion of 5-min intervals in which two individuals were observed within 1 m from each other, and social networks were generated for the overall tracking period and for each particular day. The obtained network parameters were contrasted against 1,000 null association models obtained by randomly redistributing individual trajectories within the study area. The obtained networks showed a harem-like social structure, with agonistic behavior between males and larger association indices between individuals of different sex. Occasionally, sporadic associations of large groups of females were observed conducting excursions along the study area. By providing a comprehensive view of the organizational structure of the pearly razorfish, our study demonstrates the potential of HRATS to efficiently produce high-throughput tracking data from large numbers of individuals and of proper null social model formulation to reconstruct the social networks in wild-living marine fish populations. The combination of HRATS and SNA represents a powerful tool to study key ecological processes regarding the social interactions of individuals, including social dynamics, collective movements, and the response to environmental perturbations.

Keywords: acoustic telemetry, movement ecology, high-resolution tracking, animal social networks, social organization, fish behavior

OPEN ACCESS

Edited by:
David M. P. Jacoby,
Zoological Society of London,
United Kingdom

Reviewed by:
Paula Pattrick,
South African Environmental
Observation Network, South Africa
David José Nachón,
University of Santiago
de Compostela, Spain

****Correspondence:***
Eneko Aspillaga
aspillaga@imedea.uib-csic.es

Specialty section:
This article was submitted to
Marine Biology,
a section of the journal
Frontiers in Marine Science

Received: *30 March 2021*
Accepted: *02 June 2021*
Published: *23 June 2021*

Citation:
Aspillaga E, Arlinghaus R,
Martorell-Barceló M, Barcelo-Serra M
and Alós J (2021) High-Throughput
Tracking of Social Networks in Marine
Fish Populations.
Front. Mar. Sci. 8:688010.
doi: 10.3389/fmars.2021.688010

INTRODUCTION

The complex social interactions that occur within populations and communities are a fundamental aspect in ecological research aimed at understanding the functioning of ecosystems and their resilience to external perturbations (Tylianakis et al., 2008; Ings et al., 2009). Social Network Analysis (SNA) is the predominant framework used to investigate the interactions between social animals (Wey et al., 2008; Krause et al., 2009; Jacoby and Freeman, 2016). SNA comprises a series of flexible tools that allow robust quantitative analyses to be conducted on social groups, considering them networks of nodes connected by social ties (Croft et al., 2008; Farine and Whitehead, 2015). The main aim of SNA is to analyze relevant behavioral features such as the social structure of populations (Papageorgiou et al., 2019), the individual behavioral variability (Mourier et al., 2019), the mating behavior (McDonald et al., 2013), and the transmission of information and disease (Couzin and Krause, 2003; Martínez-López et al., 2009; Stockmaier et al., 2021). Characterizing the causes that lead to the organization of animal societies provides a reference point to study social evolution in many different taxa (Grueter et al., 2020).

A crucial consideration when conducting a SNA resides in how interactions among individuals are defined and recorded because it conditions the social structure patterns that arise from the SNA (Marin and Wellman, 2011; Castles et al., 2014). Usually, SNA requires continuous monitoring of unequivocally identified individuals over long periods of time. Many traditional studies were based on observations of focal individuals or groups using visual tools, such as direct observations, video-cameras, and drones, to study the social structure of large-bodied vertebrates such as mammals (e.g., Connor et al., 2001; Cantor et al., 2012) and sharks (Mourier et al., 2012; Butcher et al., 2021). In recent years, the popularization of miniaturized GPS and other tracking devices has dramatically increased our ability to monitor the movements of terrestrial animals (Rutz et al., 2012; Kays et al., 2015), providing precise positioning data that allows interaction networks to be derived from the spatial proximity of individuals (Whitehead, 2008; Farine, 2015). Proximity-based networks are grounded on the obvious assumption that the co-occurrence of individuals in space and time is a prerequisite to form an interaction. However, proximity networks are not always a good indicator of the real interaction networks and can lead to different conclusions on the social structure of the studied organisms (Castles et al., 2014; Farine, 2015). Nevertheless, tracking devices have a great potential to gather information from a large number of individuals at the same time, especially if they are difficult to observe directly. Moreover, recent analysis tools, such as the utilization of random null models to infer the significance of the obtained network (Farine, 2017; Davis et al., 2018; Pasquaretta et al., 2021), provide analytical methods to obtain robust estimations of the observed social structures (Spiegel et al., 2016).

The application of proximity metrics for SNA in marine systems has been less used due to the limitation of tracking animals in aquatic environments at high temporal and spatial resolutions. GPS-based methods are not available underwater, posing significant challenges for assessing the high-resolution behavior of fishes in the wild (Krause et al., 2013). The most used technique to study the movement and behavior of aquatic animals, passive acoustic telemetry (Heupel et al., 2006; Hussey et al., 2015), has traditionally provided presence-absence data (i.e., detections of tagged animals by the acoustic receivers placed across the study area), and has been combined with SNA to study the connectivity between distant areas (Jacoby et al., 2012; Lédée et al., 2015) and to infer the association patterns in different fish species (Haulsee et al., 2016; Jacoby et al., 2016). In such analyses, the associations between individuals were inferred from the co-occurrence of individuals within the detection range of an acoustic receiver, either placed on a fixed position of the study area or attached to a focal individual (serving as a proximity sensor). The detection range of acoustic receivers is usually large (between 200 and 800 m) and greatly depends on the frequency of the biotransmitter. Consequently, each detection entails a considerable positional uncertainty that makes it difficult to assume an interaction when two individuals are detected by the same receiver as they might be several hundreds of meters apart from each other. Indeed, it has been seen that the network patterns that are obtained from passive acoustic telemetry are highly dependent on the acoustic range of the telemetry setup (Mourier et al., 2017). In addition, traditional passive acoustic telemetry techniques also present a limitation in terms of the number of individuals that can be monitored simultaneously due to the drastic reduction in the detection probability caused by the collisions between acoustic signals (Binder et al., 2016). These facts have limited the use of acoustic tracking and SNA to disentangle the architecture of marine societies.

With the emergence of high-resolution acoustic telemetry systems (HRATS), now it is possible to obtain trajectories of aquatic organisms with unprecedented detail (Niezgoda et al., 2002; Krause et al., 2013; Baktoft et al., 2015), allowing a better definition of the associations between individuals based on their spatial proximity. HRATS precisely locate individuals tagged with acoustic transmitters using hyperbolic multilateration algorithms (also known as reverse-GPS). To this end, acoustic signals must be detected by at least three different receivers in the array, which greatly limits the extension of the area that can be covered with a limited number of receivers. Moreover, new signal coding systems (e.g., the Binary-Phase Shift coding system, BPSK, Weiland et al., 2011) reduce the length of the emitted signals (<1 ms), decreasing the probability of signal collision to negligible levels. This allows for monitoring a representative fraction of a population (hundreds to thousands of individuals) at the same time, providing the opportunity to expand behavioral studies to the population level (Wey et al., 2008; Puga-Gonzalez et al., 2021). HRATS have been successfully used in freshwater environments, such as lakes (Baktoft et al., 2015) and rivers (Leander et al., 2020), and more recently, in marine environments (Aspillaga et al., 2021). By providing fine-scale positions of large numbers of tagged individuals, HRATS are a valuable tool to study the social structure of marine organisms based on proximity-based association networks, even with elusive small-sized species.

The objective of our study was to test the performance of HRATS and SNA characterizing the social structure of a free-living fish population in a marine environment, using the pearly razorfish (*Xyrichtys novacula*, Labridae) as a study species. The pearly razorfish is a small wrasse that inhabits coastal sandy bottoms in the Atlantic Ocean and the Mediterranean Sea and has a large socioeconomic value for local fisheries (Alós et al., 2016). It is a protogynous hermaphrodite with an evident sexual dimorphism, where males are larger than females and present a characteristic coloration pattern. It is a sedentary species with a small home range (ranging from 86 to 292 m^2, Shen and Clark, 2016), living in polygynous social systems. Males establish and protect territories or harems that enclose the smaller territories of several females (Marconato et al., 1995; Shen and Clark, 2016). The harem-like territorial organization of this species is permanent and can be observed both inside and outside the spawning period, which occurs from July to September (Cardinale et al., 1998). Here, we applied the SNA approach on high-resolution trajectory data from a free-living pearly razorfish population to obtain a complete view of the social interactions and their temporal evolution.

MATERIALS AND METHODS

High-Resolution Acoustic Telemetry System

The study was carried out in the Bay of Palma Marine Reserve (Mallorca, Balearic Islands, Spain, **Figure 1**). A small sand patch of 12.5 ha (600 m × 270 m), with depths ranging from 12 to 17 m and surrounded by a *Posidonia oceanica* seagrass meadow, was selected to install the acoustic telemetry array. This specific area was selected based on previous knowledge on the distribution and habitat preference of the species. Pearly razorfish individuals were tracked using the Juvenile Salmon Acoustic Telemetry System (JSATS, McMichael et al., 2010) manufactured by Lotek Wireless Inc. (Canada) and consisting of WHS-4250L receivers and L-AMT series transmitters (working frequency: 416.7 kHz). A total of 70 acoustic receivers were installed covering the abovementioned area using a between-receiver distance of around 50 m (**Figure 1D**). The array was installed in April 2019 and remained operational until October 2019, with the exceptions of the days from June 5–10, during which the receivers were temporally retrieved to download the data and perform maintenance tasks. The tracking period encompassed the spawning period of the pearly razorfish, which occurs between July and September (Cardinale et al., 1998). The performance of this HRATS system in the study area has been described by Aspillaga et al. (2021), demonstrating the potential of this system to generate trajectory data with a high spatial (few meters) and temporal (seconds) resolution while simultaneously monitoring hundreds of individuals without signal collision issues.

Fish Sampling and Tagging

Pearly razorfish individuals were captured within the study area from a boat using hook-and-line gear and live shrimps as bait. Individuals were anesthetized by submersion in a 0.1 $g \cdot^{-1}$ solution of tricaine methanesulfonate (MS-222). A small incision was made in the ventral area to implant the L-AMT transmitter in the peritoneal cavity. The used transmitter model depended on the size of the tagged individual, with larger individuals being tagged with larger transmitters (weight-range: 0.32–3.5 g; emission period: 2, 5, and 10 s; battery life: 75–218 days). The incision was immediately closed with a non-absorbable suture and the fish was moved to a tank filled with clean seawater until complete recovery of normal behavior was observed. Finally, individuals were released at the same capture location. The total length (size) of individuals was measured with an accuracy of 1 mm and sex was visually determined based on the sexual dimorphism of the species. A total of 320 individuals (125 males and 195 females) were tagged on 14 different days in April ($n = 49$), May ($n = 242$), June ($n = 19$), and July 2019 ($n = 10$). The size ranges were 16.3–22.3 cm for males and 9.6–18.8 cm for females. The tagging protocol followed the guidelines provided by the Spanish Government (RD 53/2013) and was approved by the Committee on the Ethics of Animal Experimentation of the University of the Balearic Islands (Ref. CEEA 107/01/19). The Department of Environment, Agriculture and Fisheries of the Government of the Balearic Islands granted permission for fishing, operating, and releasing the animals in the Bay of Palma Marine Reserve.

Data Processing

Detection data from receivers was downloaded to the computer using the WHS Host software (Lotek Wireless Inc.). The positions of transmitters were estimated from the signals that were simultaneously detected by three or more receivers applying the hyperbolic multilateration algorithm implemented in the UMAP software (Lotek Wireless Inc.). All the estimated positions were then imported to the R computing environment (R Core Team, 2020), where all the data pre-processing and analyses were conducted.

The estimated raw positions were pre-processed using the same methodology proposed by Aspillaga et al. (2021). First, twin detections (i.e., positions with duplicated timestamps generated when the positioning algorithm converged to multiple solutions) and positions with a dilution of precision value (i.e., a positioning quality indicator provided by the UMAP software, Niezgoda et al., 2002) larger than 1 were removed from the dataset. Then, a trajectory filter and a continuous-time correlated random walk movement model (CTCRWMM, Johnson et al., 2008) were applied to remove system-induced outliers and generate regular trajectories at 1-min intervals. The trajectory filter removed positions generating unrealistic movements (Freitas et al., 2008), defined by turning angles of <15°, step lengths of >15 m, or speeds of $>2\ m \cdot s^{-1}$. The CTCRWMM was fitted using the crawl package for R (Johnson and London, 2018), assuming a positioning error of 3.3 m (similar to conventional terrestrial GPS devices), value that was extracted from the precision of positioning tests conducted in the same acoustic receiver array (Aspillaga et al., 2021).

To ensure the best representation of our razorfish population case study, days with at least 100 individual trajectories were subsampled from the complete dataset. From the resulting dataset, only data from individuals with a tracking period larger than 7 days were included in the SNA. The final dataset consisted of 232 individuals (79 males, size range: 16.3–22 cm; 153 females, size range: 9.6–17.3 cm) and 55 tracking days, taking place from May to July 2019, thus encompassing periods before and after the beginning of the spawning season. The applied

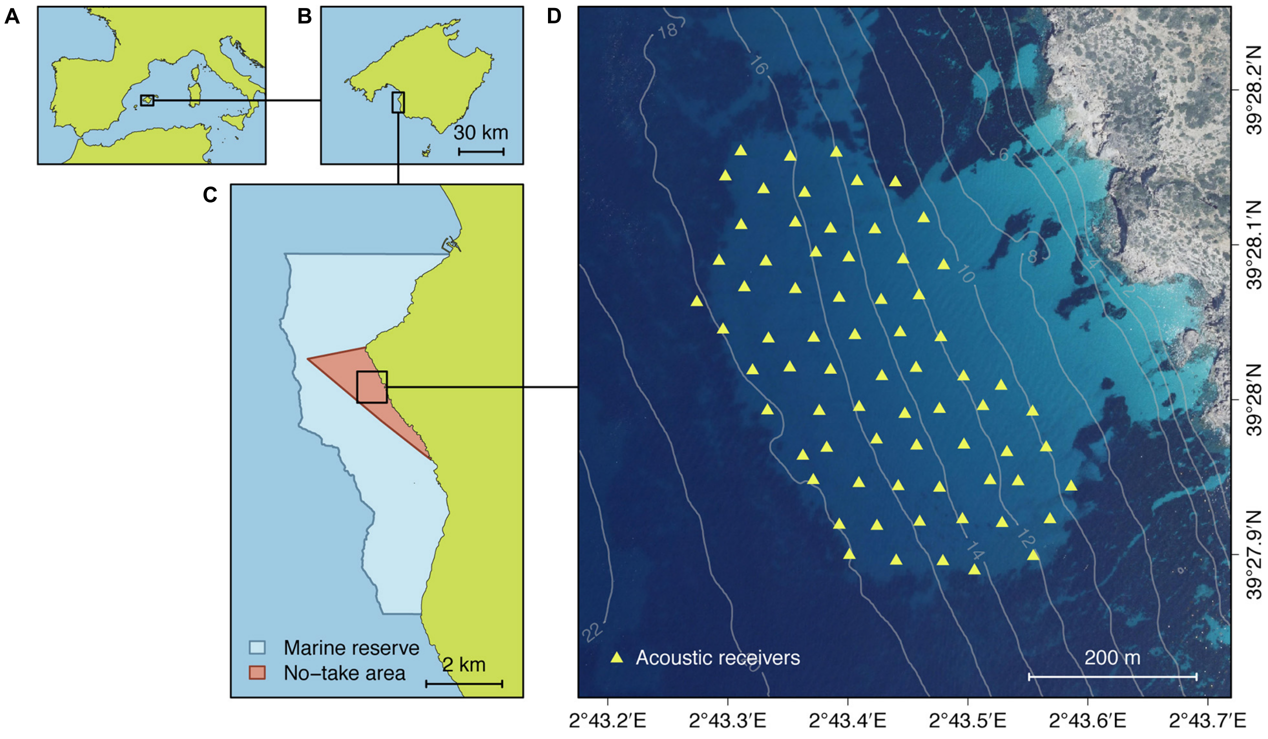


FIGURE 1 | Location of the study site within the Bay of Palma Marine Reserve (Mallorca, Balearic Islands, Spain, **A–C**) and the acoustic telemetry array (WHS-4250L receivers) used to monitor the movements of pearly razorfish individuals **(D)**. Light areas in panel D correspond to sandy bottoms and dark areas to *Posidonia oceanica* seagrass meadows.

subsampling removed data from the beginning and the end of the experiment, where fewer individuals were tracked each day, and from individuals for which few positions were obtained due to transmitter failures or post-tagging mortality.

Social Network Analysis

Associations between individuals were quantified in 5-min intervals based on the proximity between paired trajectories. During each interval, a positive interaction was considered when the minimum distance between two trajectories (calculated with the *gDistance* function from the *rgeos* package for R, Bivand and Rundel, 2020) was smaller than 1 m (i.e., we considered that two individuals interacted when they were at less than 1 m away from each other). This short distance was selected to take advantage of the high-resolution nature of the data since a sub-meter precision was reported for the trajectories obtained with this system after applying the filtering algorithm and the CTCRWMM (Aspillaga et al., 2021). Association weights were calculated as the ratio between the number of 5-min intervals in which an interaction was detected and the total number of intervals in which both individuals were observed. Given the highly resident nature of the pearly razorfish and the large amount of available data, unique associations within each day were considered spurious and therefore removed from the dataset. A general undirected network was generated from the adjacency matrix calculated for the entire tracking period. Moreover, daily networks were also generated from the adjacency matrices that were calculated for each separate day. The networks were created, analyzed, and visualized using the *igraph* package for R (Csardi and Nepusz, 2006).

To quantify and compare the rate and the intensity of the associations between individuals of the same and different sex, three sub-networks were generated dividing the general one depending on the sex of the interacting individuals: interactions between females (FF), interaction between males (MM), and interactions between males and females (MF). From the resulting subnetworks, edge-level (network-level) and node-level (individual-level) parameters were calculated. At the edge-level, the number and the mean weight of the observed associations were calculated. At the node-level, the binary degree (i.e., number of associations of an individual) and weighted degree (i.e., the sum of the weights of an individual's associations) were calculated.

The significance of the edge- and node-level parameters was quantified by comparing them against random expectations calculated from null social network models. Null models were generated using a pre-network randomization approach, using permutations of the raw positioning data to estimate the association patterns that would be expected if individuals were randomly distributed through the study area. This type of pre-network randomizations has been found to be more robust than the more commonly used node-level permutations, and it has been shown that can reduce both type I and type II error rates (Farine, 2017; Puga-Gonzalez et al., 2021).

In our case, each permutation consisted of shuffling the trajectory of each individual by changing its center (mean x and y coordinates) to a new location, which was randomly sampled within the 95% minimum convex polygon extracted from the centers of all the individual trajectories. In this way, the main characteristics of individual trajectories were maintained within each day, but the possible correlation between the space-use of the different individuals was broken. Then, general and daily networks were constructed using the same methodology as with the observed trajectories and the same parameters were calculated for each sex-specific sub-network (MM, FF, and MF). Finally, the significance (p-value) of each parameter was estimated by calculating the proportion of random iterations in which the mean value was larger or smaller (depending on the direction of the comparison) than the observed value. We used a threshold of $p < 0.05$ to consider that a parameter was significantly different from the random expectation.

RESULTS

Data Summary

The analyzed dataset contained 7,930, 1-day long trajectories corresponding to a total of 232 razorfish individuals (153 females and 79 males) distributed throughout 55 tracking days (from May 11 to July 11, 2019), with an average of 144 ± 25 individuals (mean ± SD) tracked per day (82 ± 20 females and 62 ± 8 males). A total of $2.44{\cdot}10^8$ detections were obtained by the acoustic receiver array, from which $3.05{\cdot}10^7$ raw positions were estimated using hyperbolic multilateration. The total number of positions was expanded to $7.45{\cdot}10^7$ using the CTCRWMM. Trajectories had an average duration of 13.1 ± 2 h per day (12.7 ± 2.1 h for females and 13.6 ± 1.8 h for males), coinciding with the sunlight hours during the study period.

General Network

From the entire tracking period, a total of 960 dyads (i.e., associations between individuals) were identified (**Figure 2**), from which 52% corresponded to associations between females (FF), 14% to associations between males (MM), and 34% to associations between individuals of different sex (MF) (**Figure 3A**). Overall, associations presented low edge weight values; 29% of the dyads (n = 279) had weights below $1{\cdot}10^{-3}$, representing sporadic encounters between individuals. The highest edge weight values were observed in MF associations, with a median and 95% inter-quantile range of $1.6{\cdot}10^{-3}$ [$3{\cdot}10^{-4}$–$2.6{\cdot}10^{-1}$], followed by the edge weights of FF ($3.2{\cdot}10^{-3}$ [$4{\cdot}10^{-4}$–$4.2{\cdot}10^{-2}$]) and MM ($1{\cdot}10^{-3}$ [$2{\cdot}10^{-4}$–$1.9{\cdot}10^{-2}$]) associations (**Figure 3B**). Only 8% of individuals (n = 19, 15 females and 4 males) did not present any association. When compared against null models, the number of edges of all the sex-specific sub-networks were found to be significantly higher than the values expected if individuals were randomly distributed ($p < 0.001$) (**Figure 4**). Regarding the strength of the associations, we did not find significant differences from random networks in the mean weight of FF associations (p = 0.085) (**Figure 4**). By contrast, the average weight of MM and MF associations were significantly smaller and larger, respectively, than the average weights obtained from random networks ($p < 0.001$), indicating an active avoidance of males toward other males and an association preference between males and females.

At the node (i.e., individual) level, females showed higher binary degree values when associating with other females, with a median and 95% interquantile range of 3 [0–35.4], than when associating with males (MF/F), presenting a median value of 1 [0–9.2] (**Figure 3C**). The weighted degree of both types of female associations presented similar values (FF associations: $8.6{\cdot}10^{-3}$ [0–0.35]; MF/F associations: $6.7{\cdot}10^{-3}$[0–0.45]) (**Figure 3D**). Each male interacted with a similar number of males (3 [1–10]) and females (2 [0–21]) (**Figure 3C**), but the strength of these interactions presented clear differences: the weighted degree of males interacting with other males ($6.1{\cdot}10^{-3}$ [0–0.06]) was much smaller than the weighted degree of males interacting with females (0.08 [0–0.81]) (**Figure 3D**). When compared against random expectations, the mean binary degree values in all the sex-specific networks were larger than the expected ($p < 0.001$) (**Figure 5**). The observed mean weighted degree was also significantly larger than the random expectations in all cases ($p < 0.001$), except for MM associations, in which the mean weighted degree was significantly smaller than the expected ($p < 0.001$).

Temporal Variability

Analyzing the associations of individuals on a daily basis provided a more detailed view of the patterns observed in the general network for the entire tracking period. Considerable differences were observed in some of the sex-specific sub-networks across the tracking period (**Figure 6**). For instance, the significantly higher binary and weighted degree values that could be observed in females within FF networks could not be found on all the days; 58.2% of the days (n = 32) did not present any significant departure from random expectations in terms of binary degree and 72.2% of the days (n = 40) in terms of weighted degree (**Figures 6A,B**). However, the daily association patterns between females indicated extreme departures from the random expectations in several days between May 27 and June 4, indicating sporadic but strong associations of groups of females on specific days, also observable in the whole social architecture of the population (**Figure 2**). Despite the binary degree of males interacting with other males being elevated in the general network, significantly lower values (65.5% of the days, n = 36) or no differences (34.5% of the days, n = 19) were observed in the daily networks (**Figure 6C**). By contrast, the weighted degree coincided with the observations in the general network, being significantly lower than the random expectations on every day in the tracking period (**Figure 6D**). Female and male associations in MF networks presented the same daily pattern, with significantly higher binary degrees on 59.9% of the days (n = 28) and no differences on 49.1% of the days (n = 28), while the weighted degree of interactions was higher on every single day (**Figures 6E–H**).

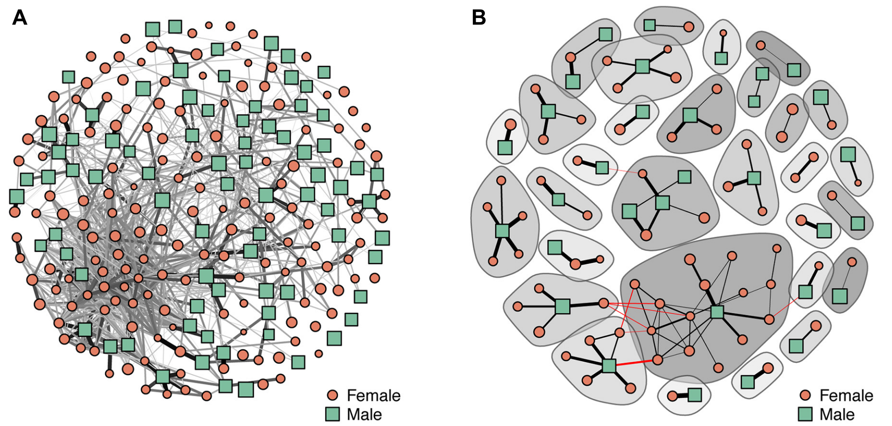


FIGURE 2 | Social network of the pearly razorfish population for the entire tracking period. **(A)** Entire network for all the 232 razorfish individuals (960 edges). **(B)** A subset of the entire network showing the strongest 10% edges (edge weight > 0.03, 90 edges, 101 individuals). Node size is proportional to the body size of each individual. Darker and thicker edges represent higher edge weights. The shadowed contours in **(B)** indicate the different groups identified by the fast greedy modularity optimization algorithm for finding community structures (Clauset et al., 2004) and red edges associations between individuals classified in different groups.

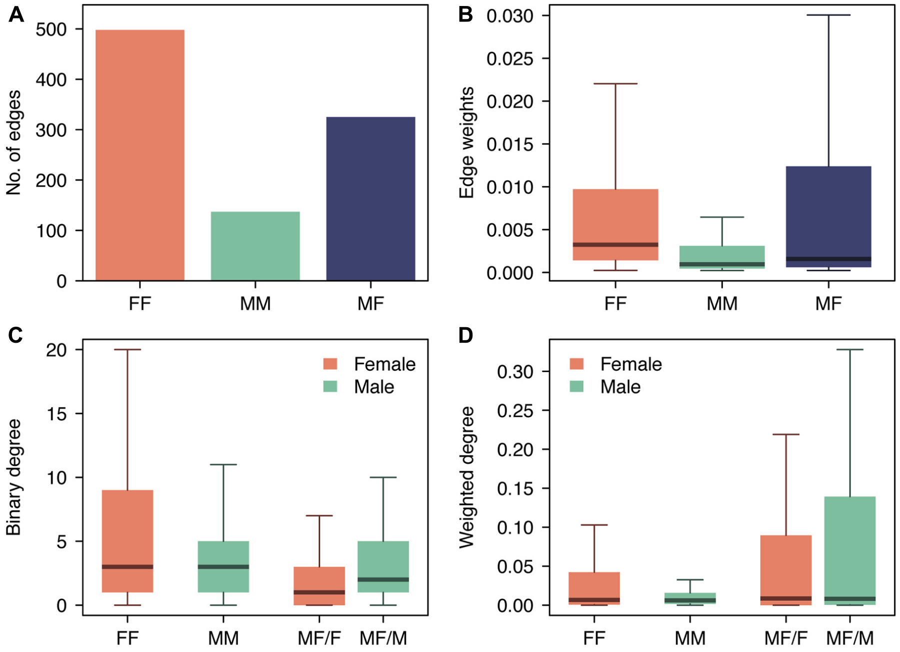


FIGURE 3 | Comparison of edge-level **(A,B)** and node-level **(C,D)** network parameters among the sex-specific social networks of the pearly razorfish population. **(A)** the number of edges and **(B)** edge weight values in each subnetwork; **(C)** binary degree and **(D)** weighted degree or strength of individuals from different sex within each subnetwork (FF: female-female associations; MM: male-male associations; MF: male-female associations; MF/F: females in male-female associations; MF/M: males in male-female associations). Boxplots indicate the median and the interquartile range and whiskers the minimum and maximum values at 1.5 times the interquantile distance.

DISCUSSION

Proximity networks are able to reproduce the complexity of social interactions that occur within animal populations and communities, improving our understanding of the function and resilience of ecosystems (Croft et al., 2008). With the proliferation of tracking and bio-logging devices, proximity metrics have gained popularity within the SNA framework (Webber and Vander Wal, 2019), despite that some discussion exists regarding the validity of proximity-based association indices as a proxy for directly measured interaction indices (Castles et al., 2014; Farine, 2015). The quantification of association indices based on direct encounters of individuals (measured here as < 1 m proximity dyads) has been neglected in aquatic systems due to the limitations that aquatic environments pose to the continuous positioning of large numbers of individuals (e.g., GPS does

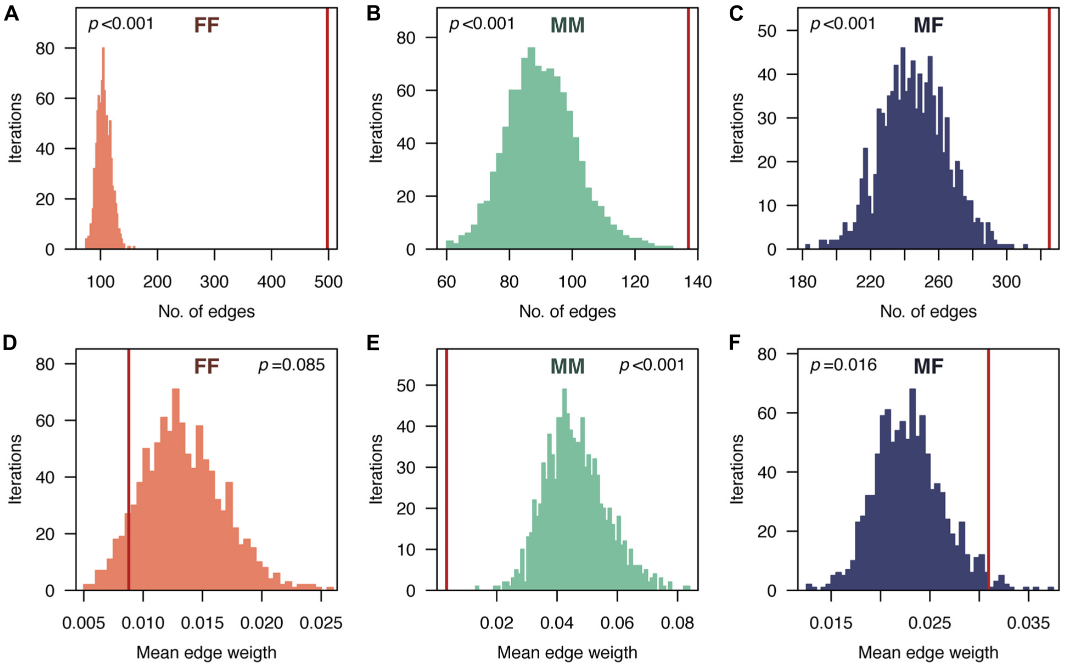


FIGURE 4 | Comparison of edge-level social network parameters (number of edges, **A–C** and mean edge weights, **D–F**) observed in the sex-specific sub-networks of the pearly razorfish population and the expected values obtained from random networks (FF: female-female; MM: male-male; MF: male-female). Histograms show the distribution of the random expectations obtained from 1,000 random networks. The vertical red lines represent the empirically observed values. *p*-values were calculated as the proportion of randomized values that were higher or lower (depending on the direction of the comparison) than the observed value.

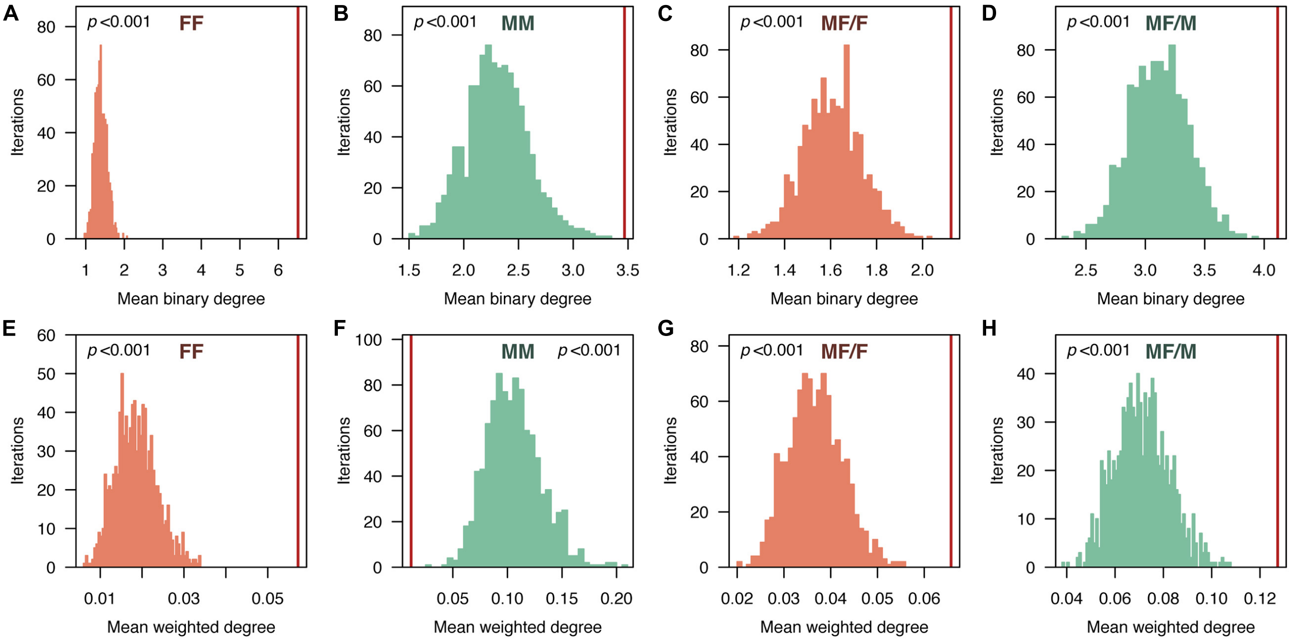


FIGURE 5 | Comparison of node-level social network parameters (**A–D**: mean binary degree; **E–H**: mean weighed degree) observed in the sex-specific sub-networks of the pearly razorfish population and the expected values obtained from random networks (FF: female-female associations; MM: male-male associations; MF/F: females in male-female associations; MF/M: males in male-female associations). Histograms show the distribution of the random expectations obtained from 1,000 random networks. The vertical red lines represent the empirically observed values. *p*-values were calculated as the proportion of randomized values that were higher or lower (depending on the direction of the comparison) than the observed value.

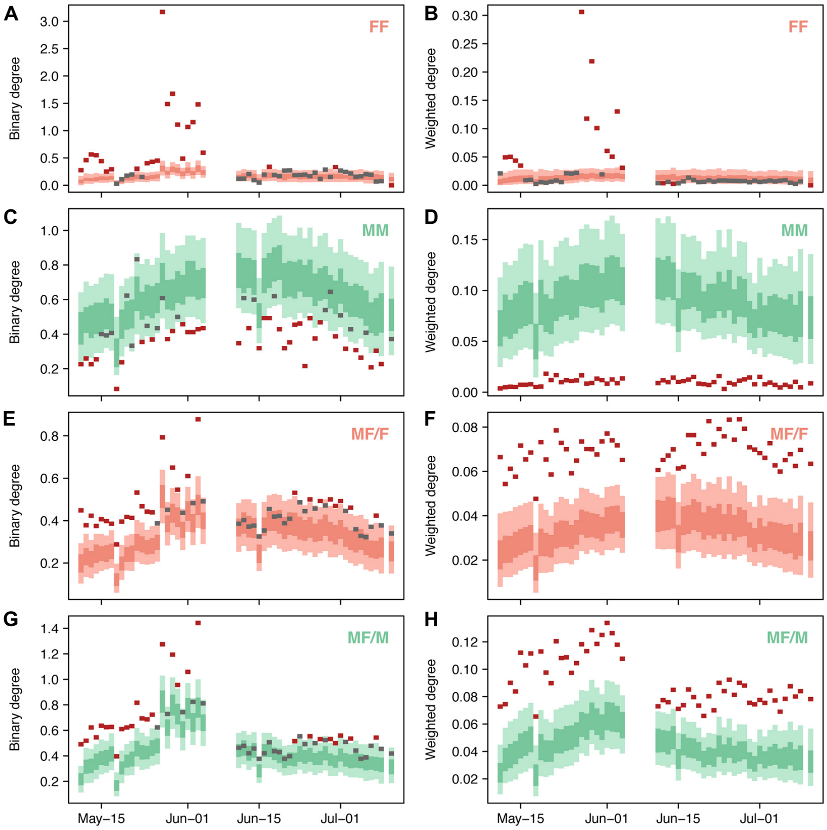


FIGURE 6 | Temporal variation of node-level parameters (**A, C, E, G**: mean binary degree; **B, D, F, H**: mean weighted degree) in sex-specific networks (FF: female-female associations; MM: male-male associations; MF/F: females in male-female associations; MF/M: males in male-female associations). The dark and light-colored bars represent the 50% and 95% inter-quantile ranges, respectively, of the average parameters obtained from random networks. Superposed segments indicate the empirically observed average parameters for each day: in red, the ones representing significant deviations from random expectations ($p < 0.05$), and in gray, the ones lacking of significant differences ($p > 0.05$).

not work underwater). Here, we demonstrate the usefulness of HRATS and SNA to study the association patterns in wild fish populations. Our method, using an approach that can be extended to other marine species, has produced the most detailed view of a marine fish society in a species that, due to its morphology and habitat, is hard to observe directly (but some works have been done underwater, e.g., Marconato et al., 1995; Shen and Clark, 2016). With the HRATS, we were able to monitor an average of 144 individuals per day (with a total of 232 monitored individuals included in the analysis), obtain high-quality spatial data from where to infer the associations between individuals, and conduct a SNA at the population level. Our study demonstrates the high potential of combining HRATS and SNA to unveil the architectural patterns of resident marine species, opening the possibility of testing a wide range of ecological hypotheses on the effect of individual traits and ecological and environmental parameters on the social structures occurring in the wild.

By combining HRATS and SNA, our findings suggest that the pearly razorfish displays a harem-like territorial behavior, where males defend territories that enclose the home range of several females. The observed low strength of the associations between males, which was significantly lower than the strength expected if individuals were randomly distributed, demonstrates that males strongly avoid individuals of the same sex. However, the number of associations between males, regardless of their strength, was significantly larger than expected, indicating sporadic contacts between males with neighboring territories. Our results agree with previous descriptions of this species' social organization based on repeated scuba diving observations on a limited number of individuals (Shen and Clark, 2016). These authors described that males divide the area into adjacent circular territories that do not overlap. They also documented occasional confrontations between males at the border of adjacent territories and against males that intruded neighboring territories, which might explain the obtained large numbers of associations with small strengths. The spatial avoidance behavior was not observed among females. Despite that the general network indicated a high number of associations with high strength between females, this pattern was not observed in most daily networks, where the number of associations and their strength did not significantly differ from the null models. The associations between males and females were, in every case, more frequent and stronger than random expectations, indicating strong and constant ties between individuals of different sex. When looking at the number of associations in MF sub-networks, we could observe that, on average, females were most often associated with only one male, while males were typically associated with two or more females, indicating the typical harem-like structure in which several females co-occur within the territory of a male. Marconato et al. (1995) and Shen and Clark (2016) described the harem-like social structure of this species, where males were observed encompassing the smaller sub-territories of two to six females. The male:female proportion of individuals included in the study (1:1.93) was similar to the ratio described for this species using underwater visual censuses (1:85, Espino et al., 2015), but higher than the ratio obtained by the same authors using trawls (1:4.9). This suggests that males could be overrepresented in our dataset, probably because they are more susceptible to be fished due to their territorial behavior. However, a thorough quantification of the population size would be required to know the exact representativeness of our study in terms of the proportion of the monitored population. Similar harem-like structures have been widely observed in marine species like parrotfishes (Mumby and Wabnitz, 2002), groupers (Zabala et al., 1997), and clownfishes (Warner, 2011). Thus, our work provides a novel method to delve into the study of the mechanisms and consequences of this social space-use behavior.

Our results also demonstrated punctual changes in the associating behavior of females. During a few days in May and June, groups of females tended to associate with each other more than during the rest of the days. In these events, high numbers of associations and high association strengths were observed between females, with groups of up to 20 females appearing strongly associated with each other. From a direct visualization of the trajectories of the females, extensive collective-like excursions were identified along the study area. Similar punctual aggregations have been found in marine species related to reproduction (e.g., Sadovy de Mitcheson and Colin, 2012; Aspillaga et al., 2016). However, the hypothesis of a spawning-related behavior is unlikely because the period in which this phenomenon was observed (May–June) was before the spawning season (July–September, Cardinale et al., 1998) and because of the lack of participation of male individuals. Indeed, we did not observe any changes in network structure patterns related to the start of the breeding season, which confirms that the establishment of harems is permanent and observable outside the spawning period (Cardinale et al., 1998). Nevertheless, the punctual collective-like movements could be representing mate choice exploratory trips pursued by females to assess quality among males in the area before settling for mating. Another possible hypothesis would be a commensalism behavior of females toward other species, such as the different ray species that also co-occur in the area during that period (pers. obs.), which males would not display due to their necessity of protecting their territories. Similar commensal relationships were also observed in the pearly razorfish and other razorfish species by Shen and Clark (2016), where groups of up to 15 individuals were attracted by the feeding activity of other sand-dwellers such as goatfishes and snake eels. However, the authors did not report any sexual specificity of such behaviors, their duration, or spatial extent. In all cases, the causes, mechanisms, and consequences of these extraordinary aggregation behavioral events in females of a territorial species deserve further attention.

Our approach combining HRATS and SNA brings out three major steps toward improving our understanding of the functioning of marine fish societies: it is based on high-resolution spatial data, considers a large number of monitored individuals, and provides raw data from which properly design null models for hypothesis testing. Regarding the ability of our system to produce high-resolution positional data, we were able to infer association patterns from extremely low spatial proximity values (<1 m). The JSATS used in this study makes it possible to track individuals with a spatial resolution of less than 1 m and a temporal resolution of a few seconds (Aspillaga et al., 2021). This is a great improvement over the conventional presence-absence acoustic tracking data, which due to its large positional uncertainty (200–800 m), may mask the real structure of the studied association networks. Instead, HRATS are able to produce high-throughput tracking data at high accuracy and resolution using hyperbolic multilateration algorithms. These systems, also known as reverse-GPS, allows transmitters to be simple and small, as most of the energy is located at the receivers, and represent one of the most promising tracking technologies to deepening insights into the most fundamental behavioral mechanisms of animals, like the allocentric representation of space (Toledo et al., 2020). Therefore, we believe that proximity metrics generated by HRATS will produce a revolution in our understanding of marine fish populations, at least for resident, home range-forming species.

A second major advance of using HRATS for SNA is that it opens the possibility of tracking a large fraction of a marine fish population simultaneously. Transmitters using the binary phase-shift keying (BPSK) coding systems allow for using thousands of transmitters emitting unique IDs on a single acoustic frequency (416 kHz in this study). This represents a significant advantage from the conventional tracking systems using the pulse position modulation (PPM) coding system, which limited the detectability of individuals co-occurring in the same area due to the effect of signal collisions. The number of monitored individuals is a crucial parameter to obtain a representative view of the social behavior of the population (Whitehead, 2008). Based on a simulation study, Silk et al. (2015) described that the social position of individuals measured in partial social networks (where some individuals were not identified) was strongly correlated with their position in the full social network, but this correlation became stronger as the proportion of identified individuals increased. In our case, we were able to track an unprecedented number of pearly razorfish individuals ($n = 232$) in a relatively small area (12.5 ha). In addition, the miniaturization of transmitters (the smallest L-AMT series transmitters weights 0.22 g) on HRATS allows tracking almost the entire range of fish sizes. Conventional tracking has always been limited to the large and adult fraction of the population (see discussion in Alós et al., 2011) due to the larger size of the transmitters, which has notably restricted our ability to study the movement of small-bodied individuals and across the ontogeny of marine species. For example, a previous study using a conventional acoustic telemetry system in a nearby area only monitored 12 pearly razorfish individuals with sizes ranging from 15.3 to 20.9 cm (Alós et al., 2012). Thus, HRATS systems emerge as a powerful tool to study the behavior and social interactions of small wild fish populations.

The third relevant point of our approach is that it generates valuable data for hypothesis testing using null models. Null models consist in generating randomized permutations of the data with the patterns that would be expected in the absence of the process of interest (Croft et al., 2011; Farine, 2017), and are especially important in the SNA framework due to the non-independence of the social data. The most commonly used and simple method to generate null models in SNA is the node-permutation, where the identity of the network nodes (i.e., the attributes of the individuals) are shuffled to break the link between the network and the trait of interest (Farine and Whitehead, 2015; Farine, 2017). More recently, conducting permutations on the raw observational data (i.e., pre-network permutations) has been proposed as a more flexible and robust alternative to network permutations because it allows for better control over the hypothesis that is being tested. Conducting pre-network permutations on animal trajectory data presents the difficulty of maintaining the autocorrelation structure of original individual tracks during the data stream randomization. For instance, Spiegel et al. (2016) generated random models of the social structure of a lizard population by randomly switching the date associated to each individual track, keeping the spatiotemporal structure of the trajectories but decoupling the possible synchronization between individuals. The pearly razorfish is a highly territorial species with a small home-range size (Alós et al., 2012; Shen and Clark, 2016). In our study, their movements were restricted to the study area, a sandy patch enclosed by a seagrass meadow. Based on these facts, we applied a pre-network permutation approach by randomly distributing the trajectories of individuals within the study area, keeping the spatial correlation of all the positions from the same individual but breaking any possible spatial pattern arisen from agonistic or affiliative behaviors between individuals. This randomization method allowed us to analyze the overall association structure of the pearly razorfish population, and more specifically, the strength of the associations between individuals of the same and different sex.

CONCLUSION

HRATS are a powerful tool to study the movements of resident fish populations and, in combination with SNA tools, can provide a complete description of their social structure. In the case of the pearly razorfish, this combination generated a unique dataset composed of more than 7,900 high-resolution daily trajectories from 232 individuals, providing the most detailed view of a marine population to date. The SNA suggested a harem-like social structure, with agonistic interactions between males and larger association indices between individuals of different sex. In addition, we were able to detect associations of large groups of females conducting synchronous movements along the study area that were not previously described in this species. The combination of HRATS and SNA opens a wide range of research questions that can be addressed for the first time with elusive or small-bodied species that would be difficult to study otherwise, such as the effect of the genetic and personality traits on the position of the individual in the network, and the effect of environmental or anthropic impacts (e.g., professional and recreational fisheries) in the overall structure of the network.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by the Committee on the Ethics of Animal Experimentation of the University of the Balearic Islands (Ref. CEEA 107/01/19).

AUTHOR CONTRIBUTIONS

EA and JA conceived the original study. RA provided the telemetry material. EA, JA, MM-B, and MB-S conducted the telemetry experiments. EA and JA led the data analysis and wrote the first manuscript. All authors made significant comments to the manuscript, and read and approved the final manuscript.

FUNDING

The telemetry system was financed by the German Federal Ministry of Education and Research (Grant No. #033W024A). EA was supported by a Margalida Comas Postdoctoral Grant from the Government of the Balearic Islands and the European Social Fund (Grant No. PD/023/2018). JA was supported by a Ramon y Cajal Grant (Grant No. RYC2018-024488-I) and received funding from the CLOCKS R&D Project (Grant No. PID2019-104940GA-I00) and the Intramural Research Project JSATS (Grant No. PIE 202030E002) funded by the Spanish Ministry of Science and Innovation and the Spanish National Research Council. The publication fee was supported by the CSIC Open Access Publication Support Initiative through its Unit of Information Resources for Research (URICI).

ACKNOWLEDGMENTS

We would like to thank David Gambin and the staff from Lotek Wireless Inc., for their technical assistance during this study. Special thanks to Sebastià Cabanellas, Guillermo Follana, Arancha Lana, and Christopher Monk for their support during the fieldwork. We are grateful to the Direcció General de Pesca i Medi Marí del Govern de las Illes Balears for the support and authorization of this work.

REFERENCES

Alós, J., Cabanellas-Reboredo, M., and Lowerre-Barbieri, S. (2012). Diel behaviour and habitat utilisation by the pearly razorfish during the spawning season. *Mar. Ecol. Prog. Ser.* 460, 207–220. doi: 10.3354/meps09755

Alós, J., March, D., Palmer, M., Grau, A., and Morales-Nin, B. (2011). Spatial and temporal patterns in *Serranus cabrilla* habitat use in the NW Mediterranean revealed by acoustic telemetry. *Mar. Ecol. Prog. Ser.* 427, 173–186. doi: 10.3354/meps09042

Alós, J., Palmer, M., Rosselló, R., and Arlinghaus, R. (2016). Fast and behavior-selective exploitation of a marine fish targeted by anglers. *Sci. Rep.* 6:38093. doi: 10.1038/srep38093

Aspillaga, E., Arlinghaus, R., Martorell-Barceló, M., Follana-Berná, G., Lana, A., Campos-Candela, A., et al. (2021). Performance of a novel system for high-resolution tracking of marine fish societies. *Anim. Biotelem.* 9:1. doi: 10.1186/s40317-020-00224-w

Aspillaga, E., Bartumeus, F., Linares, C., Starr, R. M., López-Sanz, À, Díaz, D., et al. (2016). Ordinary and extraordinary movement behaviour of small resident fish within a mediterranean marine protected area. *PLoS One* 11:e0159813. doi: 10.1371/journal.pone.0159813

Baktoft, H., Zajicek, P., Klefoth, T., Svendsen, J. C., Jacobsen, L., Pedersen, M. W., et al. (2015). Performance assessment of two whole-lake acoustic positional telemetry systems - is reality mining of free-ranging aquatic animals technologically possible? *PLoS One* 10:e0126534. doi: 10.1371/journal.pone.0126534

Binder, T. R., Holbrook, C. M., Hayden, T. A., and Krueger, C. C. (2016). Spatial and temporal variation in positioning probability of acoustic telemetry arrays: fine-scale variability and complex interactions. *Anim. Biotelem.* 4:4. doi: 10.1186/s40317-016-0097-4

Bivand, R., and Rundel, C. (2020). *Rgeos: Interface to Geometry Engine - Open Source ('GEOS'). R package version 0.5-5*. Available online at: https://cran.r-project.org/package=rgeos (accessed January 27, 2021).

Butcher, P. A., Colefax, A. P., Gorkin, R. A., Kajiura, S. M., López, N. A., Mourier, J., et al. (2021). The drone revolution of shark science: a review. *Drones* 5:8. doi: 10.3390/drones5010008

Cantor, M., Wedekin, L. L., Guimarães, P. R., Daura-Jorge, F. G., Rossi-Santos, M. R., and Simões-Lopes, P. C. (2012). Disentangling social networks from spatiotemporal dynamics: the temporal structure of a dolphin society. *Anim. Behav.* 84, 641–651. doi: 10.1016/j.anbehav.2012.06.019

Cardinale, M., Colloca, F., and Ardizzone, G. D. (1998). Growth and reproduction of *Xyrichthys novacula* (Pisces: Labridae) in the Mediterranean Sea. *Sci. Mar.* 62, 193–201. doi: 10.3989/scimar.1998.62n3193

Castles, M., Heinsohn, R., Marshall, H. H., Lee, A. E. G., Cowlishaw, G., and Carter, A. J. (2014). Social networks created with different techniques are not comparable. *Anim. Behav.* 96, 59–67. doi: 10.1016/j.anbehav.2014.07.023

Clauset, A., Newman, M. E. J., and Moore, C. (2004). Finding community structure in very large networks. *Phys. Rev. E Stat. Nonlin. Soft. Matter Phys.* 70:066111. doi: 10.1103/PhysRevE.70.066111

Connor, R. C., Heithaus, M. R., and Barre, L. M. (2001). Complex social structure, alliance stability and mating access in a bottlenose dolphin "super-alliance.". *Proc. R. Soc. B Biol. Sci.* 268, 263–267. doi: 10.1098/rspb.2000.1357

Couzin, I. D., and Krause, J. (2003). Self-organization and collective behavior in vertebrates. *Adv. Study Behav.* 32, 1–75. doi: 10.1016/S0065-3454(03)01001-5

Croft, D. P., James, R., and Krause, J. (2008). *Exploring Animal Social Networks*. Princeton: Princeton University Press.

Croft, D. P., Madden, J. R., Franks, D. W., and James, R. (2011). Hypothesis testing in animal social networks. *Trends Ecol. Evol.* 26, 502–507. doi: 10.1016/j.tree.2011.05.012

Csardi, G., and Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal Complex Syst.* 1695, 1–9. Available online at: https://igraph.org (accessed January 27, 2021).

Davis, G. H., Crofoot, M. C., and Farine, D. R. (2018). Estimating the robustness and uncertainty of animal social networks using different observational methods. *Anim. Behav.* 141, 29–44. doi: 10.1016/j.anbehav.2018.04.012

Espino, F., Triay-Portella, R., González, J. A., Haroun, R., and Tuya, F. (2015). Population structure of the pearly razorfish, *Xyrichtys novacula* (Actinopterygii: Labridae), in sand-seagrass mosaics: spatial variation according to habitat features and sampling techniques. *Sci. Mar.* 79, 179–188. doi: 10.3989/scimar.04219.05a

Farine, D. R. (2015). Proximity as a proxy for interactions: issues of scale in social network analysis. *Anim. Behav.* 104, e1–e5. doi: 10.1016/j.anbehav.2014.11.019

Farine, D. R. (2017). A guide to null models for animal social network analysis. *Methods Ecol. Evol.* 8, 1309–1320. doi: 10.1111/2041-210X.12772

Farine, D. R., and Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *J. Anim. Ecol.* 84, 1144–1163. doi: 10.1111/1365-2656.12418

Freitas, C., Lydersen, C., Fedak, M. A., and Kovacs, K. M. (2008). A simple new algorithm to filter marine mammal Argos locations. *Mar. Mammal Sci.* 24, 315–325. doi: 10.1111/j.1748-7692.2007.00180.x

Grueter, C. C., Qi, X., Zinner, D., Bergman, T., Li, M., Xiang, Z., et al. (2020). Multilevel organisation of animal sociality. *Trends Ecol. Evol.* 35, 834–847. doi: 10.1016/j.tree.2020.05.003

Haulsee, D. E., Fox, D. A., Breece, M. W., Brown, L. M., Kneebone, J., Skomal, G. B., et al. (2016). Social network analysis reveals potential fission-fusion behavior in a shark. *Sci. Rep.* 6:34087. doi: 10.1038/srep34087

Heupel, M. R., Semmens, J. M., and Hobday, A. J. (2006). Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Mar. Freshw. Res.* 57, 1–13. doi: 10.1071/MF05091

Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., et al. (2015). Aquatic animal telemetry: a panoramic window into the underwater world. *Science* 348:1255642. doi: 10.1126/science.1255642

Ings, T. C., Montoya, J. M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C. F., et al. (2009). Ecological networks - beyond food webs. *J. Anim. Ecol.* 78, 253–269. doi: 10.1111/j.1365-2656.2008.01460.x

Jacoby, D. M. P. P., and Freeman, R. (2016). Emerging network-based tools in movement ecology. *Trends Ecol. Evol.* 31, 301–314. doi: 10.1016/j.tree.2016.01.011

Jacoby, D. M. P., Brooks, E. J., Croft, D. P., and Sims, D. W. (2012). Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses. *Methods Ecol. Evol.* 3, 574–583. doi: 10.1111/j.2041-210X.2012.00187.x

Jacoby, D. M. P., Papastamatiou, Y. P., and Freeman, R. (2016). Inferring animal social networks and leadership: applications for passive monitoring arrays. *J. R. Soc. Interface* 13:20160676. doi: 10.1098/rsif.2016.0676

Johnson, D. S., and London, J. M. (2018). *Crawl: An R Package for Fitting Continuous-Time Correlated Random Walk Models to Animal Movement Data*. Geneva: Zenodo.

Johnson, D. S., London, J. M., Lea, M.-A., and Durban, J. W. (2008). Continuous-time correlated random walk model for animal telemetry data. *Ecology* 89, 1208–1215. doi: 10.1890/07-1032.1

Kays, R., Crofoot, M. C., Jetz, W., and Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science* 348:aaa2478. doi: 10.1126/science.aaa2478

Krause, J., Krause, S., Arlinghaus, R., Psorakis, I., Roberts, S., and Rutz, C. (2013). Reality mining of animal social systems. *Trends Ecol. Evol.* 28, 541–551. doi: 10.1016/j.tree.2013.06.002

Krause, J., Lusseau, D., and James, R. (2009). Animal social networks: an introduction. *Behav. Ecol. Sociobiol.* 63, 967–973. doi: 10.1007/s00265-009-0747-0

Leander, J., Klaminder, J., Jonsson, M., Brodin, T., Leonardsson, K., and Hellström, G. (2020). The old and the new: evaluating performance of acoustic telemetry systems in tracking migrating Atlantic salmon (*Salmo salar*) smolt and European eel (*Anguilla anguilla*) around hydropower facilities. *Can. J. Fish. Aquat. Sci.* 77, 177–187. doi: 10.1139/cjfas-2019-0058

Lédée, E. J. I., Heupel, M. R., Tobin, A. J., Knip, D. M., and Simpfendorfer, C. A. (2015). A comparison between traditional kernel-based methods and network analysis: an example from two nearshore shark species. *Anim. Behav.* 103, 17–28. doi: 10.1016/j.anbehav.2015.01.039

Marconato, A., And, V. T., and Marin, G. (1995). The mating system of *Xyrichthys novacula*: sperm economy and fertilization success. *J. Fish Biol.* 47, 292–301. doi: 10.1111/j.1095-8649.1995.tb01896.x

Marin, A., and Wellman, B. (2011). "Social network analysis: an introduction," in *The SAGE Handbook of Social Network Analysis*, eds J. Scott and P. J. Carrington (Thousand Oaks, CA: SAGE Publications, Inc), 25.

Martínez-López, B., Perez, A. M., and Sánchez-Vizcaíno, J. M. (2009). Social network analysis. review of general concepts and use in preventive veterinary medicine. *Transbound. Emerg. Dis.* 56, 109–120. doi: 10.1111/j.1865-1682.2009.01073.x

McDonald, G. C., James, R., Krause, J., and Pizzari, T. (2013). Sexual networks: measuring sexual selection in structured, polyandrous populations. *Philos. Trans. R. Soc. B Biol. Sci.* 368:20120356. doi: 10.1098/rstb.2012.0356

McMichael, G. A., Eppard, M. B., Carlson, T. J., Carter, J. A., Ebberts, B. D., Brown, R. S., et al. (2010). The juvenile salmon acoustic telemetry system: a new tool. *Fisheries* 35, 9–22. doi: 10.1577/1548-8446-35.1.9

Mourier, J., Bass, N. C., Guttridge, T. L., Day, J., and Brown, C. (2017). Does detection range matter for inferring social networks in a benthic shark using acoustic telemetry? *R. Soc. Open Sci.* 4:170485. doi: 10.1098/rsos.170485

Mourier, J., Lédée, E. J. I., and Jacoby, D. M. P. (2019). A multilayer perspective for inferring spatial and social functioning in animal movement networks. *bioRxiv* [Preprint]. doi: 10.1101/749085

Mourier, J., Vercelloni, J., and Planes, S. (2012). Evidence of social communities in a spatially structured network of a free-ranging shark species. *Anim. Behav.* 83, 389–401. doi: 10.1016/j.anbehav.2011.11.008

Mumby, P. J., and Wabnitz, C. C. C. (2002). Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. *Environ. Biol. Fishes* 63, 265–279. doi: 10.1023/A:1014359403167

Niezgoda, G., Benfield, M., Sisak, M., and Anson, P. (2002). Tracking acoustic transmitters by code division multiple access (CDMA)-based telemetry. *Hydrobiologia* 483, 275–286. doi: 10.1023/A:1021368720967

Papageorgiou, D., Christensen, C., Gall, G. E. C., Klarevas-Irby, J. A., Nyaguthii, B., Couzin, I. D., et al. (2019). The multilevel society of a small-brained bird. *Curr. Biol.* 29, R1120–R1121. doi: 10.1016/j.cub.2019.09.072

Pasquaretta, C., Dubois, T., Gomez-Moracho, T., Delepoulle, V. P., Le Loc'h, G., Heeb, P., et al. (2021). Analysis of temporal patterns in animal movement networks. *Methods Ecol. Evol.* 12, 101–113. doi: 10.1111/2041-210X.13364

Puga-Gonzalez, I., Sueur, C., and Sosa, S. (2021). Null models for animal social network analysis and data collected via focal sampling: pre-network or node network permutation? *Methods Ecol. Evol.* 12, 22–32. doi: 10.1111/2041-210X.13400

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rutz, C., Burns, Z. T., James, R., Ismar, S. M. H., Burt, J., Otis, B., et al. (2012). Automated mapping of social networks in wild birds. *Curr. Biol.* 22, R669–R671. doi: 10.1016/j.cub.2012.06.037

Sadovy de Mitcheson, Y., and Colin, P. L. (2012). *Reef Fish Spawning Aggregations: Biology, Research and Management*. New York, NY: Springer Netherlands.

Shen, D., and Clark, E. (2016). Territorial and reproductive behavior of the three Caribbean Razorfishes of the Genus Xyrichtys (Labridae) at bonaire. *Int. J. Ichthyol.* 22, 33–59.

Silk, M. J., Jackson, A. L., Croft, D. P., Colhoun, K., and Bearhop, S. (2015). The consequences of unidentifiable individuals for the analysis of an animal social network. *Anim. Behav.* 104, 1–11. doi: 10.1016/j.anbehav.2015.03.005

Spiegel, O., Leu, S. T., Sih, A., and Bull, C. M. (2016). Socially interacting or indifferent neighbours? Randomization of movement paths to tease apart social preference and spatial constraints. *Methods Ecol. Evol.* 7, 971–979. doi: 10.1111/2041-210X.12553

Stockmaier, S., Stroeymeyt, N., Shattuck, E. C., Hawley, D. M., Meyers, L. A., and Bolnick, D. I. (2021). Infectious diseases and social distancing in nature. *Science* 371:eabc8881. doi: 10.1126/science.abc8881

Toledo, S., Shohami, D., Schiffner, I., Lourie, E., Orchan, Y., Bartan, Y., et al. (2020). Cognitive map-based navigation in wild bats revealed by a new high-throughput tracking system. *Science* 369, 188–193. doi: 10.1126/science.aax6904

Tylianakis, J. M., Didham, R. K., Bascompte, J., and Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11, 1351–1363. doi: 10.1111/j.1461-0248.2008.01250.x

Warner, R. R. (2011). Mating behavior hermaphroditism reef fishes in coral reef fishes. *Am. Sci.* 72, 128–136.

Webber, Q. M. R., and Vander Wal, E. (2019). Trends and perspectives on the use of animal social network analysis in behavioural ecology: a bibliometric approach. *Anim. Behav.* 149, 77–87. doi: 10.1016/j.anbehav.2019.01.010

Weiland, M. A., Deng, Z. D., Seim, T. A., LaMarche, B. L., Choi, E. Y., Fu, T., et al. (2011). A cabled acoustic telemetry system for detecting and tracking juvenile salmon: part 1. engineering design and instrumentation. *Sensors* 11, 5645–5660. doi: 10.3390/s110605645

Wey, T., Blumstein, D. T., Shen, W., and Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim. Behav.* 75, 333–344. doi: 10.1016/j.anbehav.2007.06.020

Whitehead, H. (2008). *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis*. Chicago, IL: University of Chicago Press.

Zabala, M., Garcia-Rubies, A., Louisy, P., and Sala, E. (1997). Spawning behavior of the mediterranean dusky grouper *Epinephelus marginatus* (Lowe, 1834) (Pisces, Serranidae) in the medes Islands marine reserve (NW Mediterranean, Spain). *Sci. Mar.* 61, 65–77.

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 23 June 2021
doi: 10.3389/fmars.2021.678074

Companions and Casual Acquaintances: The Nature of Associations Among Bull Sharks at a Shark Feeding Site in Fiji

Thibaut Bouveroux[1,2]*, Nicolas Loiseau[3], Adam Barnett[4,5], Natasha D. Marosi[6] and Juerg M. Brunnschweiler[7]*

[1] Dauphin Island Sea Laboratory, Dauphin Island, AL, United States, [2] Department of Marine Sciences, University of South Alabama, Mobile, AL, United States, [3] MARBEC, Université de Montpellier, CNRS, IFREMER, IRD, Montpellier, France, [4] College of Science and Engineering, James Cook University, Townsville, QLD, Australia, [5] Marine Data Technology Hub, James Cook University, Townsville, QLD, Australia, [6] Beqa Adventure Divers, Pacific Harbor, Fiji, [7] Independent Researcher, Zurich, Switzerland

Edited by:
Mourier Johann,
Institut de Recherche Pour le Développement (IRD), France

Reviewed by:
Valeria Senigaglia,
Murdoch University, Australia
Quinn Webber,
University of Colorado Boulder,
United States

***Correspondence:**
Thibaut Bouveroux
tbouveroux@gmail.com
Juerg M. Brunnschweiler
juerg@gluecklich.net

Specialty section:
This article was submitted to Marine Megafauna, a section of the journal Frontiers in Marine Science

Received: 08 March 2021
Accepted: 31 May 2021
Published: 23 June 2021

Citation:
Bouveroux T, Loiseau N, Barnett A, Marosi ND and Brunnschweiler JM (2021) Companions and Casual Acquaintances: The Nature of Associations Among Bull Sharks at a Shark Feeding Site in Fiji. Front. Mar. Sci. 8:678074. doi: 10.3389/fmars.2021.678074

Provisioning activities in wildlife tourism often lead to short-term animal aggregations during the feeding events. However, the presence of groups does not necessarily mean that individuals interact among each other and form social networks. At the Shark Reef Marine Reserve in Fiji, several dozen bull sharks (*Carcharhinus leucas*) regularly visit a site, where direct feeding is conducted during tourism driven shark dives. On 3,063 shark feeding dives between 2003 and 2016, we visually confirmed the presence of 91 individual bull sharks based on external and long-lasting identification markings. We measured the intensity of associations between pairs of individuals by calculating the Simple Ratio Index (SRI) and calculated Generalized Affiliation Indices (GAIs) to distinguish true associations between dyads from structural predictor factors. Although the resulting mean SRIs were low, ranging from 0.01 to 0.12 (SRI_{mean} = 0.06; mean SRI_{max} = 0.21), preferred long-term companionships were observed between individuals. Avoidances were also observed within pairs of individuals during the second half of the study. The best fitting model describing the temporal association patterns of bull sharks revealed a social structure which is characterized by preferred companionships and casual acquaintances. Our results suggest that the aggregation resulting from direct feeding has served to facilitate the development of social associations.

Keywords: social bonds, co-occurrence, insular marine predators, fission-fusion, central place foragers, shark feeding

INTRODUCTION

The formation of aggregations and groups can be found occurring in taxa throughout the animal kingdom with considerable intra- and interspecific variation (Elgar, 1989; Whitehead, 1997). The two types of formations however, differ. The first type is driven by non-mutualistic forces, whereas the latter by forces which are typically mutualistic, in that some benefits are derived from group membership (Whitehead, 2008a). Aggregations can form for a multitude of underlying non-social reasons ranging from attraction to a food resource or specific habitat requirements (Johnson et al., 2002) to synchronized patterns of daily or seasonal activity (Guttal and Couzin, 2010). In contrast, animal groups, often termed "social groups" arise by way of underlying social drivers, with individuals actively preferring to associate with each other, therefore displaying social preferences. Within animal social networks, group members are more highly connected with other members in the group than with other individuals within the broader network (Croft et al., 2008). Social groups have been empirically investigated in a wide range of taxonomic groups including insects, fish, birds, and mammals (Chepko-Sade et al., 1989; Elena et al., 1999; Fewell, 2003; Lusseau and Newman, 2004; Cross et al., 2005; Wittemyer et al., 2005; Croft et al., 2006; Naug, 2008; McDonald, 2009; Vital and Martins, 2011).

Historically, sharks have been perceived as solitary predators, however, according to recent studies, some species may exhibit both aggregation and social grouping (Clua et al., 2013; Bass et al., 2016). Moreover aggregation may well lay the important groundwork for the development of social groups (Sims et al., 2000). Currently, it is understood that sharks have the potential to form complex social structures (Mourier et al., 2019; Papastamatiou et al., 2020). For example, blacktip reef sharks, (*Carcharhinus melanopterus*), were shown to form stable social groups over multiple years through the use of social network analysis (Mourier et al., 2012, 2017). This pattern of social group formation is likely characteristic of reef shark species which have relatively small core home ranges (consisting of a single reef or multiple reefs in close proximity) where these sharks aggregate during the day and range further at night (Barnett et al., 2012). In another reef shark species, gray reef sharks (*Carcharhinus amblyrhynchos*), formed large groups during the day which dispersed into smaller groups and individuals at night, most likely for foraging (Papastamatiou et al., 2020). Aggregation and dispersion behavior such as these can be explained by two theoretical frameworks: fission-fusion dynamics and central place foraging (CPF) (Kirkwood and Arnould, 2011; Sueur et al., 2011; Jones et al., 2020). In fission-fusion dynamics, "fission" is where individuals split from a larger group (e.g., reef sharks dispersing at night), and "fusion" is where individuals rejoin the larger group (e.g., reef sharks returning to core area the following day) (Papastamatiou et al., 2020). Conceptually similar, yet slightly nuanced, CPF theory describes behavior where animals periodically move in and out of a central place, normally associated with resting and foraging (Orians and Pearson, 1979; Papastamatiou et al., 2018). The two frameworks are non-mutually exclusive as central place foragers can display fission-fusion dynamics over short temporal periods (Papastamatiou et al., 2020).

Wildlife tourism can facilitate the formation of aggregations through provisioning activities such as using bait to attract and/or feed different shark species. Provisioning activities may be seasonal, short-term or even long-term, for example in locations such as Fiji or South Australia where direct and incidental shark feeding (Meyer et al., in press) have occurred regularly over many years or even decades (Brunnschweiler et al., 2014; Meyer et al., 2019). As such, long-term shark tourism sites offer unique platforms to collect baseline data, test specific hypotheses and more generally observe individual and group behavior and interactions in these artificial aggregations. For example, in Mourier et al. (2012) feeding was shown to promote sociality among blacktip reef sharks by attracting more potential social partners. Indeed, shark feeding may drive fission-fusion and CPF as Mourier et al. (2012) appears to indicate, however, the drivers are reversed, the central place is now a feeding location as opposed to a location used for resting.

The bull shark (*Carcharhinus leucas*) is a large, mobile species that undertakes long-range movements (Heupel et al., 2015) and is not commonly known for displaying aggregating behavior associated with CPF or fission-fusion, nor for displaying social associations under natural conditions [but see Daly et al. (2014) for example of aggregating]. Nevertheless, in the only such study for the species to date utilizing social network analysis, Loiseau et al. (2016) documented social interactions and relatively strong paired associations for two pairs of females suggesting some level of sociality among bull sharks. The study, conducted at an aquaculture farm around Reunion Island, although pioneering, was limited both in terms of sampling time (22 days) and number of identifiable individuals ($n = 8$). These constraints are not applicable to the Shark Reef Marine Reserve (SRMR), a long-term, multi-species shark provisioning site located on the southern coast of Viti Levu, Fiji (Brunnschweiler et al., 2014). At the SRMR, up to ∼80 bull sharks per day form short-term aggregations with individuals displaying different degrees of site fidelity. Visitation patterns vary with some individuals present almost year round while others remain absent for extended periods of time (Brunnschweiler and Barnett, 2013). The general pattern in diel movements for the bull sharks is to use the area around the provisioning site during the morning hours before dispersing over the broader neighboring reef systems at night (Brunnschweiler and Barnett, 2013). Direct shark feeding (Meyer et al., in press) has taken place since 2003, occurring up to five mornings per week, thus providing a unique opportunity for the assessment of long-term association patterns among individual bull sharks in an isolated insular ecosystem. The specific aims of this study were: (i) to investigate whether this artificial aggregation has facilitated social links between individuals, and (ii) if so, whether the associations persist temporally (i.e., are individuals reconnecting repeatedly at the provisioning events).

MATERIALS AND METHODS

Study Area, Data Collection, and Focal Observation

Data were collected between January 2003 and June 2016 at the SRMR (Brunnschweiler, 2010). For a detailed description of the dive and data collection protocols and for information regarding species composition, sex identification and the relative abundance of sharks at this provisioning site see Brunnschweiler and Baensch (2011) and Brunnschweiler et al. (2014). Briefly, shark feeding dives [direct feeding; see Meyer et al. (in press) for definition of the term] take place during the morning hours, 4–5 days per week. Using direct observation sampling methods (Altmann, 1974), trained observers accompany the tourist dives to collect data on the sharks encountered, which includes total number of individuals, species, identifiable individuals present on the site as well as behavioral data (Brunnschweiler and Barnett, 2013; Brunnschweiler et al., 2014). Cues and marks used to identify individual bull sharks included missing or deformed fins, notches, scratches and coloration patterns (Brunnschweiler and Baensch, 2011). This information collected is then recorded in a database.

TABLE 1 | Temporal variations of the average mean and maximum association indices (Simple Ratio Index SRI).

Time period	SRI_{mean} (±SD)	SRI_{max} (±SD)
2003–2016	0.06 (0.03)	0.21 (0.11)
Before 2009	0.06 (0.03)	0.19 (0.07)
2009–2010	0.05 (0.02)	0.20 (0.08)
From 2011	0.07 (0.03)	0.23 (0.11)

SD, standard deviation.

For this study, we used the presence-absence data for 91 individual bull sharks (77 females, 14 males; see below) encountered during 3,063 dives taking place on 1,736 diving days between 26 January 2003 and 23 June 2016 (**Supplementary Table 1**), with a mean number of diving days per year of 129.3 (SD = ± 49.6). The degree of residency to the feeding site for each individual was quantified by dividing the number of days the individual was observed by the number of days data was collected at the SRMR (site fidelity index SFI). Site fidelity values range from 0 to 1, with values closer to 0 indicating low site fidelity and values closer to 1 indicating high site fidelity.

Social Network Analyses

Associations were based on "co-occurrence," such that individuals present during the same dive were considered as part of the same group (Mourier et al., 2012). For statistical procedures, we chose a daily sampling period (i.e., the period of time within which associations are examined) to remove demographic effects occurring during the study period such as birth, death, immigration, and emigration, as well as to minimize environmental bias (e.g., tidal phase, tidal range, lunar phase, turbidity) (Whitehead and Dufault, 1999; Whitehead, 2008b; Findlay et al., 2016). In studies of social organization, restrictive observation thresholds are often applied to avoid the potential for weak and non-relevant associations between pairs of individuals and/or to reduce biases associated with small sample sizes (Baird and Whitehead, 2000; Whitehead, 2008a). In this study, out of 125 cataloged bull sharks we included only individuals which were encountered on ≥34 dives which signified the first quartile (Q1 = the median of the lower half of the dataset) (mean ± SD = 151 ± 152; median = 102). Thirty-four individuals did not meet the Q1 threshold, thus the remaining 91 individuals (77 females and 14 males) who qualified were included in analyses. Because of the large number of individuals that were added to the database during the years 2009 and 2010 (**Supplementary Table 1**), we further divided the study period into a time series as follows: the entire study period from 2003 to 2016 (91 individuals, 3,063 dives), before 2009 (27 individuals, 1,098 dives), between 2009 and 2010 (64 individuals, 609 dives), and from 2011 (88 individuals, 1,356 dives). This allowed us to investigate the effect of a significant increase in individuals observed at the feeding site, and determine what if any variations had occurred in the nature of the associations during the discrete time series.

TABLE 2 | Efficiency of predictor variables in explaining association indices between bull sharks, indicated by partial correlation coefficients and results of multiple regression quadratic assignment procedures test (MRQAP).

Time period	Predictor	Partial correlation	MRQAP *p*-values
2003–2016	Gregariousness	0.2172	0.0000*
	Temporal	0.5779	0.0000*
	Sex class	–0.0011	0.9240
Before 2009	Gregariousness	0.3998	0.0000*
	Temporal	0.3533	0.0000*
	Sex class	–0.0403	0.4740
2009–2010	Gregariousness	0.3814	0.0000*
	Temporal	0.2242	0.0000*
	Sex class	–0.0042	0.9240
From 2011	Gregariousness	0.2885	0.0000*
	Temporal	0.5872	0.0000*
	Sex class	0.0165	0.6860

Asterisks indicate significant predictors ($p < 0.001$).

To measure the intensity of associations between pairs of individuals we calculated the Simple Ratio Index (SRI), the recommended association index when calibration data are not available (Hoppitt and Farine, 2018; Mourier and Planes, 2021), in SOCPROG 2.9 (Whitehead, 2009; Whitehead et al., 2019) as follows:

$$SRI = X/[X + Y_{ab} + Y_a + Y_b]$$

where, X represents the number of times sharks a and b were observed together, Y_{ab} the total number of times shark a and b were identified during separate dives, Y_a the number of times shark a was identified and Y_b the number of times shark b was identified (Cairns and Schwager, 1987). The SRI ranges from 0 for two sharks never seen together, to 1 for two individuals always encountered together.

An association matrix between individuals was constructed by cumulating the co-occurrences over the study period. To quantify the accuracy of associations, we utilized the correlation coefficient between the true association index (AI = true SRI matrix) and the estimated values as follows:

$$r = S/CV_{est}$$

where S (social differentiation) is the measure of the variation of the social system and equals the coefficient of variation (CV) of true AIs ($S = CV_{true}$), and CV_{est} is the CV of the measured SRIs (Whitehead, 2008b). An r value > 0.4 indicates a good representation of the true social patterns,

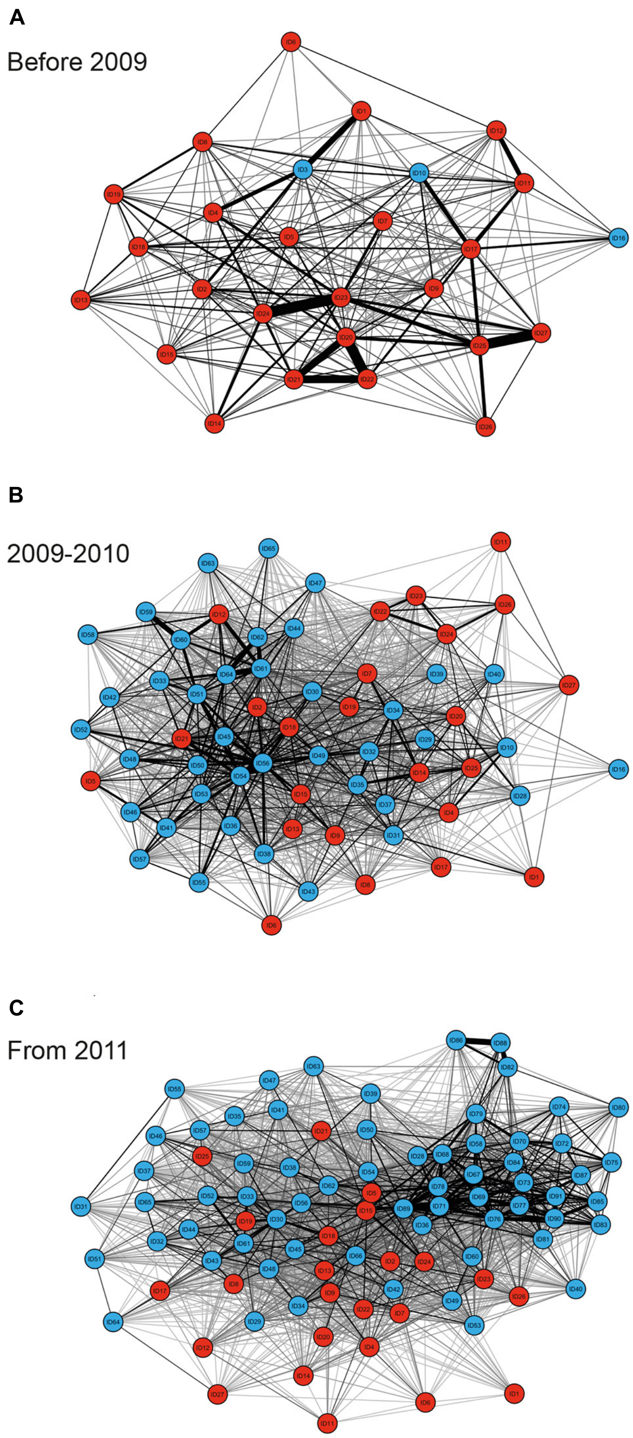


FIGURE 1 | Sociograms depicting the social ties between individual bull sharks observed on the study site on ≥34 dives for the time periods before 2009 **(A)**, between 2009 and 2010 **(B)**, and from 2011 **(C)**. Only GAI values in the highest 30% were included to highlight the strongest associations between dyads, with thicker edges indicating higher GAIs for both individuals observed throughout the entire sampling period (red nodes), and individuals which were not observed throughout the entire sampling period (blue nodes).

while an S value close to 0 reveals a very homogeneous society, and an S value close or higher to 1 indicates a highly differentiated society (Whitehead, 2008b). Social differentiation was estimated by maximizing the likelihood of observed dyadic associations using the algorithm available in SOCPROG 2.9 (Whitehead, 2009; Whitehead et al., 2019).

We then calculated Generalized Affiliation Indices (GAIs) to distinguish true associations between dyads (i.e., active preferences) from structural predictor factors such as the temporal overlap within the SRMR or differential association rates among sexes, within the social networks. GAIs are calculated as the raw residuals of a generalized linear model, where the response variables are the SRI values, and potential predictors are the structural factors (Whitehead and James, 2015). Three structural factors were considered in the analyses: temporal overlap in association patterns, the influence of sex and the difference in gregariousness between pairs of individuals following Whitehead and James (2015). First, we created a temporal overlap matrix based on the proportion of months that two individuals were found to be associated at the SRMR. This resulting index yields values ranging from 0 to 1, with a value of 0 indicating two individuals never observed together, and a value of 1 indicating two individuals seen together throughout the totality of months. We then created a sex similarity matrix where a value of 1 indicates the existence of a same sex pair and a value of 0 indicates two individuals of different sexes. Lastly, the gregariousness predictor amongst two individuals (*a* and *b*) was calculated using the log of the sum of the association indices involving *a* (except the *ab* index) multiplied by the sum of those involving *b* (except the *ba* index) (Whitehead and James, 2015). High positive values for GAIs indicate that pairs of individuals are more associated than expected given the structural predictor variables, while negative values indicate avoidance. Finally, multiple regression quadratic assignment procedure tests (MRQAP) were used to identify the relative influences of each predictor factor on associations (Whitehead and James, 2015).

Cluster Analyses and Community Division by Modularity

Average linkage hierarchical cluster analysis was used to characterize and illustrate social bonds between observed individuals. To determine the best type of cluster analysis to perform we used the cophenetic correlation coefficient (CCC), which is the correlation between real AIs and the levels of clustering between individuals. The CCC also indicates the effectiveness of the analysis (Bridge, 1993). It is assumed that a cluster with a CCC value higher than 0.8 is representative of a reliable separation among clusters (Whitehead, 2008b). To investigate whether the population of bull sharks in this study was divided into social clusters of individuals or communities based on social affiliations, we used the modularity clustering technique (Newman, 2004, 2006). This option allows for exploring the possibility that the population under study is usefully divided into clusters, such that association indices are generally high among individuals in the same cluster, and generally low among individuals in different clusters (Whitehead, 2009). The modularity coefficient (Q) for a defined set of clustered individuals represents the difference between the observed and expected proportion of the total of the association indices within clusters, where the expected AIs are calculated as proportional to a dyad's product gregariousness. Modularity analyses were assessed using the maximum modularity type 1 in SOCPROG 2.9, which controls for gregariousness by focusing on association preferences. Q-values of 0.3 or higher indicate strong community divisions in the population (Newman, 2004). Sociograms were drawn using *qgraph()* function in *qgraph* packages in R V.4.0.3.

Test for Preferred and/or Avoided Associations

To determine whether the patterns of associations between individuals differed from random, we used a permutation test (Bejder et al., 1998). The permutation test option "*permute associations within samples*" in SOCPROG 2.9 was used to test for the presence of long-term preferred and/or avoided companionships using the SRIs (co-occurrence). This procedure tests the null hypothesis that there are no preferred companions between sampling periods, given the number of associations each individual has in each sampling period (Whitehead, 2008a). In this test, the elements of the symmetric association matrix are permuted for each sampling period keeping the total number of rows and columns constant by first choosing two individuals for the rows, and then two more individuals, different from the first pair, for the columns. Significantly higher SD of the real association indices compared with the random associations reveal the presence of non-random associations in the studied population. This test is generally the most robust test because it takes into account that not all individuals are present in each sampling interval (e.g., migration or death) or have similar gregariousness (Whitehead, 2009). This test was performed starting with 1,000 permutations which were increased in a stepwise manner by 5,000 at each step until the *p*-value became stabilized (Bejder et al., 1998; Whitehead, 2009). For the analyses, the number of permutations was leveled up to 40,000 permutations for the three time periods before 2009, 2009–2010 and from 2011, and at 100,000 permutations for the entire study period (2003–2016). Similar permutation tests were applied to the GAIs to investigate social preferences amongst sharks (active decisions to interact). Significantly higher SD of the observed GAIs than expected indicates the presence of social preference amongst sharks.

Temporal Variation of Associations

The temporal stability of associations between bull sharks was investigated using the standardized lagged association rates (SLARs) available in SOCPROG 2.9 that were compared with the null association rates (Whitehead, 2008a). The SLAR analysis provides an estimate of the probability of two individuals that are associating at any given time, also the probability of being associated after various time lags (Baird and Whitehead, 2000; Whitehead, 2008a). Lagged and null association rates were standardized to take into account individuals who were actually present during a dive but were not identified for whatever reason. Temporal association patterns were then compared to four different models of lagged association rates available in SOCPROG 2.9 (*preferred companions*, *casual acquaintances*,

TABLE 3 | Tests for preferred and avoided associations of bull sharks.

	Preferred associations (SRI)			Social preferences (GAI)		
Time period	**Real**	**Random**	***p***	**Real**	**Random**	***p***
2003–2016						
Mean	0.05661	0.05661	-	0.00449	0.00442	-
SD	0.05879	0.05854	0.0000*	0.03393	0.03374	0.0158
CV	1.03848	1.03401	0.0000*	NA	NA	NA
Prop. non-zero elements	0.84567	0.84609	0.3423	NA	NA	NA
Mean non-zero elements	0.06694	0.06691	0.3373	NA	NA	NA
SD non-zero elements	0.05827	0.05797	0.0000*	NA	NA	NA
CV non-zero elements	0.87044	0.86643	0.0040*	NA	NA	NA
Before 2009						
Mean	0.06018	0.06012	-	0.00100	0.00093	-
SD	0.05825	0.05826	0.5104	0.03584	0.03584	0.4908
CV	0.96805	0.96912	0.8587	NA	NA	NA
Prop. non-zero elements	0.849	0.84791	0.6918	NA	NA	NA
Mean non-zero elements	0.07088	0.0709	0.4339	NA	NA	NA
SD non-zero elements	0.05691	0.0569	0.481	NA	NA	NA
CV non-zero elements	0.80286	0.80286	0.489	NA	NA	NA
2009–2010						
Mean	0.04812	0.04813	-	0.00117	0.00115	-
SD	0.05589	0.05507	0.0001*	0.03993	0.03916	0.0054*
CV	1.16145	1.14419	0.0000*	NA	NA	NA
Prop. non-zero elements	0.71081	0.71077	0.5093	NA	NA	NA
Mean non-zero elements	0.0677	0.06772	0.5415	NA	NA	NA
SD non-zero elements	0.0554	0.05423	0.0000*	NA	NA	NA
CV non-zero elements	0.81833	0.80079	0.0000*	NA	NA	NA
From 2011						
Mean	0.07073	0.07074	-	0.00054	0.00055	-
SD	0.06611	0.06568	0.0000*	0.03332	0.03255	0.0000*
CV	0.93466	0.85915	0.0000*	NA	NA	NA
Prop. non-zero elements	0.85893	0.85915	0.4313	NA	NA	NA
Mean non-zero elements	0.08234	0.08234	0.491	NA	NA	NA
SD non-zero elements	0.06427	0.06377	0.0000*	NA	NA	NA
CV non-zero elements	0.78057	0.77444	0.0000*	NA	NA	NA

Permute associations within samples were used with 40,000 permutations and 1,000 flips per trial for the three time series, and 100,000 permutations for the entire study period.SRIs, simple ratio indices; GAIs, general affiliation indices; SD, standard deviation; CV, coefficient of variation; NA, not available. Asterisks indicate statistical significance ($p < 0.001$).

preferred companions + casual acquaintances and *two levels of casual acquaintances*) (Whitehead, 2009). The best-fitting model was identified using the Quasi-Akaike Information Criterion value (QAIC) (Whitehead, 2008a).

RESULTS

Site Fidelity

Observation periods were defined as the cumulative number of days (including non-diving days) between the date an individual bull shark was first observed at the SRMR and recorded in the database, and the last day the individual was observed visiting the site. Observation periods within the database ranged from 128 days (ID# 91) to 4,885 days (ID# 2) with a median of 2,194 days (mean ± SD = 2,143 ± 1411) (**Supplementary Figure 1**). Presence data with respect to individual bull sharks varied greatly, with the least site visits recorded being 21 days (ID# 88) and the most site visits recorded being 554 days (ID# 2) (**Supplementary Table 1**). Site fidelity indexes (SFI) ranged from 0.03 (ID# 1 and ID# 16) to 0.84 (ID# 89) (mean ± SD = 0.23 ± 0.13).

Social Network and Cluster Analyses

Over the course of the entire study period (2003–2016), mean SRIs ranged between 0.01 (e.g., ID# 16 and ID# 27) and 0.12 (ID# 71 and ID# 89) resulting in a low overall mean association index between individuals ($SRI_{mean} = 0.06$; **Table 1**). Maximum SRIs ranged between 0.05 (ID# 6 and ID# 16) and 0.56 (ID# 71 and ID# 89) (mean $SRI_{max} = 0.21$; **Table 1**). Over the entire study period, social differentiation (S) using the likelihood method was estimated at 0.989 (SE = 0.009), indicative of a socially well-differentiated population evidenced by high variations in the dyadic probability of associations. Social differentiation was higher between 2009 and 2010 (S = 0.920, SE = 0.020) in comparison to the time periods before 2009 (S = 0.894, SE = 0.020) and from 2011 (S = 0.910, SE = 0.012). The estimated correlation between the true and estimated association indices was 0.952 (SE = 0.011) revealing the power of analysis in detecting the true social system (1 indicates maximal correlation, 0 no correlation).

MRQAP indicated that both factors of temporal overlap and of gregariousness were good predictors for explaining association patterns of bull sharks at the SRMR, and these were included in GAIs analyses (**Table 2**). Sex class was removed by the stepwise procedure from the model. Sociograms were constructed using GAIs for the three distinct time periods and presented in **Figure 1**: before 2009 (**Figure 1A**), between 2009 and 2010 (**Figure 1B**), and from 2011 (**Figure 1C**). CCC values were higher than 0.8 (CCC = 0.8273 before 2009; CCC = 0.8309 between 2009 and 2010; and CCC = 0.8266 from 2011) indicating an adequate social structure representation. The bull shark population exhibited a homogeneity for each time period as each modularity value (Q) was lower than 0.3 ($Q_{before2009}$ = 0.175; $Q_{2009-2010}$ = 0.201; $Q_{from2011}$ = 0.189).

Preferred and/or Avoided Associations

Preferred long-term companionships were observed as indicated by significantly higher SD and CV values of the real dataset compared to randomly permuted data for the entire study period, between 2009 and 2010, and from 2011 (**Table 3**). After 2011, avoided associations can be observed as the proportion of non-zero association indices are lower in the real dataset compared to the randomly permuted data, indicating that some individuals avoid others. Social preferences that investigate the active decision to interact or not were measured by GAIs (**Table 3**). Since GAIs gave similar results to SRIs, social preferences were also common and occurred within the same time series (2009–2010 and from 2011) than preferred associations. For all time series, the mean of GAI values was positive, indicating that preferred companionships were common. The SD of all observed GAIs was significantly higher, and the mean significantly lower than expected, indicating that social preferences occurred between individuals, particularly over short time periods.

Temporal Variation of Associations

The SLARs of bull sharks remained above the null association rates for the entire study period (**Figure 2**) indicating the existence of preferred associations amongst individuals in the network. However, there was a steady decay in the duration of associations for each of the four time periods without dropping below the null association rates except in 2010 when after slightly dropping below, the SLAR increased again quickly (**Figure 2C**). For the entire study period and before 2009, the best fitting model describing the temporal association pattern for these bull sharks is one of preferred companionships and casual acquaintances, with two levels of casual acquaintances characterizing the network for the time period between 2009 and 2010, and from 2011 (**Table 4**).

DISCUSSION

At the Shark Reef Marine Reserve, the ongoing wildlife tourism activity of shark diving has resulted in the formation of temporary aggregations of bull sharks. This aggregation was artificially contrived, by virtue of a non-social driving factor: that of direct feeding. Our results appear to indicate that the ongoing nature of these feeding activities, and the aggregations which ensue, have served to facilitate the development of social associations, some of which are temporally stable. With numbers reaching nowadays ∼80 individuals on a single dive, the conditions are prime for social behaviors to occur such as agonistic interactions.

Long-term preferred companionships and strong affinity between individuals were observed throughout the study. Overall and before 2009, the temporal stability of the associations was best described by preferred companionships (i.e., associations occurring more often than expected by chance) and casual acquaintances (i.e., associations lasting from a few days to a few years wherein individuals may dissociate and reassociate again), and for the time periods between 2009 and 2010, and from 2011 by two levels of casual acquaintances. This transformation within the social parameters can be explained by the numerical increase of newly identified bull sharks (Brunnschweiler and Baensch, 2011). Apart from the steady increase over time in numbers of bull sharks (whether named or unnamed) visiting the SRMR (Brunnschweiler et al., 2014), an unusually high number of individuals were identified at the beginning of 2009 (Brunnschweiler and Baensch, 2011). We can only speculate about the reasons underlying such an influx of new individuals in a relatively short period of time, but find it noteworthy. There is anecdotal evidence supporting the notion that bull sharks are indeed gregarious to an extent and travel together. Contrary to other large, apex predator species such as tiger (*Galeocerdo cuvier*) or white (*Carcharodon carcharias)* sharks, juvenile and adult bull sharks are rarely seen alone but more often observed in pairs or small groups (Brunnschweiler and Compagno, 2008; Loiseau et al., 2016). Therefore it is possible that a group of bull sharks new to the SRMR show up together at the provisioning site, causing a temporary alteration of the existing social structure by reconfiguring the nature of associations.

In natural settings, individuals form groups and associate to benefit from reduced predation risk, improved foraging efficiency or individual fitness (Krause and Ruxton, 2002). At the level of the individual, associating with conspecifics can provide a number of benefits, from increased access to resources and potential mates, social learning, and information dissemination (Krützen et al., 2005; Croft et al., 2006). Drivers of association amongst conspecifics can include overlapping core ranges, relatedness, behavioral phenotype, and familiarity (Krause and Ruxton, 2002; Croft et al., 2009). At the SRMR where bull sharks temporarily aggregate because of repeated direct feeding (Brunnschweiler and Barnett, 2013), the observed network structure and perceived possible sociality may likely be an artifact of spatio-temporal overlap and not attributed to active social interactions or behavioral strategies in grouping patterns. Hence, finding non-random associations does not necessarily mean that individuals actively choose to group

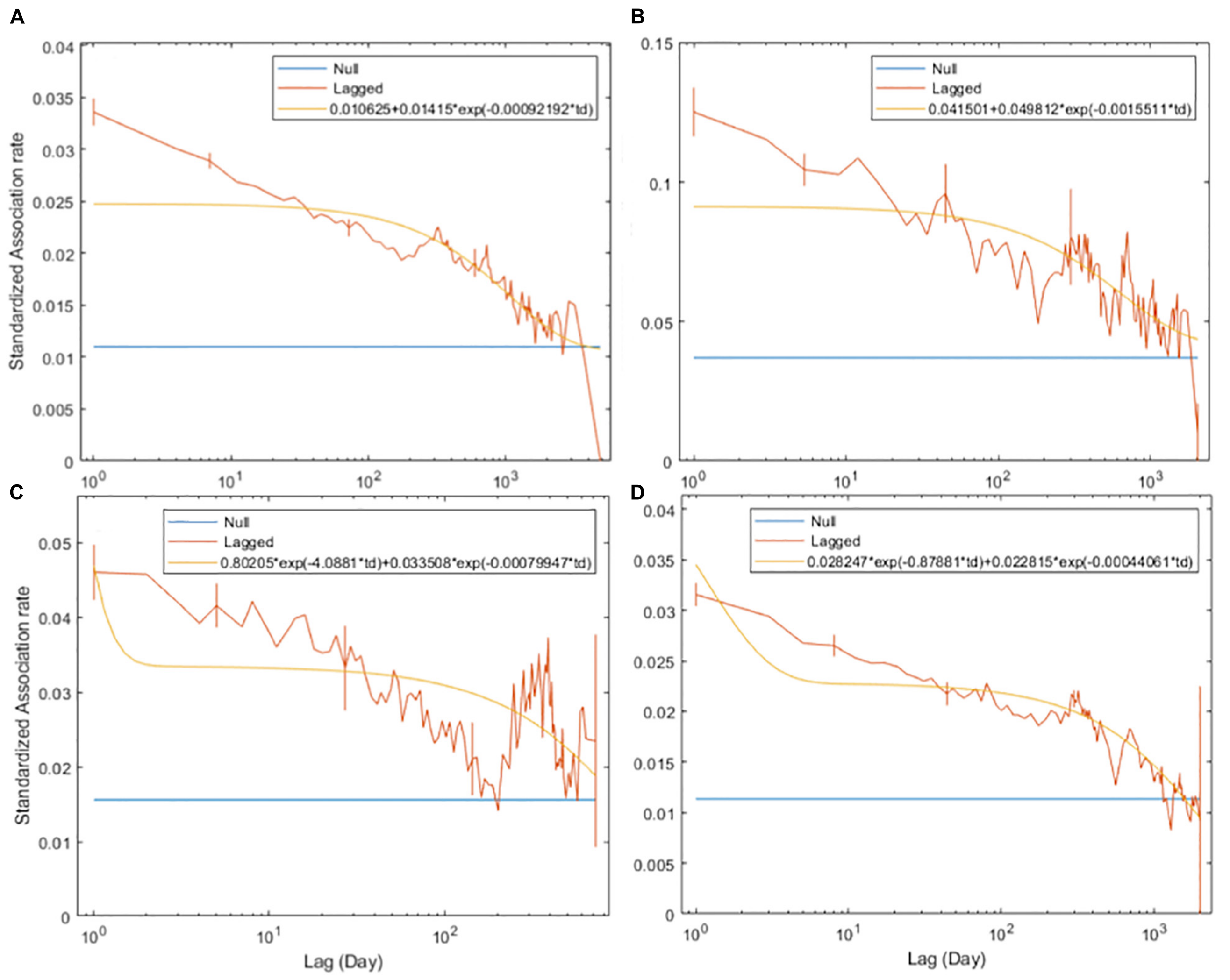


FIGURE 2 | Standardized lagged association rates (SLARs) of individual bull sharks encountered for the time periods 2003–2016 **(A)**, before 2009 **(B)**, between 2009 and 2010 **(C)**, and from 2011 **(D)**. Vertical bars indicate standard errors calculated using the temporal Jackknife method. The yellow line illustrates the best fit model characterizing the social system within the network whilst the blue line represents the null association rate, which is the theoretical SLAR if individual bull sharks were randomly associated.

with preferred social partners. The SRMR is not a natural setting, namely bull sharks form artificial aggregations solely in response to feeding by the tourism operator. This is contrary to, for example, white sharks which aggregate naturally around seal colonies and are then lured to cage-diving operators through the use of chum (Schilds et al., 2019). Yet despite the artificial driver in this instance, bull sharks aggregating to exploit a food source could be considered natural, identical to ephemeral natural feeding aggregations at whale carcasses or spawning aggregations (Graham and Castellanos, 2012; Lea et al., 2019). In this regard, the SRMR being an artificial aggregation site could have laid the groundwork for natural social interactions between sharks by simply providing regular and consistent opportunities for those interactions to occur (Clua et al., 2010; Pini-Fitzsimmons et al., 2021).

The results from this study are based on the reliable long-term identification of individual bull sharks at a single site, hence our findings come with some caveats. The individual identification of sharks using distinctive markings and coloration has its limitations (Marshall and Pierce, 2012). For example, while all individuals in this study were identified using permanent identifiable features such as scars, wounds, missing and/or damaged fins, and images and video footage was collected throughout the entire study period, it is inevitable that human error in observation, identification and recording occurred. For example, depending on the uniqueness and/or obviousness of natural marks, identification of individuals can be challenging (Brunnschweiler and Barnett, 2013). Misidentification of an individual or the failure to confirm an individual which was actually present but not recorded could also be due to ocean

TABLE 4 | Model fitting to standardized lagged association rates (SLARs) among bull shark individuals for the entire study period, before 2009, between 2009 and 2010, and from 2011.

Model	QAIC	Δ QAIC
2003–2016		
Preferred companionships + casual acquaintances	32,462,038.1179	3,853,219.8116
Two level of casual acquaintances	32,468,725.3121	3,853,219.8116
Casual acquaintances	3,2471,661.4346	3,854,360.3286
Preferred companionships	32,644,069.2658	3,874,823.2300
Before 2009		
Preferred companionships + casual acquaintances	1,109,184.6515	409,509.4936
Two level of casual acquaintances	1,109,345.1720	409,570.0190
Casual acquaintances	1,109,464.2976	409,611.4766
Preferred companionships	1,117,401.7907	412,540.7141
2009–2010		
Two level of casual acquaintances	912,608.1271	132,661.6023
Casual acquaintances	912,705.5439	132,672.3443
Preferred companionships + casual acquaintances	914,381.6500	132,917.6924
Preferred companionships	914,900.7656	132,989.7326
From 2011		
Two level of casual acquaintances	22,072,693.1589	2,805,092.6681
Preferred companionships + casual acquaintances	22,073,001.6724	2,805,130.1294
Casual acquaintances	22,075,501.1774	2,805,446.0309
Preferred companionships	22,209,400.9164	2,822,460.8089

The lowest Quasi-Akaike Information Criterion (QAIC) indicates the best-fitting model, and ΔQAIC (difference between QAIC and that of the best model) indicates the degree of support for the other models.

conditions impeding visibility or the level of experience of the trained observer. In addition, we only observed bull sharks at a single feeding site; therefore, the validity of our results is limited when compared to studies that include multiple sites (e.g., an acoustic receiver network; Armansin et al., 2016; Papastamatiou et al., 2020) or those investigating multiple areas and sampling both provisioning and non-feeding sites (Mourier et al., 2012). However, the large numbers of sharks and the long study period provides a robust data set that adequately characterizes the associations of bull sharks aggregating at the SRMR, laying the foundation for further investigating sociality in this species. For example, although kinship appears not to drive associations and affiliations among blacktip reef sharks (Mourier and Planes, 2021), group assortment in bull sharks may be influenced by genetic relatedness. Unlike most other shark species, bull sharks spend the first few years of their lives in estuaries and rivers before moving out to the ocean. Consequently, further work investigating genetic relatedness of individual bull sharks encountered at the SRMR as well as those found in known nurseries (Glaus et al., 2019) is warranted in order to explore the possibility that during those first crucial years of their lives, long lasting relationships are formed within cohorts.

Direct shark feeding at the SRMR appears to drive fission-fusion dynamics, where the feeding event temporarily fuses a large number of individual bull sharks in a central place. In terms of CPF theory, of interest is bull shark behavior following dispersion from the central place (feeding event). If bull sharks indeed choose to group with preferred associates, namely turn up together at the feeding site, specific paired associations or groups of bull sharks observed at the SRMR would be expected to be observed together at other locations as well. This hypothesis could be tested by monitoring other dive sites, feeding and not, in Fiji where bull sharks are encountered. Ward-Paige et al. (2020) reported bull shark groups of variable sizes from six areas in Fiji. Individuals would need to be independently identified at these sites to ensure that they are also visitors to the SRMR and vice versa. Anecdotal reports show that several bull sharks visually identified at the SRMR were also recorded in Kuata, an island of the Yasawa Group approx. 200 km away, where a shark feeding site was established back in 2015. In the absence of direct observation data collection at each dive site, the joint movement of individuals may be monitored using acoustic telemetry. Brunnschweiler and Barnett (2013) found that the overall diel patterns in movement are for acoustically tagged bull sharks to use the area around the feeding site in the morning before spreading out over Shark Reef throughout the day and dispersing over a larger coastal area at night. Trophic information suggests that they continue to forage on natural prey (Abrantes et al., 2018), quite possibly in the Navua estuary at night (Brunnschweiler and Barnett, 2013), nevertheless we are lacking key information including regarding resting behavior (e.g., where, when or if they rest in groups). Unfortunately, our data from acoustically tagged bull sharks are inconclusive with respect to the existence of pairs or groups free ranging together as a result of small numbers of individuals tagged together for longer time periods (Brunnschweiler and Barnett, 2013). To better understand and explore the depth and breadth of sociality within the SRMR bull shark population and determine how group behavior and dynamics align with CPF, a network analysis study including focal observations combined with tracking data should be undertaken in Fiji. A tangential study could be conducted at a location such as Mozambique where adult bull sharks aggregate without being fed (Daly et al., 2014) and the results compared and contrasted. This would provide for a more thorough examination of the associative nature of this species.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review was not required for this study; field work was carried out in the Shark Reef Marine Reserve with the knowledge and the approval of the Ministry of Fisheries and the traditional owners of Shark Reef. No animals were caught or handled.

AUTHOR CONTRIBUTIONS

JB designed the study. TB, NL, and JB analyzed the data. All authors contributed to drafting the manuscript and its revisions and read and approved the submitted version.

ACKNOWLEDGMENTS

We would like to thank Hal Whitehead and Bruno Diaz-Lopez for their advice on SOCPROG and social analyses. We would also like to thank the staff of Beqa Adventure Divers for data acquisition and for logistical support. Mike Neumann is acknowledged for implementing and maintaining the database, the content of which is the foundation of this manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.678074/full#supplementary-material

REFERENCES

Abrantes, K. G., Brunnschweiler, J. M., and Barnett, A. (2018). You are what you eat: examining the effects of provisioning tourism on shark diets. *Biol. Conserv*. 224, 300–308. doi: 10.1016/j.biocon.2018.05.021

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* 49, 227–267. doi: 10.1163/156853974x00534

Armansin, N. C., Lee, K. A., Huveneers, C., and Harcourt, R. G. (2016). Integrating social network analysis and fine-scale positioning to characterize the associations of a benthic shark. *Anim. Behav*. 115, 245–258. doi: 10.1016/j.anbehav.2016.02.014

Baird, R. W., and Whitehead, H. (2000). Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Can. J. Zool.* 78, 2096–2105. doi: 10.1139/z00-155

Barnett, A., Abrantes, K. G., Seymour, J., and Fitzpatrick, R. (2012). Residency and spatial use by reef sharks of an isolated seamount and its implications for conservation. *PLoS One* 7:e36574. doi: 10.1371/journal.pone.0036574

Bass, N. C., Mourier, J., Knott, N. A., Day, J., Brown, C., and Guttridge, T. (2016). Long-term migration patterns and bisexual philopatry in a benthic shark species. *Mar. Freshw. Res.* 68, 1414–1421. doi: 10.1071/mf16122

Bejder, L., Fletcher, D., and Bräger, S. (1998). A method for testing association patterns of social animals. *Anim. Behav.* 56, 719–725. doi: 10.1006/anbe.1998.0802

Bridge, P. D. (1993). "Classification," in *Biological Data Analysis*, ed. J. C. Fry (Oxford: Oxford University Press), 219–242.

Brunnschweiler, J. M. (2010). The shark reef marine reserve: a marine tourism project in Fiji involving local communities. *J. Sustain. Tour*. 18, 29–42. doi: 10.1080/09669580903071987

Brunnschweiler, J. M., Abrantes, K. G., and Barnett, A. (2014). Long-term changes in species composition and relative abundances of sharks at a provisioning site. *PLoS ONE* 9:e86682. doi: 10.1371/journal.pone.0086682

Brunnschweiler, J. M., and Baensch, H. (2011). Seasonal and long-term changes in relative abundance of bull sharks from a tourist shark feeding site in Fiji. *PLoS One* 6:e16597. doi: 10.1371/journal.pone.0016597

Brunnschweiler, J. M., and Barnett, A. (2013). Opportunistic visitors: long-term behavioural response of bull sharks to food provisioning in Fiji. *PLoS One* 8:e58522. doi: 10.1371/journal.pone.0058522

Brunnschweiler, J. M., and Compagno, L. J. V. (2008). First record of *Carcharhinus leucas* from Tonga, South Pacific. *Mar. Biodivers. Rec.* 1:e51.

Cairns, S. J., and Schwager, S. J. (1987). A comparison of association indices. *Anim. Behav.* 35, 1454–1469. doi: 10.1016/s0003-3472(87)80018-0

Chepko-Sade, B. D., Reitz, K. P., and Sade, D. S. (1989). Sociometrics of *Macaca mulatto* IV: network analysis of social structure of a pre-fission group. *Soc. Netw.* 11, 293–314. doi: 10.1016/0378-8733(89)90007-5

Clua, E., Buray, N., Legendre, P., Mourier, J., and Planes, S. (2010). Behavioural response of sicklefin lemon sharks *Negaprion acutidens* to underwater feeding for ecotourism purposes. *Mar. Ecol. Prog. Ser*. 414, 257–266. doi: 10.3354/meps08746

Clua, E., Chauvet, C., Read, T., Werry, J., and Lee, S. Y. (2013). Behavioural patterns of tiger shark (*Galeocerdo cuvier*) feeding aggregation at a blue whale carcass in Pony Bay, New Caledonia. *Mar. Freshwat. Behav. Physiol*. 46, 1–20. doi: 10.1080/10236244.2013.773127

Croft, D., Krause, J., Darden, S., Ramnarine, I., Faria, J., and James, R. (2009). Behavioural trait assortment in a social network: patterns and implications. *Behav. Ecol. Sociobiol.* 63, 1495–1503. doi: 10.2307/40295532

Croft, D. P., James, R., and Krause, J. (2008). *Exploring Animal Social Networks*. Princeton: Princeton University Press.

Croft, D. P., James, R., Thomas, P., Hathaway, C., Mawdsley, D., Laland, K., et al. (2006). Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata). Behav. Ecol. Sociobiol.* 59, 644–650. doi: 10.1007/s00265-005-0091-y

Cross, P. C., Lloyd-Smith, J. O., and Getz, W. M. (2005). Disentangling association patterns in fission-fusion societies using African buffalo as an example. *Anim. Behav*. 69, 499–506. doi: 10.1016/j.anbehav.2004.08.006

Daly, R., Smale, M. J., Cowley, P. D., and Froneman, P. W. (2014). Residency patterns and migration dynamics of adult bull sharks (*Carcharhinus leucas*) on the east coast of southern Africa. *PLoS One* 9:e109357. doi: 10.1371/journal.pone.0109357

Elena, V. P., Thomas, C. G., Patricia, G. P., and Paul, F. D. (1999). Patch size and composition of social groups in wintering tufted titmice. *Auk* 116, 1152–1155. doi: 10.2307/4089699

Elgar, M. (1989). Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev. Camb. Philos. Soc.* 64, 13–33. doi: 10.1111/j.1469-185X.1989.tb00636.x

Fewell, J. H. (2003). Social insect networks. *Science* 301, 1867–1870. doi: 10.1126/science.1088945

Findlay, R., Gennari, E., Cantor, M., and Tittensor, D. P. (2016). How solitary are white sharks: social interactions or just spatial proximity? *Behav. Ecol. Sociobiol.* 70, 1735–1744. doi: 10.1007/s00265-016-2179-y

Glaus, K. B. J., Brunnschweiler, J. M., Piovano, S., Mescam, G., Genter, F., Fluekiger, P., et al. (2019). Essential waters: young bull sharks in Fiji's largest riverine system. *Ecol. Evol.* 9, 7574–7585. doi: 10.1002/ece3.5304

Graham, R. T., and Castellanos, D. (2012). Apex predators target mutton snapper spawning aggregation. *Coral Reefs* 31:1017. doi: 10.1007/s00338-012-0921-0

Guttal, V., and Couzin, I. D. (2010). Social interactions, information use, and the evolution of collective migration. *Proc. Natl. Acad. Sci. U.S.A*. 107, 16172–16177. doi: 10.1073/pnas.1006874107

Heupel, M. R., Simpfendorfer, C. A., Espinoza, M., Smoothey, A. F., Tobin, A., and Peddemors, V. (2015). Conservation challenges of sharks with continental scale migrations. *Front. Mar. Sci*. 2:12. doi: 10.3389/fmars.2015.00012

Hoppitt, W. J. E., and Farine, D. R. (2018). Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. *Anim. Behav.* 136, 227–238. doi: 10.1016/j.anbehav.2017.08.029

Johnson, D. D. P., Kays, R., Blackwell, P. G., and Macdonald, D. W. (2002). Does the resource dispersion hypothesis explain group living? *Trends Ecol. Evol.* 17, 563–570. doi: 10.1016/s0169-5347(02)02619-8

Jones, T. B., Green, J. A., Patrick, S. C., Evans, J. C., Wells, M. R., Rodríguez-Malagón, M. A., et al. (2020). Consistent sociality but flexible social associations across temporal and spatial foraging contexts in a colonial breeder. *Ecol. Lett.* 23, 1085–1096. doi: 10.1111/ele.13507

Kirkwood, R., and Arnould, J. P. Y. (2011). Foraging trip strategies and habitat use during late pup rearing by lactating Australian fur seals. *Aust. J. Zool.* 59, 216–226. doi: 10.1071/zo11080

Krause, J., and Ruxton, G. D. (2002). *Living in Groups*. Oxford: Oxford University Press.

Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L., and Sherwin, W. B. (2005). Cultural transmission of tool use in bottlenose dolphins. *Proc. Natl. Acad. Sci. U.S.A*. 102, 8939–8943. doi: 10.1073/pnas.0500232102

Lea, J. S. E., Daly, R., Leon, C., Daly, C. A. K., and Clarke, C. R. (2019). Life after death: behaviour of multiple shark species scavenging a whale carcass. *Mar. Freshw. Res*. 70, 302–306. doi: 10.1071/mf18157

Loiseau, N., Kiszka, J. J., Bouveroux, T., Heithaus, M. R., Soria, M., and Chabanet, P. (2016). Using an unbaited stationary video system to investigate the behaviour and interactions of bull sharks *Carcharhinus leucas* under an aquaculture farm. *Afr. J. Mar. Sci*. 38, 73–79. doi: 10.2989/1814232x.2016.1156578

Lusseau, D., and Newman, M. E. J. (2004). Identifying the role that animals play in their social networks. *Proc. R. Soc. Lond. B*. 271, 477–481.

Marshall, A. D., and Pierce, S. J. (2012). The use and abuse of photographic identification in sharks and rays. *J. Fish Biol*. 80, 1361–1379. doi: 10.1111/j.1095-8649.2012.03244.x

McDonald, D. B. (2009). Young-boy networks without kin clusters in a lek-mating manakin. *Behav. Ecol. Sociobiol.* 63, 1029–1034. doi: 10.1007/s00265-009-0722-9

Meyer, L., Barry, C., Araujo, G., Barnett, A., Brunnschweiler, J. M., Chin, A., et al. (in press). Redefining *provisioning* in marine wildlife tourism. *J. Ecotourism*. doi: 10.1080/14724049.2021.1931253

Meyer, L., Pethybridge, H., Beckmann, C., Bruce, B., and Huveneers, C. (2019). The impact of wildlife tourism on the foraging ecology and nutritional condition of an apex predator. *Tour. Manag.* 75, 206–215. doi: 10.1016/j.tourman.2019.04.025

Mourier, J., Brown, C., and Planes, S. (2017). Learning and robustness to catch-and-release fishing in a shark social network. *Biol. Lett.* 13:20160824. doi: 10.1098/rsbl.2016.0824

Mourier, J., Lédée, E., Guttridge, T., and Jacoby, D. M. P. (2019). "Network analysis and theory in shark ecology–methods and applications," in *Shark Research: Emerging Technologies and Applications for the Field and Laboratory*, eds J. C. Carrier, M. R. Heithaus, and C. A. Simpfendorfer (Boca Raton: CRC Press), 337–356.

Mourier, J., and Planes, S. (2021). Kinship does not predict the structure of a shark social network. *Behav. Ecol.* 32, 211–222. doi: 10.1093/beheco/araa119

Mourier, J., Vercelloni, J., and Planes, S. (2012). Evidence of social communities in a spatially structured network of a free-ranging shark species. *Anim. Behav*. 83, 389–401. doi: 10.1016/j.anbehav.2011.1.008

Naug, D. (2008). Structure of the social network and its influence on transmission dynamics in a honeybee colony. *Behav. Ecol. Sociobiol.* 62, 1719–1725. doi: 10.1007/s00265-008-0600-x

Newman, M. E. J. (2004). Analysis of weighted networks. *Phys. Rev. E* 70:056131.

Newman, M. E. J. (2006). Modularity and community structure in networks. *Proc. Natl. Acad. Sci. U.S.A.* 103, 8577–8582.

Orians, G. H., and Pearson, N. E. (1979). "On the theory of central place foraging," in *Analysis of Ecological Systems*, eds D. J. Horn, R. D. Mitchell, and G. R. Stairs (Columbus: Ohio State University Press), 154–177.

Papastamatiou, Y. P., Bodey, T. W., Caselle, J. E., Bradley, D., Freeman, R., Friedlander, A. M., et al. (2020). Multiyear social stability and social information use in reef sharks with diel fission–fusion dynamics. *Proc. R. Soc. B* 287:20201063. doi: 10.1098/rspb.2020.1063

Papastamatiou, Y. P., Watanabe, Y. Y., Demsar, U., Leos-Barajas, V., Bradley, D., Langrock, R., et al. (2018). Activity seascapes highlight central place foraging strategies in marine predators that never stop swimming. *Mov. Ecol.* 6:9.

Pini-Fitzsimmons, J., Knott, N. A., and Brown, C. (2021). Heterarchy reveals social organization of a smooth stingray (*Bathytoshia brevicaudata*) population in a provisioned food context. *Front. Mar. Sci*. 8:641761. doi: 10.3389/fmars.2021.641761

Schilds, A., Mourier, J., Huveneers, C., Nazimi, L., Fox, A., and Leu, S. T. (2019). Evidence for non-random co-occurrences in a white shark aggregation. *Behav. Ecol. Sociobiol.* 73:138.

Sims, D. W., Southall, E. J., Quayle, V. A., and Fox, A. M. (2000). Annual social behaviour of basking sharks associated with coastal front areas. *Proc. R. Soc. B* 267, 1897–1904. doi: 10.1098/rspb.2000.1227

Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettle-Hofmann, C., et al. (2011). Collective decision-making and fission-fusion dynamics: a conceptual framework. *Oikos* 120, 1608–1617. doi: 10.1111/j.1600-0706.2011.19685.x

Vital, C., and Martins, E. P. (2011). Strain differences in zebrafish (*Danio rerio*) social roles and their impact on group task performance. *J. Comp. Psychol.* 125, 278–285. doi: 10.1037/a0023906

Ward-Paige, C. A., Brunnschweiler, J. M., and Skyes, H. (2020). Tourism-driven ocean science for sustainable use: a case study of sharks in Fiji. *bioRxiv [Preprint]* Available online at: https://doi.org/10.1101/2020.02.04.932236 (accessed March 7, 2021).

Whitehead, H. (1997). Analysing animal social structure. *Anim. Behav*. 53, 1053–1067. doi: 10.1006/anbe.1996.0358

Whitehead, H. (2008a). *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis*. Chicago, IL: University of Chicago Press.

Whitehead, H. (2008b). Precision and power in the analysis of social structure using associations. *Anim. Behav.* 75, 1093–1099. doi: 10.1016/j.anbehav.2007.08.022

Whitehead, H. (2009). SOCPROG programs: analysing animal social structures. *Behav. Ecol. Sociobiol.* 63, 765–778. doi: 10.1007/s00265-008-0697-y

Whitehead, H., and Dufault, S. (1999). Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. *Adv. Stud. Behav*. 28, 33–74. doi: 10.1016/S0065-3454(08)60215-6

Whitehead, H., and James, R. (2015). Generalized affiliation indices extract affiliations from social network data. *Methods Ecol. Evol*. 6, 836–844. doi: 10.1111/2041-210x.12383

Whitehead, H., Laland, K. N., Rendell, L., Thorogood, R., and Whiten, A. (2019). The reach of gene–culture coevolution in animals. *Nat. Commun.* 10:2405. doi: 10.1038/s41467-019-10293-y

Wittemyer, G., Douglas-Hamilton, I., and Getz, W. M. (2005). The socioecology of elephants: analysis of the processes creating multi-tiered social structures. *Anim. Behav*. 69, 1357–1371. doi: 10.1016/j.anbehav.2004.08.018

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

REVIEW
published: 25 June 2021
doi: 10.3389/fmars.2021.678173

Dynamics of Cetacean Mixed-Species Groups: A Review and Conceptual Framework for Assessing Their Functional Significance

Jonathan Syme[1]*, Jeremy J. Kiszka[2] and Guido J. Parra[1]

[1] Cetacean Ecology, Behaviour and Evolution Lab, College of Science and Engineering, Flinders University, Adelaide, SA, Australia, [2] Institute of Environment, Department of Biological Sciences, Florida International University, North Miami, FL, United States

Numerous species of cetaceans have been recorded in mixed-species groups (MSGs). By forming groups with individuals of different species, cetaceans may reduce predation risk, improve foraging, and gain social benefits. Most accounts of cetacean MSGs, however, are descriptive and little is known about their functions. Furthermore, research has been hindered by inconsistent use of terminology and the lack of a conceptual framework to guide investigations. We reviewed the cetacean literature to compare how MSGs have been termed and defined, to assess their characteristics, to evaluate what is known about their potential functions, and to provide directions for future study. In total, we reviewed 203 studies reporting observations of cetacean MSGs. These MSGs involved 54 different species, predominantly delphinids, that formed 216 different species pairs with varied morphologies and levels of relatedness. Cetacean MSGs occurred across the globe, from tropical to cold temperate seas, from shallow coastal waters to the open ocean, and varied in characteristics such as group size and frequency of occurrence. Only 27 of the reviewed studies proposed and discussed the potential functions of cetacean MSGs, suggesting reduced predation risk (5 species pairs), improved foraging (17 species pairs), and social benefits (12 species pairs) as the main drivers. In most cases, however, the factors that drive the formation of cetacean MSGs remain unknown. Amongst the reviewed studies, MSGs were referred to by various terms, often with no explicit definitions. To reduce this inconsistency, we recommend that future studies use only the term *mixed-species group* which we define as individuals of two or more species found in close spatial proximity due to mutual or unreciprocated attraction derived from evolutionary grouping benefits. There were also few structured investigations to confirm MSG occurrence and to analyse their potential causes and consequences. To facilitate the study of cetacean MSGs, we developed a conceptual framework that establishes diverse approaches to, firstly, distinguish MSGs from chance encounters and aggregations and to, secondly, investigate their potential functions. This is necessary if we are to advance this field of study and improve our understanding of the role that MSGs play in species and community ecology.

Keywords: grouping, interspecific association, interaction, antipredator tactics, foraging, social benefits, cetacean, mixed-species group

Edited by:
Darren Croft,
University of Exeter, United Kingdom

Reviewed by:
Mia Lykbær Kronborg Nielsen,
University of Exeter, United Kingdom
Stephanie Laura King,
University of Bristol, United Kingdom
Alexis Levengood,
University of the Sunshine Coast,
Australia

****Correspondence:***
Jonathan Syme
jonathan.syme@flinders.edu.au

Specialty section:
This article was submitted to
Marine Megafauna,
a section of the journal
Frontiers in Marine Science

Received: *09 March 2021*
Accepted: *25 May 2021*
Published: *25 June 2021*

Citation:
Syme J, Kiszka JJ and Parra GJ (2021) Dynamics of Cetacean Mixed-Species Groups: A Review and Conceptual Framework for Assessing Their Functional Significance.
Front. Mar. Sci. 8:678173.
doi: 10.3389/fmars.2021.678173

INTRODUCTION

Group living is fundamental to numerous species of animals as it conveys various benefits and costs (Alexander, 1974; Krause and Ruxton, 2002; Majolo and Huang, 2018). By forming groups, individuals may decrease the risk of predation, improve foraging, increase their reproductive chances, and decrease the energetic cost of movement (Krause and Ruxton, 2002; Majolo and Huang, 2018). Individuals may also incur costs including increased competition for resources, increased probability of detection by predators, inbreeding, and increased risk of disease transmission among group members (Alexander, 1974; Krause and Ruxton, 2002; Majolo and Huang, 2018). Studies on the costs and benefits of group living have provided a comprehensive understanding of the principles underlying group formation, particularly for groups composed of individuals of the same species. Much less is known, however, about the dynamics of groups composed of multiple species (Morse, 1977; Stensland et al., 2003; Goodale et al., 2017). Mixed-species groups (MSGs), also termed interspecific, polyspecific, or heterospecific groups or associations (Whitesides, 1989; Heymann and Buchanan-Smith, 2000; Stensland et al., 2003), are broadly defined as sets of individuals of two or more species that are seen in such close association that they can be regarded as members of the same group (Stensland et al., 2003). As such, MSGs occur when there is an attraction between heterospecific individuals (Stensland et al., 2003; Cords and Würsig, 2014). This attraction can be either mutual or unreciprocated, as long as the presence of the attracted species is tolerated by the other (Stensland et al., 2003). MSGs should be distinguished from aggregations of animals that are attracted to a common resource or that respond in a similar way to environmental stimuli and from chance encounters that result from the coincidental meeting of co-occurring species (**Table 1**; Waser, 1982, 1984; Cords and Würsig, 2014). MSGs are thought to occur because they provide evolutionary benefits over individuals, populations, or species that do not mix (Stensland et al., 2003; Whitehead, 2008; Ward and Webster, 2016; Goodale et al., 2017). These benefits form the basis of the three principal functional explanations for the formation of MSGs: reduced predation risk, improved foraging, and social advantages (Whitesides, 1989; Stensland et al., 2003; Cords and Würsig, 2014; Sridhar and Guttal, 2018). Participation in MSGs can lead to changes in behaviour and habitat use of one or more of the species involved as individuals alter their ecology in response to the presence of heterospecifics (Peres, 1992; Wolters and Zuberbühler, 2003; Porter and Garber, 2007; Sridhar et al., 2009). Thus, assessing the underlying causes and functions of MSGs is important to better understand the dynamics of ecological communities (Veit and Harrison, 2017; Zou et al., 2018).

MSGs have been recorded amongst closely and distantly related species including fishes (Lukoschek and McCormick, 2000), birds (Sridhar et al., 2009), and mammals (Stensland et al., 2003). Amongst mammals, MSGs have been most commonly documented in ungulates, primates, and cetaceans (Morse, 1977; Heymann and Buchanan-Smith, 2000; Stensland et al., 2003; Cords and Würsig, 2014; Heymann and Hsia, 2015). Cetaceans, particularly delphinids, are known to form MSGs with other cetaceans relatively frequently (Frantzis and Herzing, 2002; Stensland et al., 2003; Bearzi, 2005b; Cords and Würsig, 2014), as well as with other marine mammal species including pinnipeds (Bearzi, 2006; Bacon et al., 2017) and sirenians (Kiszka, 2007). Despite the apparent widespread occurrence of cetacean MSGs (reviewed in Stensland et al., 2003; Cords and Würsig, 2014), large gaps remain in our understanding of their function and the mechanisms underlying their formation. This is largely due to the lack of dedicated studies on the potential drivers and associated costs and benefits of cetacean MSGs (Stensland et al., 2003). The development of such studies is, in turn, hindered by inconsistent terminology and the absence of a conceptual framework to guide the development of cetacean MSG studies. In the literature, several terms, including *association*, *aggregation*, and *mixed-species group*, are used interchangeably with varying definitions (Stensland et al., 2003). Moreover, there is no clear outline of how to distinguish cetacean MSGs from chance encounters and aggregations and how to subsequently investigate their function. Consistent terminology and clear conceptual frameworks are essential when studying ecological phenomena to enable clear communication and to allow comparisons across taxa and regions (Fauth et al., 1996; Hall et al., 1997). Thus, the development and utilisation of such terminology and frameworks is key to the advancement and understanding of ecological topics.

Here, we review the literature on cetacean MSGs to: (1) address any inconsistencies in terminology and definitions; (2) assess their characteristics (i.e., the species involved, occurrence, and distribution); (3) evaluate what is known about their potential functions; and (4) use the results to propose standardised terminology and a conceptual framework to assist future studies with characterising their dynamics and functions.

METHODS

Literature Review

We used the databases Scopus, ScienceDirect, and Web of Science and the search engine Google Scholar to search for relevant journal articles, book chapters, reports, and theses that contained records of cetacean MSGs. As various terms, including *association* and *aggregation*, are often used interchangeably to refer to MSGs, we included these terms in our literature search. More

TABLE 1 | Glossary of terms.

Term	Definition	References
Mixed-species group	A set of individuals of two or more species that are seen in such close association that they can be regarded as members of the same group.	Stensland et al., 2003
Chance encounter	A set of individuals of two or more species that are found in spatial proximity due to chance alone.	Waser, 1982; Whitesides, 1989
Aggregation	A set of individuals of two or more species that are found in spatial proximity because they are attracted toward a common resource or respond to the same environmental stimuli.	Waser, 1982; Powell, 1985; Goodale et al., 2017

specifically, we combined each of several adjectives, including *mixed-species*, *interspecific*, *heterospecific*, and *polyspecific* with each of the key terms, including, but not limited to, *group*, *aggregation*, *association*, and *interaction* to form 40 phrases that refer to MSGs (see **Supplementary Table 1** for a full list of the search terms). These phrases were combined with the English names of relevant taxa (i.e., cetacean, whale, dolphin, and porpoise) to create the full search queries. Each of the search queries was entered into the databases and search engine and the citation information of all the results (e.g., titles, abstracts, authors) was downloaded. The titles and abstracts of the results were then read and analysed. Studies on captive animals were removed as they do not represent natural grouping patterns. Studies that were based entirely on data that was obtained remotely (e.g., passive acoustics) or from isotopic or genetic analyses were also removed as they do not contain the observations required to analyse grouping dynamics. The remaining studies were reviewed and those that described multiple species of cetaceans as forming *aggregations*, *associations*, *groups*, or a term that is often considered synonymous (e.g., *school*, *herd*, and *pod*) were included for further analysis. Studies that used any term with an explicit definition that clearly distinguished it from a MSG, however, were not included, as were studies that simply recorded species in the same area with no clear indication of MSG formation. Finally, the reference lists of the included studies were searched to find any additional publications that were missed by the initial searches.

Analysis

The studies that met the criteria for inclusion were then reviewed to produce a comprehensive compilation of records of cetacean MSGs. The taxonomic classification of all cetaceans involved in MSGs was recorded to the lowest taxonomic level following the 2020 Society for Marine Mammalogy Committee on Taxonomy (Committee on Taxonomy, 2020). Subsequent analyses of species composition were conducted on a species and family level. Where possible, we noted any additional information regarding group size, behaviour, and frequency of MSGs to provide a more detailed understanding of the dynamics of cetacean MSGs. All the terms used to describe MSGs, as well as any explicit definitions of those terms, were also recorded.

To gain insights into the distribution and frequency of cetacean MSGs across the major ocean basins we mapped their geographical distribution using QGIS (QGIS Development Team, 2019) and Plotly (Plotly Technologies Inc., 2015). As the precise geographical locations of the MSGs were often unavailable, we assigned a location value (i.e., ocean basin) to each study based on the study area. Additionally, to understand and visualise the spatial distribution of and the relationships between the cetacean species that most often form MSGs, we constructed a social network diagram where each node represents a species and each edge the occurrences of a species pair in MSGs. The edges were weighted according to the total number of studies reporting each species pair while the sizes of the nodes were made proportional to the total number of partner species that each species had. The average values of each species' distribution in terms of water depth and latitude were obtained from the Encyclopedia of Marine Mammals (Würsig et al., 2018) and used to position each species' node along the x and y axes, respectively, in the network diagram.

Finally, to determine the level to which cetacean MSGs have been researched, the studies were separated into those that simply reported the occurrence of cetacean MSGs and those that used observations or investigations to propose functional explanations for them. Details of these investigations and their conclusions were then compiled. Analysis of the data was conducted using Python (Python Software Foundation, 2016) and all figures were created using Plotly (Plotly Technologies Inc., 2015) in Python.

RESULTS

The literature search returned 2154 results, of which 98 were studies that met our criteria for inclusion. Additionally, 94 studies were added by tracing cited studies and a further 11 studies were obtained from a bibliography of publications on cetacean MSGs (Rowley, 2020), amounting to a total of 203 studies. Cetacean MSGs appear to have been first reported in the literature in 1961, with the majority of reports having been published since 1990 (**Figure 1**).

Definitions and Terminology

Out of the 203 studies obtained from the literature review, 116 studies (57.1%) referred to situations where multiple species of cetaceans were observed in close spatial proximity as *groups*, 95 (46.8%) as *associations*, 42 (20.7%) as *schools*, 26 (12.8%) as *aggregations*, while 11 studies (5.4%) used other terms such as *assemblage*, *encounter*, and *herd* (**Figure 2**). Over a third of the studies (36.0%) used multiple terms synonymously. Of those studies that used the term *group*, only 39 (33.6%) provided either a specific definition of a MSG or a definition of group that was applied to both single-species groups (SSGs) and MSGs. This trend was similar for the terms *association* (18 definitions, 19.0% of studies) and *aggregation* (8 definitions, 30.8% of studies), while only 3 (7.1%) studies that used the term *school* provided an explicit definition of this term (**Figure 2**). Furthermore, only five studies utilised some technique (e.g., analysis of interspecies association patterns or a minimum time limit) to confirm that potential MSGs were indeed MSGs and not simply chance encounters or aggregations.

Species Composition and Diversity

The reviewed studies revealed that 54 species of cetaceans belonging to five families of Odontocetes (Delphinidae, Kogiidae, Phocoenidae, Physeteridae, and Ziphiidae) and three families of Mysticetes (Balaenidae, Balaenopteridae, and Eschrichtiidae) were reported to form groups with other cetacean species (see **Supplementary Table 2** for full list). Of these species, 43 were Odontocetes and 11 were Mysticetes. The Odontocetes most commonly reported in MSGs belonged to the family Delphinidae, with 197 studies reporting participation in MSGs for almost all known species. The only species of the family Physeteridae, the sperm whale (*Physeter macrocephalus*), was also well represented

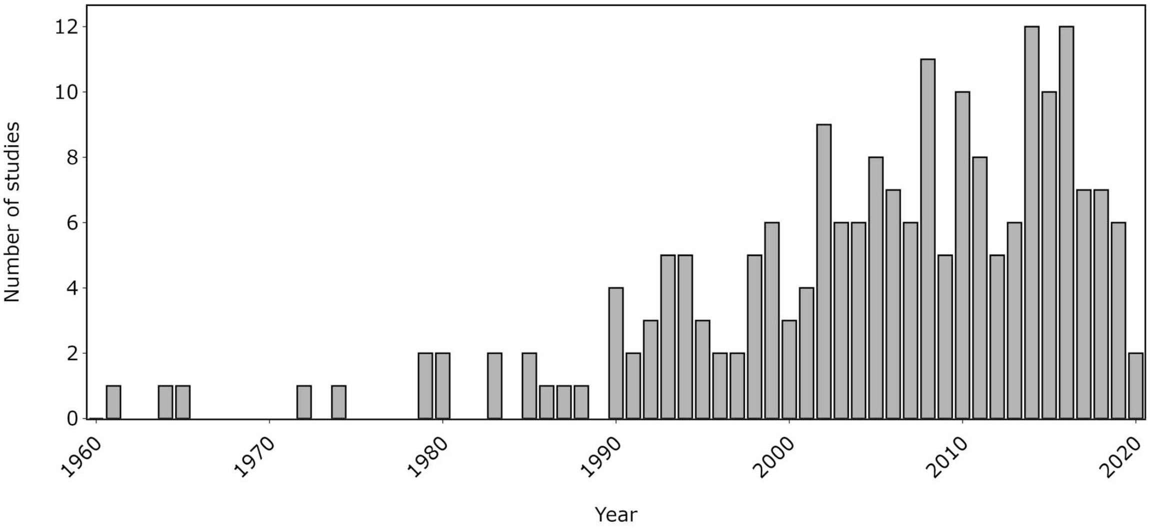


FIGURE 1 | Number of reviewed studies reporting cetacean mixed-species groups from 1961 to 2020.

with 25 studies reporting its occurrence in MSGs. In contrast, species of the remaining Odontocete families (i.e., Phocoenidae, Ziphiidae, and Kogiidae) were rarely reported in MSGs. Amongst the Mysticetes, the family Balaenopteridae accounted for most of the records (48 studies and 7 species), followed by the single Eschrichtiidae species—the grey whale (*Eschrichtius robustus*) (9 studies), and the family Balaenidae (6 studies and 3 species).

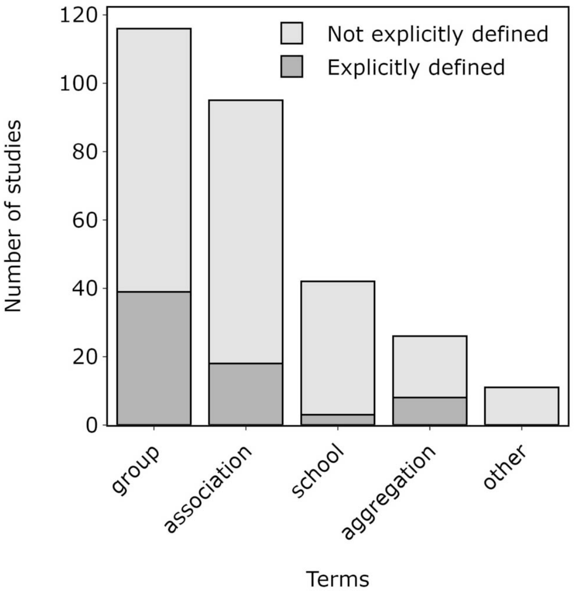


FIGURE 2 | Number of reviewed studies published between 1961 and 2020 that used several terms (i.e., *group*, *association*, *school,* and *aggregation*), with or without an explicit definition, to refer to situations where multiple species of cetaceans were observed in close spatial proximity. Other terms, including *assemblage*, *encounter*, and *herd*, are combined in the final bar. These terms were typically preceded by a variety of adjectives including *mixed-species*, *interspecific*, and *heterospecific*. The sum of the bars is greater than the total number of studies found by the review as over a third of the studies employed multiple terms.

At the species level, the common bottlenose dolphin (*Tursiops truncatus*), the common dolphin (*Delphinus delphis*), and Risso's dolphin (*Grampus griseus*) were the three most commonly reported cetacean species in MSGs (**Figure 3**). These same three species also had the greatest diversity of partner species in MSGs, with the common bottlenose dolphin associating with a total of 34 different species, the common dolphin with 27, and Risso's dolphin with 22 (**Figures 3**, **4**). Among Mysticetes, the humpback whale (*Megaptera novaeangliae*) was the most often reported species in MSGs and also the one with the highest diversity of partner species (**Figure 3**). Other delphinid species, along with several species of Balaenopteridae, made up the majority of the 33 cetacean species that were reported in MSGs by more than five studies, with only four species representing the remaining cetacean families: the sperm whale, Dall's porpoise (*Phocoenoides dalli*), the grey whale, and Longman's beaked whale (*Indopacetus pacificus*) (**Figure 3**).

The reported cetacean MSGs typically contained only two species, yet groups composed of up to four species were also observed (e.g., Ballance and Pitman, 1998; Kinzey et al., 1999; Anderson, 2005; Anderson et al., 2006; Weir, 2011; Bacon et al., 2017; Alves et al., 2018). We found records for 216 different species pairs observed within MSGs (**Supplementary Figure 1** and **Supplementary Table 2**), 47 of which were recorded by 5 or more studies (**Figure 4**). Almost all species pairs (91.7%) were from different genera yet the majority belonged to the same family (56.9%) and suborder (i.e., Odontoceti or Mysticeti) (73.2%). In particular, the majority of species pairs in cetacean MSGs consisted of two delphinid species (50.9% of reported species pairs). Furthermore, of the 47 species pairs with five or more records, 35 (74.5%) comprised two delphinid species and all

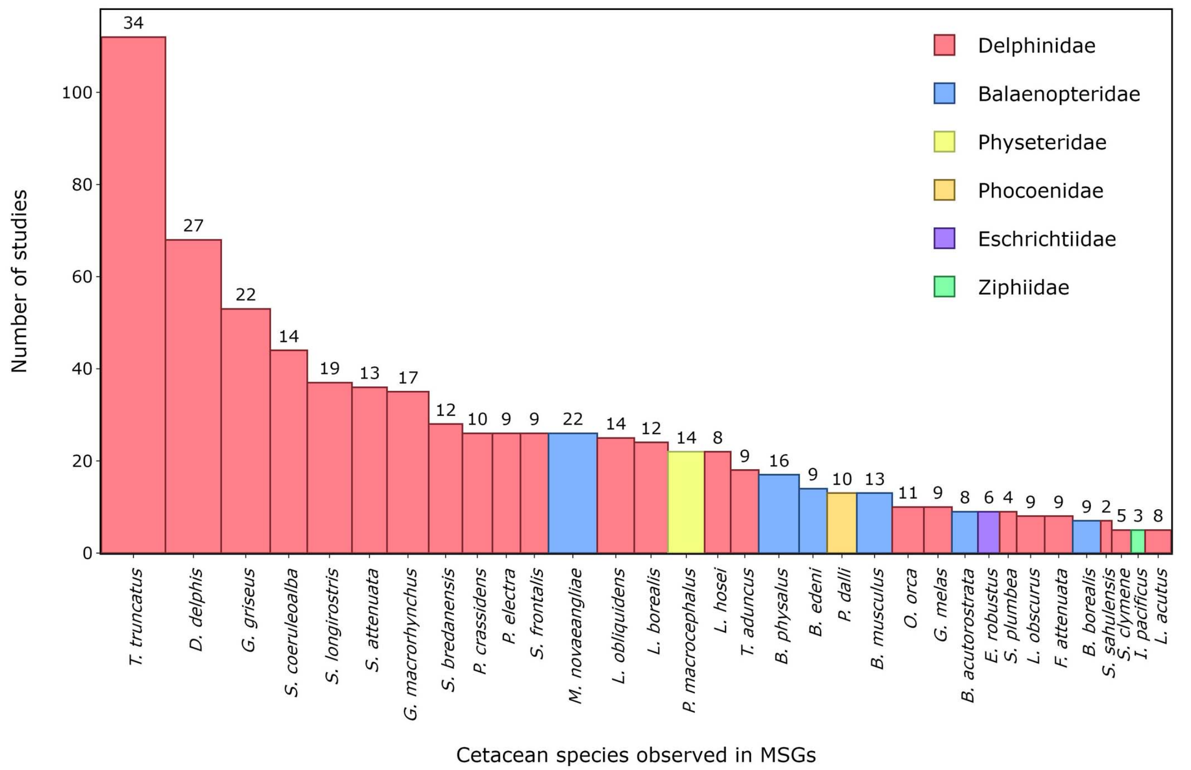


FIGURE 3 | The 33 species of cetaceans that were reported in mixed-species groups (MSGs) by five or more studies published between 1961 and 2020 that were obtained from a literature review on cetacean MSGs. The bar heights represent the number of studies reporting each species' participation in MSGs as displayed on the y axis. The bar widths are proportional to the total number of species that each species has been observed with in MSGs, i.e., the number of partner species, which is written above each bar. The bars are coloured according to the species' family.

but two involved at least one delphinid (45 species pairs, 95.7%) (**Figure 4**). The most commonly reported species pairs in MSGs were: common dolphin—striped dolphin (*Stenella coeruleoalba*) (34 studies), Risso's dolphin—common bottlenose dolphin (32 studies), and spinner dolphin (*Stenella longirostris*)—pantropical spotted dolphin (*Stenella attenuata*) (27 studies) (**Figure 4**). Many species pairs were found together much less frequently, with the majority (169 pairs) being reported by fewer than 5 studies. Marine mammal surveys across a variety of habitats and spatial scales typically gauged the proportion of cetacean groups that were mixed to be under 10% (**Table 2**). Dedicated studies of certain cetacean species that are known to form MSGs, on the other hand, reported higher frequencies, with MSGs accounting for up to a third of all groups sighted in some populations (**Table 3**; Frantzis and Herzing, 2002; Acevedo-Gutiérrez et al., 2005; Thompson, 2010; Kiszka et al., 2011).

Distribution and Habitat

Cetacean MSGs were observed from tropical to cold temperate waters in all the major ocean basins, except for the Southern Ocean (**Figure 5**). Furthermore, they were observed across a range of depths and at varying distances to shore, including: shallow coastal waters (<20 m; e.g., Acevedo-Gutiérrez et al., 2005; Hunt, 2018), over the continental shelf (20–200 m; e.g., Gowans and Whitehead, 1995; Mullin et al., 2004), around oceanic islands (e.g., Anderson, 2005; Quérouil et al., 2008; Gannier, 2009; Kiszka et al., 2011), and in the open ocean (<2,000 m; e.g., Scott and Cattanach, 1998; Jackson et al., 2008).

Functional Explanations for Cetacean Mixed-Species Group Formation

Of the 203 studies reviewed, 27 discussed potential functional explanations based on specific observations or investigations of cetacean MSGs (**Table 4**). These studies covered 25 species pairs of cetaceans, 7 of which had multiple proposed functional explanations. In total, 5 species pairs were hypothesised to form MSGs to reduce predation risk, 17 to improve foraging, and 12 to gain social benefits (**Table 4**). These hypotheses, rather than conclusions, rely on inferences drawn from behavioural observations and spatial variations in the distribution of SSGs and MSGs. Few studies (n = 5) determined that observed groupings were MSGs rather than mere chance encounters or aggregations and no study, to our knowledge, has directly tested whether participation in cetacean MSGs provides antipredator, foraging, or social benefits to group members. Nevertheless, the results provide an indication of the factors that may potentially drive cetacean MSG formation.

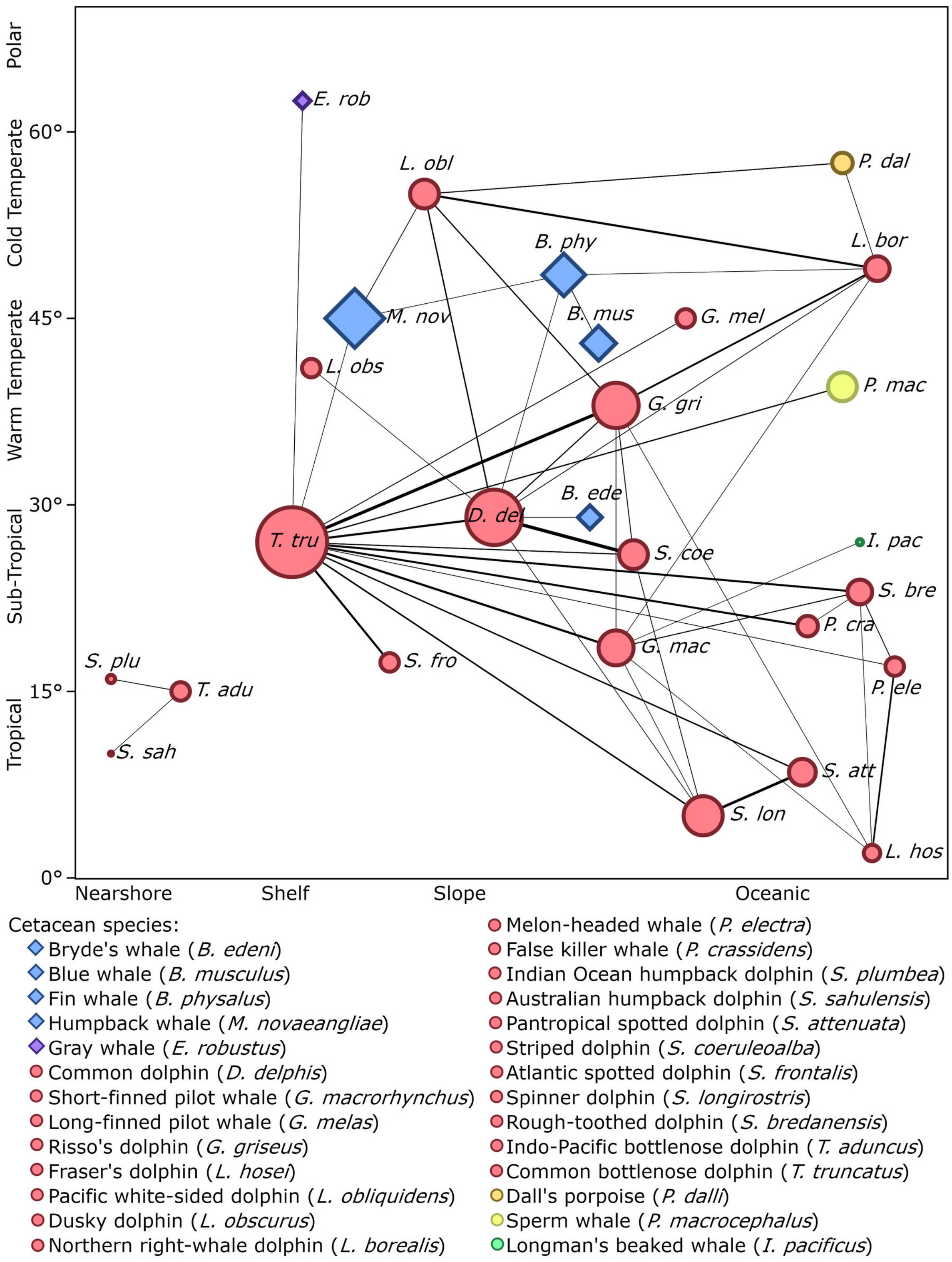


FIGURE 4 | Social network diagram showing the 47 species pairs (edges) that were reported together in mixed-species groups by five or more of the studies reviewed. The width of each edge is proportional to the total number of studies that reported that pair of species. The shape of each node indicates if the species is a Mysticete (diamond) or an Odontocete (circle) while the colours represent the species' family. The size of each node is proportional to the total number of partner species that each species has. Each species' node is placed approximately according to its average distribution with the x axis representing water depth and the y axis representing latitude. An interactive version of this network containing all 216 species pairs is available in **Supplementary Figure 1**.

TABLE 2 | Cetacean mixed-species groups as a percentage of all groups (i.e., single- and mixed-species groups) that were observed during surveys for species belonging to the target taxa.

Target taxon	Location	Mixed %	References
Odontocetes	Tropical Eastern Pacific	28.0	Oswald et al., 2008
Marine mammals	Eastern Tropical Pacific	12.0	Kinzey et al., 2000
Odontocetes	Temperate Eastern Pacific	11.0	Oswald et al., 2008
Marine mammals	Eastern Tropical Pacific	11.0	Kinzey et al., 1999
Cetaceans	Madeira	7.8	Alves et al., 2018
Cetaceans	La Réunion	6.3	Dulau-Drouot et al., 2008
Cetaceans	Santa Monica Bay, California	5.3	Bearzi and Saylan, 2011
Cetaceans	Subtropical south-western Atlantic	5.2	Di Tullio et al., 2016
Cetaceans	Maldives	4.5	Anderson, 2005
Cetaceans	Western Tropical Indian Ocean	4.4	Ballance and Pitman, 1998
Marine mammals	Southern California Bight	2.0	Bacon et al., 2017
Cetaceans	Algoa Bay, South Africa	1.9	Koper and Plön, 2016
Cetaceans	Northern Gulf of Mexico	1.4	Maze-Foley and Mullin, 2006

All surveys were boat-based except those of Bacon et al. (2017) which was aerial-based and Koper and Plön (2016) which was land- and boat-based.

TABLE 3 | Mixed-species groups (MSGs) involving delphinids recorded as a percentage of all groups (i.e., single- and mixed-species groups) of particular populations of the listed species as obtained through dedicated studies of MSGs.

Species	Location	Mixed %	References
Stenella coeruleoalba—Delphinus delphis—Grampus griseus	Gulf of Corinth, Greece	35.0	Frantzis and Herzing, 2002
Sotalia guianensis—Tursiops truncatus	Gandoca-Manzanillo, Costa Rica	32.4	Acevedo-Gutiérrez et al., 2005
Sotalia guianensis—Tursiops truncatus	Gandoca-Manzanillo, Costa Rica	23.6	Thompson, 2010
Stenella attenuata—Stenella longirostris	Mayotte	21.0	Kiszka et al., 2011
Stenella frontalis—Tursiops truncatus	Bahamas	15.2	Herzing and Johnson, 1997
Stenella frontalis—Tursiops truncatus	Bahamas	8.9	Melillo et al., 2009

Antipredator Advantage Hypothesis

One of the most common functional explanations for the formation of MSGs is that participating individuals benefit from a reduced risk of predation (Whitesides, 1989; Stensland et al., 2003). The presence of heterospecifics with a greater ability to detect predators or better defensive capabilities can lead to the formation of MSGs (Whitesides, 1989; Heymann and Buchanan-Smith, 2000; Stensland et al., 2003; Kiszka et al., 2011; Cords and Würsig, 2014). In addition, an increase in group size as a result of forming a MSG can have similar effects and can also dilute the risk of predation on individual group members (Gygax, 2002b; Cords and Würsig, 2014; Goodale et al., 2017).

In the oceanic eastern tropical Pacific, pantropical spotted and spinner dolphins often form MSGs (e.g., Au and Perryman, 1985; Reilly, 1990; Scott and Cattanach, 1998; Oswald et al., 2008). Long-term observations show no evidence of foraging when in MSGs, likely due to interspecific differences in foraging behaviour, thus making foraging benefits an unlikely driver of these MSGs (Norris and Dohl, 1980; Scott and Cattanach, 1998). Instead, given the potential high risk of predation faced by these oceanic dolphins from pelagic sharks, killer whales (*Orcinus orca*) and other large delphinids (e.g., false killer whales, *Pseudorca crassidens*), it has been suggested that these species form MSGs to reduce predation risk (Scott and Cattanach, 1998). More specifically, spinner dolphins, which feed on the deep scattering layer at night and rest during the day (Norris and Dohl, 1980), may seek refuge amongst groups of pantropical spotted dolphins, which are active and more alert during the day, and thus benefit from their vigilance (Scott and Cattanach, 1998). These species also form MSGs around the island of Mayotte in the Indian Ocean (Gross et al., 2009; Kiszka et al., 2011). Here, the absence of feeding and social interactions between the two species does not support the foraging and social benefits hypotheses, respectively. Instead, these MSGs form when spinner dolphins shift habitat to deeper waters where pantropical spotted dolphins preferentially occur, suggesting that spinner dolphins initiate these MSGs, possibly to reduce predation risk while transiting between resting areas (Kiszka et al., 2011).

Foraging Advantage Hypothesis

Foraging benefits gained from MSGs may take the form of an improved ability to detect, herd, and/or utilise food resources (Stensland et al., 2003) and may be obtained by mutual or non-mutual information exchange and coordinated foraging (Whitesides, 1989; Sridhar et al., 2009). Gatherings of different cetacean species at prey aggregations are fairly common and may also include seabirds, sharks, and large predatory fishes (Würsig and Würsig, 1979; Evans, 1982; Scott and Cattanach, 1998; Markowitz, 2004; Kiszka et al., 2015; Veit and Harrison, 2017). Although these gatherings involve the presence of different species in close spatial proximity, and so may be considered MSGs, it is not always clear if their formation is due to a mutual attraction to common prey or an attraction between species (Quérouil et al., 2008).

MSGs of common bottlenose dolphins and false killer whales have been observed in numerous locations (e.g., Scott and Chivers, 1990; Anderson, 2005; Maze-Foley and Mullin, 2006; Baird et al., 2008), including off the coast of New Zealand where they seem to engage in cooperative foraging (Zaeschmar et al., 2013). During foraging, both species feed on the same species of fishes after herding and driving them toward the surface (Zaeschmar et al., 2013). The apparent cooperative nature of the foraging suggests that these MSGs may provide mutualistic

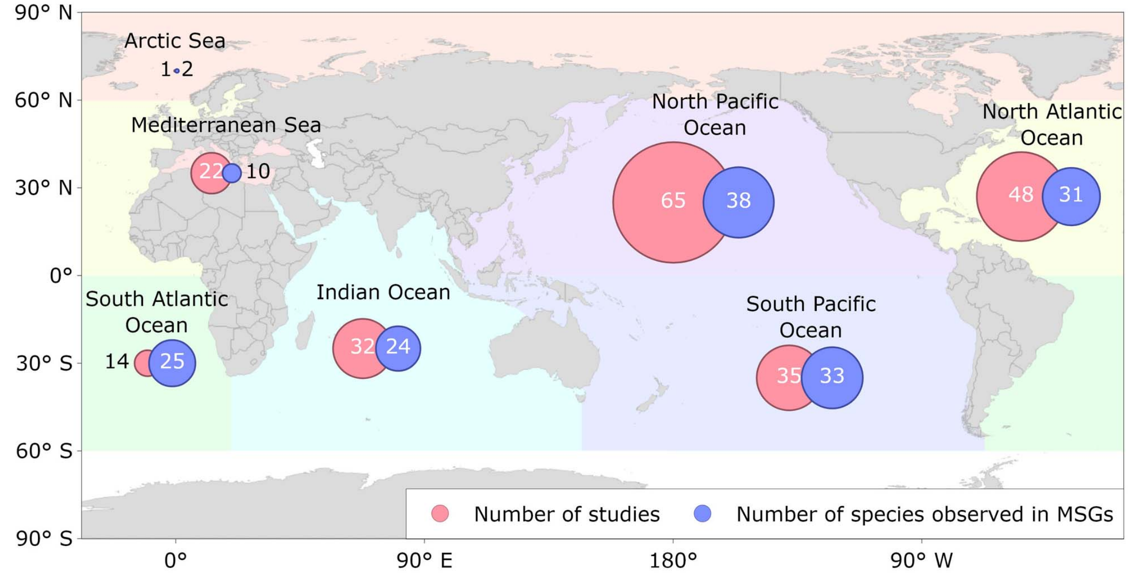


FIGURE 5 | Geographical distribution of the location of the studies reviewed that reported cetacean mixed-species groups (MSGs) across the major ocean basins from 1961 to 2020. Numbers inside circles represent the number of reviewed studies reporting the occurrence of cetacean MSGs in each ocean basin and the number of cetacean species observed in those MSGs.

benefits. Nonetheless, the degree of cooperation is unknown and the possibility of social parasitism cannot be disregarded (Zaeschmar et al., 2014).

Common bottlenose dolphins, particularly the offshore ecotype, in tropical and warm temperate waters of the Pacific and Atlantic Oceans also regularly form MSGs with short-finned pilot whales (*Globicephala macrorhynchus*) (e.g., Scott and Chivers, 1990; Mangels and Gerrodette, 1994; Gannier, 2000; Weir, 2006) and with Risso's dolphins (*Grampus griseus*) (e.g., Scott and Chivers, 1990; Bearzi, 2005b; Maze-Foley and Mullin, 2006; Weir, 2011; Bacon et al., 2017; Viana, 2019), particularly when the latter species are foraging (Norris and Prescott, 1961; Shane, 1994). The benefit here, however, may not be mutual. Common bottlenose dolphins tend to initiate the formation of MSGs and short-finned pilot whales sometimes display avoidance behaviour when common bottlenose dolphins approach. This suggests that the common bottlenose dolphins seek out the short-finned pilot whales and Risso's dolphins to improve foraging success, although it is unknown if the other species benefit from these MSGs (Shane, 1994; Bacon et al., 2017). Common bottlenose dolphins have also been frequently observed with long-finned pilot whales (*Globicephala melas*) around New Zealand (Markowitz, 2004; Zaeschmar, 2014), in the North Atlantic (Gowans and Whitehead, 1995; Weir et al., 2001), and in the Mediterranean (Cañadas et al., 2002), possibly for similar reasons, although these MSGs have not been investigated in detail.

Off the coast of New Zealand, Bryde's whales (*Balaenoptera edeni*) often follow feeding common dolphin groups and it has been hypothesised that the Bryde's whales benefit from the common dolphins' ability to herd and concentrate epipelagic fish schools (O'Callaghan and Baker, 2002; Burgess, 2006; Stockin et al., 2009). Similarly, in Norway, humpback whales (*Megaptera novaeangliae*) lunge feed on herring schools that are herded by killer whales (Jourdain and Vongraven, 2017). It is hypothesised that in this case, humpback whales benefit from the foraging effort of killer whales who may, in turn, be negatively affected by the interspecific competition for prey (Burgess, 2006; Jourdain and Vongraven, 2017).

Social Advantage Hypothesis

Cetaceans, particularly delphinids, are highly social animals with often complex social structures (Mann et al., 2000; Gowans et al., 2007). Accordingly, there are multiple contrasting social motives that have been hypothesised to lead to both agonistic and affiliative social MSGs involving aggressive, sexual, playful, and caring behaviours (e.g., Herzing and Johnson, 1997; Stensland et al., 2003; Acevedo-Gutiérrez et al., 2005; Parra, 2005; Herzing and Elliser, 2013).

Common bottlenose and Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas are often observed in MSGs, with members engaging in socio-sexual behaviours (Herzing and Johnson, 1997; Melillo et al., 2009; Herzing and Elliser, 2013). These sexual interactions are typically initiated by common bottlenose dolphins, mostly subadults, who may seek copulations with Atlantic spotted dolphins as they are unable to copulate with conspecifics due to their lower intraspecific social status (Melillo et al., 2009). Alternatively, these dolphins may use sexual behaviour to reduce levels of aggression by replacing aggressive interactions with sexual ones (Melillo et al., 2009). Furthermore, male Atlantic spotted and male common bottlenose dolphins have also been observed forming interspecific coalitions (defined as "*the joining of forces by two or more parties during a conflict of interest with other parties*": de Waal and Harcourt, 1992;

TABLE 4 | Pairs of cetacean species observed in mixed-species groups (MSGs) for which the potential functional explanations have been proposed.

Species	Functional explanation(s)	References
Balaenoptera edeni—Delphinus delphis	Foraging	Burgess, 2006; Stockin et al., 2009
Megaptera novaeangliae—Orcinus orca	Foraging	Jourdain and Vongraven, 2017
Megaptera novaeangliae—Tursiops aduncus	Foraging?	Koper and Plön, 2016
Eschrichtius robustus—Tursiops truncatus	Social	Shane, 1994
Delphinus delphis—Grampus griseus	Social?	Frantzis and Herzing, 2002
Delphinus delphis—Stenella coeruleoalba	Social	García et al., 2000; Frantzis and Herzing, 2002
	Foraging	Quérouil et al., 2008
Delphinus delphis—Stenella frontalis	Foraging	Quérouil et al., 2008
Delphinus delphis—Tursiops aduncus	Antipredator?	Koper and Plön, 2016
Delphinus delphis—Tursiops truncatus	Foraging	Quérouil et al., 2008
Globicephala macrorhynchus—Tursiops truncatus	Foraging	Shane, 1994
Grampus griseus—Lagenorhynchus obliquidens	Foraging	Black, 1994; Bacon et al., 2017
Grampus griseus—Lissodelphis borealis	Foraging	Smultea et al., 2014; Bacon et al., 2017
Grampus griseus—Stenella coeruleoalba	Social?	Frantzis and Herzing, 2002
Grampus griseus—Tursiops truncatus	Foraging; social?	Shane, 1994; Hodgins et al., 2014; Bacon et al., 2017
Lagenorhynchus obliquidens—Lissodelphis borealis	Foraging?; antipredator?	Black, 1994
Lissodelphis borealis—Physeter macrocephalus	Foraging	Smultea et al., 2014
Orcaella heinsohni—Sousa sahulensis	Social	Parra, 2005
Pseudorca crassidens—Tursiops truncatus	Foraging; antipredator?; social?	Zaeschmar et al., 2013, 2014
Sotalia guianensis—Tursiops truncatus	Social	Acevedo-Gutiérrez et al., 2005; Thompson, 2010
Sousa plumbea—Tursiops aduncus	Antipredator?; foraging?; social?	Koper and Plön, 2016
Sousa sahulensis—Tursiops aduncus	Foraging?	Corkeron, 1990
Stenella attenuata—Stenella longirostris	Antipredator; social?	Scott and Cattanach, 1998; Psarakos et al., 2003; Kiszka et al., 2011
Stenella coeruleoalba—Stenella frontalis	Foraging	Quérouil et al., 2008
Stenella frontalis—Tursiops truncatus	Social	Herzing and Johnson, 1997; Herzing et al., 2003; Melillo et al., 2009; Elliser and Herzing, 2016a,b
	Foraging	Quérouil et al., 2008
Tursiops truncatus—Physeter macrocephalus	Social	Shane, 1994; Wilson and Krause, 2013

A question mark indicates that the benefit has been hypothesised based on observations but not investigated. References are for studies that proposed functional explanations only, for a full list of references for observations of each species pair, see ***Supplementary Table 2****.*

Herzing and Johnson, 1997), to both chase away other males and pursue females of both species, although subsequent copulation is only intraspecific (Herzing and Johnson, 1997). Additionally, males of these species often engage in sexual interactions with each other (Herzing and Johnson, 1997; Herzing and Elliser, 2013). In these cases, sexual-aggressive behaviours between males and shared pursuits of females may form bonds that later provide a benefit when they form interspecific coalitions during aggressive encounters (Herzing and Johnson, 1997).

Aggressive and sexual behaviours are also typical of MSGs that involve common bottlenose dolphins and Guiana dolphins (*Sotalia guianensis*) along Costa Rica's Caribbean coast (Acevedo-Gutiérrez et al., 2005; May-Collado, 2010). Male common bottlenose dolphins exhibit aggressive behaviours toward Guiana dolphins, such as biting, body slamming, and chasing, seemingly in order to separate female Guiana dolphins from their conspecifics to mate with them (May-Collado, 2010). These observations are supported by photographic evidence and sightings of putative hybrids, although genetic confirmation of hybridisation is required (Acevedo-Gutiérrez et al., 2005). Common and Indo-Pacific (*Tursiops aduncus*) bottlenose dolphins have been observed exhibiting aggressive-sexual behaviours toward Australian (*Sousa sahulensis*) and Indian Ocean humpback dolphins (*Sousa plumbea*) (Saayman et al., 1972; Baldwin et al., 2004; Minton et al., 2010; Ansmann, 2011; Cerchio et al., 2015). Off the coast of Zanzibar, young male Indo-Pacific bottlenose dolphins harass female Indian Ocean humpback dolphins, possibly as a means of practising and developing skills involved in social behaviours in order to increase their social status (Stensland et al., 2003).

Similar interactions occur in northern Australia between Australian humpback dolphins and Australian snubfin dolphins (*Orcaella heinsohni*). In Cleveland Bay, North Queensland, Australian humpback and Australian snubfin dolphins live in sympatry, have overlapping ranges and exhibit interspecies affiliative and aggressive interactions (Parra, 2005, 2006). Aggressive interactions are more frequently observed and are mainly initiated by adult male Australian humpback dolphins, who pursue and seek physical contact with adult female Australian snubfin dolphins. The female Australian snubfin dolphins, often accompanied by calves, attempt to avoid these interactions and flee (Parra, 2005). It is hypothesised that male Australian humpback dolphins may use these interactions as opportunities for physical training or skill development, a function that would have beneficial effects for interactions with female conspecifics (Parra, 2005). This is similar to what has been suggested for incidences of male common bottlenose dolphins attacking and killing harbour porpoises (*Phocoena phocoena*) in Scotland and California (Patterson et al., 1998; Cotter et al., 2012).

Affiliative behaviours, including interspecific alloparenting are also occasionally recorded. Herzing and Johnson (1997), for example, reported two cases from the Bahamas of adult female Atlantic spotted dolphins swimming with common bottlenose dolphin calves. In New Zealand, Markowitz (2004) observed a short-term association of a calf common dolphin and an adult dusky dolphin (*Lagenorhynchus obscurus*) while Stensland et al. (2003) refer to an observation of an Indian Ocean humpback dolphin calf that travelled for several hours with a large group of Indo-Pacific bottlenose dolphin mothers and calves in Zanzibar. It is not known, however, whether these social behaviours are isolated events or if they represent broader patterns of interspecific behaviour.

Mixed-species social behaviours may also be driven by a lack of conspecifics. In the Mediterranean Sea, common dolphins regularly form MSGs with striped dolphins (e.g., Forcada et al., 1994; Cañadas and Hammond, 2008; Bearzi et al., 2011; Santoro et al., 2015; Santostasi et al., 2016) and, on occasion, Risso's dolphins (e.g., Cañadas et al., 2002; Frantzis and Herzing, 2002; Bearzi et al., 2016) and common bottlenose dolphins (e.g., Ryan et al., 2014; Pace et al., 2015; Espada et al., 2019). Common dolphin populations in the Mediterranean Sea have declined dramatically since the 1980s (Bearzi et al., 2003) and, in areas where they are now uncommon, the frequency of MSGs is higher (Frantzis and Herzing, 2002). It has, therefore, been suggested that the lack of interactions with conspecifics might be an important driver of the formation of MSGs in this region. Interactions between common dolphins and other species appear to be mainly socially driven (García et al., 2000; Frantzis and Herzing, 2002) and there are numerous records of hybrid individuals between common and striped dolphins (Bearzi et al., 2011; Santostasi et al., 2016; Antoniou et al., 2018; Bonizzoni et al., 2019) and between common and common bottlenose dolphins (Espada et al., 2019).

DISCUSSION

Many species of cetaceans in a variety of habitats have been reported to form MSGs, potentially due to the evolutionary benefits (antipredator, foraging, and social) they may gain. The studies on cetacean MSGs reviewed here often used terminology inconsistently and most did not confirm that observed sets of individuals did indeed form MSGs, rather than mere chance encounters or aggregations. Thus, we cannot be certain that all the records in this review truly represent MSGs, however, because they are potentially MSGs, they were included and treated as such. Furthermore, many studies lacked the thorough testing of hypotheses that is required to determine the potential functional explanations of the observed MSGs.

To better understand the incidence and ecological role of cetacean MSGs, we need to go beyond descriptive accounts and investigate the behavioural and ecological drivers of their formation (Stensland et al., 2003). We reviewed the literature on cetacean MSGs to: address inconsistencies in terminology; assess their characteristics (e.g., species involved, location, frequency); and evaluate what is known about their functional role. Finally, we discuss the results of this review and propose a standardised terminology and a conceptual framework to assist future research (**Figure 6**).

Current Knowledge on Cetacean Mixed-Species Groups

Amongst the cetacean species that have been reported in MSGs, delphinids are the most frequently involved and the ones with the most diversity of partner species. The dynamic and fluid social structure of many delphinid species could potentially facilitate the formation of MSGs (Stensland et al., 2003) as could a higher risk of predation when compared to the larger cetaceans, such as the baleen whales. Cetacean species with broad distributions centred on the sub-tropics and the warm temperate zone, such as the common bottlenose dolphin, also appear to be disproportionately represented, with more records of participation in MSGs and more partner species. This is possibly a result of their abundance and widespread distribution bringing them often into contact with a range of other cetacean species. These species are also, however, amongst the most studied (Wells and Scott, 2009), while many of those that are rarely, or never, reported in MSGs, such as the beaked whales, are poorly studied (MacLeod, 2018). Consequently, these results may not reflect the true composition and diversity of cetacean MSGs and may be influenced by the greater research effort dedicated to certain species.

Most of the 216 species pairs that were reported in MSGs were composed of two delphinids, however, there was considerable variation in the relatedness, morphology, and behaviour of partner species. Some MSGs were composed of pairs of closely related and morphologically similar species, such as pantropical spotted and spinner dolphins (e.g., Scott and Cattanach, 1998; Kiszka et al., 2011), while others consisted of distant and dissimilar species, such as common dolphins and Bryde's whales (e.g., Burgess, 2006; Stockin et al., 2009; Penry et al., 2011). Furthermore, some species pairs were frequently reported together (e.g., common dolphin—striped dolphin and spinner dolphin—pantropical spotted dolphin) (**Table 3**), while others (e.g., common bottlenose dolphin—dusky dolphin) have been rarely, if ever, observed together in MSGs (Würsig and Würsig, 1979; Markowitz, 2004). Most cetacean species pairs belonged to different genera but the same family and suborder, suggesting that a moderate level of dissimilarity between cetacean species is favourable to MSG formation. This is in accordance with research on other taxa, including primates and birds, where it has been shown that optimum levels of dissimilarity in characteristics such as diet, habitat use, and body size increase the frequency of MSG occurrence (Heymann and Buchanan-Smith, 2000; Sridhar et al., 2009; Heymann and Hsia, 2015; Sridhar and Guttal, 2018). Currently, however, it is not well understood which are the biological factors that determine if and how often cetacean

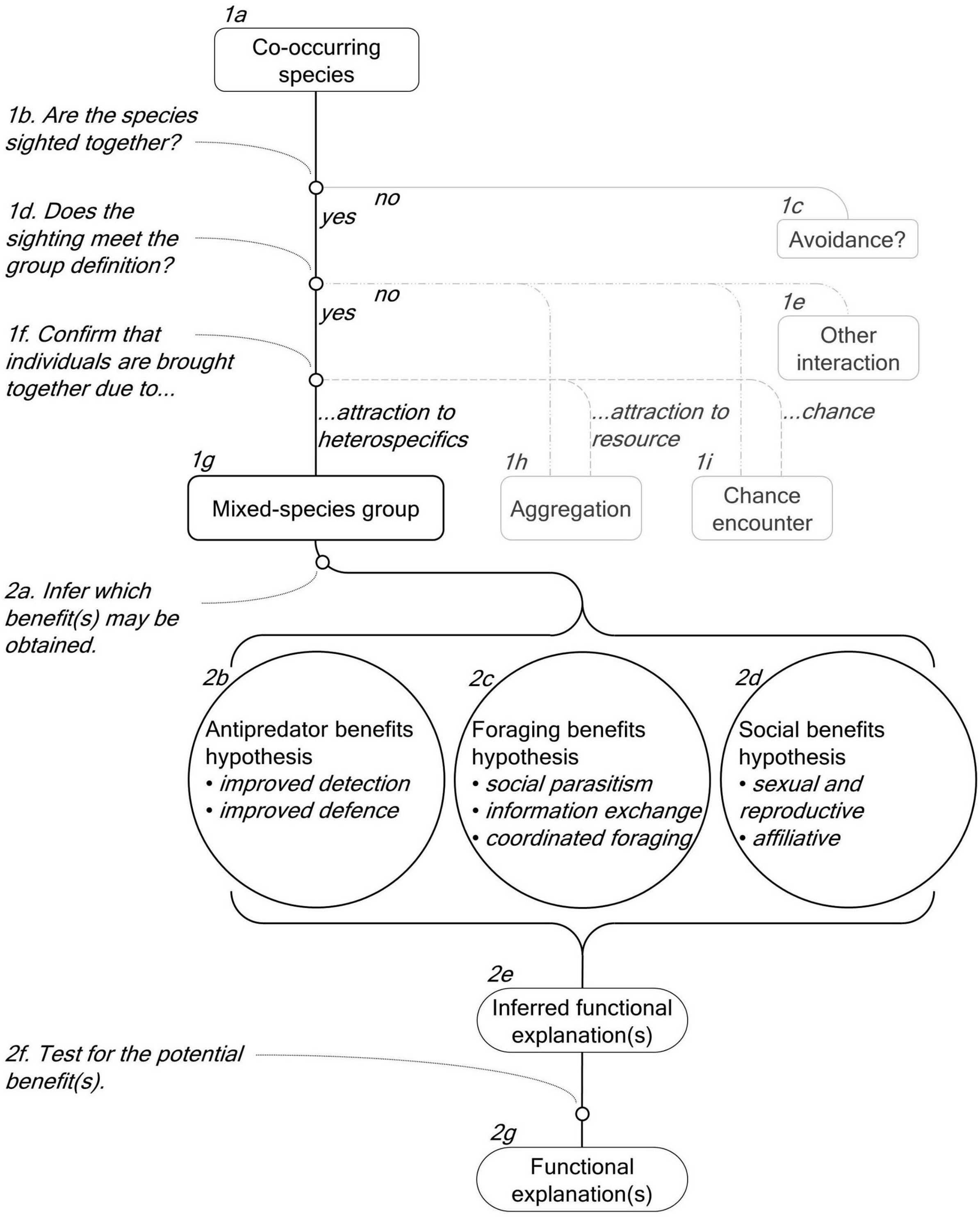


FIGURE 6 | A conceptual framework for studying cetacean mixed-species groups (MSGs). The framework details the steps required to determine that the species form a MSG (Boxes 1b, 1d, and 1f) and to establish the potential function(s) of the MSG (Boxes 2a and 2f).

species form MSGs, but future analysis of the similarities and dissimilarities in corresponding characteristics between pairs of cetacean species could provide insight into this question.

It is apparent that MSGs are formed by both inshore and offshore species of cetaceans in a variety of habitats, however, the lack of available information regarding the distribution and grouping dynamics of cetacean MSGs makes it challenging to establish any detailed patterns. We can, nonetheless, observe several potential trends pertaining to the influence of environmental factors. Water depth and distance to shore appear to affect MSGs in the same way they do SSGs (Wells et al., 1980), with coastal species often forming small groups of 5–20 individuals (e.g., Herzing and Johnson, 1997; Acevedo-Gutiérrez et al., 2005; Thompson, 2010) and oceanic species forming large groups of hundreds and even thousands (e.g., Hill and Barlow, 1992; Wade and Gerrodette, 1993; Scott and Cattanach, 1998; Appler et al., 2004; Dulau-Drouot et al., 2008). For some species, such as the common bottlenose dolphin, MSGs have been shown to be more common in oceanic waters (Scott and Chivers, 1990). Potentially higher predation risk offshore may drive certain species to form larger groups (Gygax, 2002a) including MSGs when faced with a low abundance of conspecifics. However, some species that inhabit shallow coastal waters also frequently form MSGs (e.g., Herzing and Johnson, 1997; Acevedo-Gutiérrez et al., 2005; Thompson, 2010), so the drivers of MSG formation likely vary across taxa and habitats. Cetacean MSGs were most commonly reported in the North Pacific and North Atlantic, potentially due to the higher species diversity within those areas (Kaschner et al., 2011; Pompa et al., 2011), although this result may also be influenced by uneven research effort (Kaschner et al., 2012).

A Conceptual Framework for Investigating the Functional Significance of Cetacean Mixed-Species Groups

To facilitate future studies, we use the results of this review to propose a standardised terminology and a conceptual framework that (1) defines and characterises cetacean MSGs (**Figure 6**, Boxes 1a-1i) and (2) details how to investigate their functions by testing relevant hypotheses (**Figure 6**, Boxes 2a-2g).

Defining and Characterising Cetacean Mixed-Species Groups

After evaluating the terms and definitions used in the reviewed studies and the underlying processes involved in the formation of MSGs, we propose to expand on the definition provided by Stensland et al. (2003) (**Table 1**). This definition considered a MSG to be a set of individuals of two or more species that are seen in such close association that they can be regarded as members of the same group.

Firstly, the application of this definition to MSGs requires an explicit definition of *group* that contains rules that can be applied in field research settings (**Figure 6**, Box 1d). Definitions of *group* should be biologically meaningful and consistent across species and studies (Krause and Ruxton, 2002; Whitehead, 2008). However, what defines a cetacean group remains a contentious and unresolved issue (Connor et al., 1998, 2000; Gibson and Mann, 2009). The spatial proximity of individuals is the most often used criterion for determining group membership along with behaviour and directionality, although there is considerable variation in how each of these criteria is applied (Whitehead, 2008; Gibson and Mann, 2009). In the studies obtained by this literature review the threshold distances for delimiting group membership ranged from 10 to 1,000 m. In the broader cetacean literature, commonly used definitions are equally varied and include: a 10 m chain rule (Smolker et al., 1992); a 100 m fixed point rule (Irvine et al., 1981); and individuals "in apparent association, moving in the same direction and often, but not always, engaged in the same activity" (Shane, 1990). The inconsistency in definitions of group causes confusion and weakens comparisons between studies, yet, as it stands, there is no clear solution to this problem. Dedicated work on this subject is needed to, firstly, determine how groups are defined in the cetacean literature and to, secondly, formulate biologically meaningful definitions via quantitative analyses of parameters such as inter-individual distances or the coordination between individuals (Krause and Ruxton, 2002; Croft et al., 2008; Whitehead, 2008). Until such work is done, we recommend that studies of cetacean MSGs explicitly state the definition used and any justification for their choice.

Secondly, we emphasise that, as a type of group, MSGs provide evolutionary benefits to at least some participants and are consequently formed and maintained by a mutual or unreciprocated attraction between individuals. Therefore, they should be distinguished from chance encounters that occur at random and aggregations of individuals that are attracted toward a common resource or that respond to the same environmental stimuli (Waser, 1982; Powell, 1985; Whitesides, 1989; Goodale et al., 2017; **Figure 6**, Box 1f). Null models can be used to assess whether sightings of multiple species in close proximity correspond to non-random patterns. For example, gas models and computer simulations recreate the movement of individuals in their environment and can be used to test whether encounter rates and durations occur at random or not (**Figure 6**, Box 1f; Waser, 1982; Whitesides, 1989; Hutchinson and Waser, 2007). Such approaches are all but absent from studies of cetaceans, likely because they require input data regarding the travel speed and diameter of groups that may be difficult to acquire (Cords and Würsig, 2014). Nevertheless, these data could be obtained through dedicated studies that incorporate group focal follows and technologies that facilitate their acquisition such as unmanned aerial vehicles (UAVs), satellite tracking, and theodolite observations.

Analyses of individual association patterns can be conducted on multiple species, provided that individuals of each species can be feasibly identified (Farine et al., 2012; Zaeschmar et al., 2014; Elliser and Herzing, 2016b). Null models can be used to analyse these networks in order to determine if individuals display non-random patterns of association and, therefore, are not found together by chance (Whitehead, 2008; Farine, 2017). Additionally, by accounting for alternate factors that may bring individuals together, such as spatial overlap or shared resource use, it is possible to determine the influence that social preference (i.e., attraction and avoidance) has on observed patterns of association (Whitehead, 2008; Farine, 2017). This has been done for single-species social networks and could be done on a mixed-species basis (Frère et al., 2010; Farine et al., 2012; Strickland et al., 2017; Zanardo et al., 2018; Hunt et al., 2019; Diaz-Aguirre et al., 2020). In this case, evidence of strong and/or preferential associations between individuals of different species after alternate factors are taken into account would be indicative of attraction between individuals, suggesting that the species form groups and not aggregations (**Figure 6**, Box 1f).

Alternative modelling approaches include occupancy modelling based on presence/absence data, which can be used to analyse species co-occurrence patterns to determine if there is avoidance or attraction between co-occurring species (Richmond et al., 2010; MacKenzie et al., 2017). Where such modelling is not practical, alternative criteria can be used. For example, situations where species are observed together for less than a minimum time limit can be considered to have occurred by chance (Kiszka et al., 2011; Jourdain and Vongraven, 2017). Such time limits may be arbitrary, but, alternatively, could be based on a comparison of the duration of single-species groups (SSGs) and MSGs.

Thirdly, although the overall attraction amongst participants in a MSG may be mutual or unreciprocated, the presence of each species must be tolerated by the other (Stensland et al., 2003). Consequently, there are several interspecific relationships that we do not consider to fall within the scope of MSGs because they exclusively involve agonistic interactions where species do not congregate for the purpose of group formation (**Figure 6**, Box 1e). More specifically, we exclude predator-prey relationships, competition-based relationships (e.g., Shane, 1995), and incidences where heterospecifics are used as "objects" in object-oriented play (e.g., Baird, 1998; Patterson et al., 1998; Cotter et al., 2012). MSGs that, on occasion, involve agonistic behaviours, but that also involve affiliative and neutral behaviours (e.g., Herzing and Johnson, 1997; Acevedo-Gutiérrez et al., 2005) are not excluded. Finally, we recommend the use of the term *mixed-species group* rather than other terms such as *interspecific*, *polyspecific*, or *heterospecific group* or *association*, as it was the most commonly employed in the studies that we reviewed and is also widely applied in the study of other taxa (Stensland et al., 2003; Goodale et al., 2017).

In summary, we define a MSG as individuals of two or more species found in close spatial proximity due to a mutual or unreciprocated attraction derived from evolutionary grouping benefits. MSGs may involve affiliative, neutral, and agonistic behaviours excluding instances of predation, competition, and heterospecific "object" play.

Investigating the Functional Explanations for Cetacean MSG Formation

Once it has been established that the occurrence of different species of cetaceans in close proximity does represent a MSG, and not a chance encounter nor an aggregation, the next step should be to investigate what drives species to group (**Figure 6**, Box 2a). Throughout any investigation, all three functional explanations (**Figure 6**, Boxes 2b-2d) should ideally be considered for each species involved as the functional explanations are not mutually exclusive and each species will not necessarily obtain the same benefits and costs (Stensland et al., 2003; Goodale et al., 2017). Furthermore, it is best to independently consider and compare MSGs to SSGs of each species because the differences between them will demonstrate how participation in MSGs affects each species' biology, in turn revealing what drives them to form MSGs (Sridhar and Guttal, 2018).

To investigate the function of cetacean MSGs, one needs to identify which benefits each species may obtain by analysing ecological, behavioural, and group characteristic data that are relevant to each hypothesis being tested. This should begin with reviewing the existing knowledge of each species' ecology and grouping dynamics through the perspective of the theory on MSG formation to evaluate which functional explanations are more probable. Data should then be obtained directly from the study populations, including species distributions and abundance, group characteristics (e.g., size, composition, and cohesiveness), encounter rates, and behaviour (e.g., behavioural states, events, and transitions) of both SSGs and MSGs. These data should be combined with relevant environmental (e.g., depth, habitat, and distance to shore) (Scott and Chivers, 1990; Kiszka et al., 2011), food availability (e.g., distribution, abundance, and prey biomass), predation risk (e.g., predator distribution and abundance), and temporal data (e.g., time of day, season, and group duration). This will enable the identification of important factors for MSG formation and can be indicative of the functional explanations for MSGs formation, as detailed in the following sections.

Data on cetacean distribution, abundance, grouping dynamics, and behaviour may be obtained by dedicated boat- and land-based surveys with appropriate sampling protocols and, potentially, the integration of new technologies such as UAVs, acoustic recording, and biologging (Nowacek et al., 2016; Andrews et al., 2019). These technologies provide great potential to acquire data that are relevant to investigations of potential functional explanations but remain underutilised in the study of cetacean MSGs. For example, radio-tags have been used to record the location and diving patterns of dolphins and the tuna that associate with them to track and compare the movements and behaviours of the different species (Scott et al., 2012). Innovative approaches and new technologies, such as those listed above (Nowacek et al., 2016), may also allow the direct measurement of parameters that are indicative of any benefits (e.g., predation attempts and successes, prey capture success rate, food intake rate, reproductive success, and social standing). This would make it possible to confirm that a benefit is gained by determining if these parameters are affected by MSG participation. Here, we discuss several analytical approaches and present potential results which lend support to each of the three principal hypotheses for MSG formation. Each of these approaches presents its own unique challenges that may make them practically and financially unfeasible in certain situations. Therefore, we provide a range of suggestions and entrust to researchers the decision of which approaches are most suitable to be implemented in their studies.

Antipredator Advantage Hypothesis

Individuals are more likely to form MSGs for antipredator benefits (**Figure 6**, Box 2b) when the perceived risk of predation is high and when other avoidance tactics cannot be used (e.g., use of safer habitats, formation of large SSGs). Increased MSG size can be indicative of increased group vigilance and, therefore, decreased predation risk for individuals involved in MSGs (Herzing and Johnson, 1997; Scott and Cattanach, 1998; Gygax, 2002b; Majolo et al., 2008; Melillo et al., 2009; Kiszka et al., 2011). A shift to habitat with a higher perceived predation risk when in MSGs compared to SSGs also supports the antipredator benefits hypothesis, as does increased travelling and resting behaviours (Kiszka et al., 2011). Additionally, a predation risk landscape, based on the distribution of predators or bite scars on each species, could be employed to determine how predation risk, potentially combined with environmental factors, influences the prevalence and characteristics of MSGs. Playback experiments and biologging have been employed to record the reactions of SSGs of cetaceans to the simulated presence of potential predators (Curé et al., 2012, 2019; Bowers et al., 2018) and similar experiments could be undertaken to determine if simulated predator presence increases the propensity of species to form MSGs, as has been done for primates (Noë and Bshary, 1997). Finally, and although it is undoubtedly a logistical challenge, the level of predation risk would ideally be compared between SSGs and MSGs by recording failed and successful predation attempts or by analysing individual vigilance rates as a measure of perceived predation risk (Wolters and Zuberbühler, 2003; Sridhar et al., 2009; Stojan-Dolar and Heymann, 2010).

Foraging Advantage Hypothesis

Co-occurring species may form MSGs in order to gain potential foraging benefits (**Figure 6**, Box 2c; Smultea et al., 2014; Sridhar and Guttal, 2018). A high or increased prevalence of feeding when in MSGs argues in favour of this hypothesis (Quérouil et al., 2008; Zaeschmar et al., 2014; Bacon et al., 2017), as do observations of species foraging together or following foraging heterospecifics (Shane, 1994; Burgess, 2006; Zaeschmar et al., 2013; Smultea et al., 2014; Bacon et al., 2017; Jourdain and Vongraven, 2017). Evidence, from playback experiments incorporating biologging or UAVs, that a species is attracted to vocalisations of foraging heterospecifics could also be indicative of a foraging benefit (Suzuki and Kutsukake, 2017). Rates of prey capture success and energy intake have been used in studies of primates and birds to determine whether the presence of heterospecifics increases feeding success (Peres, 1992; Sridhar et al., 2009). The use of underwater video of feeding events, potentially recorded with a camera integrated into a biologger (Pearson et al., 2019; Linsky et al., 2020), could allow this, although the difficulties and costs would be considerable. For species that are assumed to improve foraging when in MSGs, one could record and compare the time that individuals spend searching for food when in SSGs and MSGs to see if search time is reduced when heterospecifics are present.

Social Advantage Hypothesis

Species that may gain social benefits (**Figure 6**, Box 2d) typically exhibit high or increased levels of social activity when in MSGs compared to when they are in SSGs (Herzing and Johnson, 1997; García et al., 2000; Acevedo-Gutiérrez et al., 2005; Melillo et al., 2009), while a lack of social interactions argues against this hypothesis (Quérouil et al., 2008; Kiszka et al., 2011). Additionally, the presence of aggressive (e.g., tail slaps and open-mouth postures), sexual (e.g., erections, mating, and presence of hybrids), and affiliative behaviours (e.g., alloparental care, play, and non-aggressive body contact) provides evidence of social benefits and may also assist in unravelling the complexity of social interactions by providing insight into their nature (Herzing and Johnson, 1997; Acevedo-Gutiérrez et al., 2005; Parra, 2005; Melillo et al., 2009). Increased group size of MSGs can also be related to social behaviour (Acevedo-Gutiérrez et al., 2005) while a preferential attraction to the vocalisations of socialising heterospecifics (demonstrated with playback experiments) would be expected from species that form MSGs to obtain social benefits. Social advantages are more difficult to quantify and measure (Stensland et al., 2003), however, from a long-term study, it may be possible to record and compare the mating and reproductive success or the social status of individuals with regard to how often they are observed interacting with heterospecifics.

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

Our findings show that cetacean MSGs are potentially diverse and complex in various aspects: the species involved, the habitats where they occur, their frequency, and their ecological functions. There are, however, two main impediments to the advancement of our understanding of cetacean MSGs: (1) inconsistent terminology and the lack of approaches to distinguish them from mere aggregations and chance encounters and (2) the lack of studies designed to investigate their dynamics and function. We believe that our proposed terminology and conceptual framework can aid in overcoming these impediments by serving as a guide for future studies of cetacean MSGs. Thus, we strongly encourage our colleagues to employ this framework and to improve upon it as new information and technological developments become available. Research on MSGs of terrestrial species has, so far, led the way by developing the theoretical basis for MSG formation, by detailing ideal approaches for their investigation, and by revealing the broader influence that MSGs can have on the behaviour and ecology of the species involved (Stensland et al., 2003; Sridhar et al., 2009; Goodale et al., 2020). By conducting detailed and structured investigations of cetacean MSGs, we will likewise be able to further unravel their ecological functions and improve our understanding of the role that they play in community ecology.

AUTHOR CONTRIBUTIONS

JS conducted the literature review and data analysis with advice from GP and JK. JS wrote the manuscript with contributions to drafting, critical review, and editorial input from GP and JK. All authors conceived and designed the study.

FUNDING

JS was the recipient of a Flinders University Postgraduate Scholarship while conducting this work.

ACKNOWLEDGMENTS

We would like to thank the reviewers for their comments which helped to improve this work and Flinders University for providing funding. This is contribution #274 of the Coastal and Oceans Division within the Institute of Environment at Florida International University.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.678173/full#supplementary-material

REFERENCES

Acevedo-Gutiérrez, A., DiBerardinis, A., Larkin, S., Larkin, K., and Forestell, P. (2005). Social interactions between tucuxis and bottlenose dolphins in Gandoca-Manzanillo, Costa Rica. *Lat. Am. J. Aquat. Mamm.* 4, 49–54. doi: 10.5597/lajam00069

Alexander, R. D. (1974). The evolution of social behavior. *Annu. Rev. Ecol. Syst.* 5, 325–383. doi: 10.1146/annurev.es.05.110174.001545

Alves, F., Ferreira, R., Fernandes, M., Halicka, Z., Dias, L., and Dinis, A. (2018). Analysis of occurrence patterns and biological factors of cetaceans based on long-term and fine-scale data from platforms of opportunity: Madeira Island as a case study. *Mar. Ecol.* 39:e12499. doi: 10.1111/maec.12499

Anderson, R. C. (2005). Observations of cetaceans in the Maldives, 1990-2002. *J. Cetacean Res. Manag.* 7, 119–135.

Anderson, R. C., Clark, R., Madsen, P. T., Johnson, C., Kiszka, J., and Breysse, O. (2006). Observations of Longman's beaked whale (*Indopacetus pacificus*) in the Western Indian Ocean. *Aquat. Mamm.* 32, 223–231. doi: 10.1578/am.32.2.2006.223

Andrews, R. D., Baird, R. W., Calambokidis, J., Goertz, C. E. C., Gulland, F. M. D., Heide-Jørgensen, M. P., et al. (2019). Best practice guidelines for cetacean tagging. *J. Cetacean Res. Manag.* 20, 27–66. doi: 10.47536/JCRM.V20I1.237

Ansmann, I. C. (2011). *Fine-Scale Population Structure of Indo-Pacific Bottlenose Dolphins, Tursiops aduncus, in Moreton Bay, Queensland, Australia*. Doctor of Philosophy. Australia: The University of Queensland.

Antoniou, A., Frantzis, A., Alexiadou, P., Paschou, N., and Poulakakis, N. (2018). Evidence of introgressive hybridization between *Stenella coeruleoalba* and *Delphinus delphis* in the Greek Seas. *Mol. Phylogenet. Evol.* 129, 325–337. doi: 10.1016/j.ympev.2018.09.007

Appler, J., Barlow, J., and Rankin, S. (2004). *Marine mammal data collected during the Oregon, California, and Washington Line-Transect Expedition (ORCAWALE) conducted aboard the NOAA ships McArthur and David Starr Jordan, July - December 2001*. La Jolla, CA: National Oceanic and Atmospheric Administration.

Au, D., and Perryman, W. (1985). Dolphin habitats in the eastern Tropical Pacific. *Fish. Bull.* 83, 623–644.

Bacon, C. E., Smultea, M. A., Fertl, D., Würsig, B., Burgess, E. A., and Hawks-Johnson, S. (2017). Mixed-species associations of marine mammals in the Southern California bight, with emphasis on Risso's dolphins (*Grampus griseus*). *Aquat. Mamm.* 43, 177–184. doi: 10.1578/AM.43.2.2017.177

Baird, R. W. (1998). An interaction between Pacific white-sided dolphins and a neonatal harbor porpoise. *Mammalia* 62, 129–134.

Baird, R. W., Gorgone, A. M., McSweeney, D. J., Webster, D. L., Salden, D. R., Deakos, M. H., et al. (2008). False killer whales (*Pseudorca crassidens*) around the main Hawaiian Islands: Long-term site fidelity, inter-island movements, and association patterns. *Mar. Mamm. Sci.* 24, 591–612. doi: 10.1111/j.1748-7692.2008.00200.x

Baldwin, R. M., Collins, M., Van Waerebeek, K., and Minton, G. (2004). The Indo-Pacific Humpback Dolphin of the Arabian Region: A Status Review. *Aquat. Mamm.* 30, 111–124. doi: 10.1578/am.30.1.2004.111

Ballance, L. T., and Pitman, R. L. (1998). Cetaceans of the western tropical Indian Ocean: Distribution, relative abundance, and comparisons with cetacean communities of two other tropical ecosystems. *Mar. Mamm. Sci.* 14, 429–459. doi: 10.1111/j.1748-7692.1998.tb00736.x

Bearzi, G., Bonizzoni, S., Agazzi, S., Gonzalvo, J., and Currey, R. J. C. (2011). Striped dolphins and short-beaked common dolphins in the Gulf of Corinth, Greece: Abundance estimates from dorsal fin photographs. *Mar. Mamm. Sci.* 27, E165-E184. doi: 10.1111/j.1748-7692.2010.00448.x

Bearzi, G., Bonizzoni, S., Santostasi, N. L., Furey, N. B., Eddy, L., Valavanis, V. D., et al. (2016). Dolphins in a Scaled-Down Mediterranean: The Gulf of Corinth's Odontocetes. *Adv. Mar. Biol.* 75, 297–331. doi: 10.1016/bs.amb.2016.07.003

Bearzi, G., Reeves, R. R., Notarbartolo-Di-Sciara, G., Politi, E., Canadas, A., Frantzis, A., et al. (2003). Ecology, status and conservation of short-beaked common dolphins *Delphinus delphis* in the Mediterranean Sea. *Mamm. Rev.* 33, 224–252. doi: 10.1046/j.1365-2907.2003.00032.x

Bearzi, M. (2005a). Aspects of the ecology and behaviour of bottlenose dolphins (*Tursiops truncatus*) in Santa Monica Bay, California. *J. Cetacean Res. Manag.* 7, 75–83.

Bearzi, M. (2005b). Dolphin sympatric ecology. *Mar. Biol. Res.* 1, 165–175. doi: 10.1080/17451000510019132

Bearzi, M. (2006). California sea lions use dolphins to locate food. *J. Mamm.* 87, 606–617. doi: 10.1644/04-MAMM-A-115R4.1

Bearzi, M., and Saylan, C. A. (2011). Cetacean ecology for Santa Monica Bay and nearby areas, California, in the context of the newly established MPAs. *Bull. South. Calif. Acad. Sci.* 110, 35–51. doi: 10.3160/10-12.1

Black, N. A. (1994). *Behavior and ecology of Pacific white-sided dolphins (Lagenorhynchus obliquidens) in Monterey Bay, California*. Master of Science. California: San Francisco State University.

Bonizzoni, S., Furey, N. B., Santostasi, N. L., Eddy, L., Valavanis, V. D., and Bearzi, G. (2019). Modelling dolphin distribution within an important marine mammal area in Greece to support spatial management planning. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 29, 1665–1680. doi: 10.1002/aqc.3148

Bowers, M. T., Friedlaender, A. S., Janik, V. M., Nowacek, D. P., Quick, N. J., Southall, B. L., et al. (2018). Selective reactions to different killer whale call categories in two delphinid species. *J. Exp. Biol.* 221, 1–12. doi: 10.1242/jeb.162479

Burgess, E. A. (2006). *Foraging Ecology of Common Dolphins (Delphinus sp.) in the Hauraki Gulf, New Zealand*. Master of Science. Auckland: Massey University.

Cañadas, A., and Hammond, P. S. (2008). Abundance and habitat preferences of the short-beaked common dolphin *Delphinus delphis* in the southwestern Mediterranean: Implications for conservation. *Endanger. Species Res.* 4, 309–331. doi: 10.3354/esr00073

Cañadas, A., Sagarminaga, R., and García-Tiscar, S. (2002). Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. *Deep. Res. Part I Oceanogr. Res. Pap.* 49, 2053–2073. doi: 10.1016/S0967-0637(02)00123-1

Cerchio, S., Andrianarivelo, N., and Andrianantenaina, B. (2015). "Ecology and conservation status of indian ocean humpback dolphins (Sousa plumbea) in Madagascar," in *Advances in Marine Biology*, eds T. A. Jefferson and B. E. Curry (San Diego, California: Academic Press), 163–199. doi: 10.1016/bs.amb.2015.09.004

Committee on Taxonomy (2020). *List of marine mammal species and subspecies*. Available Online at: https://marinemammalscience.org/science-and-publications/list-marine-mammal-species-subspecies/ [Accessed December 11, 2020].

Connor, R. C., Mann, J., Tyack, P. L., and Whitehead, H. (1998). Social evolution in toothed whales. *Trends Ecol. Evol.* 13, 228–232. doi: 10.1016/S0169-5347(98)01326-3

Connor, R., Wells, R., Mann, J., and Read, A. (2000). "The bottlenose dolphin: Social relationships in a fission-fusion society" in *Cetacean Societies: Field Studies of Whales and Dolphins*, eds J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead (Chicago, IL: The University of Chicago Press), 91–126.

Cords, M., and Würsig, B. (2014). "A Mix of species: associations of heterospecifics among primates and dolphins," in *Primates and Cetaceans: Field Research and Conservation of Complex Mammalian Societi*es, eds J. Yamagiwa and L. Karczmarski (Tokyo: Springer Japan), 409–431. doi: 10.1007/978-4-431-54523-1_21

Corkeron, P. J. (1990). "Aspects of the behavioral ecology of inshore dolphins *Tursiops truncatus* and *Sousa chinensis* in Moreton Bay, Australia," in *The Bottlenose Dolphin*, eds S. Leatherwood and R. R. Reeves (San Diego, California: Academic Press, Inc.), 285–293. doi: 10.1016/b978-0-12-440280-5.50018-4

Cotter, M. P., Maldini, D., and Jefferson, T. A. (2012). "Porpicide" in California: killing of harbor porpoises (*Phocoena phocoena*) by coastal bottlenose dolphins (*Tursiops truncatus*). *Mar. Mamm. Sci.* 28, E1–E15. doi: 10.1111/j.1748-7692.2011.00474.x

Croft, D. P., James, R., and Krause, J. (2008). *Exploring Animal Social Networks*. Princeton: Princeton University Press.

Curé, C., Antunes, R., Samarra, F., Alves, A. C., Visser, F., Kvadsheim, P. H., et al. (2012). Pilot whales attracted to killer whale sounds: acoustically-mediated interspecific interactions in cetaceans. *PLoS One* 7:e52201. doi: 10.1371/journal.pone.0052201

Curé, C., Isojunno, S., I. Vester, H., Visser, F., Oudejans, M., Biassoni, N., et al. (2019). Evidence for discrimination between feeding sounds of familiar fish and unfamiliar mammal-eating killer whale ecotypes by long-finned pilot whales. *Anim. Cogn.* 22, 863–882. doi: 10.1007/s10071-019-01282-1

de Waal, F. B. M., and Harcourt, A. H. (1992). *Coalitions and Alliances in Humans and Other Animals*. eds A. H. Harcourt and F. B. M. de Waal Oxford: Oxford University Press.

Di Tullio, J. C., Gandra, T. B. R., Zerbini, A. N., and Secchi, E. R. (2016). Diversity and distribution patterns of cetaceans in the subtropical Southwestern Atlantic outer continental shelf and slope. *PLoS One* 11:e0155841. doi: 10.1371/journal.pone.0155841

Diaz-Aguirre, F., Parra, G. J., Passadore, C., and Möller, L. (2020). Kinship and reproductive condition correlate with affiliation patterns in female southern Australian bottlenose dolphins. *Sci. Rep.* 10:1891. doi: 10.1038/s41598-020-58800-2

Dulau-Drouot, V., Boucaud, V., and Rota, B. (2008). Cetacean diversity off La Réunion Island (France). *J. Mar. Biol. Assoc. U.K.* 88, 1263–1272. doi: 10.1017/S0025315408001069

Elliser, C. R., and Herzing, D. L. (2016a). Changes in interspecies association patterns of Atlantic bottlenose dolphins, *Tursiops truncatus*, and Atlantic spotted dolphins, *Stenella frontalis*, after demographic changes related to environmental disturbance. *Mar. Mamm. Sci.* 32, 602–618. doi: 10.1111/mms.12289

Elliser, C. R., and Herzing, D. L. (2016b). Long-term interspecies association patterns of Atlantic bottlenose dolphins, *Tursiops truncatus*, and Atlantic spotted dolphins, *Stenella frontalis*, in the Bahamas. *Mar. Mamm. Sci.* 32, 38–56. doi: 10.1111/mms.12242

Espada, R., Olaya-Ponzone, L., Haasova, L., Martín, E., and García-Gómez, J. C. (2019). Hybridization in the wild between *Tursiops truncatus* (Montagu 1821) and *Delphinus delphis* (Linnaeus 1758). *PLoS One* 14:e0215020. doi: 10.1371/journal.pone.0215020

Evans, P. (1982). Associations between seabirds and cetaceans: a review. *Mamm. Rev.* 12, 187–206. doi: 10.1111/j.1365-2907.1982.tb00015.x

Farine, D. R. (2017). A guide to null models for animal social network analysis. *Methods Ecol. Evol.* 8, 1309–1320. doi: 10.1111/2041-210X.12772

Farine, D. R., Garroway, C. J., and Sheldon, B. C. (2012). Social network analysis of mixed-species flocks: Exploring the structure and evolution of interspecific social behaviour. *Anim. Behav.* 84, 1271–1277. doi: 10.1016/j.anbehav.2012.08.008

Fauth, J. E., Bernardo, J., Camara, M., Resetarits, W. J., Van Buskirk, J., and McCollum, S. A. (1996). Simplifying the jargon of community ecology: A conceptual approach. *Am. Nat.* 147, 282–286. doi: 10.1086/285850

Forcada, J., Aguilar, A., Hammond, P. S., Pastor, X., and Aguilar, R. (1994). Distribution and numbers of striped dolphins in the western Mediterranean Sea after the 1990 epizootic outbreak. *Mar. Mamm. Sci.* 10, 137–150. doi: 10.1111/j.1748-7692.1994.tb00256.x

Frantzis, A., and Herzing, D. (2002). Mixed-species associations of striped dolphins (*Stenella coeruleoalba*), short-beaked common dolphins (*Delphinus delphis*), and Risso's dolphins (*Grampus griseus*) in the Gulf of Corinth (Greece, Mediterranean Sea). *Aquat. Mamm.* 28, 188–197.

Frère, C. H., Krützen, M., Mann, J., Watson-Capps, J. J., Tsai, Y. J., Patterson, E. M., et al. (2010). Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. *Anim. Behav.* 80, 481–486. doi: 10.1016/j.anbehav.2010.06.007

Gannier, A. (2000). Distribution of cetaceans off the Society Islands (French Polynesia) as obtained from dedicated surveys. *Aquat. Mamm.* 26, 111–126.

Gannier, A. (2009). Comparison of odontocete populations of the Marquesas and Society Islands (French Polynesia). *J. Mar. Biol. Assoc. U.K.* 89, 931–941. doi: 10.1017/S0025315408002713

García, S., Knouse, D., Sagarminaga, R., and Cañadas, A. (2000). An Insight on the biological significance of mixed groups of common dolphins (*Delphinus delphis*) and striped dolphins (*Stenella coeruleoalba*) in the Alboran Sea. *Eur. Res. Cetaceans* 14, 135–137.

Gibson, Q. A., and Mann, J. (2009). Do sampling method and sample size affect basic measures of dolphin sociality? *Mar. Mammal Sci.* 25, 187–198. doi: 10.1111/j.1748-7692.2008.00242.x

Goodale, E., Beauchamp, G., and Ruxton, G. D. (2017). *Mixed-Species Groups of Animals: Behavior, Community Structure, and Conservation*. Cambridge, MA: Academic Press.

Goodale, E., Sridhar, H., Sieving, K. E., Bangal, P., Colorado Z. G. J., Farine, D. R., et al. (2020). Mixed company: a framework for understanding the composition and organization of mixed−species animal groups. *Biol. Rev.* 95, 889–910. doi: 10.1111/brv.12591

Gowans, S., and Whitehead, H. (1995). Distribution and habitat partitioning by small odontocetes in the Gully, a submarine canyon on the Scotian Shelf. *Can. J. Zool.* 73, 1599–1608. doi: 10.1139/z95-190

Gowans, S., Würsig, B., and Karczmarski, L. (2007). The social structure and strategies of Delphinids: predictions based on an ecological framework. *Adv. Mar. Biol.* 53, 195–294. doi: 10.1016/S0065-2881(07)53003-8

Gross, A., Kiszka, J., Van Canneyt, O., Richard, P., and Ridoux, V. (2009). A preliminary study of habitat and resource partitioning among co-occurring tropical dolphins around Mayotte, southwest Indian Ocean. *Estuar. Coast. Shelf Sci.* 84, 367–374. doi: 10.1016/j.ecss.2009.05.017

Gygax, L. (2002a). Evolution of group size in the dolphins and porpoises: Interspecific consistency of intraspecific patterns. *Behav. Ecol.* 13, 583–590. doi: 10.1093/beheco/13.5.583

Gygax, L. (2002b). Evolution of group size in the superfamily Delphinoidea (Delphinidae, Phocoenidae and Monodontidae): A quantitative comparative analysis. *Mamm. Rev.* 32, 295–314. doi: 10.1046/j.1365-2907.2002.00114.x

Hall, L. S., Krausman, P. R., and Morrison, M. L. (1997). The habitat concept and a plea for standard terminology. *Wildl. Soc. Bull.* 25, 173–182.

Herzing, D. L., and Elliser, C. R. (2013). Directionality of sexual activities during mixed-species encounters between atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*). *Int. J. Comp. Psychol.* 26, 124–134. doi: 10.5811/westjem.2011.5.6700

Herzing, D. L., and Johnson, C. M. (1997). Interspecific interaction between Atlantic spotted dolphins and bottlenose dolphins in the Bahamas, 1985-1995. *Aquat. Mamm.* 23, 85–99.

Herzing, D. L., Moewe, K., and Brunnick, B. J. (2003). Interspecies interactions between Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*, on Great Bahama Bank, Bahamas. *Aquat. Mamm.* 29, 335–341. doi: 10.1578/01675420360736505

Heymann, E. W., and Buchanan-Smith, H. M. (2000). The behavioural ecology of mixed-species troops of callitrichine primates. *Biol. Rev.* 75, 169–190. doi: 10.1111/j.1469-185X.1999.tb00044.x

Heymann, E. W., and Hsia, S. S. (2015). Unlike fellows - a review of primate-non-primate associations. *Biol. Rev. Camb. Philos. Soc.* 90, 142–156. doi: 10.1111/brv.12101

Hill, P. S., and Barlow, J. (1992). *Report of a marine mammal survey of the California coast aboard the research vessel McArthur, July 28-November 5, 1991*. La Jolla, CA: National Oceanic and Atmospheric Administration.

Hodgins, N. K., Dolman, S. J., and Weir, C. R. (2014). Potential hybridism between free-ranging Risso's dolphins (*Grampus griseus*) and bottlenose dolphins (*Tursiops truncatus*) off north-east Lewis (Hebrides, UK). *Mar. Biodivers. Rec.* 7, 1–7. doi: 10.1017/S175526721400089X

Hunt, T. (2018). *Demography, habitat use and social structure of Australian humpback dolphins (Sousa sahulensis) around the North West Cape, Western Australia: Implications for conservation and management*. Doctor of Philosophy. Bedford Park, Australia: Flinders University.

Hunt, T. N., Allen, S. J., Bejder, L., and Parra, G. J. (2019). Assortative interactions revealed in a fission–fusion society of Australian humpback dolphins. *Behav. Ecol.* 30, 914–927. doi: 10.1093/beheco/arz029

Hutchinson, J. M. C., and Waser, P. M. (2007). Use, misuse and extensions of "ideal gas" models of animal encounter. *Biol. Rev.* 82, 335–359. doi: 10.1111/j.1469-185X.2007.00014.x

Irvine, A. B., Scott, M. D., Wells, R., and Kaufmann, J. (1981). Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, Near Sarasota, Florida. *Fish. Bull.* 79, 671–688.

Jackson, A., Gerrodette, T., Chivers, S., Lynn, M., Rankin, S., and Mesnick, S. (2008). *Marine Mammal Data Collected during a Survey in the Eastern Tropical Pacific Ocean Aboard NOAA Ships David Starr Jordan and McArthur II, July 28-December 7, 2006*. La Jolla, CA: National Oceanic and Atmospheric Administration.

Jourdain, E., and Vongraven, D. (2017). Humpback whale (*Megaptera novaeangliae*) and killer whale (*Orcinus orca*) feeding aggregations for foraging on herring (*Clupea harengus*) in Northern Norway. *Mamm. Biol.* 86, 27–32. doi: 10.1016/j.mambio.2017.03.006

Kaschner, K., Quick, N. J., Jewell, R., Williams, R., and Harris, C. M. (2012). Global coverage of cetacean line-transect surveys: status Quo, data gaps and future challenges. *PLoS One* 7:e44075. doi: 10.1371/journal.pone.0044075

Kaschner, K., Tittensor, D. P., Ready, J., Gerrodette, T., and Worm, B. (2011). Current and future patterns of global marine mammal biodiversity. *PLoS One* 6:e19653. doi: 10.1371/journal.pone.0019653

Kinzey, D., Gerrodette, T., Barlow, J., Dizon, A., Perryman, W., and Olson, P. (2000). *Marine Mammal Data Collected during a Survey in the Eastern Tropical Pacific Ocean Aboard the NOAA Ships McArthur and David Starr Jordan, July 28-December 9, 1999*. La Jolla, CA: National Oceanic and Atmospheric Administration.

Kinzey, D., Gerrodette, T., Barlow, J., Dizon, A., Perryman, W., Olson, P., et al. (1999). *Marine Mammal Data Collected during a Survey in the Eastern Tropical Pacific Ocean Aboard the NOAA Ships McArthur and David Starr Jordan and the UNOLS Ship Endeavor, July 31-December 9, 1998*. La Jolla, CA: National Oceanic and Atmospheric Administration.

Kiszka, J., Perrin, W. F., Pusineri, C., and Ridoux, V. (2011). What drives island-associated tropical dolphins to form mixed-species associations in the southwest Indian Ocean? *J. Mammal.* 92, 1105–1111. doi: 10.1644/10-MAMM-A-376.1

Kiszka, J. J. (2007). Atypical associations between dugongs (*Dugong dugon*) and dolphins in a tropical lagoon. *J. Mar. Biol. Assoc. U.K.* 87, 101–104. doi: 10.1017/S0025315407055129

Kiszka, J. J., Heithaus, M. R., and Wirsing, A. J. (2015). Behavioural drivers of the ecological roles and importance of marine mammals. *Mar. Ecol. Prog. Ser.* 523, 267–281. doi: 10.3354/meps11180

Koper, R. P., and Plön, S. (2016). Interspecific interactions between cetacean species in Algoa Bay, South Africa. *Aquat. Mamm.* 42, 454–461. doi: 10.1578/AM.42.4.2016.454

Krause, J., and Ruxton, G. D. (2002). *Living in Groups*. New York, NY: Oxford University Press.

Linsky, J. M. J., Wilson, N., Cade, D. E., Goldbogen, J. A., Johnston, D. W., and Friedlaender, A. S. (2020). The scale of the whale: using video-tag data to evaluate sea-surface ice concentration from the perspective of individual Antarctic minke whales. *Anim. Biotelem.* 8, 1–12. doi: 10.1186/s40317-020-00218-8

Lukoschek, V., and McCormick, M. I. (2000). A review of multi-species foraging associations in fishes and their ecological significance. *Proc. Ninth Int. Coral Reef Symp.* I, 467–474.

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., and Hines, J. E. (2017). *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Second Edition. London, England: Academic Press.

MacLeod, C. D. (2018). "Beaked Whales, Overview," in *Encyclopedia of Marine Mammals*, eds B. Würsig, J. G. M. Thewissen, and K. Kovacs (Cambridge, MA: Academic Press), 80–83. doi: 10.1016/b978-0-12-804327-1.00062-5

Majolo, B., de Bortoli Vizioli, A., and Schino, G. (2008). Costs and benefits of group living in primates: group size effects on behaviour and demography. *Anim. Behav.* 76, 1235–1247. doi: 10.1016/j.anbehav.2008.06.008

Majolo, B., and Huang, P. (2018). "Group Living," in *Encyclopedia of Animal Cognition and Behavior*, eds J. Vonk and T. Shackelford (Cham: Springer International Publishing), 1–12.

Mangels, K. F., and Gerrodette, T. (1994). *Report of cetacean sightings during a marine mammal survey in the eastern tropical Pacific Ocean and the Gulf of California aboard the NOAA ships McArthur and David Starr Jordan, July 28-November 6, 1993*. La Jolla, CA: National Oceanic and Atmospheric Administration.

Mann, J., Connor, R. C., Tyack, P. L., and Whitehead, H. eds (2000). *Cetacean Societies: Field Studies of Dolphins and Whales*. Chicago: The University of Chicago Press.

Markowitz, T. M. (2004). *Social organization of the New Zealand dusky dolphin*. Doctor of Philosophy. College Station, TX: Texas A&M University.

May-Collado, L. J. (2010). Changes in whistle structure of two dolphin species during interspecific associations. *Ethology* 116, 1065–1074. doi: 10.1111/j.1439-0310.2010.01828.x

Maze-Foley, K., and Mullin, K. D. (2006). Cetaceans of the oceanic Northern Gulf of Mexico: distributions, group sizes and interspecific associations. *J. Cetacean Res. Manag.* 8, 2003–2013.

Melillo, K. E., Dudzinski, K. M., and Cornick, L. A. (2009). Interactions between Atlantic spotted (*Stenella frontalis*) and bottlenose (*Tursiops truncatus*) dolphins off Bimini, The Bahamas, 2003-2007. *Aquat. Mamm.* 35, 281–291. doi: 10.1578/AM.35.2.2009.281

Minton, G., Collins, T., Findlay, K., and Baldwin, R. (2010). Cetacean distribution in the coastal waters of the Sultanate of Oman. *J. Cetacean Res. Manag.* 11, 301–313.

Morse, D. H. (1977). Feeding behavior and predator avoidance in heterospecific groups. *Bioscience* 27, 332–339. doi: 10.2307/1297632

Mullin, K. D., Hoggard, W., and Hansen, L. J. (2004). Abundance and seasonal occurence of cetaceans in outer continental shelf and slope waters of the north-central and northwestern Gulf of Mexico. *Gulf Mex. Sci.* 22, 62–73. doi: 10.18785/goms.2201.06

Noë, R., and Bshary, R. (1997). The formation of red colobus-diana monkey associations under predation pressure from chimpanzees. *Proc. R. Soc. B Biol. Sci.* 264, 253–259. doi: 10.1098/rspb.1997.0036

Norris, K. S., and Dohl, T. P. (1980). Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. *Fish. Bull.* 77, 821–849.

Norris, K. S., and Prescott, J. H. (1961). Observations on Pacific cetaceans of Californian and Mexican Waters. *Univ. Calif. Publ. Zool.* 63, 291–402.

Nowacek, D. P., Christiansen, F., Bejder, L., Goldbogen, J. A., and Friedlaender, A. S. (2016). Studying cetacean behaviour: new technological approaches and conservation applications. *Anim. Behav.* 120, 235–244. doi: 10.1016/j.anbehav.2016.07.019

O'Callaghan, T. M., and Baker, C. S. (2002). *Summer cetacean community, with particular reference to Bryde's whales, in the Hauraki Gulf, New Zealand*. New Zealand: Department of Conservation.

Oswald, J. N., Rankin, S., and Barlow, J. (2008). To whistle or not to whistle? geographic variation in the whistling behavior of small odontocetes. *Aquat. Mamm.* 34, 288–302. doi: 10.1578/AM.34.3.2008.288

Pace, D. S., Mussi, B., Airoldi, S., Alessi, J., Arcangeli, A., Atzori, F., et al. (2015). New insights on the presence and distribution of the short-beaked common dolphin, *Delphinus delphis*, in Italian Waters. *Biol. Mar. Mediterr.* 22, 262–263.

Parra, G. J. (2005). *Behavioural ecology of Irrawaddy, Orcaella brevirostris (Owen in Grey 1866), and Indo-Pacific Humpback dolphins, Sousa chinensis (Osbeck, 1765), in northwest Queensland, Australia: A comparative study*. Doctor of Philosophy. Douglas: James Cook University.

Parra, G. J. (2006). Resource partitioning in sympatric delphinids: Space use and habitat preferences of Australian snubfin and Indo-Pacific humpback dolphins. *J. Anim. Ecol.* 75, 862–874. doi: 10.1111/j.1365-2656.2006.01104.x

Patterson, I. A. P., Reid, R. J., Wilson, B., Grellier, K., Ross, H. M., and Thompson, P. M. (1998). Evidence for infanticide in bottlenose dolphins: An explanation for violent interactions with harbour porpoises? *Proc. R. Soc. B Biol. Sci.* 265, 1167–1170. doi: 10.1098/rspb.1998.0414

Pearson, H. C., Jones, P. W., Brandon, T. P., Stockin, K. A., and Machovsky-Capuska, G. E. (2019). A biologging perspective to the drivers that shape gregariousness in dusky dolphins. *Behav. Ecol. Sociobiol.* 73:155. doi: 10.1007/s00265-019-2763-z

Penry, G. S., Cockcroft, V. G., and Hammond, P. S. (2011). Seasonal fluctuations in occurrence of inshore Bryde's whales in Plettenberg Bay, South Africa, with notes on feeding and multispecies associations. *Afr. J. Mar. Sci.* 33, 403–414. doi: 10.2989/1814232X.2011.637617

Peres, C. A. (1992). Prey-capture benefits in a mixed-species group of Amazonian tamarins, *Saguinus fuscicollis* and *S. mystax*. *Behav. Ecol. Sociobiol.* 31, 339–347. doi: 10.1007/BF00177774

Plotly Technologies Inc. (2015). *Collaborative Data Science*. Montréal: Plotly Technologies Inc.

Pompa, S., Ehrlich, P. R., and Ceballos, G. (2011). Global distribution and conservation of marine mammals. *Proc. Natl. Acad. Sci. U. S. A.* 108, 13600–13605. doi: 10.1073/pnas.1101525108

Porter, L. M., and Garber, P. A. (2007). Niche expansion of a cryptic primate, *Callimico goeldii*, while in mixed species troops. *Am. J. Primatol.* 69, 1340–1353. doi: 10.1002/ajp.20441

Powell, G. V. N. (1985). Sociobiology and adaptive significance of interspecific foraging flocks in the neotropics. *Ornithol. Monogr.* 36, 713–732. doi: 10.2307/40168313

Psarakos, S., Herzing, D. L., and Marten, K. (2003). Mixed-species associations between Pantropical spotted dolphins (*Stenella attenuata*) and Hawaiian spinner dolphins (*Stenella longirostris*) off Oahu, Hawaii. *Aquat. Mamm.* 29, 390–395. doi: 10.1578/01675420360736578

Python Software Foundation (2016). *Python Language Reference, version 3.8.0*. Available Online at: https://www.python.org/.

QGIS Development Team (2019). *QGIS Geographic Information System, version 3.8.3 Zanzibar*. Available Online at: http://qgis.osgeo.org.

Quérouil, S., Silva, M. A., Cascão, I., Magalhães, S., Seabra, M. I., Machete, M. A., et al. (2008). Why do dolphins form mixed-species associations in the Azores? *Ethology* 114, 1183–1194. doi: 10.1111/j.1439-0310.2008.01570.x

Reilly, S. (1990). Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. *Mar. Ecol. Prog. Ser.* 66, 1–11. doi: 10.3354/meps066001

Richmond, O. M. W., Hines, J. E., and Beissinger, S. R. (2010). Two-species occupancy models: A new parameterization applied to co-occurrence of secretive rails. *Ecol. Appl.* 20, 2036–2046. doi: 10.1890/09-0470.1

Rowley, K. (2020). Mixed-Species Cetacean Groups. Maryland: National Oceanic and Atmospheric Administration.

Ryan, C., Cucknell, A., Romagosa, M., Boisseau, O., Moscrop, A., Frantzis, A., et al. (2014). *A Visual and Acoustic Survey for Marine Mammals in the Eastern Mediterranean Sea during Summer 2013*. Kelvedon, UK: Marine Conservation Research International.

Ryan, C., Macleod, G., Dinsdale, C., and Cook, S. (2017). Long-term association between a solitary common dolphin (*Delphinus delphis delphis*) and a harbour porpoise (*Phocoena phocoena*). *Aquat. Mamm.* 43, 113–115. doi: 10.1578/AM.43.1.2017.113

Saayman, G. S., Bower, D., and Tayler, C. K. (1972). Observations on inshore and pelagic Dolphins on the South-Eastern Cape coast of South Africa. *Koedoe* 15, 1–24. doi: 10.4102/koedoe.v15i1.664

Santoro, R., Sperone, E., Tringali, M. L., Pellegrino, G., Giglio, G., Tripepi, S., et al. (2015). Summer distribution, relative abundance and encounter rates of cetaceans in the Mediterranean waters off southern Italy (western Ionian Sea and southern Tyrrhenian Sea). *Mediterr. Mar. Sci.* 16, 613–620. doi: 10.12681/mms.1007

Santostasi, N. L., Bonizzoni, S., Bearzi, G., Eddy, L., and Gimenez, O. (2016). A robust design capture-recapture analysis of abundance, survival and temporary emigration of three Odontocete species in the Gulf of Corinth, Greece. *PLoS One* 11:e0166650. doi: 10.1371/journal.pone.0166650

Scott, M. D., and Cattanach, K. L. (1998). Diel patterns in aggregations of pelagic dolphins and tunas in the eastern Pacific. *Mar. Mammal Sci.* 14, 401–422. doi: 10.1111/j.1748-7692.1998.tb00735.x

Scott, M. D., and Chivers, S. J. (1990). "Distribution and herd structure of bottlenose dolphins in the eastern tropical pacific ocean," in *The Bottlenose Dolphin*, eds S. Leatherwood and R. R. Reeves (San Diego: Academic Press), 387–402. doi: 10.1016/b978-0-12-440280-5.50026-3

Scott, M. D., Chivers, S. J., Olson, R. J., Fiedler, P. C., and Holland, K. (2012). Pelagic predator associations: Tuna and dolphins in the eastern tropical Pacific Ocean. *Mar. Ecol. Prog. Ser.* 458, 283–302. doi: 10.3354/meps09740

Shane, S. (1994). Occurrence and habitat use of marine mammals at Santa Catalina Island, California from 1983-91. *Bull. South. Calif. Acad. Sci.* 93:13.

Shane, S. H. (1990). "Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida," in *The Bottlenose Dolphin*, eds S. Leatherwood and R. R. Reeves (San Diego, CA: Academic Press), 245–265. doi: 10.1016/b978-0-12-440280-5.50016-0

Shane, S. H. (1995). Relationship between pilot whales and Risso's dolphins at Santa Catalina Island, California, USA. *Mar. Ecol. Prog. Ser.* 123, 5–12. doi: 10.3354/meps123005

Smolker, R. A., Richards, A. F., Connor, R. C., and Pepper, J. W. (1992). Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour* 123, 38–69. doi: 10.1163/156853992X00101

Smultea, M. A., Bacon, C. E., Lomac-MacNair, K., Visser, F., and Bredvik, J. (2014). Rare mixed-species associations between sperm whales and Risso's and northern right whale dolphins off the southern california bight: Kleptoparasitism and social parasitism? *Northwest. Nat.* 95, 43–49. doi: 10.1898/nwn13-11.1

Sridhar, H., Beauchamp, G., and Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim. Behav.* 78, 337–347. doi: 10.1016/j.anbehav.2009.05.008

Sridhar, H., and Guttal, V. (2018). Friendship across species borders: Factors that facilitate and constrain heterospecific sociality. *Philos. Trans. R. Soc. B Biol. Sci.* 373:20170014. doi: 10.1098/rstb.2017.0014

Stensland, E., Angerbjörn, A., and Berggren, P. (2003). Mixed species groups in mammals. *Mamm. Rev.* 33, 205–223. doi: 10.1046/j.1365-2907.2003.00022.x

Stockin, K. A., Binedell, V., Wiseman, N., Brunton, D. H., and Orams, M. B. (2009). Behavior of free-ranging common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand. *Mar. Mammal Sci.* 25, 283–301. doi: 10.1111/j.1748-7692.2008.00262.x

Stojan-Dolar, M., and Heymann, E. W. (2010). Vigilance of mustached tamarins in single-species and mixed-species groups-the influence of group composition. *Behav. Ecol. Sociobiol.* 64, 325–335. doi: 10.1007/s00265-009-0848-9

Strickland, K., Levengood, A., Foroughirad, V., Mann, J., Krzyszczyk, E., and Frère, C. H. (2017). A framework for the identification of long-term social avoidance in longitudinal datasets. *R. Soc. Open Sci.* 4:170641. doi: 10.1098/rsos.170641

Suzuki, T. N., and Kutsukake, N. (2017). Foraging intention affects whether willow tits call to attract members of mixed-species flocks. R. Soc. Open Sci. 4:170222. doi: 10.1098/rsos.170222

Thompson, L. M. (2010). *Long-term inter- and intra- species interactions of marine tucuxi (Sotalia guianensis) and common bottlenose (Tursiops truncatus) dolphins in Gandoca-Manzanillo, Costa Rica*. Master of Science. Hempstead, NY: Hofstra University.

Veit, R. R., and Harrison, N. M. (2017). Positive interactions among foraging seabirds, marine mammals and fishes and implications for their conservation. *Front. Ecol. Evol.* 5:121. doi: 10.3389/fevo.2017.00121

Viana, Y. (2019). *Are Tursiops truncatus modulating the whistles parameters in different mixed groups contexts?* Master of Science. Juiz de Fora: MG Universidade Federal de Juiz de Fora.

Wade, P. R., and Gerrodette, T. (1993). Estimates of cetacean abundance and distribution in the eastern tropical Pacific. *Rep. Int. Whal. Comm.* 43, 477–493.

Ward, A., and Webster, M. (2016). *Sociality: The Behaviour of Group-Living Animals*. Cham: Springer International Publishing.

Waser, P. M. (1982). Primate polyspecific associations: do they occur by chance? *Anim. Behav.* 30, 1–8. doi: 10.1016/S0003-3472(82)80230-3

Waser, P. M. (1984). "Chance" and mixed-species associations. *Behav. Ecol. Sociobiol.* 15, 197–202. doi: 10.1007/BF00292975

Weir, C. R. (2006). Occurrence and distribution of cetaceans off northern Angola, 2004/05. *J. Cetacean Res. Manag.* 9, 225–240.

Weir, C. R. (2011). Distribution and seasonality of cetaceans in tropical waters between Angola and the Gulf of Guinea. *Afr. J. Mar. Sci.* 33, 1–15. doi: 10.2989/1814232X.2011.572333

Weir, C. R., Pollock, C., Cronin, C., and Taylor, S. (2001). Cetaceans of the Atlantic frontier, north and west of Scotland. *Cont. Shelf Res.* 21, 1047–1071. doi: 10.1016/S0278-4343(00)00124-2

Wells, R. S., Irvine, A. B., and Scott, M. D. (1980). "The social ecology of inshore Odontocetes," in *Cetacean Behavior: Mechanisms & Functions*, ed. L. M. Herman (New York: Wiley), 263–317.

Wells, R. S., and Scott, M. D. (2009). "Common bottlenose dolphin: *Tursiops truncatus*," in *Encyclopedia of Marine Mammals*, eds B. Würsig, J. G. M. Thewissen, and K. M. Kovacs (Amsterdam: Elsevier), 249–255.

Whitehead, H. (2008). *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis*. Chicago, IL: University of Chicago Press.

Whitesides, G. H. (1989). Interspecific associations of Diana monkeys, *Cercopithecus diana*, in Sierra Leone, West Africa: biological significance or chance? *Anim. Behav.* 37, 760–776. doi: 10.1016/0003-3472(89)90062-6

Wilson, A. D. M., and Krause, J. (2013). Repeated non-agonistic interactions between a bottlenose dolphin (*Tursiops truncatus*) and sperm whales (*Physeter macrocephalus*) in Azorean Waters. *Aquat. Mamm.* 39, 89–96. doi: 10.1578/AM.39.1.2013.89

Wolters, S., and Zuberbühler, K. (2003). Mixed-species associations of Diana and Campbell's monkeys: The costs and benefits of a forest phenomenon. *Behaviour* 140, 371–385. doi: 10.1163/156853903321826684

Würsig, B., Thewissen, J. G. M., and Kovacs, K. M. (2018). *Encyclopedia of Marine Mammals*. San Diego: Academic Press.

Würsig, B., and Würsig, M. (1979). Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. *Fish. Bull.* 77, 871–890.

Zaeschmar, J. R. (2014). *False killer whales (Pseudorca crassidens) in New Zealand Waters. Master of Science*. New Zealand: Massey University.

Zaeschmar, J. R., Dwyer, S. L., and Stockin, K. A. (2013). Rare observations of false killer whales (*Pseudorca crassidens*) cooperatively feeding with common bottlenose dolphins (*Tursiops truncatus*) in the Hauraki Gulf, New Zealand. *Mar. Mammal Sci.* 29, 555–562. doi: 10.1111/j.1748-7692.2012.00582.x

Zaeschmar, J. R., Visser, I. N., Fertl, D., Dwyer, S. L., Meissner, A. M., Halliday, J., et al. (2014). Occurrence of false killer whales (*Pseudorca crassidens*) and their association with common bottlenose dolphins (*Tursiops truncatus*) off northeastern New Zealand. *Mar. Mammal Sci.* 30, 594–608. doi: 10.1111/mms.12065

Zanardo, N., Parra, G. J., Diaz-Aguirre, F., Pratt, E. A. L., and Möller, L. M. (2018). Social cohesion and intra-population community structure in southern Australian bottlenose dolphins (*Tursiops* sp.). *Behav. Ecol. Sociobiol.* 72, 1–13. doi: 10.1007/s00265-018-2557-8

Zou, F., Jones, H., Colorado Z. G. J., Jiang, D., Lee, T. M., Martínez, A., et al. (2018). The conservation implications of mixed-species flocking in terrestrial birds, a globally-distributed species interaction network. *Biol. Conserv.* 224, 267–276. doi: 10.1016/j.biocon.2018.06.004

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

REVIEW
published: 14 July 2021
doi: 10.3389/fmars.2021.688842

Diversity and Consequences of Social Network Structure in Toothed Whales

Michael N. Weiss[1,2]*, *Samuel Ellis*[1] *and Darren P. Croft*[1]

[1] Department of Psychology, Centre for Research in Animal Behaviour, University of Exeter, Exeter, United Kingdom, [2] Center for Whale Research, Friday Harbor, WA, United States

Toothed whales (suborder Odontoceti) are highly social, large brained mammals with diverse social systems. In recent decades, a large body of work has begun investigating these dynamic, complex societies using a common set of analytical tools: social network analysis. The application of social network theory to toothed whales enables insight into the factors that underlie variation in social structure in this taxon, and the consequences of these structures for survival, reproduction, disease transmission, and culture. Here, we perform a systematic review of the literature regarding toothed whale social networks to identify broad patterns of social network structure across species, common drivers of individual social position, and the consequences of network structure for individuals and populations. We also identify key knowledge gaps and areas ripe for future research. We recommend that future studies attempt to expand the taxonomic breadth and focus on standardizing methods and reporting as much as possible to allow for comparative analyses to test evolutionary hypotheses. Furthermore, social networks analysis may provide key insights into population dynamics as indicators of population health, predictors of disease risk, and as direct drivers of survival and reproduction.

Keywords: cetacea, Odontoceti, social structure, social evolution, socioecology

Edited by:
Lyne Morissette,
M – Expertise Marine, Canada

Reviewed by:
Olivier Adam,
Sorbonne Université, France
John Gatesy,
University of California, Riverside,
United States

Correspondence:
Michael N. Weiss
m.weiss@exeter.ac.uk

Specialty section:
This article was submitted to
Marine Megafauna,
a section of the journal
Frontiers in Marine Science

Received: *31 March 2021*
Accepted: *22 June 2021*
Published: *14 July 2021*

Citation:
Weiss MN, Ellis S and Croft DP (2021) Diversity and Consequences of Social Network Structure in Toothed Whales. Front. Mar. Sci. 8:688842. doi: 10.3389/fmars.2021.688842

INTRODUCTION

The structure of social interactions between individuals is a fundamental feature of animal populations, with far reaching consequences (Kurvers et al., 2014). In recent decades, toothed whales (suborder Odontoceti) have emerged as a key subject of behavioural research into the diversity and function of social structure in animals. Highly social, large brained, and inhabiting a wide variety of marine and freshwater environments, these species exhibit a diverse array of social systems, some of which (such as lifelong bisexual social philopatry) are apparently unique among mammals (Connor et al., 1998).

Studying cetacean sociality presents a number of significant challenges. Social structure is defined by the pattern of repeated social interactions between individuals (Hinde, 1976). In cetaceans, the relevant social interactions typically occur underwater, and are therefore difficult to observe. In addition, individual cetaceans are highly mobile, often over large home ranges, which can make it challenging to conduct adequate repeated sampling of individuals to quantify their social interactions. The composition of toothed whale groups also tends to be highly dynamic, with individuals regularly joining and leaving temporary groupings ("fission-fusion dynamics"). Finally, toothed whale social relationships tend to be highly individualized, and thus a full accounting of social structure requires information at the individual and dyadic level, rather than groups or classes of individuals.

These characteristics make social network analysis the ideal framework to answer many questions about toothed whale societies. Social networks represent social actors (typically individuals) as nodes in a graph, connected by edges representing social relationships (Croft et al., 2008). In practice, these edges can be measured in many ways (Farine and Whitehead, 2015), however, in toothed whales they most often represent the rate of association between individuals. Association is typically defined as co-membership in the same group, as these individuals are assumed to have the opportunity to interact ("gambit of the group," Whitehead and Dufault, 1999; **Figure 1**). This framework allows researchers to model individualized, dynamic social systems based on patterns of group membership or spatial occurrence.

Several in-depth reviews exist discussing patterns of social structure in cetaceans (Connor et al., 1998; Gowans et al., 2007; Möller, 2011; Rendell et al., 2019) and the application of social network analysis to animals (Brent et al., 2011; Webber and Vander Wal, 2019), however, the widespread quantification of toothed whale social systems using network analysis warrants greater attention. This growing body of research provides the opportunity to study social structure in toothed whales in a comparative framework. Here, we perform a systematic review of the literature on the structure, function and consequences of toothed whale social networks. We extract network metrics and general results from these studies to point toward patterns across toothed whale species, and to evaluate and expand previously proposed models of cetacean sociality.

REVIEW METHODOLOGY AND TAXONOMIC BREADTH

We used the Web of Science database (accessed March 27, 2020) to search for relevant literature. We searched for articles by pairing taxonomic terms ("cetacean," "whale," "dolphin," or "porpoise") with sociality terms ("social organisation," "social structure," or "social network"). We only retained peer-reviewed studies that generated or analysed matrices of social relationship measures between identified individuals; we did not include studies which analysed social behaviour without quantifying individual relationship. We further exclude studies that only analysed genetic networks without comparing them to behaviourally defined social networks; While kinship can be a basis for social relationships (see section 3.2), genetic relatedness does not necessarily indicate social affiliation, and thus genetic networks are not social networks. Furthermore, we do not include studies on captive groups of animals. We did not exclude studies developing methods for analysing animal social systems, however, we did exclude network science papers that used the Doubtful Sound bottlenose dolphin network (originally described by Lusseau, 2003) as a baseline for algorithm development without reference to the animals' biology. Where data were available, we extracted measures of network modularity and social differentiation as general measures of global network structure, along with the results of statistical tests of network structure at the dyadic and nodal level. In some cases, a particular study did not report relevant social network measures from their data set, but these measures were reported in later studies that did not appear in our review. In these cases, we extracted measures from these later studies. Our initial search returned 732 studies, of which 179 were retained. Studies on bottlenose dolphins (*Tursiops* spp.) are by far the most common, representing a majority of all studies (51%), followed by killer whales (*Orcinus orca,* 13%) and sperm whales (*Physeter macrocephalus,* 9%). A single study on porpoises was found, which used animal-borne sensors to derive measures of synchrony between individuals (Sakai et al., 2011). While a valuable methodological study, these results are not broadly comparable with most studies of social network structure in toothed whales which are generally based on information of the co-occurence of individuals within groups. We found only one study on small pelagic dolphins, conducted on island associated spinner dolphins (*Stenella longirostris,* Karczmarski et al., 2005). Entirely absent from our review are studies of exclusively freshwater dolphin species, and members of Monodontidae (beluga whales *Delphinapterus leucas* and narwhals *Monodon monoceros*). We found 4 studies on members of the family Ziphiidae conducted on 4 species (northern bottlenose whale, *Hyperoodon ampullatus,* Baird's beaked whale, *Berardius bairdii,* Blainville's beaked whale, *Mesoplodon densirostris,* and Cuvier's beaked whale, *Ziphius cavirostris*). Thus, our data for deriving cross-species patterns is limited to delphinids, sperm whales, and a small sampling of beaked whales (see **Supplementary Table 1** for number of studies for each species, and the **supplementary data** for a dataset of all studies). Future studies focusing on beaked whales, porpoises, belugas, and narwhals, may be crucial for a broad comparative understanding of social structure in this taxon (see section 5).

THE STRUCTURE OF TOOTHED WHALE SOCIAL NETWORKS

The unifying feature of all studied toothed whale social networks is relatively densely connected population-level social networks and fairly rapid fission fusion dynamics. In contrast to most primate societies, where social interactions and fission-fusion dynamics typically occur within well-defined social units (Kappeler and van Schaik, 2002), most toothed whale populations exhibit open social networks, and thus the relevant level of analysis is typically the population. Even where stable social units are present, interactions between units are common (e.g., in killer whales, Parsons et al., 2009).

There are countless features of social network structure that could be examined. Here, we focus on those aspects of social network topology which are both commonly measured in toothed whale studies, and are potentially particularly relevant to the biology of these animals: social modularity and social differentiation, the role of kinship, sex, and behavioural phenotypes in shaping these networks, and what factors correlate with variation in social centrality.

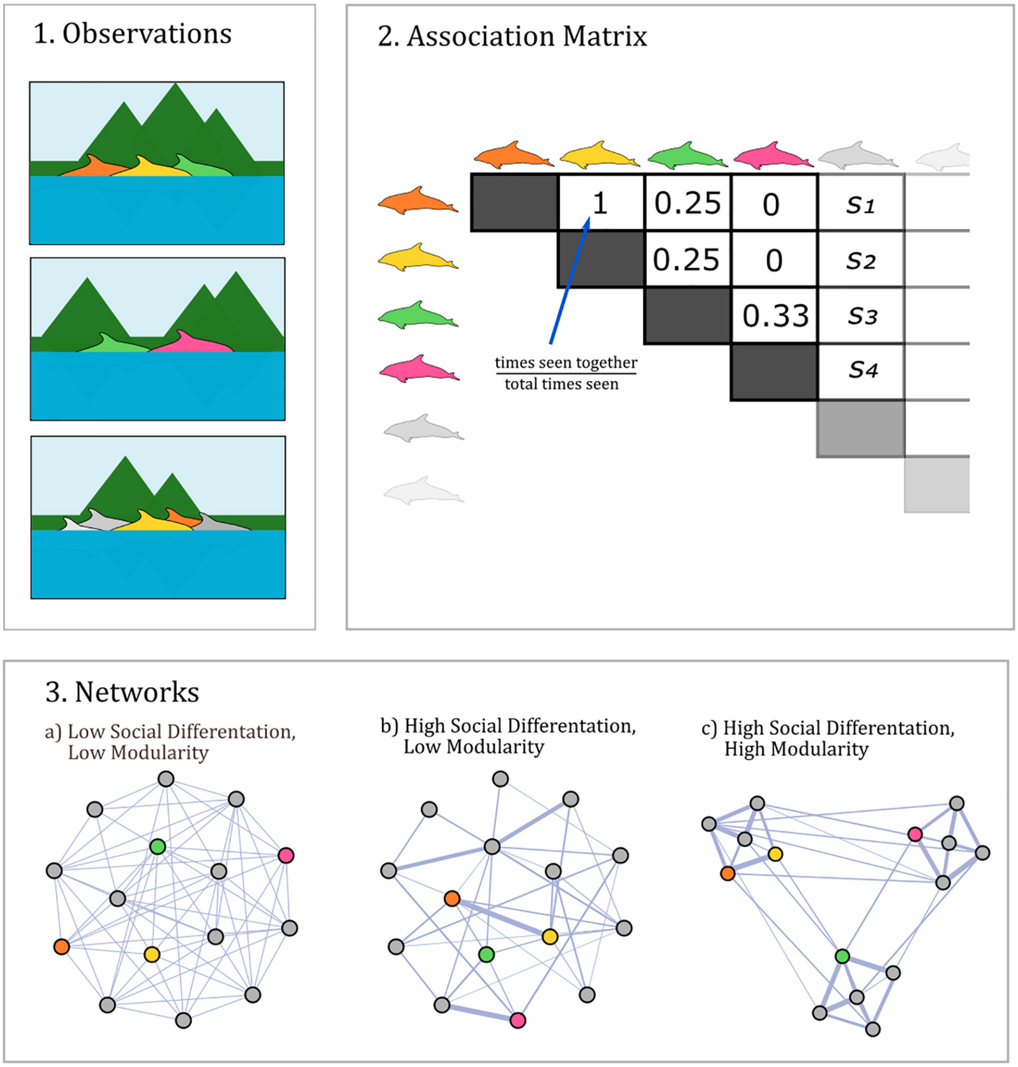


FIGURE 1 | Measuring and analysing toothed whale social networks. Associations between individuals are typically derived from repeated photo-ID surveys (1). These samples are used to generate pairwise association indices between individuals and a corresponding association matrix (2). These matrices can be analysed as weighted social networks to quantify aspects of social structure, such as social differentiation and modularity (3). Dolphin silhouettes are by Chris Huh, re-used here with alteration under a Creative Commons Share-alike license (https://creativecommons.org/licenses/by-sa/3.0).

Community Structure and Social Differentiation

Among the most common measures of global social structure in our review are social differentiation (28% of studies) and modularity (34% of studies). These measures describe easily interpretable aspects of social structure, and can be calculated from any association dataset, without the need for any information about individual attributes. For this reason, they serve as useful metrics to compare social structure between species and populations. However, some caution is needed in interpreting comparisons between species, as aspects of sampling (e.g., duration, intensity, environmental context) and network size can affect these measures. In addition, the methods used to collect network data, define associations, and calculate edge weights can have strong impacts on social network measures (Castles et al., 2014; Farine and Whitehead, 2015). Therefore, we restrict our review of social differentiation and modularity to studies using the most common sampling regime (association networks based on group membership, derived from photo identification, 94% of studies) and association index (the half-weight index, 79% of studies).

Social differentiation (abbreviated *S*) is an index of variation, or non-randomness, in association indices (see **Box 1**). Networks with high social differentiation have large variation in association strength, with individuals exhibiting strongly preferred and avoided associates. In practice, this is calculated by estimating the coefficient of variation of the underlying association probabilities using maximum likelihood (Whitehead, 2008), thus attempting to remove sampling noise from the estimate. This measure is

BOX 1 | Glossary of social network terms.

Adjacency matrix: Representation of a social network as an $N \times N$ matrix A, with the entries A_{ij} indicating the relationship between individuals i and j.

Association: The occurrence of a pair of individuals in close enough proximity (often approximated membership in the same group) to engage in social interactions.

Association index: A measure of the frequency with which pairs of individuals associate, usually expressed as the probability of association in a given sampling period. Commonly used indices include the simple ratio index (SRI) and the half-weight index (HWI). Typically these take the general form X/D, where X is the number of sampling periods in which a given pair of individuals were seen together, and D is the number of sampling periods in which they could have been seen together (often with some form of correction).

Edge: A connection between nodes in a network. In social networks, edges represent some aspect of social relationships.

Group: A temporary collection of individuals in close physical proximity with some degree of coordination in behaviour.

Matrix correlation: The correlation (or regression coefficient) between the entries of a social adjacency matrix and a predictor matrix, with statistical significance determined through randomisations. Special cases include the Mantel test and multiple regression quadratic assignment procedure (MRQAP).

Modularity: Degree to which a social network is separated into social communities, ranging from 0 to 1. Usually represented by the letter Q. Mathematically, the modularity of a weighted network, for a particular community structure, is $Q = \frac{1}{2m}\sum_{ij}\left[A_{ij} - \frac{k_i k_j}{2m}\right]\delta(c_i, c_j)$. Here, A_{ij} is the edge weight between i and j, k_i and k_j are the weighted degree (sum of weights) for i and j, m is the sum of all edge weights in the network, and $\delta(c_i, c_j)$ is 1 if i and j are in the same community, and 0 otherwise.

Node: A point where edges in a network connect. In social networks, these represent social entities, typically individuals.

Social community: Subsets of individuals within a social network such that most associations or interactions occur within rather than between sets. These may or may not represent social units (see below).

Social differentiation: Estimated coefficient of variation of underlying association probabilities. High values indicate highly non-random associations. Usually estimated by fitting the parameters of a beta-binomial distribution to association index numerators and denominators using maximum likelihood.

Social network: A set of nodes and edges representing social entities and the social relationships between them, respectively.

Social unit: A stable set of individuals in near-constant association with one another.

strictly positive, with no natural upper bound. Typically, values of S below 0.5 indicate fairly homogenous associations, while values greater than 1 indicate extremely differentiated associations (Whitehead, 2008).

In our review, we found strong variation in S across species. Reported values of S are lowest in the smaller dolphin species, with the lowest reported value being 0.24 in Sepetiba Bay Guiana dolphins (*Sotalia guianensis,* Beirao-Campos et al., 2016), and peaks in larger dolphins, particularly killer whales and pilot whales (*Globicephala* spp.), with values approaching $S = 2$ (Alves et al., 2013; Wierucka et al., 2014; Esteban et al., 2016a). Australian humpback dolphins (*Sousa sahulensis*) in Moreton Bay have been reported to have similarly high levels of social differentiation ($S = 1.98$, Hawkins et al., 2019). We did not find any reported population-level values of S for sperm whales, however, high within ($S \approx 1$) and between social unit values ($S > 1$) suggest that this species has similarly high social differentiation as the largest dolphins (Gero et al., 2015). Lying between these two extremes are the mid-sized dolphins, including spotted dolphins (*Stenella frontalis,* $S \approx 0.7$), bottlenose dolphins ($S \approx 0.8$), and most populations of humpback dolphins (*Sousa* spp., $S \approx 1.1$), as well as Baird's beaked whales (*Berardius bairdii*, $S = 0.56$, Fedutin et al., 2015). For a complete dataset of average S values for each species and references, see **Supplementary Table 1**. We also find a great deal of between-population variance within species. In common bottlenose dolphins (*T. truncatus*), for example, reported values range from 0.29 in Bahia San Antonio (Vermeulen, 2018) to 1.08 in the northern Adriatic Sea (Genov et al., 2019). Some studies have also reported variations within populations between seasons, such as dusky dolphins (*Lagenorhynchus obscurus*) in Golfo Nuevo, where social differentiation is considerably higher during the winter (Degrati et al., 2018).

Social modularity (abbreviated Q) measures a slightly different aspect of social structure than social differentiation (see **Box 1** and **Figure 1**). Modularity quantifies the degree of subgrouping in the network; values of Q very close to 1 indicate that the network is divided into extremely clear subgroups, while values close to 0 indicate little to no subgrouping (Newman, 2006). Networks with high modularity, by definition, have strong social differentiation, as associations cannot be both random and organized into subgroups, but socially differentiated networks are not necessarily modular (Whitehead, 2008; **Figure 1**). Because of this inherent correlation, cross-species patterns of social modularity correspond to those of social differentiation: smaller delphinids such as Guiana dolphins generally have lower modularity ($Q < 0.3$), followed by mid-sized dolphins and beaked whales ($0.3 < Q < 0.5$), with modularity peaking in the largest dolphins and sperm whales ($Q > 0.5$) (**Supplementary Table 1**). As with social differentiation, there is significant variance between population within species, again epitomized by differences across bottlenose dolphin populations.

What drives cross-species variation in modularity and social differentiation? Several hypotheses have been proposed to explain variations in toothed whale social systems, with implications relevant to social network structure. Bräger (1999) and Rendell et al. (2019) both point toward the importance of the mother-calf bond, suggesting that the extent of maternal investment and the need for cooperative care positively correlates with the stability of social groups (and thus the modularity and differentiation of social networks). Gowans et al. (2007) suggested that the predictability and distribution of resources may drive variation in social systems. Species feeding on locally abundant and predictable resources are predicted to have small home ranges, small groups, and fluid relationships (and thus less differentiated and modular networks). Finally, Möller (2011) suggested that the presence of stable social modules in the largest dolphins is a response to the increased threat of male harassment due to the strong sexual size dimorphism in these species.

We will attempt here to use the results from our review to very roughly evaluate these three hypotheses. In interpreting the patterns found in our review, we must again caution that differences in methodology between studies make solid comparisons difficult. In addition, data on individual species do not constitute independent data points, due to likely phylogenetic signal that must be accounted for in robust statistical tests. Nonetheless, the broad patterns between species may be useful for formulating hypotheses to test in future comparative analyses.

From our review, we find patterns that could support each of the three hypotheses outlined above. While the smaller dolphins that exhibit loose networks have calving intervals averaging around 2 years, the large dolphins and sperm whales have intervals in excess of 5 years, indicating greater maternal care (Ferguson and Higdon, 2013). In addition, the species with more modular social networks tend to exhibit greater sexual size dimorphism, with males 20 to 60% larger than females (Dines et al., 2015). Finally, while smaller dolphins tend to have home ranges spanning tens or perhaps hundreds of square kilometres, the species with the largest dolphins and sperm whales have ranges that may span many thousands or tens of thousands of square kilometres (Bräger and Bräger, 2019). Distinguishing which of these mechanisms is most important for determining social structure is difficult, as all three potential drivers are themselves correlated, primarily due to covariance with body size: larger species tend to have large home ranges, more extensive maternal care, and greater sexual dimorphism.

A potentially useful case study may be the social network structure of northern bottlenose whales (**Figure 2**). Recent evidence suggests that these whales, contrary to previous thought, exhibit prolonged maternal care, comparable to that of sperm and killer whales (Feyrer et al., 2020). Additionally, males are approximately 13% longer than females and have sex-specific weaponry (large melons used for headbutting; Gowans and Rendell, 1999), and thus under Möller's sociosexual hypothesis males would pose a risk to females. These whales, however, exhibit very different social structure from the matrilineal whales, with undifferentiated relationships between females and weak community structure (Gowans et al., 2001; Whitehead and James, 2015). Aside from social structure, where bottlenose whales apparently differ from the matrilineal toothed whale species is in their ecology and ranging patterns. Northern bottlenose whales feed preferentially on relatively small squid (*Gonatus* spp., Hooker et al., 2001) within small home ranges (~ 25 km^2, Hooker et al., 2002). This contrast may point toward ecological factors, rather than sociosexual pressures or maternal investment, as a key determinant of toothed whale social modularity and differentiation. The convergence of northern bottlenose whales' social network structure with that of the smaller coastal dolphins may therefore reflect some fundamental similarities in their ecology, with animals feeding on abundant, predictable resources, despite the extreme differences in their habitat. While instructive, this contrast is far from definitive evidence for a cross-species link between ecology and social network structure, and phylogenetically controlled comparative analyses are needed to address this hypothesis robustly.

Why might the modularity and differentiation of social networks be linked to the distribution of resources in time and space? Sueur et al. (2019) suggested that when food resources are patchily distributed, individuals may limit their associations to kin and dominant individuals as they attempt to monopolize resources through contest competition, resulting in more modular networks. This mechanism could give rise to the pattern we've identified here, in which populations apparently feeding on more dispersed, patchy prey (manifesting in their more widespread movement patterns) have more modular, differentiated networks. Observations of cetaceans monopolizing prey patches, however, are sparse, and doing so in a three-dimensional environment is likely challenging. Alternatively, the presence of stable social bonds may relate to a need for cooperation in order to find and exploit large, unpredictable prey patches. Another possibility is that the distribution of resources modulates individuals' dependence on different forms of social information. Theoretical studies suggest that dependence on social information during foraging is more likely to evolve when resources are unevenly distributed (Smolla et al., 2015), which may promote greater sociality in population relying on patchy resources. In toothed whales, the time-scale over which resources change may be key in modulating what type of social information is most beneficial. For example, in salmon-eating killer whales, the availability and distribution of prey changes over several decades, making vertical transmission of information from older females key (Brent et al., 2015), which may promote the formation of stable groups along maternal lines. In contrast, if the timescale of resource variation is shorter, individuals may rely on horizontal transmission, which may select for less exclusive social relationships as modularity is predicted to slow the spread of social information (Whitehead and Rendell, 2015). These potential mechanisms have yet to be thoroughly tested, and doing so will require new studies on poorly understood species, phylogenetically controlled statistical methods, and novel methods to correct for differences in methodology between studies.

Kinship Structure

While understanding the differentiation of social relationships and the degree of subgrouping gives us a general picture of social network structure, it does not provide any information about which individual and dyadic factors are associated with stronger social bonds or drive community structure. One factor that often drives social relationships in mammals generally (Smith, 2014) and toothed whales specifically (Möller, 2011; Rendell et al., 2019) is relatedness, or kinship. Studying variations in the patterns of kinship between associates is key for understanding the evolution of sociality in this taxon, as relatedness between social partners has profound implications for social evolution (Hamilton, 1964; Kay et al., 2020).

Measuring the correlation between social relationships and kinship requires either pedigrees derived from observed maternities, which take decades to estimate with confidence in long-lived mammals and only provides information about maternal relatedness, or genetic data which are often not available in cetacean populations. Studies of kin structuring in our review were limited to pilot whales (Alves et al., 2013; Van Cise et al., 2017), killer whales (e.g., Esteban et al., 2016a; Reisinger et al., 2017), sperm whales (e.g., Gero et al., 2008; Konrad et al., 2018a), and bottlenose dolphins (e.g.,

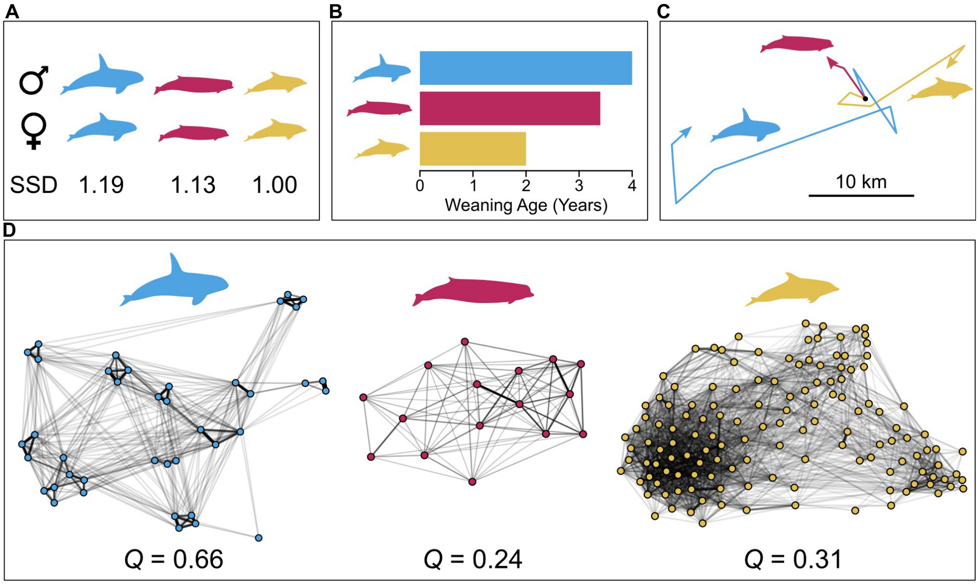


FIGURE 2 | Comparison of network structure and hypothesized drivers in three species of toothed whale, killer whales (blue), northern bottlenose whales (red), and common bottlenose dolphins (yellow). Top panels indicate sexual size dimorphism (SSD) **(A)**, maternal investment, approximated by weaning age **(B)**, and the distribution of resources, as approximated by movement patterns **(C)**. The bottom panel **(D)** contains plots of group-based half-weight index networks for each species with accompanying modularity estimate. Sexual size dimorphism estimates are the ratio of male to female lengths, and are taken from Dines et al. (2015). Weaning ages are based on stable isotope analysis of dental layers (killer whales: Newsome et al., 2009; bottlenose whales: Feyrer et al., 2020; bottlenose dolphins: Fruet et al., 2015). Movement data are tracks of single individuals obtained from animal-borne devices (radio tag for bottlenose whales, satellite tags for bottlenose dolphins and killer whales) over approximately 24 h, with a common initial point and tracks rotated for clarity. Movement and social data are taken from killer whales at the Prince Edward Islands, bottlenose whales at the Gully, Nova Scotia, and bottlenose dolphins off Georgia, United States. Movement data are replotted from Hooker et al. (2002); Reisinger et al. (2015), and Balmer et al. (2018), and social networks are replotted from Whitehead and James (2015); Reisinger et al. (2017), and Kovacs et al. (2017). Species silhouettes are by Chris Huh, re-used here with alteration under a Creative Commons Share-alike license (https://creativecommons.org/licenses/by-sa/3.0).

Louis et al., 2018; Diaz-Aguirre et al., 2019; Foroughirad et al., 2019). The lack of studies on smaller dolphins and beaked whales means our picture here is incomplete, and our knowledge is clearly taxonomically biased toward species with stable social units.

In the large dolphins, genetic studies and long-term observation suggest that social units are mixed sex groups of maternal kin (Pilot et al., 2010; Alves et al., 2013). In addition to determining social unit membership, kinship may determine associations between units in these populations. In pilot whales, between unit association rates correlate with genetic similarity (Alves et al., 2013). In killer whales, results are mixed with respect to the role of kinship in shaping between-unit social relationships, with some populations organized into semi-stable pods composed of genetically related matrilineal social units (Parsons et al., 2009; Pilot et al., 2010), while in other populations there does not appear to be a correlation between kinship and association between social units (Deecke et al., 2010; Reisinger et al., 2017).

Sperm whales, like the large dolphins, have primarily matrilineal societies. Unlike these species, however, sperm whale males disperse at maturity (Whitehead, 2003), and social units may contain multiple matrilines (Richard et al., 1996). Variations in kinship drive social association rates within units (Gero et al., 2008), however, kinship between units does not appear to predict cross-unit affiliation patterns (Konrad et al., 2018a).

In Indo-Pacific bottlenose dolphins, where males tend to form stable alliances, most studies have found that associations between females are structured according to kinship, however, bonds between males do not appear to be kin structured (Möller et al., 2001, 2006; Wiszniewski et al., 2010, 2012; Chabanne et al., 2017; Foroughirad et al., 2019). Studies on bottlenose dolphins in Coffin Bay, Australia (of the contested species *T. australis*), in contrast, suggest that male alliances are kin-biased, and the network is generally structured by genetic relatedness (Diaz-Aguirre et al., 2018, 2019). In our review, studies of common bottlenose dolphins almost universally found no correlation between genetic relatedness and association rates (Louis et al., 2018; Nykanen et al., 2018; Machado et al., 2019), with the exception of one study of male alliances in the Bahamas (Parsons et al., 2003).

In summary, it appears that kin-biased associations between adult males are rare in toothed whale social networks, perhaps only present in the largest dolphins and a few populations of bottlenose dolphins. In contrast, bonds between female kin are a fundamental aspect of many toothed whale societies. Rendell et al. (2019) suggested that maternal kinship structure is an important driver of modular social structure in cetaceans, with stronger maternal kin structure associated with greater modularity. While we do not have data on enough species to evaluate this hypothesis robustly, it allows us to make some predictions. If social modularity and kinship structure are inherently linked in cetaceans, we should expect to find strong kinship structuring in the social networks of highly modular systems, such as Australian humpback dolphins in Moreton Bay (Hawkins et al., 2019), and we expect to find little or no kinship structure in the beaked whales and small dolphins.

Sexual Segregation

In animal population, the sexes often differ in their nutritional needs and predation risk, and are under fundamentally different pressures. This often leads to the sexes segregating, either spatially or socially (Ruckstuhl, 2007). In our review, studies have reported social segregation between the sexes in both species of bottlenose dolphins (e.g., Kent et al., 2008; Mann et al., 2012), Australian humpback dolphins (Hawkins et al., 2019; Hunt et al., 2019), Risso's dolphins (Hartman et al., 2007), Atlantic spotted dolphins (e.g., Herzing et al., 2017; Danaher-Garcia et al., 2019), and northern bottlenose whales (Gowans et al., 2001). In contrast, studies have found no evidence for sexual segregation in the association networks of killer whales (Baird and Whitehead, 2000; Williams and Lusseau, 2006; Tavares et al., 2017), pilot whales (Augusto et al., 2017), and spinner dolphins (Karczmarski et al., 2005). In addition, while not addressed directly by studies in our review, sperm whales are known to exhibit extreme spatial segregation between males and females (Whitehead, 2003). This has likely not been addressed directly using social network methods due to the extreme degree of segregation in this species meaning that individualized relationships need not be measured to identify sexual segregation. Importantly, in bottlenose dolphins, there appears to be intraspecific variation, with some populations showing no sexual segregation (Baker et al., 2018; Louis et al., 2018).

In terrestrial ungulates, sexual segregation is thought to be linked to sex differences in body size and weaponry leading to different energetic requirements and predation risk (Ruckstuhl and Neuhaus, 2002). This does not appear to be the case in toothed whales; while the most sexually segregated species, the sperm whale, does also have the most extreme sexual size dimorphism, the highly sexually dimorphic killer and pilot whales show no segregation, and many of the other sexually segregated species show almost no dimorphism. Instead, patterns of sexual segregation appear to be linked to species' mating systems. Among the species that sexually segregate, there is evidence that males engage in direct contests when competing for females (Kato, 1984; Dines et al., 2015; Allen et al., 2017; Volker and Herzing, 2021), and coercion of females by groups of males has been observed in some of these species, particularly spotted dolphins (Herzing, 1996) and Indo-Pacific bottlenose dolphins (Connor and Krützen, 2015). With the notable exception of sperm whales, males in these sexually segregated species tend to have more stable intrasexual social bonds than females. It therefore seems likely that sexual segregation in these systems is driven by females avoiding harassment from males, while males form social bonds with each other in order to cooperatively monopolize females. Studies within bottlenose dolphin populations support this mechanism, suggesting that male social bonds are associated with variation in reproductive success (see below), and that sexual segregation is primarily driven by females avoiding males (Galezo et al., 2017).

Interesting variations and exceptions to this pattern are found in sperm whales and Risso's dolphins. Sperm whales are highly sexually segregated generally, however, males regularly associate with units of females and offspring in mating grounds. While associated with females, males behave similarly to other group members, and do not exhibit aggression toward females or calves (Whitehead, 1993). It may be that the stable social units of females make coercion impossible, promoting alternative strategies. There is however, evidence that sperm whale males engage in aggressive contests (Kato, 1984), and relatively small testes suggest that males are able to monopolize access to females (Dines et al., 2015), however, direct observation of males defending groups of females from competitors are lacking. Importantly, the segregation between male and female sperm whales is not strictly social; for most of the year males inhabit higher latitudes than females, and males inhabit a different ecological niche than females (Whitehead, 2003). In Risso's dolphins, males form stable long-term groups, while females exhibit fission-fusion sociality, a social structure with some similarities to those of some bottlenose dolphins (Hartman et al., 2007). However, anatomical evidence suggests strong post-copulatory competition, and therefore a lack of monopolisation of females (Dines et al., 2015). It is unclear, then, whether the stable male-male bonds of Risso's dolphins provide benefits in terms of mating access or are instead useful for increasing foraging success or predator defense (Hartman et al., 2007).

Behavioural Assortment

Social bonds existing primarily between phenotypically similar individuals ("homophily") is a common trait of social networks in humans (McPherson et al., 2001) and other animals (Croft et al., 2009). In toothed whales, several studies have found evidence that individuals preferentially associate with individuals that exhibit similar behaviours, such as foraging strategies and vocal repetoires. Hunting behaviour, particularly with respect to strategies that rely on human fisheries and aquaculture, have been of particular focus in social network studies.

Bottlenose dolphins often exhibit human-associated foraging, either in an opportunistic or cooperative context. In our systematic review, several studies report that bottlenose dolphins interacting with fisheries and aquaculture preferentially associate with each other (Chilvers and Corkeron, 2001; Kovacs et al., 2017; Genov et al., 2019; Machado et al., 2019; Methion and Diaz Lopez, 2020). This pattern is also present in Strait of Gibraltar killer whales, where social community structure perfectly correlates with degree of interaction with the local tuna fishery (Esteban et al., 2016a). Other evidence for assortment by foraging phenotype comes from stable isotope analysis. Studies in pilot whales, killer whales, and bottlenose dolphins have found that individuals with more similar stable isotope profiles, and thus likely have similar prey choice, have higher rates of association (de Stephanis et al., 2008; Esteban et al., 2016b; Louis et al., 2018).

An important caveat to these findings is that they are correlative, and the direction of causality, or even whether the causality is direct, is unclear. Correlations between behavioural similarity and association strength could be the result of social transmission of behaviour (see below). Associations and behavioural similarity could also be driven by a common underlying factor, such as kinship or space use (although many studies account for these confounds).

A study conducted on Moreton Bay bottlenose dolphins provides perhaps the strongest evidence that behavioural homophily can (directly or indirectly) drive social structure in toothed whales. In this population, a subset of individuals regularly interacted with the trawler fishery, and this set of individuals were socially segregated from non-interacting individuals (Chilvers and Corkeron, 2001). When the trawler fishery was reduced, the population's social network became less differentiated and less modular, suggesting that interaction with the fishery drove the initial population split (Ansmann et al., 2012).

It is unclear if similar patterns are present in other species. In pilot whales and killer whales, social learning within maternal lineages may be a more parsimonious explanation for correlations between behaviour and association, however, some degree of behavioural homophily, perhaps based on acoustic cues, may be present.

Social Network Centrality

So far, we have focused on global aspects of social network structure. Also important, however, are individuals' positions within their network. In social network analysis, the term "centrality" can have many meanings depending on the specific research question, but generally refers to how well connected or embedded individuals are in a social system, either directly or indirectly. Some centrality measures have clear parallels to individual behavioural phenotypes. For example, strength centrality (the sum of an individual's connections) in association networks can be directly related to their typical group size, and thus their gregariousness (Whitehead, 2008). Other measures, particularly those that quantify an individual's position within the broader network, are less clearly linked to individual behaviour, but can also be driven by relatively simple behavioural differences (Firth et al., 2017). Regardless of the behavioural substrate underlying variations in social position, social network centrality is often a key driver of individual fitness in social species (see below). In addition, variations in centrality between different age and sex classes can provide clues about the function of sociality in these species.

The correlates of social centrality are less well understood in toothed whales than global aspects of social network structure, but have been examined in several species. In our review, 25% of studies performed analyses of individual centrality, however, only 9% of studies investigated the relationship between network centrality and individual characteristics (such as age, sex, and behaviour).

One of the most commonly investigated correlates of centrality is sex. In Indo-Pacific bottlenose dolphins, spotted dolphins, and Hector's dolphins, males tend to be more socially central than females (Slooten et al., 1993; Mann et al., 2012; Danaher-Garcia et al., 2019). In contrast, in common bottlenose dolphins and Australian humpback dolphins, females have been found to be more central, even if male-male bonds tend to be more stable than female-female bonds (Baker et al., 2018; Hawkins et al., 2019; Hunt et al., 2019). Age has also been found to be an important factor in shaping social centrality. In sperm whale social units, calves are the most central individuals, likely reflecting the function of social units in cooperative care (Gero et al., 2013). In both killer whales (Williams and Lusseau, 2006) and Indo Pacific bottlenose dolphins (Stanton et al., 2011), young individuals appear to be more socially explorative, having many social connections to diverse individuals that may not be connected to one another. In some populations of bottlenose dolphins, however, young individuals are less central in the networks (Louis et al., 2018). Reproductive state may also be an important determinant of social position; in both sperm whales and Indo Pacific bottlenose dolphins, females with infant offspring are more socially central than other females (Gero et al., 2013; Nishita et al., 2017). This suggests that social relationships may be partially driven by cooperative care in these systems.

Individual behavioural phenotypes can also play a role in determining centrality. Two studies have found correlations between centrality and interactions with human aquaculture and fisheries in bottlenose dolphins, however, the reported effects are in different directions (Pace et al., 2012; Methion and Diaz Lopez, 2020). In addition, levels of pollutants, likely reflecting differences in foraging and habitat use, correlate with centrality in bottlenose dolphins in the Indian River Lagoon (Titcomb et al., 2017).

The few studies of centrality in toothed whales, and the different methods used, precludes any robust interpretation of the drivers of centrality in a comparative context. There is no clear relationship between sexual segregation or mating systems and sex differences in centrality. While males apparently form stable bonds that are useful for gaining access to females in Indo-Pacific bottlenose dolphins (Connor et al., 2001) and potentially in Australian humpback dolphins (Allen et al., 2017) and Atlantic spotted dolphins (Elliser and Herzing, 2014), these three species do not show consistent effects of sex on network centrality. Young individuals apparently being socially explorative in killer whales and bottlenose dolphins resembles results in some terrestrial taxa (e.g., Goldenberg et al., 2016), and may reflect a strategy to establish important social bonds early in life. We recommend that more studies investigate the correlates of centrality in toothed whale social networks, particularly in terms of the relationship between centrality, age, and sex, and how these might relate to life history characteristics and mating systems.

CONSEQUENCES OF SOCIAL NETWORK STRUCTURE

As discussed above, social network structure is predicted to have important implications for evolutionary and ecological processes, including variations in individual fitness (Snyder-Mackler et al., 2020), the spread of infectious disease (Craft, 2015), and the emergence of culture in animal populations (Cantor and Whitehead, 2013). Here, we'll review the current state of our understanding of how these processes are influenced by social network structure in toothed whales.

Correlates of Survival and Reproduction

Social connections are vital for survival and health in humans and other social animals (Snyder-Mackler et al., 2020). Some of the key studies elucidating the link between social network structure and components of fitness have been conducted in toothed whale populations, particularly killer whales and bottlenose dolphins. There are multiple studies correlating survival with social network structure in these two species. In Indo-Pacific bottlenose dolphins, young males that are more central in their association networks are more likely to survive to adulthood, possibly due to increased protection from harassment by older males (Stanton and Mann, 2012). In the heavily studied southern resident killer whale population, both direct and indirect centrality within social communities correlated with increased survival in male, but not female, killer whales (Ellis et al., 2017). This effect was particularly important in years of low salmon, suggesting that social network position modulates individuals' access to resources, either through providing food sharing opportunities or increasing access to social information. Similar results have been reported in sub-Antarctic killer whales (Busson et al., 2019).

Effects of social network centrality on reproduction are less well understood, with no study in our systematic review directly investigating this relationship. Some evidence for social centrality determining reproductive success comes from Shark Bay bottlenose dolphins, where males in larger and more stable alliances have greater mating success (Connor et al., 2001). Another study, which did not appear in our literature search, found that females in this population have correlated reproductive success with their social partners (Frère et al., 2010), however, this does not indicate whether more socially central females have enhanced fecundity or calf survival.

Social Information and Culture

Social learning, and the group specific, stable behavioural traditions that can emerge from it ("culture") has been increasingly recognized as an important aspect of animal ecology. While culture was long considered to be a human-specific phenomenon, it has become clear that social transmission of information and behaviour, often resulting in multi-generation traditions, are likely present in many non-human animals (Schuppli and van Schaik, 2019). Much of the data fueling the early non-human culture debate was derived from studies of toothed whales. These species have a well-documented penchant for social learning, and the presence of group specific foraging tactics and vocal traditions in wild populations suggests that social learning is an important contributor to behavioural diversity in these species (Whitehead and Rendell, 2015).

Social network structure defines the opportunities that individuals have for social learning, and therefore is predicted to correlate with the occurrence, spread, and diversity of socially learned behaviours (Cantor and Whitehead, 2013). In toothed whales, correlations between behavioural similarity and association strength have often been used to test for the presence of cultural processes, particularly with respect to the acoustic repertoires of killer whales and sperm whales. In these species, results are mixed. While vocal similarity between matrilines correlates with association strength in killer whales, suggesting horizontal transmission (Deecke et al., 2010), there is no apparent correlation between association strength and vocal similarity within sperm whale clans (Konrad et al., 2018b).

Other evidence comes from analysis of foraging behaviour. Several species of toothed whale exhibit group or population specific foraging behaviours that are thought to be the result of cultural transmission, with perhaps the most notable example being the highly specialized foraging strategies found in killer whale populations (Riesch et al., 2012). Social network studies have born out the likelihood that foraging strategies are socially learned in several species. Similarity in foraging behaviour and stable isotope profiles correlate with association strength in pilot whales, killer whales, and bottlenose dolphins (de Stephanis et al., 2008; Esteban et al., 2016b; Louis et al., 2018). However, as discussed above, these results could be the result of either social learning or behavioural homophily. More solid evidence of social transmission within toothed whale social networks has been gained from diffusion modelling of novel foraging techniques in Shark Bay bottlenose dolphins. The "sponging" behaviour, where individuals utilize marine sponges to protect their rostrum while bottom feeding, has been found to socially spread along maternal lines (Wild et al., 2019). In contrast, the "shelling" behaviour, where individuals catch fish by chasing them into a shell before raising the shell to the surface, spreads horizontally between associates (Wild et al., 2020).

One of the key hypotheses linking social structure and social transmission is that more structured (i.e., modular and differentiated) social networks should have slower rates of social transmission and generate greater behavioural diversity than relatively random networks (Cantor and Whitehead, 2013). We found no studies investigating this hypothesis empirically in toothed whales, and we are unaware of any study investigating this question in natural systems. This question may be of particular interest in future comparative studies, perhaps using indices of diversity in foraging behaviour (such as isotopic niche widths) or vocal repertoires.

Disease Transmission

As in the case of information transmission, social network structure is a major factor shaping the pattern of disease transmission in animal populations, as social networks represent potential disease transmission pathways (Craft, 2015). Understanding disease transmission risk is toothed whale populations is crucial for evaluating the relative risk to populations and potentially informing strategies to manage outbreaks. Several unusual mortality events in toothed whale populations have been attributed to disease outbreaks, and the risk of these outbreaks may be increasing as oceans grow warmer (Sanderson and Alexander, 2020).

In our review, only three studies explicitly addressed the transmission of diseases in toothed whale social networks. Guimaraes Paulo et al. (2007) modelled the spread of a hypothetical pathogen over the social network of mammal eating killer whales, finding that the network was more vulnerable than random networks. The remaining two studies both analysed the impacts of observed disease outbreaks in relationship to social structure. Wierucka et al. (2014) found that increased mortality in Mediterranean long-finned pilot whales following a morbillivirus epizootic was limited to two social clusters, suggesting that sociality shaped the transmission of this disease. Similarly, Felix et al. (2019) found that the occurrence of lobomycosis-disease was linked to the structure of social communities in bottlenose dolphins. Interestingly, neither of these studies directly analysed the specific transmission pathway thought to be involved in the spread of these diseases (respiratory transmission and physical contact, respectively), but still found an influence of association network structure. This suggests that, at least in some cases, broad-scale associations can be a useful proxy for actual disease transmission pathways in toothed whales.

FUTURE RESEARCH DIRECTIONS

The application of social networks to animals has expanded greatly over the last 2 decades, and has been used to answer numerous biological questions (Webber and Vander Wal, 2019). In sync with this explosion of social network research, studies on toothed whale sociality has provided additional insight into the ecological and evolutionary forces shaping social structure (Rendell et al., 2019). Our review highlights some clear gaps in our current knowledge on toothed whale social networks, as well as some exciting opportunities for future research.

Most obviously, our review highlights severe taxonomic bias toward three genera, *Tursiops, Orcinus,* and *Physeter.* In particular, the majority of the studies in our review concerned bottlenose dolphins. Bottlenose dolphins are widespread, many populations inhabit coastal areas that are relatively easily accessible, and their relatively small home ranges of individuals mean that individuals can be reliably re-located, making them attractive research subjects. In addition, the presence of several forms of cooperation, social transmission, and multilevel alliances make this genus theoretically interesting. However, studies of a wider array of species will be important for understanding the origins and diversity of social structure in this taxon. In particular, further research on beaked whales, open ocean dolphins, river dolphins, beluga, and narwhals will faciliate more extensive comparative work to uncover the drivers and consequences of cetacean social structure. Studying these animals' social systems comes with significant challenges. Many of them inhabit remote or challenging habitats, such as the open ocean, the high Arctic, and complex river systems. In the open ocean dolphins, the sheer size of groups makes identifying a reasonable portion of group members difficult, and the lack of dorsal fins in Monodonts and river dolphins makes traditional photo ID challenging. Developments in research technology, such as machine learning for individual identification (Kierdorf et al., 2020) and unoccupied aerial systems for observing submerged individuals and markings typically not visible from the surface (Torres et al., 2018) may begin to unravel the structure of these species' social networks.

Our literature search also demonstrated a lack of studies investigating the consequences of social network centrality on reproductive success in toothed whales. Given the central role of cooperative calf care in many hypotheses about the evolution of social structure in this taxon, understanding how sociality influences female reproductive success is crucial. We would predict that, in the species where cooperative care is thought to be important, females with greater social centrality will have greater reproductive success due to increased calf survival.

As we have discussed throughout our review, the growing body of work in toothed whales has begun to provide the necessary data for comparative studies to investigate the drivers and consequences of social network structure. Such studies will require not only social metrics from a large number of species derived using the same methods, but will need to correct for effects of sampling intensity and network size. In addition, the observed features of social networks have inherent uncertainty (Lusseau et al., 2008), which will need to be incorporated into any such analyses. We recommend that all descriptive studies of toothed whale social systems report standard errors for global network metrics to allow for principled comparisons.

While this body of work studying association networks is undoubtedly valuable, it may be necessary for studies of toothed whales to begin to move past the gambit of the group and study social interactions themselves. The development of research technologies such as animal borne devices may again prove useful for these studies. Recent studies have demonstrated the usefulness of unoccupied aerial systems to observe sociality in greater detail in odontocetes (Hartman et al., 2020), and continued development of these methods have the potential to greatly expand our understanding of these systems.

Finally, there is an opportunity to incorporate social network structure more fully into the conservation of toothed whales. The application of social network theory to conservation problems generally has the potential to improve outcomes in endangered populations (Snijders et al., 2017), and social structure has been proposed as a key determinant of population dynamics in cetaceans (Wade et al., 2012). Several studies have utilized social networks to help define management units (Alves et al., 2013; Wang et al., 2015; Esteban et al., 2016b) or to better understand populations' response to mortality and removal events (Williams and Lusseau, 2006; Herzing et al., 2017; Busson et al., 2019), however, we feel there are additional roles for social network analysis in conservation generally, and in toothed whales specifically. In many toothed whale populations, one large source of mortality is fisheries bycatch, which can simultaneously and suddenly remove entire social units. The effect of these removals on the stability of population-level social network structure, and the consequences of possible social disruption to population function, may be a vital area for further research.

Some studies have found that social network dynamics share common drivers with population dynamics (Parsons et al., 2009; Foster et al., 2012a; Herzing et al., 2017; Busson et al., 2019). This suggests that social network dynamics may serve as a useful behavioural indicator of population health. In other species, changes in behaviour have been used to detect novel stressors (e.g., Caro, 2005), indicate the success of management actions (e.g., Al-Shaer et al., 2018), and predict future population growth (van Gils et al., 2009). Given the apparently widespread link between ecological variables and social network dynamics in toothed whales, and the relative ease with which social network measures can be derived from photographic identification data, the application of social networks as a behavioural indicator in these populations bears further investigation.

In addition, social networks could help managers understand disease risk and target vaccinations. While our systematic review found only three studies explicitly linking social networks and disease, more recent work has expanded the application of social networks to disease management, by estimating age and sex specific risk (Leu et al., 2020), explicitly modelling the spread of specific pathogens along with possible vaccination strategies (Weiss et al., 2020), and using randomisation procedures to determine the relevance of association networks to observed disease outbreaks (Powell et al., 2020). Further work determining the impact of social network structure on population-level disease risk in a comparative context could further inform conservation efforts.

Disease mitigation is only one aspect of what Snijders et al. (2017) refer to as "relationship-based management strategies." Understanding the relationships between individuals in threatened populations can additionally help maintain animal welfare, and potentially aid in predicting which animals are experiencing greater mortality risk. For example, in resident killer whales, the death of an individuals' mother or grandmother increases their mortality risk, likely due to the loss of social benefits such as information and food sharing (Foster et al., 2012b; Nattrass et al., 2019). Social network methods may help identify other important social partners, the removal of which might cause increased stress or mortality.

CONCLUSION

The application of social network methods to free-ranging odontocetes has revealed a great diversity of social structures, and has elucidated some of the drivers and consequences of sociality in this taxon. Our review highlights both the vast body of knowledge generated through the applications of social network analysis to these interesting species, and the great potential of these methods for further study. We have attempted to summarize the current state of our knowledge, but as this is a young field, there is still a great deal of uncertainty, and some of the results we discuss here may be further confirmed or refuted by further study. Future research focusing on applying new methods, studying less well understood species, and applying this knowledge directly to conservation problems may provide important components of continued efforts to understand and conserve toothed whale populations worldwide.

DATA AVAILABILITY STATEMENT

The database of studies generated for this study can be found in the **Supplementary Material**.

AUTHOR CONTRIBUTIONS

MW conceived of the project and carried out the systematic review, with input from DC. MW wrote the initial draft of the manuscript, which was then developed with input from all authors. All authors contributed to the article and approved the submitted version.

FUNDING

This work was supported by a UK Natural Environmental Research Council Grant (NE/S010327/1) awarded to DC. SE was funded by a Leverhulme Early Career Research Fellowship.

ACKNOWLEDGMENTS

We thank our colleagues at the Centre for Research in Animal Behaviour, particularly the CRAB Social Network Club, for discussion and comments that helped shape this manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.688842/full#supplementary-material

REFERENCES

Allen, S. J., King, S. L., Krützen, M., and Brown, A. M. (2017). Multi-modal sexual displays in Australian humpback dolphins. *Sci. Rep.* 7:13644.

Al-Shaer, L., Bloch, A., Little, K., and Itzkowitz, M. (2018). Monitoring social behaviour as an assessment of translocation success in a reintroduced population of the endangered Leon Springs pupfish (*Cyprinodon bovis*). *Aqu. Conserv. Mar. Freshw. Ecosyst.* 28, 559–566. doi: 10.1002/aqc.2889

Alves, F., Querouil, S., Dinis, A., Nicolau, C., Ribeiro, C., Freitas, L., et al. (2013). Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. *Aqu. Conserv.* 23, 758–776.

Ansmann, I. C., Parra, G. J., Chilvers, B. L., and Lanyon, J. M. (2012). Dolphins restructure social system after reduction of commercial fisheries. *Anim. Behav.* 84, 575–581. doi: 10.1016/j.anbehav.2012.06.009

Augusto, J. F., Frasier, T. R., and Whitehead, H. (2017). Social structure of long-finned pilot whales (*Globicephala melas*) off northern Cape Breton Island, Nova Scotia. *Behaviour* 154, 509–540. doi: 10.1163/1568539x-00003432

Baird, R. W., and Whitehead, H. (2000). Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Can. J. Zool.* 78, 2096–2105. doi: 10.1139/z00-155

Baker, I., O'Brien, J., McHugh, K., Ingram, S. N., and Berrow, S. (2018). Bottlenose dolphin (*Tursiops truncatus*) social structure in the Shannon Estuary, Ireland, is distinguished by age- and area-related associations. *Mar. Mammal Sci.* 34, 458–487. doi: 10.1111/mms.12462

Balmer, B., Zolman, E., Rowles, T., Smith, C., Townsend, F., Fauquier, D., et al. (2018). Ranging patterns, spatial overlap, and association with dolphin morbillivirus exposure in common bottlenose dolphins (*Tursiops truncatus*) along the Georgia, USA coast. *Ecol. Evol.* 8, 12890–12904. doi: 10.1002/ece3.4727

Beirao-Campos, L., Cantor, M., Flach, L., and Simoes-Lopes, P. C. (2016). Guiana dolphins form social modules in a large population with high ranging overlap and small demographic changes. *Behav. Ecol. Sociobiol.* 70, 1821–1830. doi: 10.1007/s00265-016-2188-x

Bräger, S. (1999). Association patterns in three populations of Hector's Dolphin, Cephalorhynchus hectori. *Can. J. Zool.* 77, 13–18. doi: 10.1139/cjz-77-1-13

Bräger, S., and Bräger, Z. (2019). "Movement patterns of Odontocetes through space and time," in *Ethology and Behavioural Ecology of Odontocetes*, ed. B. Würsig (Cham: Springer), 117–144. doi: 10.1007/978-3-030-16663-2_6

Brent, L. J., Lehmann, J., and Ramos-Fernandez, G. (2011). Social network analysis in the study of nonhuman primates: a historical perspective. *Am. J. Primatol.* 73, 720–730. doi: 10.1002/ajp.20949

Brent, L. J. N., Franks, D. W., Foster, E. A., Balcomb, K. C., Cant, M. A., and Croft, D. P. (2015). Ecological knowledge, leadership, and the evolution of menopause in killer whales. *Curr. Biol.* 25, 746–750. doi: 10.1016/j.cub.2015.01.037

Busson, M., Authier, M., Barbraud, B., Tixier, P., Reisinger, R. R., Janc, A., et al. (2019). Role of sociality in the response of killer whales to an additive mortality event. *Proc. Natl. Acad. Sci. U.S.A.* 116, 11812–11817.

Cantor, M., and Whitehead, H. (2013). The interplay between social networks and culture: theoretically and among whales and dolphins. *Philos. Trans. R. Soc. B Biol. Sci.* 368:20120340. doi: 10.1098/rstb.2012.0340

Caro, T. M. (2005). Behavioural indicators of exploitation. *Ethol. Ecol. Evol.* 17, 189–194. doi: 10.1080/08927014.2005.9522608

Castles, M., Heinsohn, R., Marshall, H. H., Lee, A. E. G., Cowlisha, G., and Carter, A. J. (2014). Social networks created with different techniques are not comparable. *Anim. Behav.* 96, 59–67. doi: 10.1016/j.anbehav.2014.07.023

Chabanne, D. B. H., Finn, H., and Bejder, L. (2017). Identifying the relevant local population for environmental impact assessments of mobile marine fauna. *Front. Mar. Sci.* 4:148. doi: 10.3389/fmars.2017.00148

Chilvers, B. L., and Corkeron, P. J. (2001). Trawling and bottlenose dolphins' social structure. *Proc. R. Soc. B Biol. Sci.* 268, 1901–1905. doi: 10.1098/rspb.2001.1732

Connor, R. C., Heithaus, M. R., and Barre, L. M. (2001). Complex social structure, alliance stability and mating access in a bottlenose dolphin "super-alliance". *Proc. R. Soc. B Biol. Sci.* 268, 263–267. doi: 10.1098/rspb.2000.1357

Connor, R. C., and Krützen, M. (2015). Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. *Anim. Behav.* 103, 223–235. doi: 10.1016/j.anbehav.2015.02.019

Connor, R. C., Mann, J., Tyack, P. L., and Whitehead, H. (1998). Social evolution in toothed whales. *Trends Ecol. Evol.* 13, 228–232. doi: 10.1016/s0169-5347(98)01326-3

Craft, M. E. (2015). Infectious disease transmission and contact networks in wildlife and livestock. *Philos. Trans. R. Soc. B Biol. Sci.* 370, 20140107. doi: 10.1098/rstb.2014.0107

Croft, D. P., James, R., and Krause, J. (2008). *Exploring Animal Social Networks*. Princeton, NJ: Princeton University Press.

Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J., and James, R. (2009). Behavioural trait assortment in a social network: patterns and implications. *Behav. Ecol. Sociobiol.* 63, 1495–1503. doi: 10.1007/s00265-009-0802-x

Danaher-Garcia, N. A., Melillo-Sweeting, K., and Dudzinski, K. M. (2019). Social structure of Atlantic spotted dolphins (*Stenella frontalis*) off Bimini, The Bahamas (2003-2016): alternate reasons for preferential association in delphinids. *Acta Ethol.* 23, 9–21. doi: 10.1007/s10211-019-00329-3

de Stephanis, R., Garcia-Tiscar, S., Verborgh, P., Esteban-Pavo, R., Perez, S., Minvielle-Sebastia, L., et al. (2008). Diet of social groups of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar. *Mar. Biol.* 154, 603–612. doi: 10.1007/s00227-008-0953-8

Deecke, V. B., Barrett-Lennard, L. G., Spong, P., and Ford, J. K. B. (2010). The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (*Orcinus orca*). *Naturwissenchaften* 97, 513–518. doi: 10.1007/s00114-010-0657-z

Degrati, M., Coscarella, M. A., Crespo, E. A., and Dans, S. L. (2018). Dusky dolphin group dynamics and association patterns in Peninsula Valdes. Argentina. *Mar. Mammal Sci.* 35, 416–433. doi: 10.1111/mms.12536

Diaz-Aguirre, F., Parra, G. J., Passadore, C., and Möller, L. (2018). Kinship influences social bonds among male southern Australian bottlenose dolphins (*Tursiops cf. australis*). *Behav. Ecol. Sociobiol.* 72:190.

Diaz-Aguirre, F., Parra, G. J., Passadore, C., and Möller, L. (2019). Genetic relatedness delineates the social structure of southern Australian bottlenose dolphins. *Behav. Ecol.* 30, 948–959. doi: 10.1093/beheco/arz033

Dines, J. P., Mesnick, S. L., Ralls, K., May-Collado, L., Agnarsson, I., and Dean, M. D. (2015). A trade-off between precopulatory and postcopulatory trait investment in male cetaceans. *Evolution* 69, 1560–1572. doi: 10.1111/evo.12676

Elliser, C. R., and Herzing, D. L. (2014). Long-term social structure of a resident community of Atlantic spotted dolphins, Stenella Frontalis, in the Bahamas 1991–2002. *Mar. Mammal Sci.* 30, 308–328.

Ellis, S., Franks, D. W., Nattrass, S., Cant, M. A., Weiss, M. N., Giles, D., et al. (2017). Mortality risk and social network position in resident killer whales: sex differences and the importance of resource abundance. *Proc. R. Soc. B* 284:20171313. doi: 10.1098/rspb.2017.1313

Esteban, R., Verborgh, P., Gauffier, P., Gimenez, J., Foote, A. D., and de Stephanis, R. (2016a). Maternal kinship and fisheries interactions influence killer whale social structure. *Behav. Ecol. Sociobiol.* 70, 111–122. doi: 10.1007/s00265-015-2029-3

Esteban, R., Verborgh, P., Gauffier, P., Gimenez, J., Martin, V., Perez-Gil, M., et al. (2016b). Using a multi-disciplinary approach to identify a critically endangered killer whale management unit. *Ecol. Indicat.* 66, 291–300. doi: 10.1016/j.ecolind.2016.01.043

Farine, D., and Whitehead, H. (2015). Constructing, conducting, and interpreting animal social network analysis. *J. Anim. Ecol.* 84, 1144–1163.

Fedutin, I. D., Filatova, O. A., Mamaev, E. G., Burdin, A. M., and Hoyt, E. (2015). Occurrence and social structure of Baird's beaked whales, Berardius bairdii, in the Commander Islands, Russia. *Mar. Mammal Sci.* 31, 853–865. doi: 10.1111/mms.12204

Felix, F., Van Bressem, M.-F., and Van Waerebeek, K. (2019). Role of social behaviour in the epidemiology of lobomycosis- like disease (LLD) in estuarine common bottlenose dolphins from Ecuador. *Dis. Aqu. Organ.* 134, 75–87. doi: 10.3354/dao03356

Ferguson, S. H., and Higdon, J. W. (2013). Grouping world cetaceans according to life-history characteristics indicates two divergent strategies. *Can. Wildlife Biol. Manag.* 2, 51–66.

Feyrer, L. J., Zhao, S., Whitehead, H., and Mattews, C. J. D. (2020). Prolonged maternal investment in northern bottlenose whales alters our understanding of beaked whale reproductive life history. *PLoS One* 15:e0235114. doi: 10.1371/journal.pone.0235114

Firth, J. A., Sheldon, B. C., and Brent, L. J. (2017). Indirectly connected: simple social differences can explain the causes and apparent consequences of complex social network positions. *Proc. R. Soc. B Biol. Sci.* 284:20171939.

Foroughirad, V., Levengood, A. L., Mann, J., and Frere, C. H. (2019). Quality and quantity of genetic relatedness data affect the analysis of social structure. *Mol. Ecol. Resour.* 19, 1181–1194. doi: 10.1111/1755-0998.13028

Foster, E. A., Franks, D. W., Mazzi, S., Darden, S. K., Balcomb, K. C., Ford, J. K., et al. (2012b). Adaptive prolonged postreproductive life span in killer whales. *Science* 337, 1313–1313. doi: 10.1126/science.1224198

Foster, E. A., Franks, D. W., Morrell, L. J., Balcomb, K. C., Parsons, K. M., van Ginneken, A., et al. (2012a). Social network correlates of food availability in an endangered population of killer whales, *Orcinus orca*. *Anim. Behav.* 83, 731–736. doi: 10.1016/j.anbehav.2011.12.021

Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L., and Sherwin, W. B. (2010). Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proc. Natl. Acad. Sci. U.S.A.* 107, 19949–19954. doi: 10.1073/pnas.1007997107

Fruet, P. F., Genoves, R. C., Möller, L. M., Botta, S., and Secchi, E. R. (2015). Using mark-recapture and stranding data to estimate reproductive traits in female bottlenose dolphins (*Tursiops truncatus*) of the Southwestern Atlantic Ocean. *Mar. Biol.* 162, 661–673. doi: 10.1007/s00227-015-2613-0

Galezo, A. A., Krzyszczyk, E., and Mann, J. (2017). Sexual segregation in Indo-Pacific bottlenose dolphins is driven by female avoidance of males. *Behav. Ecol.* 29, 377–386. doi: 10.1093/beheco/arx177

Genov, T., Centrih, T., Kotnjek, P., and Hace, A. (2019). Behavioural and temporal partitioning of dolphin social groups in the northern Adriatic Sea. *Mar. Biol.* 166:11.

Gero, S., Engelhaupt, D., and Whitehead, H. (2008). Heterogeneous social associations within a sperm whale, Physeter macrocephalus, unit reflect pairwise relatedness. *Behav. Ecol. Sociobiol.* 63, 143–151. doi: 10.1007/s00265-008-0645-x

Gero, S., Gordon, J., and Whitehead, H. (2013). Calves as social hubs: dynamics of the social network within sperm whale units. *Proc. R. Soc. B Biol. Sci.* 280:20131113. doi: 10.1098/rspb.2013.1113

Gero, S., Gordon, J., and Whitehead, H. (2015). Individualized social preferences and long-term social fidelity between social units of sperm whales. *Anim. Behav.* 102, 15–23. doi: 10.1016/j.anbehav.2015.01.008

Goldenberg, S. Z., Douglas-Hamilton, I., and Wittemyer, G. (2016). Vertical transmission of social roles drives resilience to poaching in elephant networks. *Curr. Biol.* 26, 75–79. doi: 10.1016/j.cub.2015.11.005

Gowans, S., and Rendell, L. (1999). Head-butting in northern bottlenose whales (Hyperoodon ampullatus): A possible function for big heads? *Mar. Mammal Sci.* 15, 1342–1350. doi: 10.1111/j.1748-7692.1999.tb00896.x

Gowans, S., Whitehead, H., and Hooker, S. K. (2001). Social organization in northern bottlenose whales, Hyperoodon ampullatus: not driven by deep-water foraging? *Anim. Behav.* 62, 369–377. doi: 10.1006/anbe.2001.1756

Gowans, S., Würsig, B., and Karczmarski, L. (2007). The social structure and strategies of delphinids: predictions based on an ecological framework. *Adv. Mar. Biol.* 53, 195–294. doi: 10.1016/s0065-2881(07)53003-8

Guiamares, P. R. Jr., de Menezes, M. A., Baird, R. W., Lusseau, D., Guimaraes, P., and dos Reis, S. F. (2007). Vulnerability of a killer whale social network to disease outbreaks. *Phys. Rev. E* 76:042901.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. *J. Theor. Biol.* 7, 1–16. doi: 10.1016/0022-5193(64)90038-4

Hartman, K., van der Harst, P., and Vilela, R. (2020). Continuous focal group follows operated by a drone enable analysis of the relation between sociality and position in a group of male Risso's Dolphins (Grampus griseus). *Front. Mar. Sci.* 7:283. doi: 10.3389/fmars.2020.00283

Hartman, K. L., Visser, F., and Hendriks, A. J. E. (2007). Social structure of Risso's dolphins (Grampus griseus) in the Azores: a stratified community based on highly associated units. *Can. J. Zool.* 86, 294–306. doi: 10.1139/z07-138

Hawkins, E. R., Pogson-Manning, L., Jaehnichen, C., and Meager, J. J. (2019). Social dynamics and sexual segregation of Australian humpback dolphins (Sousa *sahulensis*) in Moreton Bay, Queensland. *Mar. Mammal Sci.* 36, 500–521. doi: 10.1111/mms.12657

Herzing, D. (1996). Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, Stenella frontalis and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals* 22, 61–79.

Herzing, D. L., Augliere, B. N., Elliser, C. R., Green, M. L., and Pack, A. A. (2017). Exodus! Large-scale displacement and social adjustments of resident Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas. *PLoS One* 12:e0180304. doi: 10.1371/journal.pone.0180304

Hinde, R. A. (1976). Interactions, relationships and social structure. *Man* 11, 1–17. doi: 10.2307/2800384

Hooker, S., Iverson, S., Ostrom, P., and Smith, S. (2001). Diet of northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy samples. *Can. J. Zool.* 79, 1442–1454. doi: 10.1139/z01-096

Hooker, S. K., Whitehead, H., Gowans, S., and Baird, R. W. (2002). Fluctuations in distribution and patterns of individual range use of northern bottlenose whales. *Mar. Ecol. Progress Ser.* 225, 287–297. doi: 10.3354/meps225287

Hunt, T. N., Allen, S. J., Bejder, L., and Parra, G. J. (2019). Assortative interactions revealed in a fission-fusion society of Australian humpback dolphins. *Behav. Ecol.* 30, 914–927. doi: 10.1093/beheco/arz029

Kappeler, P. M., and van Schaik, C. P. (2002). Evolution of primate social systems. *Int. J. Primatol.* 23, 707–740.

Karczmarski, L., Würsig, B., Gailey, G., Larson, K. W., and Vanderlip, C. (2005). Spinner dolphins in a remote Hawaiian atoll: social grouping and population structure. *Behav. Ecol.* 16, 675–685. doi: 10.1093/beheco/ari028

Kato, H. (1984). Observation of tooth scars on the head of male sperm whale, as an indication of intra-sexual fightings. *Sci. Rep. Whales Res. Inst.* 35, 39–46.

Kay, T., Keller, L., and Lehmann, L. (2020). The evolution of altruism and the serial rediscovery of the role of relatedness. *Proc. Natl. Acad. Sci. U.S.A.* 117, 28894–28898. doi: 10.1073/pnas.2013596117

Kent, E. E., Mazzoil, M., McCulloch, S. D., and Defran, R. H. (2008). Group characteristics and social affiliation patterns of bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon, Florida. *Florida Sci.* 71, 149–168.

Kierdorf, J., Garcke, J., Behley, J., Cheeseman, T., and Roscher, R. (2020). Whate identified a whale by its fluke? On the benefit of interpretable machine learning for whale identification. *ISPRS Ann. Photogr. Remote Sen. Spatial Inform. Sci.* 2, 1005–1012. doi: 10.5194/isprs-annals-v-2-2020-1005-2020

Konrad, C. M., Frasier, T. R., Rendell, L., Whitehead, H., and Gero, S. (2018b). Kinship and association do not explain vocal repertoire variation among individual sperm whales or social units. *Anim. Behav.* 145, 131–140. doi: 10.1016/j.anbehav.2018.09.011

Konrad, C. M., Gero, S., Frasier, T., and Whitehead, H. (2018a). Kinship influences sperm whale social organization within, but generally not among, social units. *R. Soc. Open Sci.* 5:180914. doi: 10.1098/rsos.180914

Kovacs, C. J., Perrtree, R. M., and Cox, T. M. (2017). Social differentiation in common bottlenose dolphins (*Tursiops truncatus*) that engage in human-related foraging behaviors. *PLoS One* 12:e0170151. doi: 10.1371/journal.pone.0170151

Kurvers, R. H. J. M., Krause, J., Croft, D. P., Wilson, A. D. M., and Wolf, M. (2014). The evolutionary and ecological consequences of animal social networks: emerging issues. *Trends Ecol. Evol.* 29, 326–335. doi: 10.1016/j.tree.2014.04.002

Leu, S. T., Sah, P., Krzyszczyk, E., Jacoby, A., Mann, J., and Bansal, S. (2020). Sex, synchrony, and skin contact: integrating myultiple behaviours to assess pathogen transmission risk. *Behav. Ecol.* 31, 651–660.

Louis, M., Simon-Bouhet, B., Viricel, A., Lucas, T., Gally, F., Cherel, Y., et al. (2018). Evaluating the influence of ecology, sex and kinship on the social structure of resident coastal bottlenose dolphins. *Mar. Biol.* 165:80.

Lusseau, D. (2003). The emergent properties of a dolphin social network. *Proc. R. Soc. B Biol. Sci.* 270, S186–S188.

Lusseau, D., Whitehead, H., and Gero, S. (2008). Incorporating uncertainty into the study of animal social networks. *Anim. Behav.* 75, 1809–1815. doi: 10.1016/j.anbehav.2007.10.029

Machado, A. M. S., Cantor, M., Costa, A. P. B., Righetti, B. P. H., Bezamat, C., Valle-Pereira, J. V. S., et al. (2019). Homophily around specialized foraging underlies dolphin social preferences. *Biol. Lett.* 15:20180909. doi: 10.1098/rsbl.2018.0909

Mann, J., Stanton, M. A., Patterson, E. M., Bienenstock, E. J., and Singh, L. O. (2012). Social networks reveal cultural behaviour in tool-using using dolphins. *Nat. Commun.* 3:980.

McPherson, M., Smith-Lovin, L., and Cook, J. M. (2001). Birds of a feather: homophily in social networks. *Ann. Rev. Sociol.* 27, 415–444. doi: 10.1146/annurev.soc.27.1.415

Methion, S., and Diaz Lopez, B. (2020). Individual foraging variation drives social organization in bottlenose dolphins. *Behav. Ecol.* 31, 97–106.

Möller, L. M. (2011). Sociogenetic structure, kin associations and bonding in delphinids. *Mol. Ecol.* 21, 745–764. doi: 10.1111/j.1365-294x.2011.05405.x

Möller, L. M., Beheregaray, L. B., Allen, S. J., and Harcourt, R. G. (2006). Association patterns and kinship in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Behav. Ecol. Sociobiol.* 61, 109–117. doi: 10.1007/s00265-006-0241-x

Möller, L. M., Beheregaray, L. B., Harcourt, R. G., and Krutzen, M. (2001). Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proc. R. Soc. B Biol. Sci.* 268, 1941–1947. doi: 10.1098/rspb.2001.1756

Nattrass, S., Croft, D. P., Ellis, S., Cant, M. A., Weiss, M. N., Wright, B. M., et al. (2019). Postreproductive killer whale grandmothers improve the survival of their grandoffspring. *Proc. Natl. Acad. Sci. U.S.A.* 116, 26669–26673. doi: 10.1073/pnas.1903844116

Newman, M. E. J. (2006). Modularity and community structure in networks. *Proc. Natl. Acad. Sci. U.S.A.* 103, 8577–8582.

Newsome, S. D., Etnier, M. A., Monson, D. H., and Fogel, M. L. (2009). Retrospective characterization of ontogenetic shifts in killer whale diets via δ13C and δ15N analysis of teeth. *Mar. Ecol. Progress Ser.* 374, 229–242. doi: 10.3354/meps07747

Nishita, M., Shirakihara, M., and Amano, M. (2017). Patterns of association among female Indo-Pacific bottlenose dolphins (Tursiops aduncus) in a population forming large groups. *Behaviour* 154, 1013–1028. doi: 10.1163/1568539x-00003453

Nykanen, M., Dillane, E., Englund, A., Foote, A. D., Ingram, S. N., Louis, M., et al. (2018). Quantifying dispersal between marine protected areas by a highly mobile species, the bottlenose dolphin. *Tursiops truncatus*. Ecol. Evol. 8, 9241–9258. doi: 10.1002/ece3.4343

Pace, D. S., Pulcini, M., and Triossi, F. (2012). Anthropogenic food patches and association patterns of *Tursiops truncatus* at Lampedusa island. Italy. *Behav. Ecol.* 23, 254–264. doi: 10.1093/beheco/arr180

Parsons, K. M., Balcomb, K. C., Ford, J. K. B., and Durban, J. W. (2009). The social dynamics of southern resident killer whales and conservation implications for this endangered population. *Anim. Behav.* 77, 963–971. doi: 10.1016/j.anbehav.2009.01.018

Parsons, K. M., Durban, J. W., Claridge, D. E., Balcomb, K. C., Noble, L. R., and Thompson, P. M. (2003). Kinship as a basis for alliance formation between male bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Anim. Behav.* 66, 185–194. doi: 10.1006/anbe.2003.2186

Pilot, M., Dahlheim, M. E., and Hoelzel, A. R. (2010). Social cohesion among kin, gene flow without dispersal and the evolution of population genetic structure in the killer whale (*Orcinus orca*). *J. Evol. Biol.* 23, 20–31. doi: 10.1111/j.1420-9101.2009.01887.x

Powell, S. N., Wallen, M. M., Miketa, M. L., Krzyszczyk, E., Foroughirad, V., Bansal, S., et al. (2020). Sociality and tattoo skin disease among bottlenose dolphins in Shark Bay. Australia. *Behav. Ecol.* 31, 459–466. doi: 10.1093/beheco/arz207

Reisinger, R. R., Keith, M., Andrews, R. D., and de Bruyn, N. (2015). Movement and diving of killer whales (*Orcinus orca*) at a Southern Ocean archipelago. *J. Exp. Mar. Biol. Ecol.* 473, 90–102. doi: 10.1016/j.jembe.2015.08.008

Reisinger, R. R., van Rensburge, C., Hoelzel, A. R., and de Bruyn, P. J. N. (2017). Kinship and association in a highly social apex predator population, killer whales at Marion Island. *Behav. Ecol.* 28, 750–759. doi: 10.1093/beheco/arx034

Rendell, L., Cantor, M., Gero, S., Whitehead, H., and Mann, J. (2019). Causes and consequences of female centrality in cetacean societies. *Philos. Trans. R. Soc. B Biol. Sci.* 374:20180066. doi: 10.1098/rstb.2018.0066

Richard, K. R., Dillon, M. C., Whitehead, H., and Wright, J. M. (1996). Patterns of kinship in groups of free-living sperm whales (Physeter macrocephalus) revealed by multiple molecular genetic analyses. *Proc. Natl. Acad. Sci. U.S.A.* 93, 8792–8795. doi: 10.1073/pnas.93.16.8792

Riesch, R., Barrett-Lennard, L. G., Ellis, G. M., Ford, J. K. B., and Deecke, V. B. (2012). Cultural traditions and the evolution of reproductive isolation: ecological speciation in killer whales? *Biol. J. Linnean Soc.* 106, 1–17. doi: 10.1111/j.1095-8312.2012.01872.x

Ruckstuhl, K. E. (2007). Sexual segregation in vertebrates: proximate and ultimate causes. *Integr. Comparative Biol.* 47, 245–257. doi: 10.1093/icb/icm030

Ruckstuhl, K. E., and Neuhaus, P. (2002). Sexual segregation in ungulates: a comparative test of three hypotheses. *Biol. Rev.* 77, 77–96. doi: 10.1017/s1464793101005814

Sakai, M., Wang, D., Wang, K., Li, S., and Akamatsu, T. (2011). Do porpoises choose their associates? A new method for analysing social relationships among cetaceans. *PLoS One* 6:e28836. doi: 10.1371/journal.pone.0028836

Sanderson, C. E., and Alexander, K. A. (2020). Unchartered waters: Climate change likely to intensify infectious disease outbreaks causing mass mortality events in marine mammals. *Global Change Biol.* 26, 4284–4301. doi: 10.1111/gcb.15163

Schuppli, C., and van Schaik, C. P. (2019). Animal cultures: how we've only seen the tip of the iceberg. *Evol. Hum. Sci.* 1:E2.

Slooten, E., Dawson, S. M., and Whitehead, H. (1993). Associations among photographically identified Hector's dolphins. *Can. J. Zool.* 71, 2311–2318. doi: 10.1139/z93-324

Smith, J. E. (2014). Hamilton's legacy: kinship, cooperation, and social tolerance in mammalian groups. *Anim. Behav.* 92, 291–304. doi: 10.1016/j.anbehav.2014.02.029

Smolla, M., Gilman, R. T., Galla, T., and Shultz, S. (2015). Competition for resources and explain patterns of social and individual learning in nature. *Proc. R. Soc. B Biol. Sci.* 282:20151405. doi: 10.1098/rspb.2015.1405

Snijders, L., Blumstein, D. T., Stanley, C. R., and Franks, D. W. (2017). Animal social network theory can help wildlife conservation. *Trends Ecol. Evol.* 32, 567–577. doi: 10.1016/j.tree.2017.05.005

Snyder-Mackler, N., Burger, J. R., Gaydosh, L., Belsky, D. W., Noppert, G. A., Campos, F. A., et al. (2020). Social determinants of health and survival in humans and other animals. *Science* 368:eaax9553. doi: 10.1126/science.aax9553

Stanton, M. A., Gibson, Q. A., and Mann, J. (2011). When mum's away: a study of mother and calf ego networks during separations in wild bottlenose dolphins (*Tursiops sp.*). *Anim. Behav.* 82, 405–412. doi: 10.1016/j.anbehav.2011.05.026

Stanton, M. A., and Mann, J. (2012). Early social networks predict survival in wild bottlenose dolphins. *PLoS One* 7:e47508. doi: 10.1371/journal.pone.0047508

Sueur, C., Romano, V., Sosa, S., and Puga-Gonzalez, I. (2019). Mechanisms of network evolution: a focus on socioecological factors, intermediary mechanisms, and selection pressures. *Primates* 60, 167–181. doi: 10.1007/s10329-018-0682-7

Tavares, S. B., Samarra, F. I. P., and Miller, P. J. O. (2017). A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics. *Behav. Ecol.* 28, 500–514. doi: 10.1093/beheco/arw179

Titcomb, E. M., Reif, J. S., Fair, P. A., Stavros, H.-C. W., Mazzoil, M., Bossart, G. D., et al. (2017). Blood mercury concentrations in common bottlenose dolphins from the Indian River Lagoon, Florida: patterns of social distribution. *Mar. Mammal Sci.* 33, 771–784. doi: 10.1111/mms.12390

Torres, L. G., Nieukirk, S. L., Lemos, L., and Chandler, T. E. (2018). Drone up! Quantifying whale behavior from a new perspective improves observational capacity. *Front. Mar. Sci.* 5:319. doi: 10.3389/fmars.2018.00319

Van Cise, A. M., Martien, K. K., Mahaffy, S. D., Baird, R. W., Webster, D. L., Fowler, J. H., et al. (2017). Familial social structure and socially driven genetic differentiation in Hawaiian short-finned pilot whales. *Mol. Ecol.* 26, 6730–6741. doi: 10.1111/mec.14397

van Gils, J. A., Kraan, C., Dekinga, A., Koolhaas, A., Drent, J., de Goeij, P., et al. (2009). Reversed optimality and predictive ecology: burrowing depth forecasts population change in a bivalve. *Biol. Lett.* 5, 5–8. doi: 10.1098/rsbl.2008.0452

Vermeulen, E. (2018). Association patterns of bottlenose dolphins (*Tursiops truncatus*) in Bahia San Antonio, Argentina. *Mar. Mammal Sci.* 34, 687–700. doi: 10.1111/mms.12481

Volker, C. L., and Herzing, D. L. (2021). Aggressive behaviors of adult male spotted dolphins: making signals count during intraspecific and interspecific conflicts. *Anim. Behav. Cogn.* 8, 36–51.

Wade, P. R., Reeves, R. R., and Mesnick, S. L. (2012). Social and behavioural factors in cetacean responses to overexploitation: Are Odontocetes less "resilient" than mysticetes? *J. Mar. Sci.* 2012:567276.

Wang, X., Wu, F., Turvey, S. T., Rosso, M., Tao, C., Ding, X., et al. (2015). Social organization and distribution patterns inform conservation management of a threatened Indo-Pacific humpback dolphin population. *J. Mammol.* 96, 964–971. doi: 10.1093/jmammal/gyv097

Webber, Q. M. R., and Vander Wal, E. (2019). Trends and perspectives on the use of animal social network analysis in behavioural ecology: a bibliometric approach. *Anim. Behav.* 149, 77–87. doi: 10.1016/j.anbehav.2019.01.010

Weiss, M. N., Franks, D. W., Balcomb, K. C., Ellifrit, D. K., Silk, M. J., Cant, M. A., et al. (2020). Modelling cetacean morbillivirus outbreaks in an endangered killer whale population. *Biol. Conserv.* 242:108398. doi: 10.1016/j.biocon.2019.108398

Whitehead, H. (1993). The behaviour of mature male sperm whales on the Galapagos Islands breeding grounds. *Can. J. Zool.* 71, 689–699. doi: 10.1139/z93-093

Whitehead, H. (2003). *Sperm Whales: Social Evolution in the Ocean*. Chicago, IL: The University of Chicago Press.

Whitehead, H. (2008). Precision and power in the analysis of social structure using associations. *Anim. Behav.* 75, 1093–1099. doi: 10.1016/j.anbehav.2007.08.022

Whitehead, H., and Dufault, S. (1999). Techniques for analyzing vertebrate social structure unsing identified individuals. *Adv. Study Behav.* 28, 33–74. doi: 10.1016/s0065-3454(08)60215-6

Whitehead, H., and James, R. (2015). Generalized affiliation indices extract affiliations from social network data. *Methods Ecol. Evol.* 6, 836–844. doi: 10.1111/2041-210x.12383

Whitehead, H., and Rendell, L. (2015). *The Cultural Lives of Whales and Dolphins*. Chicago, IL: The University of Chicago Press.

Wierucka, K., Verborgh, P., Meade, R., Colmant, L., Gauffier, P., Esteban, R., et al. (2014). Effects of a morbillivirus epizootic on long-finned pilot whales *Globicephala melas* in Spanish Mediterranean waters. *Mar. Ecol. Progress Ser.* 502, 1–10. doi: 10.3354/meps10769

Wild, S., Allen, S. J., Krutzen, M., King, S. L., Gerber, L., and Hoppitt, W. J. E. (2019). Multi-network-based diffusion analysis reveals vertical cultural transmission of sponge tool use within dolphin matrilines. *Biol. Lett.* 15:20190227. doi: 10.1098/rsbl.2019.0227

Wild, S., Hoppit, W. J. E., Allen, S. J., and Krützen, M. (2020). Integregating genetic, environmental, and social networks to reveal transmission pathways of a dolphin foraging innovation. *Curr. Biol.* 30, 3024–3030. doi: 10.1016/j.cub.2020.05.069

Williams, R., and Lusseau, D. (2006). A killer whale social network is vulnerable to targeted removals. *Biol. Lett.* 2, 497–500. doi: 10.1098/rsbl.2006.0510

Wiszniewski, J., Brown, C., and Moeller, L. M. (2012). Complex patterns of male alliance formation in a dolphin social network. *J. Mammol.* 93, 239–250. doi: 10.1644/10-mamm-a-366.1

Wiszniewski, J., Lusseau, D., and Moeller, L. M. (2010). Female bisexual kinship ties maintain social cohesion in a dolphin network. *Anim. Behav.* 80, 895–904. doi: 10.1016/j.anbehav.2010.08.013

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 23 July 2021
doi: 10.3389/fmars.2021.695100

Environmental Reconstruction and Tracking as Methods to Explore Social Interactions in Marine Environments: A Test Case With the Mediterranean Rainbow Wrasse *Coris julis*

Zoë Goverts[1,2,3], Paul Nührenberg[1,2,3] and Alex Jordan[1,2,3]*

[1] Department of Collective Behaviour, Max Planck Institute of Animal Behavior, Konstanz, Germany, [2] Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany, [3] Department of Biology, University of Konstanz, Konstanz, Germany

OPEN ACCESS

Edited by:
David M. P. Jacoby,
Zoological Society of London,
United Kingdom

Reviewed by:
Josep Alos,
Mediterranean Institute for Advanced Studies (IMEDEA), Spain
Michele Gristina,
National Research Council (CNR), Italy

***Correspondence:**
Alex Jordan
ajordan@ab.mpg.de

Specialty section:
This article was submitted to
Marine Biology,
a section of the journal
Frontiers in Marine Science

Received: 14 April 2021
Accepted: 28 June 2021
Published: 23 July 2021

Citation:
Goverts Z, Nührenberg P and Jordan A (2021) Environmental Reconstruction and Tracking as Methods to Explore Social Interactions in Marine Environments: A Test Case With the Mediterranean Rainbow Wrasse Coris julis. Front. Mar. Sci. 8:695100. doi: 10.3389/fmars.2021.695100

A key aspect of understanding social interactions in marine animals is determining whether individuals freely interact in fission-fusion groups, or have spatially structured interactions, for example territories or home ranges. Territoriality can influence access to mates, food resources, or shelter sites, and may also impact conservation efforts, as the delineation of marine protected areas relies on knowledge of home ranges and movement patterns. However, accurately determining distribution and movement is challenging for many marine species, especially small and medium species, which cannot carry beacons or tags to automatically measure movement, and are also difficult for human observers to accurately follow. Yet these smaller species comprise the bulk of near-shore assemblages, and are essential conservation targets. As such, novel solutions for monitoring movement and behavior are required. Here we use a combination of tracking and environmental reconstruction to explore territoriality, aggression, and navigation in a small marine fish, explicitly applying this technique to questions of sociality in the marine environment. We use the Mediterranean Rainbow Wrasse, *Coris julis*, as a test case, but this approach can be extended to many other species and contexts. In contrast with previous reports for this species, we find that during our observation period, female *C. julis* occupy consistent territories over sand patches, and that they defend these territories against same-sex conspecifics. Displacement experiments revealed two further important social behavioral traits – first that displaced individuals were able to navigate back to their territory, avoiding almost all other female territories as they returned. Second that when displaced fish approached the territories of others, residents of these territories were often aggressive to the non-neighboring fish, in contrast with our observations of low aggression counts toward their natural neighbors. Resident fish therefore appear to show differing levels of aggressiveness depending on their social relationship with same-sex conspecifics. Overall, these results suggest a sophisticated degree of social behavior in this marine wrasse, dependent on social and structural environment, but which can only effectively be revealed by state-of-the-art tracking and environment reconstruction techniques.

Keywords: territory, range, social, marine, wrasse

INTRODUCTION

Animals interact dynamically with their environment and can develop specific relationships with their surroundings, as for example expressed through home ranges, defined as the areas where individuals spend most of their time with activities such as foraging, resting, or mating (Pearl, 2000). For many animals, the core of their home range is the most important area and is often considered the territory, and by defending such an area, individuals can monopolize resources, including food, shelter [e.g., in rodents *Meriones unguiculatus*: (Ågren et al., 1989), and mates (e.g., butterflies *Papilio zelicaon*: (Lederhouse, 1982)]. In the Tuatara, *Sphenodon punctatus*, territory structure also depends on the distribution of mates and competitors. Females and males of this species occupy independent territories, and for the males the size of territory scales with body size. Large males are more likely to own and defend larger territories that overlap with female home ranges, increasing their access to mates and providing a strong benefit (Moore et al., 2009).

Defending territories against intruders may involve displays or fights between residents and intruders, which come at a high cost to both winners and losers because of the energetic requirements and the possibility of physical damage and mortality (Dugatkin et al., 1998). From a game theoretic perspective, both individuals would benefit by avoiding confrontation if they could predict the outcome of the confrontation. However, it is often unclear which individual will win a fight, resulting in physical interactions. One way to avoid these costly interactions is to establish social relationships, the formation of which may lead to spatial structuring within populations as territory borders are established. In teleost fish, it has been suggested that spatial learning and social interactions are necessary prerequisites for territoriality (Bronstein, 1986). Territorial individuals might benefit from neighboring conspecifics and form integrated social groups within territorial neighborhoods (Stamps, 1988).

As well as the ecological impacts of territoriality, an understanding of the spatial structure of animal populations is essential for conservation efforts and management strategies. Protected areas, for example, can only be an effective conservation management tool if they are larger than the home ranges of the occurring species [as shown in a case study for the Mediterranean Sea: (Di Franco et al., 2018)]. To protect animals that are habitat specialists (for example the swift fox *Vulpes velox* in short-grass prairies), knowledge about their habitat preference and utilization are of primary importance (Kamler et al., 2003). In terrestrial systems, monitoring the movement and home ranges of animals can be achieved through tracking or remote telemetry, but this presents a major problem in marine habitats, where approaches such as Global Positioning System (GPS) or Pop-up Satellite Archival Tags (PSATs) are mostly applicable for larger, or in the case of acoustic telemetry, medium-sized aquatic animals (Hussey et al., 2015; Thys et al., 2015). For reasons of animal size, species abundance, and habitat complexity, many available tracking methods are poorly suited to these inshore regions and are not easily applied in smaller animals, despite these comprising the bulk of vertebrate species assemblages. To address this knowledge gap, alternative methods are necessary, and in the present study we employ a computer-vision based tracking methodology (Francisco et al., 2020) to track and analyse the movement and social interactions of a small inshore species, the Mediterranean rainbow wrasse (*Coris julis*). This study provides a demonstration of the potential for this type of approach to generate unprecedented quantitative insight into the behavior and movement of a class of marine vertebrates that was previously inaccessible to modern tracking approaches.

The Mediterranean rainbow wrasse belongs to the family Labridae and lives in coastal regions up to a depth of 120 m on rocky bottoms or seagrass (e.g., *Posidonia oceanica*) beds (Lejeune, 1987). As for many Labrids, it is a protogynous hermaphrodite, with a temporal separation of the sexes in one individual (Bentivegna et al., 1985). Sex change to the secondary male phase usually occurs at four years of age and is accompanied with a color change and testes function. Most *C. julis* are born as females but some are initially born as males (primary males) that phenotypically resemble females (Linde et al., 2011). The females live in harems and mate with the dominant and much larger secondary male, producing pelagic eggs (Lejeune, 1987). Lejeune (1987) states that only secondary phase males are territorial and that initial phase individuals have home ranges between 5 and 10 m. Males defend their territories because of the benefit of having multiple mates living in their home range.

No reports of female territoriality exist for *C. julis*, but harems have previously been suggested to form when females are defendable and thus site attached (Gladstone, 1987; Lejeune, 1987). Female territoriality could be adaptive because the defended area provides food resources or shelter sites (Bujalska and Saitoh, 2000). This may be particularly pertinent for this species, as *C. julis* rest in holes that they dig in the sand, so it may be advantageous for females to defend sandy areas (Videler et al., 1986). The question of female territoriality in *C. julis* is therefore important at many levels; to understand the social and breeding system of the species, to understand the home range and therefore efficacy of protection measures, and more generally to better understand sex-specific territoriality in fish, for example the assumed relationship that when one sex of a species is territorial, the other one is not (Ostfeld, 1985). This relationship may not always hold, for example in the haremic dwarf hawkfish *Cirrhitichtys falco* both males and females are territorial; territorial behavior in males depends on female access, whereas female territoriality is based on food resources (Kadota et al., 2011).

A theoretical approach of studying territoriality in a standardized way is to assume that the benefits and costs of defending a territory are measurable. Here, the territory is defined as the core area where an animal spends the majority of its time and which it actively defends against intruders, located in the potentially larger home range, the area that it frequently visits (Powell, 2000). The costs of holding such a territory are caused by the behavioral activities used to defend their area against con- or heterospecific individuals, such as aggressive behavior and patrols, while benefits are defined as the access to limited resources or mates (Stamps, 1994). The interaction between resource exploitability and exploration difficulty, which both directly link to costs and benefits, can drive territorial behavior when both the exploitation potential and the exploration difficulty are high (Monk et al., 2018). In contrast with the approach that concentrates on a focal resident and its responses to the costs and benefits of defense, alternative models exist that mainly consider the interactions with other individuals. One example is focusing on interactions among direct neighbors and how these interactions shape their use of space and another one defines territory size as the result of the interactions between residents and potential settlers seeking to gain territory (Adams, 2001). In this study, we combine both of these focal resident models by collecting information on direct neighbor interactions as well as interactions with unfamiliar conspecifics. We predict female *C. julis* will show territorial defense and have home ranges, because secondary males are territorial and are assumed to defend female harems. In order to test this, we use a novel method for underwater animal tracking to measure the home ranges of female *C. julis* in a non-invasive way. Furthermore, to test their spatial memory and their tendency to stay within their home ranges, we displaced focal fish from their territories and observed if and how they returned to their original putative territories.

MATERIALS AND METHODS

Field Experiments

All experiments were conducted by scuba diving at the STARESO Field Station, Calvi, France from mid-June to mid-July 2019 at two sandy patches embedded in a *P. oceanica* seagrass bed (see **Figure 1A**). These patches were located approximately 100 m from the coast (42°34′48.4′′N 8°43′31.8′′E), at a depth of 13 to 15.3 m, spanning an area of 261 m^2 with 60.4 m as the longest side (north-to-south).

First, we aimed to capture and tag all phenotypically female *C. julis* in this area were with a visible, unique elastomer code (Northwest Marine Technology, Inc.) to maintain the identity of fish across all experiments and tracking observations. The least invasive way to determine sex in *C. julis* is measuring the body length and identifying the phenotype. Individuals bigger than 18 cm are considered to be secondary males (Bertoncini et al., 2009). Therefore, targeted fish for this study were phenotypic females ranging from 8.5 cm to 12.5 cm standard length. In total, 11 fish were captured, of which 10 were within this range. Much larger or smaller individuals were not used in the experiments to avoid including secondary males and juveniles. After capturing the fish, the elastomer was injected below the skin, parallel to the dorsal fin, to allow visual identification of the tagged individuals. During the tagging procedure, a picture was taken of each fish to measure the standard body length (for details on the sizes of all tagged fish see **Supplementary Table 2**). Afterward, the individuals were released at the location of capture. At no point were the fish removed from the water (nor their depth changed), and all procedures were conducted in accordance with the STARESO field station's general scientific permit.

To determine if the tagged *C. julis* had territories or home ranges, we followed a repeated observation protocol in which each fish was observed for 10 min on a total of three days (repeated on day 3 and 5 after the first observation on day 1, see **Supplementary Table 1** for a summary of all tracking observations). During these observations, a diver followed the focal fish at a distance of approximately 2 m and recorded from a top-down perspective using a T-shaped stereo-camera setup (2x GoPro Hero 7, see **Supplementary Table 3** for further GoPro parameters and **Supplementary Figures 1A,D** for a picture of the setup). This setup ensured that the disturbance of the focal fish by the diver was minimized, apparent through the naturally behaving *C. julis*. Additionally, a video covering the sandy patches was recorded using the same setup for spatial reference.

In these observations, the female *C. julis* appeared to have defined home ranges. To further analyse their territorial behavior, each fish was captured, placed inside a transparent container (**Supplementary Figures 1B,C**) and displaced between 30 to 40 m from its roughly estimated core area to the core area of another tagged individual. The behavioral responses of the resident *C. julis* toward the displaced fish were recorded for 5 min. Then, the displaced fish were released and recorded by a diver with the stereo-camera setup until they entered their respective home range.

Video Analysis

A combination of tracking and structure-from-motion (SfM) was employed to determine the home ranges of individual *C. julis*. We mainly followed the methodology presented by Francisco et al. (2020), but implemented a few changes to tailor the technique to our specific use case. Firstly, the corresponding videos that resulted from the stereo-camera setup were temporally synchronized using their audio signals (Francisco et al., 2020). Then, one video frame was extracted every 2 s of the sandy patch footage and one frame every 3 s of each individual fish tracking observation. Secondly, we used COLMAP, an open-source SfM pipeline, to reconstruct the visual environment in 3D (Schönberger and Frahm, 2016; Schönberger et al., 2016). In addition to the reconstruction of environmental features, SfM also estimated camera positions and orientations for each of the extracted video frames. This resulted in one reconstruction for each tracking observation, all referenced within the reconstruction of the sandy patch. Finally, we used COLMAP to merge all reconstructions into a single one that was then used to triangulate 3D fish trajectories.

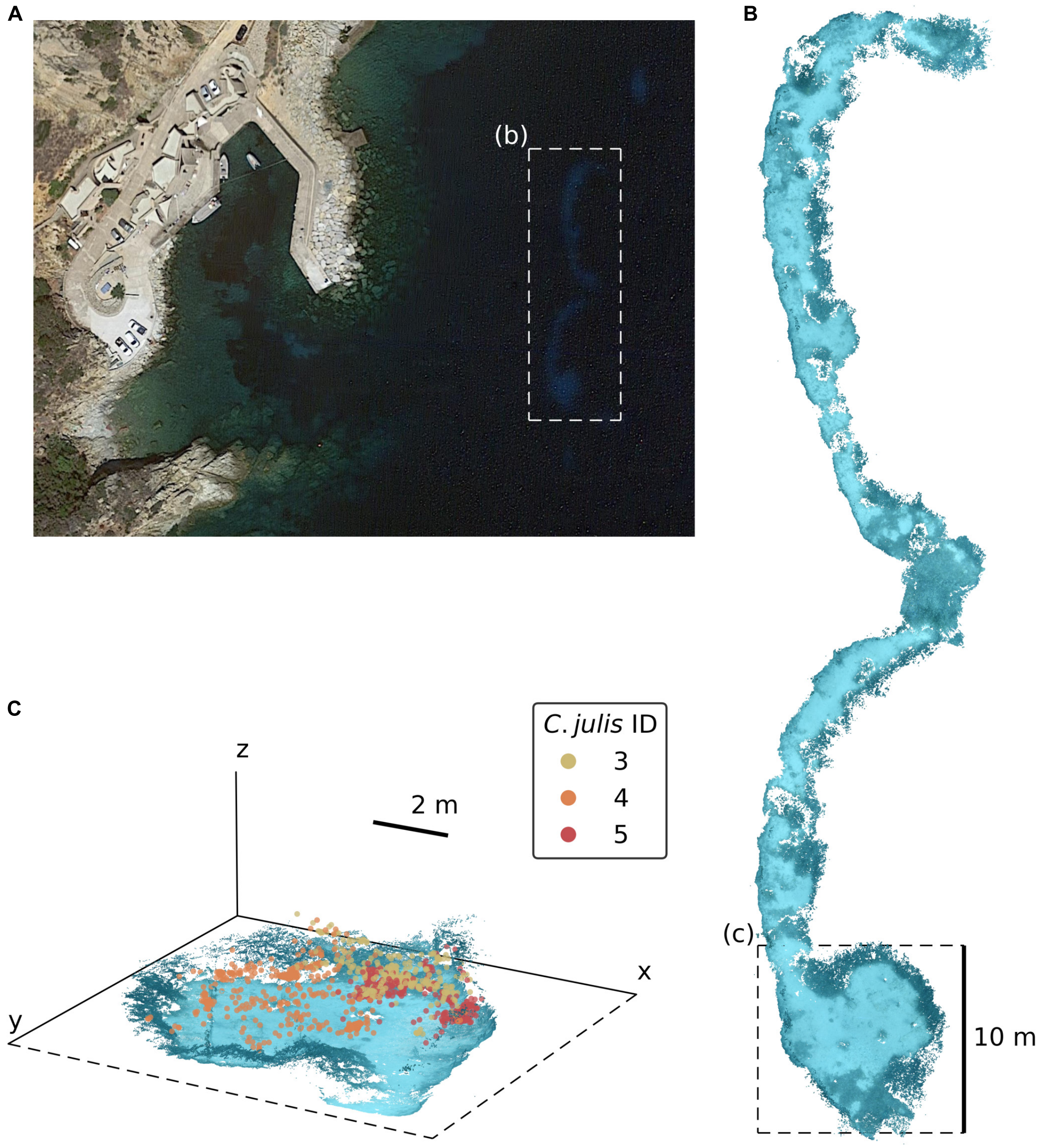


FIGURE 1 | (A) Satellite image of the STARESO bay near Calvi on Corsica, France (image source: Google Earth). The dashed rectangle (b) marks the location of the experimental area, the two sandy patches embedded in a *Posidonia oceanica* seagrass bed. **(B)** Dense SfM reconstruction of the sandy patches. **(C)** Detailed 3D view of the environmental reconstruction [the dashed rectangle marked as (c) in panel **(B)**] with the triangulated positions of *Coris julis* 3, 4, and 5.

For the latter, the focal individuals were tracked in both videos from the stereo-camera setup for each observation. Diverging from Francisco et al. (2020), we chose to manually track the fish using a custom-written Python video interface to record the pixel coordinates at a sampling frequency of 0.33 Hz (in the same video frames that were extracted for SfM). This resulted in corresponding, stereo-view pixel coordinates for each observation of each fish. Subsequently, these coordinates were triangulated into 3D trajectories (again, with a temporal resolution of 0.33 Hz) using "multiviewtracks" (Francisco et al., 2020). For an overview of trajectory completeness, we calculated the track coverage of each trajectory as the percentage of successfully triangulated 3D positions.

Statistical Analyses

For further analysis of home ranges, the 2D kernel density utilization distribution (UD) of the trajectory points from all three tracking observations (using only X and Y components) was calculated for each fish using the "adehabitatHR" package in R (Calenge, 2006). Utilization distribution is a well-established, objective technique to estimate the home range area from location data, calculating the probability that an individual is found at a specific point in space. The kernel density estimator is one of the common non-parametric statistical methods for estimating these probabilities. Using the UD, we calculated the home range and territory area (the core area of the home range) as the commonly used UD_{95} and UD_{50} contours, respectively (Worton, 1989; Nicholls et al., 2005).

Since no detailed description of aggressive behavior was found for this species, we created an ethogram based on aggressive behavior described in other teleost species [see **Table 1**, derived from Balzarini et al. (2014)]. The interactions between the focal individual and other *C. julis* in the 10 min tracking observations were manually scored and then spatially referenced into the 3D reconstructions. We then used BORIS to further analyse the video recordings obtained from the displacement experiments (Friard and Gamba, 2016). Here, the same ethogram was used to analyse the interactions of territory holders and displaced fish. Additionally, the paths of all individuals returning to their home ranges from the release locations of respective displacement trials were manually estimated on the map of the sandy patches based on observations and key features recognized in the video. The lengths of these paths were measured, as well as the "beeline" (the Euclidean distance between release and arrival locations) and the shortest distance through the sandy patch (following a path consisting of linear segments between the release and arrival location, bounded by the sandy patch). Further, the interactions between the released fish and any other *C. julis* were scored using the same ethogram.

Using this data, we conducted a series of statistical analyses. First, we tested whether the standard length of a fish has an effect on the size of its home range area (UD_{95}) or core area (UD_{50}). Next, we tested if the fraction of UD_{95} and UD_{50} that an individual shares with neighbors is dependent on the difference in their body lengths. For both tests, we used linear models in R (Zeileis and Hothorn, 2002). The parametric assumptions were tested using the Shapiro-Wilk (for normality of residuals) and the Breusch-Pagan test (for homoscedasticity). If the model did not meet the parametric assumptions, the response variable was log-transformed. All proportional data (area overlaps) was logit-transformed.

TABLE 1 | Ethogram of *Coris julis* with behaviors and respective descriptions.

Category	Behavior	Description
Neutral	Approach	Slow frontal swimming toward another *C. julis*
	Cleaning	*C. julis* cleaning a conspecific that is in a still vertical position with its head upward
Restrained aggression	S-bend	Stiff and still body in an "S" shape, often connected to approach
	Lateral display	*C. julis* aligning laterally with a conspecific, dorsal fin erected
Overt aggression	Ramming	Fast approach toward opponent with strong physical contact toward opponent
	Bumping	Intended attack with nose against opponent

The behaviors were grouped into categories for subsequent statistical analysis. Overt behaviors involve physical contact between the interacting individuals, or in the case of presented fish, physical contact of the behaving fish with the transparent presentation container.

Furthermore, equivalent models were used to test two behavioral hypotheses: (1) the body size difference between the resident and displaced fish affects the aggression presented by the resident individual and (2) the frequency of the territory holder's aggression toward the displaced intruder is dependent on the size of its home range or core area (UD_{95} and UD_{50}). Here, we modeled the behavior frequency as the response, dividing the count of observed behaviors by the time the resident fish showed attention toward the displaced individual. Lastly, we tested whether the released *C. julis* traveled a significantly longer distance than the beeline or the shortest way through the sandy patches, avoiding the territories of other individuals located in the patches. After testing that the differences of the sample pairs are normally distributed using the Shapiro-Wilk test, we used paired t-tests to compare the path length to the beeline and the shortest way through the sandy patch.

RESULTS

Using the three repeated observations for each of the 10 tracked fish, we were able to obtain 27 SfM reconstructions and successfully reference them into a common reconstruction. 85.8% of all extracted images were reconstructed into this 3D scene (**Figure 1B**). The observations of two individuals (*C. julis* 1 and 8) were only partially reconstructed with 46.2% and 33.3% of the images, respectively. For the remaining individuals, the fraction of reconstructed images varied between 93% and 99.3%. Since both of the stereo-images needed to be reconstructed with the focal individual visible in both of them for a location to be successfully triangulated, the track coverage (percentage of time points with obtained 3D location) can be lower than the percentage of reconstructed images. The mean track coverage of the three observations per fish varied between a minimum of 27.6% (*C. julis* 1) and a maximum of 85.1% (*C. julis* 4), with an overall mean track coverage of 66.7%. See **Figure 1C** for a detailed 3D view of triangulated fish locations and **Figure 2A** for all locations embedded in the reconstruction of the sandy patches.

Using the triangulated fish positions, we were able to estimate the UD_{95} and UD_{50} and shared areas for each fish (**Figure 2B**; **Supplementary Tables 2, 4**). The statistical models showed that fish size does not significantly affect UD_{95} (**Figure 2C**; estimate ± SE = 0.3 ± 0.13, $t = 2.26$, $p = 0.054$, $N = 10$) or UD_{50} (est. ± SE = 0.33 ± 0.16, $t = 2.07$, $p = 0.073$, $N = 10$). Further, we found that neither the shared fraction of UD_{95} or UD_{50} is affected by the pairwise size difference of the individuals (**Figure 2D**; UD_{95}: est. ± SE = -0.271 ± 0.39, $t = -0.696$, $p = 0.494$, $N = 24$; UD_{50}: est. ± SE = -0.319 ± 0.364, $t = -0.088$, $p = 0.931$, $N = 24$).

The behavioral scorings that were obtained with BORIS (Friard and Gamba, 2016) using the established ethogram (**Table 1**) and the displacement experiment recordings are

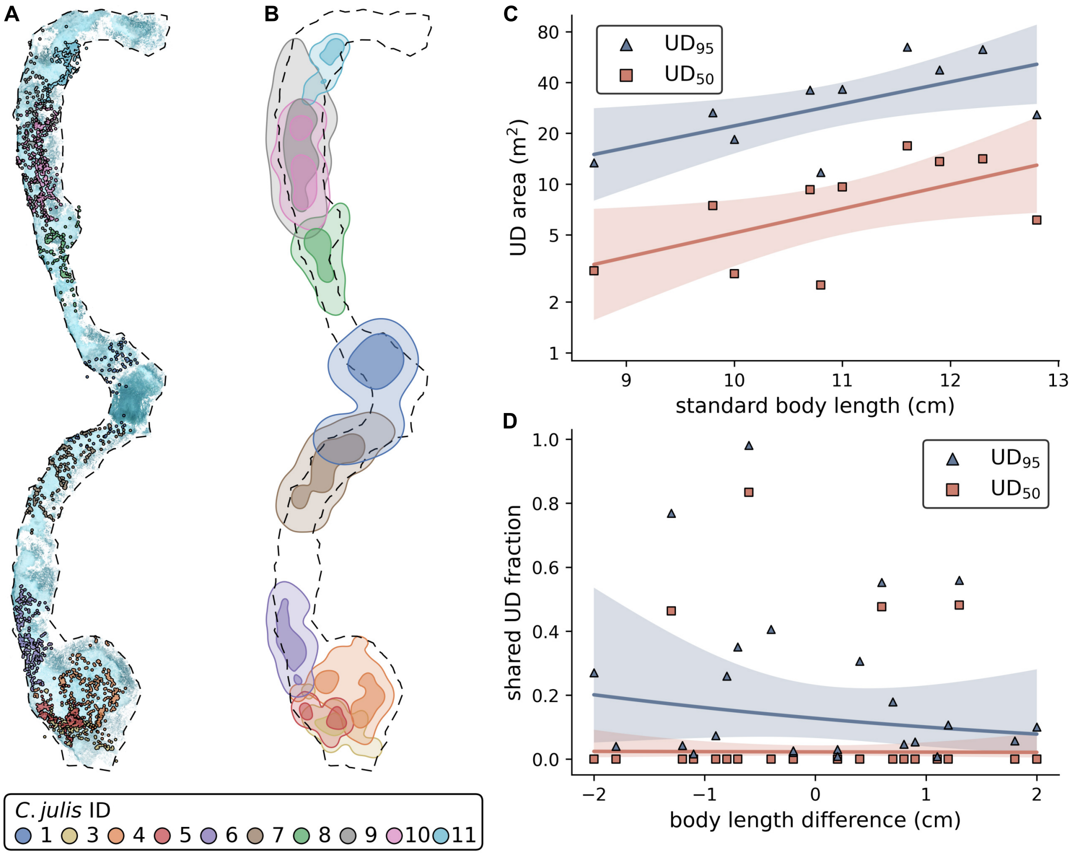


FIGURE 2 | (A) All *Coris julis* locations embedded in the reconstruction of the sandy patches. The dashed outline represents a contour approximation of the sandy patches that was used to estimate the size of this area. **(B)** UD_{95} (light areas) and UD_{50} (darker areas) contours of each fish. **(C)** Effect of standard body length on UD area. Note the log-scale of the y-axis. **(D)** Effect of body length differences on the shared UD areas (shared fraction of focal fish area). **(C,D)** Solid lines represent non-significant model fits, shaded areas 90% confidence intervals.

summarized in **Supplementary Table 5**. With this data, we found that (i) the body length of the resident fish does not influence its aggression toward the presented individual (**Figure 3A**; *overt behaviors*: est. ± SE = 0.027 ± 0.023, $t = 1.18$, $p = 0.28$, $N = 8$; *restrained behaviors*: est. ± SE 0.004 ± 0.004, $t = 1.026$, $p = 0.345$, $N = 8$), (ii) the difference in body length between both fish does not influence the aggressive response of the resident fish (**Figure 3B**; *overt behaviors*: est. ± SE = 0.017 ± 0.016, $t = 1.038$, $p = 0.339$, $N = 8$; *restrained behaviors*: est. ± SE = 0.002 ± 0.003, $t = 0.637$, $p = 0.5475$, $N = 8$); and that (iii) neither UD_{95} nor UD_{50} of the resident fish have an effect on its aggressive response (**Figures 3C,D**; UD_{95}: est. ± SE = 0.0008 ± 0.0027, $t = 0.295$, $p = 0.778$, $N = 8$; UD_{50}: est. ± SE = 0.0027 ± 0.009, $t = 0.283$, $p = 0.786$, $N = 8$). Note that we could not successfully identify all individuals based on their elastomer tags during these experiments due to the distance between the cameras and the diver to the resident fish that was adhered to, minimizing the diver's disturbance of the fish. Therefore, the sample size in these models was limited to 8 unique resident/presented fish pairs. Further, we were able to spatially map the behavioral interactions during the tracking observations, however, due to the small sample sizes within the different behaviors, we chose not to statistically analyse the relationship between behavior counts and *C. julis* density (**Figure 3E**).

The displacements were made at distances ranging from 30 to 46 m from each estimated core area. After the release from the transparent container, the fish took between 3.25 and 14.3 min to return to their respective home range, with average velocities of the fish varying from 0.09 m/s to 0.28 m/s (mean velocity 0.18 m/s, for more details see **Supplementary Table 6**). *Coris julis* 9 was lost directly after the release, but was found at its home range the day after. We manually mapped the path that the fish swam from their locations of displacement to their respective home ranges, and the interactions that they had during these observations (**Figure 4A**). All displaced individuals swam through the *P. oceanica* with little to no contact with the sand and other home ranges. Noticeably, all behavioral interactions between the returning *C. julis* and other individuals took place in the sandy patches. Using paired *t*-tests, we showed that the paths used by *C. julis* after they were released were significantly longer than the 'beeline' and the more direct paths over the sand (**Figure 4B**; "*beeline*": $p < 0.001$, mean of differences = 26.6, $N = 9$; *shortest path on sand*: $p < 0.001$, mean of differences = 21.0, $N = 9$).

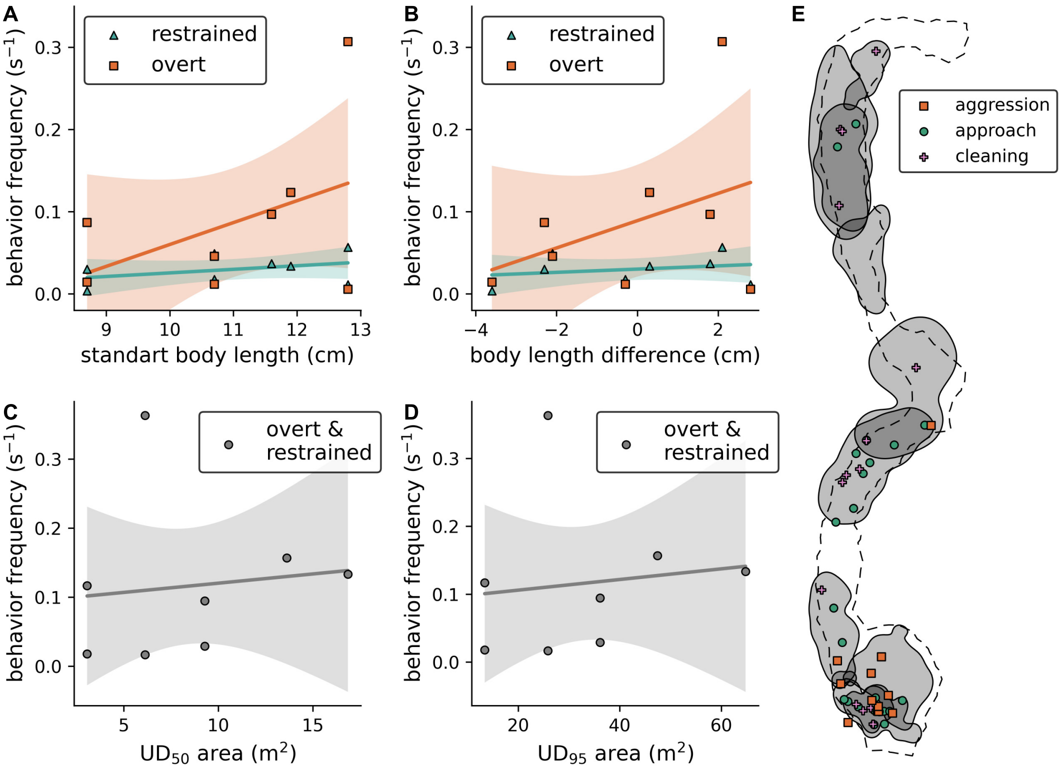


FIGURE 3 | (A) Effect of resident fish size on the frequency of aggressive behaviors toward the presented intruder. **(B)** Effect of the size difference between resident and presented fish on the frequency of aggressive behaviors. **(C,D)** Effect of UD area (UD$_{50}$ and UD$_{95}$, respectively) on the frequency of aggressive behaviors (both overt and restrained). **(A–D)**: Solid lines represent non-significant model fits, shaded areas 90% confidence intervals. **(E)** Visualization of UD$_{95}$ contours (gray areas) with the locations of behavioral interactions of fish during the tracking observations.

DISCUSSION

Territoriality is an important aspect of animal behavior. Defending an area and therefore monopolizing its associated resources, such as food, cover, shelter or mates, may increase fitness if these resources are limiting. Territoriality is therefore not only expressed in the spatial relationship the individual has with its surroundings, but also the social relationship it has with its neighbors and intruders. In the case of *C. julis*, only second phase males were previously described as being territorial, potentially defending harems of females (Lejeune, 1987). Because of the potential site fidelity of females, we were also interested in testing whether females were territorial. In order to examine this apparent knowledge gap, we deployed a novel technique to measure the movement behavior of not only individual females, but also their interactions with neighbors and unknown conspecifics. Based on video imaging, this non-invasive method yielded highly detailed positional data and allowed the estimation of home ranges and territories. We were able to determine the home ranges and territories of ten female *C. julis* which were largely confined to sandy regions during our observations, in contrast to the more broadly ranging males. We showed that every individual returned to its home range when displaced, which took between 3 and 14 min. This result suggests these fish have good spatial memory or an existing cognitive map, although further experimental tests would be required to fully test for this possibility. Furthermore, we studied the social relationships that the individuals had with their neighbors and possible intruders. The interactions among neighbors were mostly non-aggressive, but when we presented a possible settler to territory holders, the behavioral response was overwhelmingly aggressive. This may be due to dear-enemy effects (Aires et al., 2015), providing further suggestions of long-term fixed territories in females of this species.

In addition, we found that the observed female *C. julis* were site attached. Each of the individuals was spotted within a relatively small, confined area in all of its respective observations. These areas were considered as home ranges and were estimated as UD$_{95}$, varying between 11.7 and 64.8 m^2, with a mean of 34.37 ± 19 m^2. Most territories were of similar sizes and the observed *C. julis* barely left the sand (**Figure 2B**), as shown with the UD$_{50}$ estimates, which range between 3 and 16.8 m^2, with a mean of 8.6 ± 5 m^2. A similar relationship was found in a previous study made with six different Caribbean wrasse species (Jones, 2005). Although *C. julis* has been reported to live on rocky bottoms or seagrass (Lejeune, 1987; Fruciano et al., 2011), our study suggests that the observed female individuals mostly live on sand. Presumably, sand is of importance because they feed during the day and dig themselves into the sand to rest during the night (Videler et al., 1986). Almost the entire area of the two

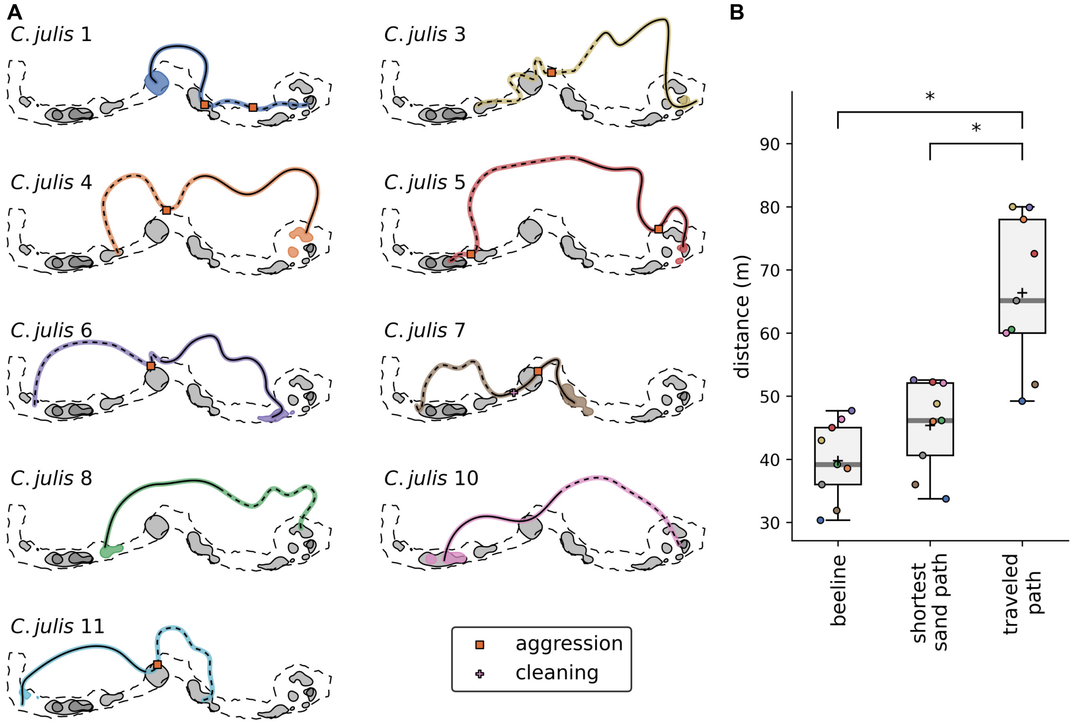


FIGURE 4 | (A) Estimated paths of *Coris julis* after their release at the locations of the displacement experiments. The paths start with the dashed and end with the solid lines. Shaded areas represent the UD_{50} contours of each fish with the colored area marking the core area of the displaced individual. *Coris julis* 10 was lost directly after its release, so no path could be estimated. Note that visualizations were rotated 90°counter-clockwise. **(B)** Distances of the "beeline" (the Euclidean distance between the points of release and arrival), the shortest path on the sand (a path consisting of linear segments bounded within the sandy patch), and the estimated traveled path. Asterisks denote significant differences.

sandy patches in our study site was part of an observed home range. We found only two spots in which no camera positions from the individual observations were reconstructed. In one case, we assume that it belongs to the home ranges of the adjacent individuals that were not completely reconstructed (missing 53.7% and 66.66% of the images, respectively, **Supplementary Table 1**). Structure-from-motion relies on a static background with detectable keypoints, and it is possible there was moving debris in this location, making it difficult to reconstruct. In the other case, only 2.6% and 0.74% of the adjacent territories did not get reconstructed, so this spot is either not habitable or already occupied by an individual that was not tagged and filmed.

From the video recordings, we not only calculated the home ranges and territories, but also scored the observed interactions (**Figure 3E**). Aggression was mainly observed in areas with at least two overlapping UD_{95}, however, due to the small sample size we did not statistically test this potential effect of fish density. A general limitation of our study is the small sample size of observed individuals; although we aimed to tag and track the movement behavior of all female individuals in the experimental area, we only found 10 individuals that matched our target range of fish sizes within the sandy patches. We later observed one other female that also matched this range, but it is unclear whether it was a new settler in this area or if we missed it during the tagging dives. With this limited data, we did not find that larger individuals were significantly more aggressive toward intruders in the displacement experiments or that the aggressiveness of the resident depended on the size difference between the presented and the resident fish. The non-significant trend in the first case, however, implies that such an effect could exist if a larger sample of female *C. julis* with a broader range of body lengths were studied. In addition to aggressive interactions, we also observed cleaning behavior, which was only presented by juveniles (fish smaller than the ones targeted in this study) toward the focal fish. This substantiates the assumption that only juvenile *C. julis* are frequent cleaners in the Mediterranean (Vasco-Rodrigues and Cabrera, 2015). Some wrasses have fixed "cleaning stations," for example *Halichoeres cyanocephalus* (Sazima et al., 1998) but our current dataset cannot fully investigate such site-specific cleaning behaviors in *C. julis*. However, cleaning was observed in almost every territory, and the spatial relationships between cleaning, territories and potential "cleaning stations" should be addressed in further research.

We found that body size does not significantly affect the UD_{95} or UD_{50}, and that the shared fraction of the UD_{95} is not affected by the difference in body length of the individuals (**Figures 2C,D**). However, these results are likely to be influenced by the small sample size, as we only observed the interactions and territories of 10 individuals in this study. For example, it has been shown in a study on six different wrasse species that body length and territory size correlate (Jones, 2005). An alternative explanation for our results could be that territory size depends on the time and energy an animal has spent in a specific area, more than on its body size. For example, smaller individuals that hold a territory for a longer time might own larger territories than large individuals that have recently settled in a territorial neighborhood. Again, this is an area of fruitful future research. The territories (UD_{50}) do not frequently overlap (**Figures 2A, D**), except between *C. julis* 3 and 5, and *C. julis* 9 and 10, where we observed almost complete overlaps in UD_{50}. This indicates shared territories between these individuals and potential benefits from forming a social group within a territorial neighborhood. It might be less costly to cooperate at defending against intruders than to fight over the territory to decide which of the individuals keeps the area (Stamps, 1988). Close neighbors also might act as an early warning system to detect intruders [for example described in red-capped cardinals, *Paroaria gularis* (Eason and Stamps, 1993)]. However, it should be considered that initial phase males have the same phenotype as females, and thus, a small fraction of our focal rainbow wrasse are likely to be males. A previous study in the same study site showed that 14.7% of initial phase individuals were initial phase males, suggesting that even if some of the focal fish where initial phase males, the vast majority were likely to be females (Lejeune, 1987). This presents the alternative that the observed territory overlaps were the result of initial phase males courting females, although we did not observe courtship behavior between these individuals. Our observations were made in June and July, overlapping with the peak of sexual activity that was described to last from April to mid-September in *C. julis* (Lejeune, 1987). Furthermore, territories of initial phase males vary between 5 and 10 m^2, which is in the range of area sizes that we estimated as territories (UD_{50}, 8.6 ± 5 m^2).

SUMMARY

Here, we used a novel method to test for territoriality and to measure home ranges and territories in a highly quantitative manner based on video recordings and individual tracking. Our results show that female *C. julis* can be territorial, and that none of the observed fish changed its location throughout three consecutive trials in the course of seven days, demonstrating high site-specificity in this period. It is possible that at other periods of the day, or season, this species has different distributions for example outside of breeding periods, a possibility requiring further research attention. Interactions with neighbors were mostly non-aggressive, but territory holders defended their area against potential settlers. Moreover, when displaced, individuals immediately returned to their original territory, mostly avoiding territories of other individuals. When they did enter the territory of other individuals, they were frequently met with aggression. We assume that the observed female *C. julis* defended territories in sandy areas because they monopolize food resources and their presumed resting sites. Further, the territoriality of female *C. julis* during our observations suggests that they form harems in the broader territories of males. These two aspects are fruitful avenues for future research on how female *C. julis* use the habitat within their home ranges and which resources they defend inside their territories. When including other habitat types such as rocky reefs and considering the context of male territoriality, follow-up experiments could provide an in-depth description of the mating, homing and territorial behavior of one of the abundant species in the Mediterranean Sea using these approaches. This non-invasive, quantitative study of social interactions and movement in a small marine fish reveals the insight that can be gained in previously understudied systems, contributing further understanding species social systems, relationships with their environment, and ultimately, effective conservation measures.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because all research was conducted under the general scientific permit of the STARESO Marine Station.

AUTHOR CONTRIBUTIONS

ZG, PN, and AJ designed experiments and wrote the manuscript. ZG performed experiments and filming in the field. ZG and PN performed tracking and performed statistical analysis. All authors contributed to the article and approved the submitted version.

FUNDING

This research was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy – EXC 2117 – 422037984 and by the Max Planck Institute of Animal Behavior.

ACKNOWLEDGMENTS

We thank members of the Jordan lab for many fruitful discussions. We thank Myriam Knöpfle, Jakob Gübel, and Karina Weiler for their assistance in the field. We also thank the staff at STARESO Marine Station, in particular Cyril Steibel, for kindly supporting our research in the field.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.695100/full#supplementary-material

REFERENCES

Adams, E. S. (2001). Approaches to the study of territory size and shape. *Annu. Rev. Ecol. Syst.* 32, 277–303. doi: 10.1146/annurev.ecolsys.32.081501.114034

Ågren, G., Zhou, Q., and Zhong, W. (1989). Ecology and social behaviour of *Mongolian gerbils*, *Meriones unguiculatus*, at Xilinhot, Inner Mongolia, China. *Anim. Behav.* 37, 28–32. doi: 10.1016/0003-3472(89)90003-1

Aires, R. F., Oliveira, G. A., Oliveira, T. F., Ros, A. F. H., and Oliveira, R. F. (2015). Dear enemies elicit lower androgen responses to territorial challenges than unfamiliar intruders in a cichlid fish. *PLoS One* 10:e0137705. doi: 10.1371/journal.pone.0137705

Balzarini, V., Taborsky, M., Wanner, S., Koch, F., and Frommen, J. G. (2014). Mirror, mirror on the wall: the predictive value of mirror tests for measuring aggression in fish. *Behav. Ecol. Sociobiol.* 68, 871–878. doi: 10.1007/s00265-014-1698-7

Bentivegna, F., Cirino, P., and Rasotto, M. B. (1985). Further investigations into sex reversal of *Coris julis* L. (Pisces, Labridae). *Bolletino di Zool.* 52, 355–358. doi: 10.1080/11250008509440539

Bertoncini, ÁA., MacHado, L. F., Barreiros, J. P., Hostim-Silva, M., and Verani, J. R. (2009). Cleaning activity among *Labridae* in the Azores: the rainbow wrasse *Coris julis* and the Azorean blue wrasse *Centrolabrus caeruleus*. *J. Mar. Biol. Assoc. U.K.* 89, 859–861. doi: 10.1017/S002531540900040X

Bronstein, P. M. (1986). Socially mediated learning in male betta splendens. *J. Comp. Psychol.* 100, 279–284. doi: 10.1037/0735-7036.100.3.279

Bujalska, G., and Saitoh, T. (2000). Territoriality and its consequences. *Polish J. Ecol.* 48, 37–49.

Calenge, C. (2006). The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Modell.* 197, 516–519. doi: 10.1016/j.ecolmodel.2006.03.017

Di Franco, A., Plass-Johnson, J. G., Di Lorenzo, M., Meola, B., Claudet, J., Gaines, S. D., et al. (2018). Linking home ranges to protected area size: the case study of the Mediterranean Sea. *Biol. Conserv.* 221, 175–181. doi: 10.1016/j.biocon.2018.03.012

Dugatkin, L. A., Reeve, H. K., and Mangel, M. (1998). Game theory and animal behaviour. *Nature* 395:32.

Eason, P. K., and Stamps, J. A. (1993). An early warning system for detecting intruders in a territorial animal. *Anim. Behav.* 46, 1105–1109. doi: 10.1006/anbe.1993.1300

Francisco, F. A., Nührenberg, P., and Jordan, A. (2020). High-resolution, non-invasive animal tracking and reconstruction of local environment in aquatic ecosystems. *Mov. Ecol.* 8:27. doi: 10.1186/s40462-020-00214-w

Friard, O., and Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol. Evol.* 7, 1325–1330. doi: 10.1111/2041-210X.12584

Fruciano, C., Tigano, C., and Ferrito, V. (2011). Geographical and morphological variation within and between colour phases in *Coris julis* (L. 1758), a protogynous marine fish. *Biol. J. Linn. Soc.* 104, 148–162. doi: 10.1111/j.1095-8312.2011.01700.x

Gladstone, W. (1987). Role of female territoriality in social and mating systems of *Canthigaster valentini* (Pisces: Tetraodontidae): evidence from field experiments. *Mar. Biol.* 96, 185–191. doi: 10.1007/BF00427018

Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., et al. (2015). Aquatic animal telemetry: a panoramic window into the underwater world. *Science* 348:1255642. doi: 10.1126/science.1255642

Jones, K. M. M. (2005). Home range areas and activity centres in six species of caribbean wrasses (Labridae). *J. Fish Biol.* 66, 150–166. doi: 10.1111/j.0022-1112.2005.00589.x

Kadota, T., Osato, J., Hashimoto, H., and Sakai, Y. (2011). Harem structure and female territoriality in the dwarf hawkfish *Cirrhitichthys falco* (Cirrhitidae). *Environ. Biol. Fishes* 92, 79–88. doi: 10.1007/s10641-011-9817-z

Kamler, J. F., Ballard, W. B., Fish, E. B., Lemons, P. R., Mote, K., and Perchellet, C. C. (2003). Habitat use, home ranges, and survival of swift foxes in a fragmented landscape: conservation implications. *J. Mammal.* 84, 989–995. doi: 10.1644/BJK-033

Lederhouse, R. C. (1982). Territorial defense and lek behavior of the black swallowtail butterfly, *Papilio polyxenes*. *Behav. Ecol. Sociobiol.* 10, 109–118. doi: 10.1007/BF00300170

Lejeune, P. (1987). The effect of local stock density on social behavior and sex change in the mediterranean labrid *Coris julis*. *Environ. Biol. Fishes* 18, 135–141. doi: 10.1007/BF00002601

Linde, M., Palmer, M., and Alós, J. (2011). Why protogynous hermaphrodite males are relatively larger than females? Testing growth hypotheses in mediterranean rainbow wrasse *Coris julis* (Linnaeus, 1758). *Environ. Biol. Fishes* 92, 337–349. doi: 10.1007/s10641-011-9844-9

Monk, C. T., Barbier, M., Romanczuk, P., Watson, J. R., Alós, J., Nakayama, S., et al. (2018). How ecology shapes exploitation: a framework to predict the behavioural response of human and animal foragers along exploration–exploitation trade-offs. *Ecol. Lett.* 21, 779–793. doi: 10.1111/ele.12949

Moore, J. A., Daugherty, C. H., and Nelson, N. J. (2009). Large male advantage: phenotypic and genetic correlates of territoriality in tuatara. *J. Herpetol.* 43, 570–578. doi: 10.1670/08-290.1

Nicholls, D. G., Robertson, C. J. R., and Naef-Daenzer, B. (2005). Evaluating distribution modelling using kernel functions for northern royal albatrosses (Diomedea sanfordi) at sea off South America. *Notornis* 52:223.

Ostfeld, R. S. (1985). Limiting resources and territoriality in microtine rodents. *Am. Nat.* 126, 1–15. doi: 10.1086/284391

Pearl, M. C. (2000). *Research Techniques in Animal Ecology*. New York, NY: Columbia University Press.

Powell, R. (2000). "Animal home ranges and territories and home range estimators," in *Research Techniques in Animal Ecology: Controversies and Consequences*, eds M. C. Pearl, L. Boitani, and T. Fuller (New York, NY: Columbia University Press), 65–110.

Sazima, I., Moura, R. L., and Luiz Gasparini, J. (1998). The wrasse *Halichoeres cyanocephalus* (Labridae) as a specialized cleaner fish. *Bull. Mar. Sci.* 63, 605–610.

Schönberger, J. L., and Frahm, J. M. (2016). "). Structure-from-motion revisited," in *Proceedings of the IEEE Computer Society Conference on Computer Vision and Pattern Recognition (CVPR)* (Las Vegas, NV: IEEE), 4104–4113. doi: 10.1109/CVPR.2016.445

Schönberger, J. L., Zheng, E., Pollefeys, M., and Frahm, J.-M. (2016). "Pixelwise view selection for unstructured multi-view stereo," in *Proceedings of the 14th European Conference on Computer Vision (ECCV)*, Amsterdam.

Stamps, J. A. (1988). Conspecific attraction and aggregation in territorial species. *Am. Nat.* 131, 329–347. doi: 10.1086/284793

Stamps, J. A. (1994). Territorial behavior: testing the assumptions. *Adv. Study Behav.* 23:232.

Thys, T. M., Ryan, J. P., Dewar, H., Perle, C. R., Lyons, K., O'Sullivan, J., et al. (2015). Ecology of the ocean sunfish, mola mola, in the southern California current system. *J. Exp. Mar. Bio. Ecol.* 471, 64–76. doi: 10.1016/j.jembe.2015.05.005

Vasco-Rodrigues, N., and Cabrera, P. M. (2015). *Coris julis* cleaning a mola mola, a previously unreported association. *Cybium* 39, 315–316.

Videler, J. J., Koella, W. P., Obál, F., and Schulz, H. (1986). "Sleep under sand cover of the labrid fish *Coris julis*," in *Sleep*, eds W. Koella, F. Obal, H. Schulz, and P. Visser (Stuttgart, FRG: Fischer), 145–147.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home- range studies. *Ecology* 70, 164–168. doi: 10.2307/1938423

Zeileis, A., and Hothorn, T. (2002). Diagnostic checking in regression relationships. *R News* 2, 7–10.

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Marine Science

ORIGINAL RESEARCH
published: 03 September 2021
doi: 10.3389/fmars.2021.665726

Social Network Analysis Reveals the Subtle Impacts of Tourist Provisioning on the Social Behavior of a Generalist Marine Apex Predator

David M. P. Jacoby[1,2*†], Bethany S. Fairbairn[1,3], Bryan S. Frazier[4], Austin J. Gallagher[5†], Michael R. Heithaus[6†], Steven J. Cooke[7†] and Neil Hammerschlag[8,9†]

[1] Institute of Zoology, Zoological Society of London, London, United Kingdom, [2] Lancaster Environment Centre, Lancaster University, Lancaster, United Kingdom, [3] Centre for Biodiversity and Environmental Research, University College London, London, United Kingdom, [4] South Carolina Department of Natural Resources, Marine Resources Research Institute, Charleston, SC, United States, [5] Beneath the Waves, Herndon, VA, United States, [6] Institute of Environment, Department of Biological Science, Florida International University, North Miami, FL, United States, [7] Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, Ottawa, ON, Canada, [8] Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL, United States, [9] Leonard and Jayne Abess Center for Ecosystem Science and Policy, University of Miami, Coral Gables, FL, United States

Edited by:
David W. Sims,
Marine Biological Association of the United Kingdom, United Kingdom

Reviewed by:
Charlie Huveneers,
Flinders University, Australia
Nick Humphries,
Marine Biological Association of the United Kingdom, United Kingdom

****Correspondence:***
David M. P. Jacoby
d.jacoby@lancaster.ac.uk;
davidjacoby1@gmail.com

†ORCID:
David M. P. Jacoby
0000-0003-2729-3811
Austin J. Gallagher
0000-0003-1515-3440
Michael R. Heithaus
0000-0002-3219-1003
Steven J. Cooke
0000-0002-5407-0659
Neil Hammerschlag
0000-0001-9002-9082

Specialty section:
This article was submitted to Marine Megafauna, a section of the journal Frontiers in Marine Science

Received: *09 February 2021*
Accepted: *04 August 2021*
Published: *03 September 2021*

Citation:
Jacoby DMP, Fairbairn BS, Frazier BS, Gallagher AJ, Heithaus MR, Cooke SJ and Hammerschlag N (2021) Social Network Analysis Reveals the Subtle Impacts of Tourist Provisioning on the Social Behavior of a Generalist Marine Apex Predator. Front. Mar. Sci. 8:665726. doi: 10.3389/fmars.2021.665726

Shark dive ecotourism is a lucrative industry in many regions around the globe. In some cases, sharks are provisioned using bait, prompting increased research on how baited dives influence shark behavior and yielding mixed results. Effects on patterns of habitat use and movement seemly vary across species and locations. It is unknown, however, whether wide-ranging, marine apex predators respond to provisioning by changing their patterns of grouping or social behavior. We applied a tiered analytical approach (aggregation-gregariousness-social preferences) examining the impact of provisioning on the putative social behavior of tiger sharks (*Galeocerdo cuvier*) at a dive tourism location in The Bahamas. Using network inference on three years of acoustic tracking data from 48 sharks, we tested for non-random social structure between non-provisioned and provisioned monitoring sites resulting in 12 distinct networks. Generally considered a solitary nomadic predator, we found evidence of sociality in tiger sharks, which varied spatiotemporally. We documented periods of both random ($n = 7$ networks) and non-random aggregation ($n = 5$ networks). Three of five non-random aggregations were at locations unimpacted by provisioning regardless of season, one occurred at an active provisioning site during the dry season and one at the same receivers during the wet season when provision activity is less prevalent. Aggregations lasted longer and occurred more frequently at provisioning sites, where gregariousness was also more variable. While differences in gregariousness among individuals was generally predictive of non-random network structure, individual site preferences, size and sex were not. Within five social preference networks, constructed using generalized affiliation indices, network density was lower at provisioning sites, indicating lower connectivity at these locations. We found no evidence of size assortment on preferences. Our data suggest that sociality may occur naturally within the Tiger Beach area, perhaps due to the unusually high density of individuals there. This study demonstrates the existence of periodic social behavior, but also considerable variation in association between tiger sharks, which we argue may help to mitigate any long-term impacts of provisioning on this population. Finally, we illustrate the utility of combining telemetry and social network approaches for assessing the impact of human disturbance on wildlife behavior.

Keywords: behavioral ecology, ecotourism, gregariousness, predators, shark diving, social affiliations, sociality, tiger shark (*Galeocerdo cuvier*)

INTRODUCTION

Shark dive ecotourism has grown significantly as an enterprise over the last two decades, bolstering support for the argument that sharks are more valuable alive than they are dead where ecotourism is viable (Gallagher and Hammerschlag, 2011; Cisneros-Montemayor et al., 2013; Gallagher et al., 2015). This argument resonates particularly when we consider that many of these iconic, large-bodied species are often the focus of ecotourism dive ventures, but are continuing to decline amid widespread and persistent overexploitation (Worm et al., 2013; Queiroz et al., 2019; MacNeil et al., 2020; Pacoureau et al., 2021).

To ensure reliable experiences can be offered to paying clients, the provisioning of food to attract sharks to divers is commonplace (Meyer et al., 2021). This has led to debate within the public and scientific community as to whether the potential economic and conservation advantages outweigh the possible negative impacts, which might include changes in shark behavior, increased human-wildlife conflict, increased prevalence of disease, or a possible reliance of sharks on provisioned food sources (Semeniuk and Rothley, 2008; Brena et al., 2015; Gallagher et al., 2015; Macdonald et al., 2017). At face value, shark ecotourism appears to be a conservation "win-win" providing localized protection to species, while generating local income and employment (of particular importance in developing countries) and raising public awareness of imperiled species (Apps et al., 2018). Since the initial boom of these tourism operations, considerable research effort has focused on the potential ecological impacts of this industry, resulting in a number of species-specific studies exploring the influence of shark dive tourism on movement ecology (Hammerschlag et al., 2012), residency patterns (Mourier et al., 2020), trophic ecology (Abrantes et al., 2018), community composition (Clarke et al., 2013), field metabolic rates (Barnett et al., 2016), and harmful human-wildlife encounters such as shark bites [see Brena et al. (2015), Gallagher et al. (2015) for reviews]. On balance, each operation, as well as each species/ecosystem response to dive ecotourism are different. Past research examining the ecological implications of provisioning have ranged from negligible behavioral impacts (e.g., Hammerschlag et al., 2017) to community-level reorganization (Brunnschweiler et al., 2014) of large shark species, suggesting that further research is needed to begin to build a framework for predicting the consequences of different types of provisioning ecotourism.

Diverse behavioral tactics, in conjunction with the ability of many species of apex predatory sharks to undertake long-range movements, make quantifying the potential impacts of seasonal provisioning challenging. In some instances, these very characteristics might buffer these species from any persistent biological impacts. For example, individuals with large activity spaces (and no or diffuse core areas) are unlikely to be exposed to the same intensity of provisioning as site-attached sharks such as reef sharks (Mourier et al., 2020). At a well-studied dive tourism site in The Bahamas, tiger sharks (*Galeocerdo cuvier*) appear to neither change their long-range migratory behavior – compared to sharks from areas unimpacted by human activities – nor their short-term diel space use in response to provisioning (Hammerschlag et al., 2012, 2017). By contrast, equally wide-ranging white sharks (*Carcharodon carcharias*) have been found to shift their three dimensional, fine-scale, space use to spend more time in close proximity to the dive boats during berleying (chumming) activities that attract individuals to shark cage-diving operators, with sharks spending significantly more time in close proximity to the dive boats (Huveneers et al., 2013). Broad variation in provisioning practices, species ecology and habitats indicate that only through the investigation of more contexts and species will any widespread predictable impacts be revealed.

While the impacts of provisioning on individual shark behavior appears to vary both within and among species (Brena et al., 2015), impacts at the group level on species that form aggregations (groups of sharks forming on a regular to semi-regular basis) or engage in social association behavior (i.e., non-random co-occurrence in space and time) are less well studied (Becerril-García et al., 2019). With increasing numbers of shark populations found to feature social associations (Jacoby et al., 2012; Mourier et al., 2018) and compelling evidence that conditioning can occur leading to anticipatory behaviors at dive sites (Bruce and Bradford, 2013; Clarke et al., 2013; Heinrich et al., 2021), understanding both the direct and indirect impacts of provisioning on the potential social structuring of shark groups remains an important and unexplored area of research. Indeed, compelling evidence from long-term studies on highly social cetaceans (Indo-Pacific bottlenose dolphins, *Tursiops aduncus*) suggests that tourist provisioning can have significant implications beyond simple changes in space use and movement. Specifically, daily provisioning of dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia, negatively affected the reproductive success of female dolphins through reduced parental care, changes in calf foraging behavior, and higher calf mortality (Mann et al., 2000). However, long-term monitoring and Before-After-Control-Impact approaches to the evolution of tourism practices, has proven crucial for this species in Shark Bay, not least because it has been tailored to the ecological nuances of the species in question (e.g., slow life histories; complex, structured societies that allow for the social transmission of behaviors), resulting in positive changes to management practices and feeding protocols in the area (Foroughirad and Mann, 2013). Management of Shark Bay dolphins suggests that significant progress could be made by working closely with dive operators and managers to refine tourism activities for other areas and species. In addition, such studies emphasize the importance of understanding the complexities of species responses to provisioning at both the individual and population level, which has implications for human safety, and is particularly important for social species (Gallagher and Huveneers, 2018). For shark dive tourism, these group-level responses remain largely unexplored. Social network analyses can offer important insights that will likely help to reveal the extent to which social behavior and social structure might provide a degree of resilience against potential anthropogenic impacts (Snijders et al., 2017) or conversely reveal the potential for indirect costs associated with shark dive tourism.

Here, we use long-term acoustic tracking (across years) and social network inference to explore the potential existence of social behavior in a wide-ranging, generalist, marine apex predator, as well investigating the group-level impacts of dive tourist food provisioning on the patterns of association in tiger sharks. Large numbers of female tiger sharks occur naturally, particularly during colder months (November to April), on the northwestern edge of Little Bahama Bank, The Bahamas (Hammerschlag et al., 2012). Within the region is a popular dive site, nicknamed "Tiger Beach", where tiger sharks are chummed and provisioned regularly at specific locations to support shark dive tourism that occurs almost exclusively during colder months, coinciding with the seasonally high numbers of tiger sharks found there (Hammerschlag et al., 2017).

Thought to be predominantly solitary for large proportions of their life histories, tiger sharks are observed to aggregate predictably at this female-dominated site. Although the specific reasons for this aggregation are not fully resolved, it is hypothesized that subadult females may benefit from reduced male harassment and the warm shallow waters may aid gestation for pregnant females (Sulikowski et al., 2016). Regardless of the reasons for this aggregation, high densities of sharks facilitate the potential for non-random associations and social preferences to form. Here social preferences are defined as pairs of individuals occurring together in space and time more than would be expected from chance, after controlling for individual patterns of space use and an individual's propensity to group with others (hereafter termed "gregariousness"). It is not yet known whether tiger sharks exhibit such preferential associations with conspecifics at Tiger Beach or elsewhere, nor is it known whether provisioning might influence potential structuring of associations within the population. What is known, however, is that tiger sharks at this location occur at densities that are higher than usual for large apex sharks, raising the prospect that sociality might exist within the population. Indeed, non-random co-occurrences have been observed in another large, apex shark (white sharks, *Carcharodon carcharias*) when observed aggregating at pinniped colonies off South Australia, where provisioning for shark dive tourism also occurs (Schilds et al., 2019). Given these recent findings and the widespread evidence of social structuring in more site-attached and smaller shark species (Mourier et al., 2018), it is not inconceivable that tiger sharks structure themselves through non-random associations.

In this study, we use tracking data from acoustic receivers on the northwestern edge of Little Bahama Bank to explore whether tiger sharks form non-random associations with one another, and if such associations differ at provisioning and non-provisioning sites at Tiger Beach. We took a tiered approach to analyze social behavior (from aggregation, to individual gregariousness, to distinct social preferences – all defined above) to address the following hypotheses: (1) provisioning increases the level of aggregation behavior at dive sites, (2) tiger sharks are capable of forming non-random social associations maintained by individual social preferences that break down when food is made available at the dive sites, and (3) social preferences are assorted by size.

MATERIALS AND METHODS

Study Site

This study was carried out on the north-western side of Little Bahama Bank, which extends off Grand Bahama Island, The Bahamas (**Figure 1A**). Formed of relatively shallow carbonate platforms, this area is predominantly sand flats interspersed with patches of seagrass and coral. On the bank edge, lies an area known as Tiger Beach (26.86° N, 79.04° W) where dive operators have been reliably operating shark dives since 2003. Sharks are attracted using crates of minced fish and on occasion are fed fish carcasses during dives. This activity occurs at several key dive sites (used to define our assignment of provisioned or non-provisioned receivers) predominantly during the colder months (i.e., the subtropical dry season; November through April), to coincide with the seasonal occurrence of large female tiger sharks that dominate the site (Hammerschlag et al., 2017). Up to seven dive tourism boats operate at Tiger Beach, with four regular live-a-board vessels operating weekly during the dry season, and provisioning occurring during daylight hours. While obtaining information on precisely when and where all shark diving activity occurred was not possible, we were able to obtain summaries from the logbook from one regular operator, which was used to infer shark diving provisioning activity. The logbook, while not overlapping entirely with the study period, contained 163 entries (tourism events) between 1 Nov 2013–16 Oct 2015 (714 days). The average duration of presence at dive sites was 7.33 h per day (range 1:10–17:00 h) all during daylight hours and predominantly during the dry season. Given that this log represents just one of four regular vessels, we estimate that during the dry season there is likely at least one vessel chumming at the dive sites during all available daylight hours.

Shark Tagging and Acoustic Telemetry

Tiger sharks were predominantly tagged near Tiger Beach in Grand Bahama (n = 41), but several individuals that frequent Tiger Beach were tagged in Florida (n = 2) and South Carolina (n = 5) using the same methodology. Sharks were captured using standardized circle-hook drum-lines following

Tinari and Hammerschlag (2021), and acoustic transmitters (Vemco V16, 69 kHz, 68 × 16 mm, 60–90 s nominal delay) were surgically implanted in the body cavity of tiger sharks as per Hammerschlag et al. (2017) while the sharks were in tonic immobility (Kessel and Hussey, 2015). Individual sex was recorded, total length (TL) was measured, and reproductive status of each individual at the time of tagging was determined from a combination of ultrasonography and hormone analysis of blood samples (see Sulikowski et al., 2016 for details).

An acoustic array of 32 VR2W receivers (VEMCO Division, AMIRIX systems) were installed by June 2014, with receivers anchored to the seafloor approximately 750 m apart in a 12 km × 3.2 km rectangular format (**Figure 1**). Due to receiver failure, the final array of functioning receivers to the completion of the study consisted of 23 receivers (**Figures 1B,C**). This included receivers placed within the proximity of four primary dive sites at Tiger Beach which were considered provisioned receivers ($n = 5$, **Figure 1C**). Diurnal range testing revealed that on average receivers had a detection efficiency of 50% at 200 m. See Hammerschlag et al. (2017) for more detail on the study site, receivers and tagging procedures.

Data Manipulation and Social Network Construction

Data from the receivers were downloaded every 6 months and raw detections were filtered to remove false detections which can arise from tag collisions (i.e., when two tags within a receiver's range ping at the exact same time) and from acoustic pollution (Simpfendorfer et al., 2015). A time-series of the detection data was then visually inspected to determine the final data set, which was chosen as the time window that maximized the overlap of individuals at liberty within the array. This window spanned Nov 2014–Oct 2017 providing three complete years of data. We removed the first 24 h of data for any individuals that were tagged during this study period (∼15% of studies individuals). We deemed 24 h as sufficient as tiger sharks are known for being robust to capture and handling, exhibiting a muted capture stress response (Gallagher et al., 2014a,b). Previous studies have revealed strong seasonal trends in the detection of tiger sharks at Tiger Beach with increased detection probabilities during the cold, "dry" season (Nov–April) relative to the warmer "wet" season (May–Oct). There are no apparent diel differences in shark use of this area (Hammerschlag et al., 2017). Consequently, the data were divided into dry and wet seasons in addition to "non-provisioned" (hereafter, NP) and "provisioned" (hereafter, P) sites for each year, producing 12 subsets of data, grouped by year, season, and provisioning status, in which social structure was explored.

Importantly, provisioning occurred predominantly during the dry season when sharks were already there in high densities; provisioning during the wet season was negligible; however, the distinction between NP and P receivers was retained into the wet season to account for any carryover effects between seasons and to ensure that each network represented an aggregation of six months of data.

To infer social associations from the telemetry data, a Gaussian mixture model (GMM) was first applied to the acoustic time-series to identify clustering events at each location where multiple sharks were detected within the same receiver range (approximately 200 m) at the same time, signified by temporally and spatially overlapping clusters of detections (Jacoby et al., 2016). Crucially, the GMM retrieves clusters of detections that vary in duration, which likely better reflects the fact that some pairs of individuals may socialize for short periods while others might socialize for tens of minutes to hours. This approach also nullifies the subjective assignment of a specific and fixed temporal sampling window, favoring instead that this is determined by

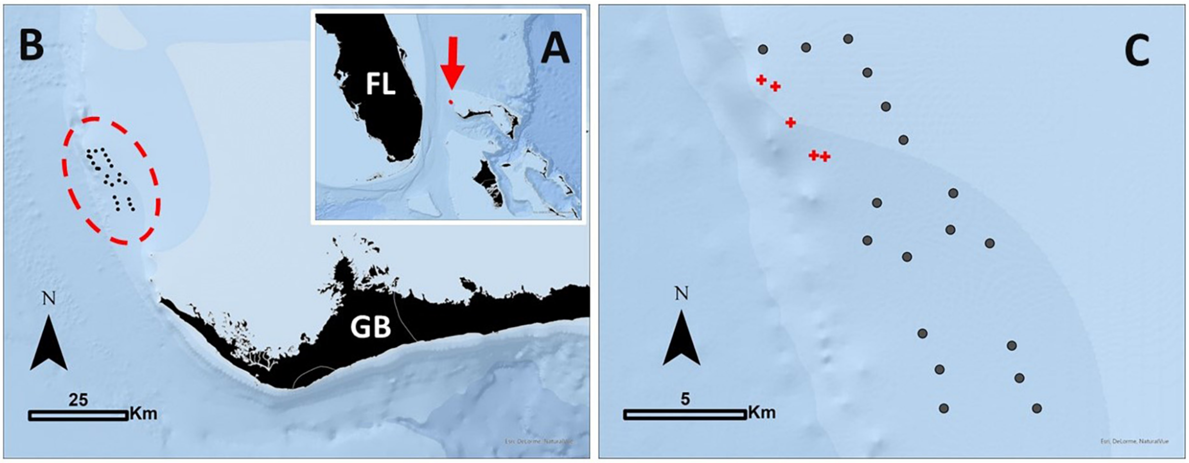


FIGURE 1 | (A) The location of the study area in the northern Bahamas identified with a red arrow. FL, Florida, United States, as a spatial reference. **(B)** Positioning of the telemetry array on the north-western edge of the Little Bahama Bank, off Grand Bahama [GB] Island. The 23 receivers used in this study are outlined in a red dashed oval. **(C)** Receivers were arranged in a roughly 12 km × 3 km rectangle, with the western line just inshore of the bank edge. Receivers in locations exposed to provisioning from commercial shark dive operations are identified with red crosses, referred to in the text as provisioning [P] sites. All other receivers are identified with gray circles, referred to in the text as non-provisioning [NP] sites.

the distribution of the data (Psorakis et al., 2015). Using the "gmmevents" function in the R package *asnipe* (Farine, 2013), a group-by-individual bipartite graph was generated across the relevant receiver locations combined, which outlined individual co-occurrences through time. The GMM was applied separately to all 12 subsets of the data and a matrix of association extracted using the Simple Ratio Index (SRI).

Analysis of Social Data

Aggregation and Group-Level Social Structure

From the GMM metadata, the frequency of clustering events, that is the number of times that two or more sharks were deemed to be aggregating at a location based on their detection profile, and typical duration of these events were explored qualitatively between NP and P sites across the three years of the study. The median, interquartile ranges, 95% confidence intervals and density spread of the data were visualized using violin plots. We then used a chi-squared test to assess whether the frequency of aggregations was dependent on whether provisioning occurred at a receiver location or not. Finally, we tested for differences in the mean duration of these aggregations between NP and P receivers with independent Mann-Whitney U tests on the dependent variable of aggregation duration (min). To explore the potential relationship between the number of aggregation events as a function of distance from the nearest provisioning site we used a GLM with a quasipoisson (log) link function to account for overdispersion in the count data. The models were run for both dry and wet seasons separately to determine whether there was a spatial influence of provisioning in both seasons.

To explore the overall structuring of the sharks across each of the data subsets, we extracted the weighted degree (node strength, S_i) of individuals present within the subset networks and compared the mean S_i to that of 30,000 randomized networks – constrained to swaps within location – using the "network_permutation" function in the package *asnipe* (Farine, 2013). Importantly the null model included all individuals that were detected within the subset which resulted in networks (both observed and null) containing unconnected nodes (i.e., individuals within that area that did not participate in any aggregation behavior). Mean S_i of our observed networks that fell within the upper or lower 2.5% threshold for our posterior null distribution were deemed to be highly structured, and significantly more or less connected than might be expected by chance (two tailed test). Those networks that showed significant non-random structure were then explored in greater detail to determine whether social preferences between conspecifics were driving this structure. Binomial logistic regressions were used to explore whether shark attribute data [number of individuals, mean and standard deviation of size (TL)], presence or absence of provisioning, while controlling for year as a random effect, were predictive of non-random social structure as a binary response variable.

Gregariousness, Social Preferences and Assortment

To explore non-random networks in more detail, we were interested in testing and consequently controlling for possible non-social drivers of social network structure. To do so we used generalized affiliation indices (GAIs) that use the deviance residuals from a generalized linear model with binomial error structure as an indication of significant dyadic affiliations or avoidances (Whitehead and James, 2015). To explore the role of individual variation in gregariousness on social network structure we first calculated pairwise gregariousness between individuals (Godde et al., 2013), using the equation, $G_{ab} = \log(\Sigma \mathrm{SRI}_a \Sigma \mathrm{SRI}_b)$, as implemented in Perryman et al. (2019) where ΣSRI are the sums of all simple ratio indices for individuals a and b (0 being individuals that had exactly the same level of gregariousness with all other conspecifics). Pairwise gregariousness took the form of a matrix that corresponded to the SRI matrix of association derived from the GMM. A size matched matrix was also constructed to reflect the pairwise distance in meters between individual site preferences. For each individual, the receiver location that recorded the highest number of detections was used as a proxy for individual site preferences. The distance matrix was produced from an edge list of coordinates using the "distm" function in the package *geosphere* (Hijmans et al., 2017).

Matrices of pairwise gregariousness and site preference dissimilarity were then regressed (with 5000 permutations) against the adjacency matrix of SRIs using Multiple Regression Quadratic Assignment Procedure (MRQAP) implementing the double semi-partialing, DSP approach advocated by Dekker et al. (2007). This enabled us to determine whether social network structure of any non-random networks was predicted by these non-social, potentially confounding variables. Estimates of social affiliations and avoidances (GAIs) were then derived as the residuals from our regression of significant structural predictor variables on our association indices for each network (Whitehead and James, 2015) using the "assoc.gfi" in the Animal Network Toolkit Software (*ANTs*) package in R (Sosa et al., 2020). Controlling for both gregariousness and site preference like this we then constructed networks of tiger shark social preferences. Networks were visualized and edge density extracted using the *igraph* package in R (Csardi and Nepusz, 2006).

To explore size assortment, tiger sharks were categorized into three size classes based on their total length (TL). Previous analysis of reproductive hormones and use of ultrasonography on tiger sharks at this site, suggest that size of sexual maturity is typically at 300 cm (Sulikowski et al., 2016). Therefore, sharks were assigned to a size class of "small" (TL < 300 cm), "medium" (TL = 300–350 cm), or "large" (TL > 350 cm) corresponding to immature, recently matured, and matured older individuals and the *assortnet* package in R was used to calculate weighted assortativity (Farine, 2014). This was then compared to a null distribution from an edge-swap permutation test. This way we could test whether social preferences (GAIs) were assorted non-randomly based on size class.

RESULTS

Aggregation and Group-Level Social Structure

The final acoustic data set consisted of 154,897 detections from 48 different tiger sharks (**Table 1**). The mixture models revealed

TABLE 1 | Summary of the 48 tiger sharks tagged with acoustic transmitters that occurred during our three-year study at Tiger Beach, The Bahamas.

TAG ID	Tag Code Space	Tag Life (days)	Number of Detections*	Number of Receivers†	Capture Location	Capture Latitude	Capture Longitude	Pre-Caudal Length (cm)	Fork Length (FL)	Total length (cm)	Life-Stage	Sex	Date
18402	9001	1910	15	5	Florida	25.64	−80.17	197	202	269	Immature	F	2016-10-16
18412	9001	1910	78	10	Florida	25.42	−80.05	105	117	150	Immature	F	2016-09-24
20562	9001	1910	1485	23	Grand Bahama	26.91	−79.06	295	321	387	Gravid	F	2016-01-06
23340	1601	1616	2579	20	Grand Bahama	26.90	−79.08	272	300	356	Not Gravid	F	2014-11-14
23341	1601	1616	879	21	Grand Bahama	27.02	−79.16	207	231	283	Immature	F	2014-11-16
23343	1601	1616	2642	16	Grand Bahama	27.02	−79.16	267	294	355	Not Gravid	F	2014-11-16
23345	1601	1616	20	4	Grand Bahama	27.02	−79.16	272	300	352	Mature	M	2014-11-14
23346	1601	1616	20	1	Grand Bahama	27.02	−79.16	169	182	236	Immature	F	2014-11-16
24643	1601	1616	164	15	Grand Bahama	27.02	−79.16	.	.	346	Mature	M	2014-11-16
24644	1601	1616	800	23	Grand Bahama	27.02	−79.16	296	311	349	Not Gravid	F	2014-05-12
24645	1601	1616	1696	23	Grand Bahama	25.91	−79.06	188	221	262	Immature	F	2014-05-13
24646	1601	1616	109	15	Grand Bahama	25.91	−79.06	246	266	324	Not Gravid	F	2014-05-14
24647	1601	1616	109	2	Grand Bahama	25.91	−79.06	152	174	213	Immature	F	2014-05-13
24648	1601	1616	717	22	Grand Bahama	27.02	−79.16	275	309	356	Not Gravid	F	2014-05-12
24649	1601	1616	385	15	Grand Bahama	27.02	−79.16	.	.	144	Immature	M	2014-11-15
24650	1601	1616	779	23	Grand Bahama	27.02	−79.16	279	292	352	Gravid	F	2014-05-12
24651	1601	1616	539	20	Grand Bahama	27.02	−79.16	175	192	242	Immature	F	2014-05-13
24652	1601	1616	1189	17	Grand Bahama	26.91	−79.06	294	324	383	Not Gravid	F	2014-05-13
24653	1601	1616	93	13	Grand Bahama	25.91	−79.06	226	247	301	Not Gravid	F	2014-05-14
24654	1601	1616	887	19	Grand Bahama	27.02	−79.16	203	223	273	Immature	F	2014-05-12
24656	1601	1616	494	21	Grand Bahama	25.91	−79.06	272	297	358	Not Gravid	F	2014-05-13
24657	1601	1616	3453	23	Grand Bahama	27.02	−79.16	259	282	342	Not Gravid	F	2014-11-15
24658	1601	1616	4061	23	Grand Bahama	26.90	−79.08	259	282	336	Gravid	F	2014-11-14
24659	1601	1616	6697	22	Grand Bahama	26.91	−79.08	277	300	366	Not Gravid	F	2014-05-14
24662	1601	1616	651	17	Grand Bahama	27.02	−79.16	194	210	264	Immature	F	2014-05-13
26750	1601	854	11618	23	Grand Bahama	25.91	−79.06	200	223	273	Immature	F	2013-10-17
26751	1601	854	87	3	Grand Bahama	25.91	−79.06	233	259	307	Gravid	F	2013-10-17
26753	1601	854	4598	23	Grand Bahama	25.91	−79.06	.	.	331	Gravid	F	2013-10-18
26754	1601	854	2266	21	Grand Bahama	25.91	−79.06	190	212	260	Gravid	F	2013-10-19
26755	1601	854	13813	23	Grand Bahama	25.91	−79.06	243	271	322	Not Gravid	F	2013-10-18
26756	1601	854	8292	23	Grand Bahama	25.91	−79.06	225	253	325	Not Gravid	F	2013-10-18
26757	1601	854	54	8	Grand Bahama	26.91	−79.08	281	317	373	Gravid	F	2013-10-18
26758	1601	854	131	8	Grand Bahama	25.91	−79.06	278	306	357	Gravid	F	2013-10-19
26759	1601	854	196	13	Grand Bahama	25.91	−79.06	286	315	368	Gravid	F	2013-10-19
26760	1601	854	2395	23	Grand Bahama	25.91	−79.06	290	313	380	Not Gravid	F	2013-10-19
26761	1601	854	3073	22	Grand Bahama	26.91	−79.08	242	273	344	Gravid	F	2013-10-18
26762	1601	854	35	3	Grand Bahama	25.91	−79.06	265	296	360	Gravid	F	2013-10-19
26764	1601	854	1633	22	Grand Bahama	26.91	−79.08	303	323	378	Not Gravid	F	2013-10-17
26765	1601	854	1411	23	Grand Bahama	26.91	−79.08	269	300	356	Mature	M	2013-10-20
26766	1601	854	2029	23	Grand Bahama	25.91	−79.06	286	315	369	Gravid	F	2013-10-20
26767	1601	854	410	18	Grand Bahama	25.91	−79.06	272	298	357	Gravid	F	2013-10-20
26768	1601	854	713	21	Grand Bahama	25.91	−79.06	273	295	357	Gravid	F	2013-10-20
58399	1601	1616	1700	22	Grand Bahama	26.91	−79.06	255	273	324	Gravid	F	2016-01-05
21911	9001	2538	77	8	South Carolina	32.43	−80.36	.	288	361	Mature	F	2015-11-03
21912	9001	2538	44	3	South Carolina	32.21	−80.61	.	315	368	Mature	F	2015-11-04
21916	9001	2538	194	10	South Carolina	32.21	−80.63	.	316	383	Mature	F	2015-09-28
22382	9001	2538	104	3	South Carolina	32.22	−80.63	.	252	319	Mature	F	2015-08-17
32151	1601	1633	69483	22	South Carolina	32.44	−80.39	.	290	338	Not Gravid	F	2014-10-31

**These values only represents the detections in the truncated dataset used in this study. Additional detections for individuals occurred outside of the three year study period.*
†Out of a possible 23.

9201 aggregation events in total across three years, 23 locations [including both non-provisioned (NP; $n = 3389$) and provisioned (P; $n = 5812$) sites] and both seasons each year. Aggregation events occurred more frequently at provisioned sites during the provisioning (dry) season ($\chi^2 = 153.61$, d.f. = 2, $p < 0.001$, **Figure 2A**). Regardless of season, these aggregations typically

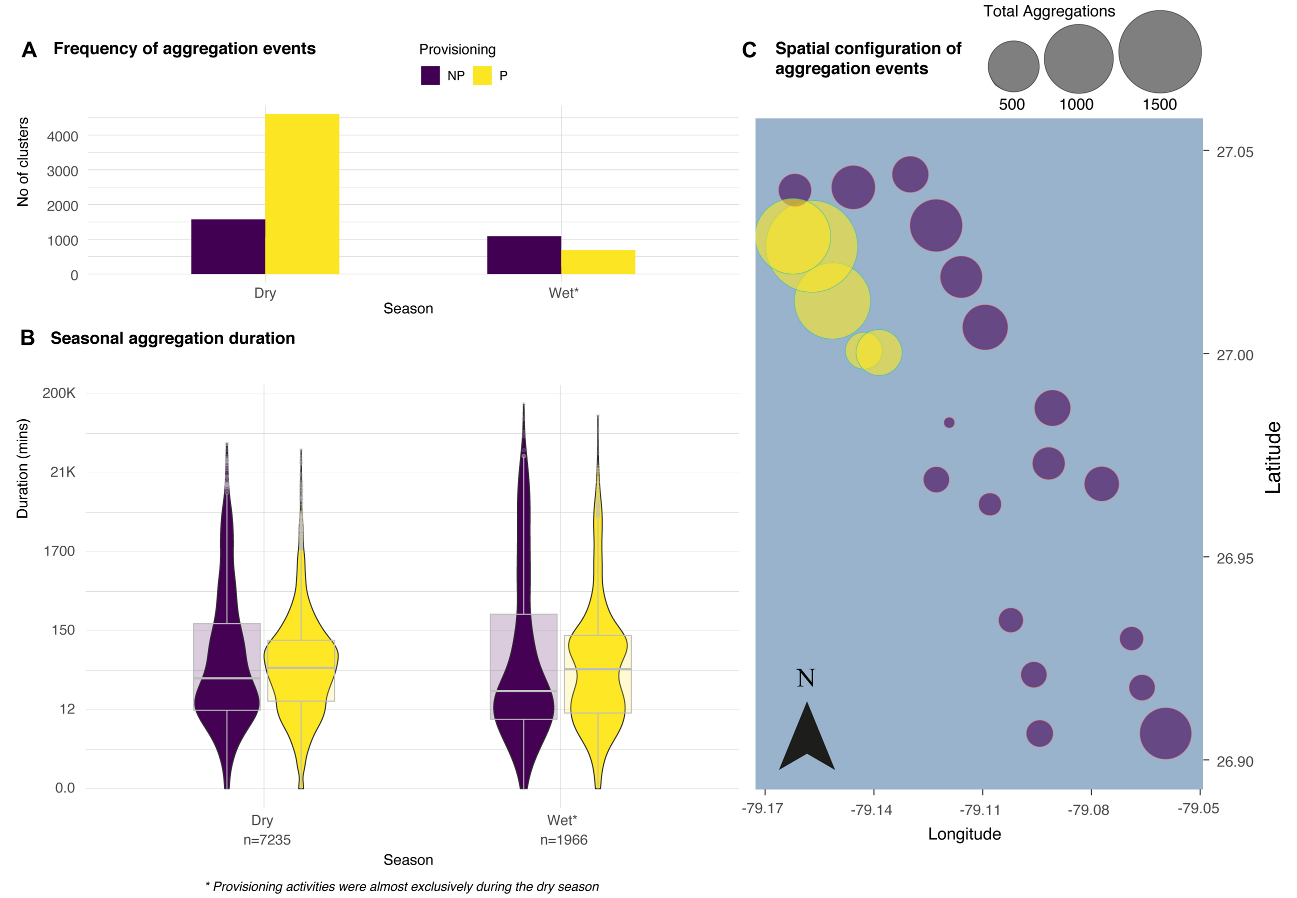


FIGURE 2 | The frequency, duration and configuration of aggregations derived from spatio-temporal clustering events from the GMM between non-provisioned and provisioned sites from data spanning three years. The bar chart **(A)** reveals more frequent clustering events at provisioned locations and the violin plots **(B)** illustrate the median, interquartile range, 95% confidence interval and spread of the typical duration (in min, log scale) of aggregations between NP and P (*n* represents the number of aggregations per year). No relationship was found between the number of aggregations at each receiver and the distance to the nearest provisioning site **(C)**.

lasted twice as long at P sites over NP sites (Dry: W = 5816600, $p < 0.01$, Wet: W = 432652, $p < 0.05$, **Figure 2B**). There was no significant effect of distance from the nearest provisioning site on the number of aggregations in either the dry season (GLM: NS $p = 0.599$) or the wet season (GLM: NS $p = 0.533$, **Figure 2C**).

Of the 12 networks split by season and year, five had a mean weighted degree higher than would be expected by chance ($p < 0.025$, two tailed), meaning that seven of the 12 networks were characterized by random assortment and mixing. Of the five non-random networks, three were at locations not impacted by provisioning (NP) in either season, one represented receivers influenced by active provisioning during the dry season (Dry P) and one at the same receivers but during the wet season (Wet P_{neg}) when provision activity is negligible (**Table 2**). Mean weighted degree was higher at NP sites for all seasons and all years, than P sites. The binomial logistic regression revealed that the number of sharks within the network, as a proxy for shark density ($p = 0.225$), nor the mean ($p = 0.883$) or standard deviation ($p = 0.475$) of shark size, nor the presence of provisioning ($p = 0.492$) were predictive of whether non-random social structure was found.

Gregariousness, Social Preference and Assortment

Site preference was not predictive of network structure within any of the five non-random networks, and pairwise gregariousness was predictive of just three (**Table 3**). Gregariousness appeared to be more variable at the provisioned site [CV: NP = −34.71 (mean); $P_{neg} = -20.41$, $P = -50.33$]. Significant social preferences (visualized in **Figure 3**) represent the positive GAIs with edge weights indicative of the relative strength of those affiliations. For those receivers impacted by provisioning, either directly during the dry season or indirectly during the wet season through possible carryover effects and low level provisioning, network density was typically lower ($NP_{mean} = 0.277$, $P_{mean} = 0.199$) representing a near 10% decrease in connectivity of social preferences at P sites. Finally, there was no evidence that social preferences were assorted by size class either at NP sites ($r = 0.056$, 0.139, and −0.102 all NS) or at P sites ($r = -0.112$ and 0.094, both NS). Interestingly, there was surprising little year-to-year or season-to-season consistency in pairwise GAIs, as well as high variation in within-individual GAI scores (i.e.,

TABLE 2 | Testing for non-random social structure across season and provisioned (P)/non-provisioned (NP) sites monitored by acoustic receivers (note P_{neg} indicates the wet season when provisioning was negligible).

		n	mean w.degree$_{obs}$	mean w.degree$_{null}$	Effect	*p*
Y1	**Dry NP**	**34**	**0.245**	**0.229**	**+0.016**	**0.024**
	Dry P	32	0.164	0.159	+0.005	0.221
	Wet NP	**23**	**0.173**	**0.148**	**+0.025**	**0.008**
	Wet P_{neg}	**18**	**0.135**	**0.105**	**+0.030**	**0.023**
Y2	Dry NP	25	0.203	0.183	+0.020	0.051
	Dry P	**24**	**0.158**	**0.11**	**+0.048**	**0.003**
	Wet NP	14	0.264	0.29	−0.026	0.805
	Wet P_{neg}	16	0.083	0.095	−0.012	0.650
Y3	**Dry NP**	**18**	**0.356**	**0.233**	**+0.123**	**0.000**
	Dry P	16	0.14	0.164	−0.024	0.909
	Wet NP	11	0.269	0.260	+0.009	0.365
	Wet P_{neg}	10	0.225	0.216	+0.009	0.310

Mean weighted degree was used to compare the observed network and the 30,000 random networks comprising each null model (the effect size, direction, and p value are displayed). Network structure was explored prior to controlling for individual gregariousness and site use behavior to identify which networks warranted further investigation of social preferences.

an individual's level of preference to all other individuals within any given time period, **Figure 3**). Because reproductive status was only determined at tagging, we excluded any statistical analyses that included this information.

DISCUSSION

Sharks are a valuable commodity within the dive tourism industry (Gallagher and Hammerschlag, 2011) and there are potential conservation benefits to be gained through these practices (Vianna et al., 2012; Macdonald et al., 2017; Apps et al., 2018). Attracting wide-ranging, apex marine predators in high densities to areas through food provisioning however, may have unintended consequences at both the individual and group level (Brena et al., 2015), and it is the latter that we still know very little about. In this study we demonstrate for the first time that tiger sharks, often considered a solitary nomadic species, are highly flexible in their capacity to associate with one another, and that provisioning of food for tourism can enhance gregarious behavior, as well as subtly influence the level of social behavior within the population.

Supporting our first hypothesis, provisioning activities increased the frequency of aggregations during the dry season when this practice was most prevalent. The provisioning site also featured longer durations of aggregations year-round. This might be indicative of continued effects during much lower levels of provisioning and/or possible anticipatory aggregation during the wet season. With no evidence of a linear reduction in the number of aggregations with distance from provisioning activity, this might simply be evidence that this particular area of Tiger Beach is highly suitable for tiger sharks, for example offering increased natural foraging opportunities, thus supporting higher numbers. In partial support of our second hypotheses, we demonstrated that tiger sharks are capable of sociality but that at Tiger Beach this sociality is highly variable: sometimes they mix randomly with one another and at other times aggregate in ways that are structured by distinct social preferences. Only 1 of 3 possible networks, demonstrated non-random social structure at provisioning locations during times of the year when provisioning occurred (Y2 Dry P), while 4 of 9 networks were non-random when provisioning was minimal or non-existent. Consequently, the probability of social preferences was not detectably different at provisioned and non-provisioned locations, but statistical power remains relatively low, as does our knowledge of the number of untagged sharks that might complicate this picture. It is also important to mention that our knowledge of the scale of provisioning activity is not perfect due to a lack of information. While difficult to conclusively determine whether non-random preferences at provisioned sites were the result of provisioning or natural preferences (regardless of provisioning), the social preference networks that did occur at provisioned sites (both dry and wet) were less well connected, indicated by lower network density suggestive of a qualitative reduction in strength and diversity of associations amongst individuals. Finally, our third hypothesis was rejected following no evidence of assortment based on individual size categories indicative of maturity and age.

Aside from regular provisioning and natural prey sources, Tiger Beach appears to provide other benefits to female tigers sharks which may include a potential refuge site from male harassment for sub-adult and gravid female sharks and warm shallow waters that could aid female gestation (Sulikowski

TABLE 3 | Matrix regression of non-social predator variables on association matrices across the five non-random networks.

	Y1 Dry NP		Y1 Wet NP		Y1 Wet P		Y2 Dry P		Y3 Dry NP	
Predictor	**Partial correl.**	***p***	**Partial correl.**	***p***	**Partial correl.**	***p***	**Partial correl.**	***p***	**Partial correl.**	***p***
Intercept	0.0105	0	0.0122	0.001	0.0304	0	0.0116	0	0.0604	0
Pairwise gregariousness	0.0013	**0.025**	0.0009	0.2348	0.0052	**0.001**	0.0010	0.065	0.0140	**0**
Site attachment similarity*	0.0000	0.668	−0.0001	0.359	0.0000	0.4214	−0.0001	0.64	0.0000	0.981

MRQAP analyses representing the partial correlation coefficient and p values.
** was not included as a predictor variable in the calculation of GAIs.*
Bold values indicate significant predictors of network structure.

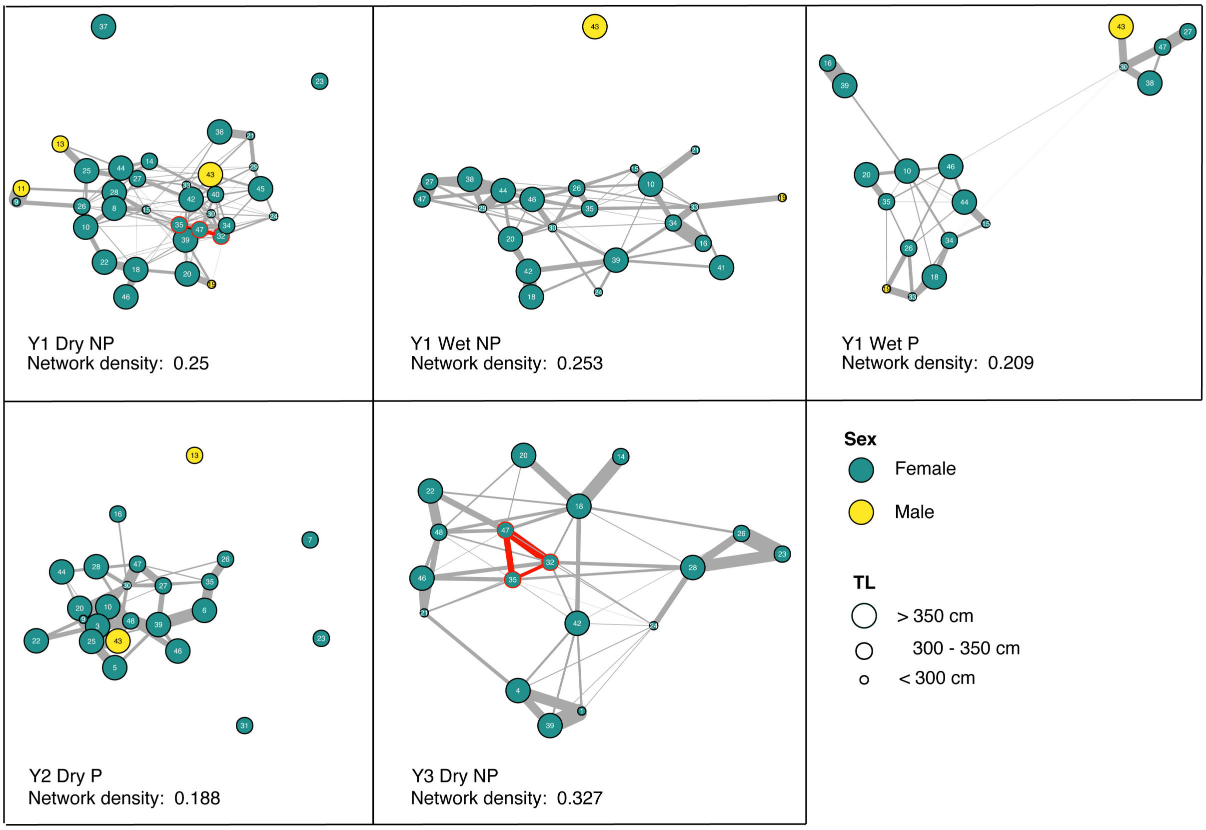


FIGURE 3 | Generalized Affiliation Indices (GAIs) indicating social preferences between tiger sharks within the five non-random social networks. Edge weight (gray) is indicative of the strength of social preference, while node color indicates sex and node size, the size class of the individual. Network density (0–1 scale) is reported illustrating the relative connectedness of the network, where 1 would indicate a network with all conspecifics preferentially associated with all others and 0, no social preferences exist at all. Red nodes and edges illustrate a particular triad of tiger sharks that preferentially socialize in both years 1 and 3.

et al., 2016). These could explain the heavy female bias of the population at this location. Aside from one individual male tiger shark ("43," **Figure 3**), the small number of males that showed social preferences were more loosely connected to the network providing further evidence of socially mediated segregation and female refuging behavior as a potential male avoidance strategy in elasmobranchs (Sims et al., 2001; Wearmouth and Sims, 2008; Jacoby et al., 2010).

Differences in the reproductive status of females co-occurring at this site (Sulikowski et al., 2016) may explain the high variability in site preferences seen amongst these wide-ranging individuals which appeared not to influence the formation of social preferences. Most tagged individuals in this study did appear to be detected on a high proportion of the available receivers (**Table 1**) suggesting that these are genuine preferences for specific locations rather than limited use of the overall area. In a previous study, tiger sharks at this location tagged with Smart Position and Temperature Transmitting (SPOT) tags were found to travel as far as 3500 km from Tiger Beach and exhibited a collective activity space of 8549 km^2 (Hammerschlag et al., 2012). It is thus unsurprising then that individuals have different site preferences within Tiger Beach, perhaps determined by timing of arrival, density of conspecifics or human presence. Wide-ranging movements may also explain why space use and diel movement patterns were found to be relatively unimpacted by provisioning in this species (Hammerschlag et al., 2017), compared to highly site-attached and resident species of elasmobranchs that exhibit marked shifts in behavior in response to provisioning (Fitzpatrick et al., 2011; Mourier et al., 2020).

The mixed and emerging results within this study, which are perhaps emphasized by the largely nomadic and solitary nature of this species, indicate that social preferences amongst conspecifics are, in fact, preferences. The occurrence of social preferences within this population might be entirely dependent on the composition of sharks that arrive at Tiger Beach attracted either by the promise of regular food during the dry season or the presence of warm sheltered waters that could be beneficial given their reproductive state. Interestingly, the preferences of individual sharks varied across seasons and years. In spite of a largely similar suite of individuals present in non-random networks that we detected, as well as some pairs of individuals that prefer one another across multiple spatial or temporal network representations (**Figure 3**), high pairwise-associations of individuals varied considerably across these networks. A lack of year-to-year or season-to-season consistency in pairwise preferences, as well as high within-individual variation in GAI scores, seems to imply that generally social preferences are not particularly long-lasting. The occurrence of a triad of social preferences between three individuals in year 1 ("47," "35," and "32," **Figure 3**), which appeared again at the NP sites in year 3, however, is indication that perhaps under the certain conditions, social preferences among individuals are able to reform within future aggregations. The putative benefits of long-term, preferential associations remains an interesting area of investigation in tiger sharks, particularly in the context of a recent study that demonstrated possible foraging benefits to such long-term stable preferences in reef sharks (Papastamatiou et al., 2020).

Studies of sociality in another large, apex predatory sharks (white sharks, *Carcharodon carcharias*), have also produced mixed results. Within natural aggregations of this species around pinniped colonies in South Africa, biological traits (e.g., sex and size) were a more important determinant of aggregation than social preferences (Findlay et al., 2016). Conversely, at a pinniped colony in Southern Australia which also supports shark cage-diving operators, similar photo-identification methods revealed four distinct communities of white sharks underpinned by non-random co-occurrences of individuals (Schilds et al., 2019). With only a proportion of the population tagged with acoustic transmitters in our study, the results here reveal only a component of the social behavior within this population. More in depth examination of dyadic and triadic preferences, as well as exploration of the longevity of sociality and within the context of reproduction for this species in the future, may help to tease apart some of the ecological drivers of these affiliations (Perryman et al., 2019; Papastamatiou et al., 2020).

Our binomial regression indicated that neither provisioning, shark density nor size were predictive of whether non-random networks formed. Significant structure during the dry season in years 1 and 3, and a marginally non-significant result from the permutation test in year 2 (**Table 2**), however, suggest that social structuring may occur naturally under higher densities of individuals (e.g., dry season) which can shape the formation of social traits within a population (Webber and Vander Wal, 2018). Indeed, our proxy for density was limited to the number of tagged individuals within a network (our independent variable with the regression models) and while this was not predictive of non-random structure, it did appear to be the most likely candidate; a result that perhaps reflects the fact that social structure was also underpinned by numerous associations between tagged/untagged and untagged/untagged individuals. The interpretation that the provisioning activity at Tiger Beach is not pervasive enough to influence the long-term structuring of the population through social associations, is not unreasonable. However, further data from this species from areas completely free of tourism, which would serve as a full control location, would be useful for comparison of network metrics in the future.

In summary, we revealed that provisioning influences the opportunities for tiger sharks to socialize by promoting a higher turnover of aggregations and increased mixing resulting in lower likelihood of social preferences forming. How the sharks respond to this disruption, however, appears quite nuanced and variable. It is plausible that the social flexibility demonstrated here may buffer the population, to some extent, from any long-term changes to social behavior at the group level.

The impacts of dive tourist food provisioning on shark biology and behavior should continue to be assessed on a case by case basis (Brena et al., 2015; Gallagher et al., 2015). We advocate that such assessments should also evaluate the impacts of provisioning at the group level and in ways that incorporate the social ecology of the species in question (Foroughirad and Mann, 2013; Meyer et al., 2021). Social network analyses offer a useful toolkit for the quantitative appraisal of such impacts as they consider behavior at both the individual and group/population level. Applied here, we were able to partially reveal the social complexity (and flexibility) of a wide-ranging, "solitary" marine apex predator and demonstrate that the impacts of provisioning on gregariousness and social behavior were limited both spatially (to the specific dive locations) and temporally (to predominantly the dry season when most diving occurs). By continuing to limit provisioning activities to certain times of year, our study suggests that tourism is unlikely to be significantly disruptive to the structuring of the tiger shark population at Tiger Beach. The extent to which that may hold true elsewhere remains unclear.

DATA AVAILABILITY STATEMENT

Raw acoustic tracking data are archived in the Ocean Tracking Network (Project V2LUMI): https://members.oceantrack.org/OTN/project?ccode=V2LUMI.

ETHICS STATEMENT

This work was conducted under permits from the Bahamas Department of Marine Resources, South Carolina Department of Natural Resources, Florida Fish and Wildlife Conservation Commission, National Oceanic and Atmospheric Administration and the University of Miami Institutional Animal Care and Use Committee (Protocol #18-154).

AUTHOR CONTRIBUTIONS

NH and DJ conceived the study. NH obtained funding and alongside AG and BrF conducted fieldwork. MH and SC loaned equipment for the study. BeF contributed to data analysis. DJ conducted the data analysis and wrote the manuscript. All authors contributed to manuscript editing and writing.

FUNDING

DJ was funded by the Bertarelli Foundation through the Bertarelli Programme in Marine Science and through Research England. SC was supported by the Canada Research Chairs Program and NSERC. NH was supported by the Batchelor Foundation. Equipment and field work were supported by the Batchelor Foundation and the Disney Conservation Fund. Twenty receivers were obtained through a grant from the Ocean Tracking Network via support from the Canada Foundation for Innovation.

ACKNOWLEDGMENTS

We thank Captain Jim Abernethy and the past and present crew of Jim Abernethy Scuba Adventures who provided logistical support for this research, in particular George Hughes, Jamin Martineli, Jay Castellano, Matt Heath, and Mike Black. For donating their time and expertise as well as enabling receiver deployments and data downloads, thank you to Carl Hampp, Bill Parks, Cheryl Carroll, and Angela Rosenberg. This research benefited greatly from the dedicated contributions of all the University of Miami's Shark Research and Conservation Program team leaders and interns who assisted infield expeditions as well as data organization for this project, especially Stephen Cain, Mitchel Rider, and Abby Tinari. Data organization was facilitated by the FACT Network and the Ocean Tracking Network. We thank the International SeaKeepers Society as well as the owners, captain, and crew of the yachts Fugitive, Penne Mae, and Xiang for providing boats for this research.

REFERENCES

Abrantes, K. G., Brunnschweiler, J. M., and Barnett, A. (2018). You are what you eat: examining the effects of provisioning tourism on shark diets. *Biol. Conserv.* 224, 300–308. doi: 10.1016/j.biocon.2018.05.021

Apps, K., Dimmock, K., and Huveneers, C. (2018). Turning wildlife experiences into conservation action: can white shark cage-dive tourism influence conservation behaviour? *Mar. Policy* 88, 108–115. doi: 10.1016/j.marpol.2017.11.024

Barnett, A., Payne, N. L., Semmens, J. M., and Fitzpatrick, R. (2016). Ecotourism increases the field metabolic rate of whitetip reef sharks. *Biol. Conserv.* 199, 132–136. doi: 10.1016/j.biocon.2016.05.009

Becerril-García, E. E., Hoyos-Padilla, E. M., Micarelli, P., Galván-Magaña, F., and Sperone, E. (2019). The surface behaviour of white sharks during ecotourism: a baseline for monitoring this threatened species around Guadalupe Island, Mexico. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 29, 773–782. doi: 10.1002/aqc.3057

Brena, P. F., Mourier, J., Planes, S., and Clua, E. (2015). Shark and ray provisioning functional insights into behavioral, ecological and physiological responses across multiple scales. *Mar. Ecol. Prog. Ser.* 538, 273–283. doi: 10.3354/meps11492

Bruce, B. D., and Bradford, R. W. (2013). The effects of shark cage-diving operations on the behaviour and movements of white sharks, Carcharodon carcharias, at the Neptune Islands, South Australia. *Mar. Biol.* 160, 889–907. doi: 10.1007/s00227-012-2142-z

Brunnschweiler, J. M., Abrantes, K. G., and Barnett, A. (2014). Long-term changes in species composition and relative abundances of sharks at a provisioning site. *PLoS One* 9:e86682. doi: 10.1371/journal.pone.0086682

Cisneros-Montemayor, A. M., Barnes-Mauthe, M., Al-Abdulrazzak, D., Navarro-Holm, E., and Sumaila, U. R. (2013). Global economic value of shark ecotourism: implications for conservation. *Oryx* 47, 381–388. doi: 10.1017/S0030605312001718

Clarke, C., Lea, J. S. E., and Ormond, R. F. G. (2013). Changing relative abundance and behaviour of silky and grey reef sharks baited over 12 years on a Red Sea reef. *Mar. Freshw. Res.* 64, 909–919.

Csardi, G., and Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal Complex Syst.* 1695, 1–9. doi: 10.3724/sp.j.1087.2009.02191

Dekker, D., Krackhardt, D., and Snijders, T. A. B. (2007). Sensitivity of MRQAP tests to collinearity and autocorrelation conditions. *Psychometrika* 72, 563–581. doi: 10.1007/s11336-007-9016-1

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using asnipe. *Methods Ecol. Evol.* 4, 1187–1194. doi: 10.1111/2041-210X.12121

Farine, D. R. (2014). Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges. *Anim. Behav.* 89, 141–153. doi: 10.1016/j.anbehav.2014.01.001

Findlay, R., Gennari, E., Cantor, M., and Tittensor, D. P. (2016). How solitary are white sharks: social interactions or just spatial proximity? *Behav. Ecol. Sociobiol.* 70, 1735–1744. doi: 10.1007/s00265-016-2179-y

Fitzpatrick, R., Abrantes, K. G., Seymour, J., and Barnett, A. (2011). Variation in depth of whitetip reef sharks: does provisioning ecotourism change their behaviour? *Coral Reefs* 30, 569–577. doi: 10.1007/s00338-011-0769-8

Foroughirad, V., and Mann, J. (2013). Long-term impacts of fish provisioning on the behavior and survival of wild bottlenose dolphins. *Biol. Conserv.* 160, 242–249. doi: 10.1016/j.biocon.2013.01.001

Gallagher, A. J., and Hammerschlag, N. (2011). Global shark currency: the distribution, frequency, and economic value of shark ecotourism. *Curr. Issues Tour.* 14, 797–812. doi: 10.1080/13683500.2011.585227

Gallagher, A. J., and Huveneers, C. P. M. (2018). Emerging challenges to shark-diving tourism. *Mar. Policy* 96, 9–12. doi: 10.1016/j.marpol.2018.07.009

Gallagher, A. J., Orbesen, E. S., Hammerschlag, N., and Serafy, J. E. (2014a). Vulnerability of oceanic sharks as pelagic longline bycatch. *Glob. Ecol. Conserv.* 1, 50–59. doi: 10.1016/j.gecco.2014.06.003

Gallagher, A. J., Serafy, J. E., Cooke, S. J., and Hammerschlag, N. (2014b). Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. *Mar. Ecol. Prog. Ser.* 496, 207–218. doi: 10.3354/meps10490

Gallagher, A. J., Vianna, G. M. S., Papastamatiou, Y. P., Macdonald, C., Guttridge, T. L., and Hammerschlag, N. (2015). Biological effects, conservation potential, and research priorities of shark diving tourism. *Biol. Conserv.* 184, 365–379. doi: 10.1016/j.biocon.2015.02.007

Godde, S., Humbert, L., Côté, S. D., Réale, D., and Whitehead, H. (2013). Correcting for the impact of gregariousness in social network analyses. *Anim. Behav.* 85, 553–558. doi: 10.1016/j.anbehav.2012.12.010

Hammerschlag, N., Gallagher, A. J., Wester, J., Luo, J., and Ault, J. S. (2012). Don't bite the hand that feeds: assessing ecological impacts of provisioning ecotourism on an apex marine predator. *Funct. Ecol.* 26, 567–576. doi: 10.1111/j.1365-2435.2012.01973.x

Hammerschlag, N., Gutowsky, L. F. G., Gallagher, A. J., Matich, P., and Cooke, S. J. (2017). Diel habitat use patterns of a marine apex predator (tiger shark, *Galeocerdo cuvier*) at a high use area exposed to dive tourism. *J. Exp. Mar. Bio. Ecol.* 495, 24–34. doi: 10.1016/j.jembe.2017.05.010

Heinrich, D., Dhellemmes, F., Guttridge, T. L., Smukall, M., Brown, C., Rummer, J., et al. (2021). Short-term impacts of daily feeding on the residency, distribution and energy expenditure of sharks. *Anim. Behav.* 172, 55–71. doi: 10.1016/j.anbehav.2020.12.002

Hijmans, R., Williams, E., Vennes, C., and Hijmans, M. (2017). *Geosphere: Spherical Trigonometry. R Package.* Available online at: https://CRAN.R-project.org/package=geosphere

Huveneers, C., Rogers, P. J., Beckmann, C., Semmens, J. M., Bruce, B. D., and Seuront, L. (2013). The effects of cage-diving activities on the fine-scale swimming behaviour and space use of white sharks. *Mar. Biol.* 160, 2863–2875. doi: 10.1007/s00227-013-2277-6

Jacoby, D. M. P., Busawon, D. S., and Sims, D. W. (2010). Sex and social networking: the influence of male presence on social structure of female shark groups. *Behav. Ecol.* 21, 808–818. doi: 10.1093/beheco/arq061

Jacoby, D. M. P., Croft, D. P., and Sims, D. W. (2012). Social behaviour in sharks and rays: analysis, patterns and implications for conservation. *Fish Fish.* 13, 399–417. doi: 10.1111/j.1467-2979.2011.00436.x

Jacoby, D. M. P., Papastamatiou, Y. P., and Freeman, R. (2016). Inferring animal social networks and leadership: applications for passive monitoring arrays. *J. R. Soc. Interface* 13:20160676. doi: 10.1098/rsif.2016.0676

Kessel, S. T., and Hussey, N. E. (2015). Tonic immobility as an anaesthetic for elasmobranchs during surgical implantation procedures. *Can. J. Fish. Aquat. Sci.* 72, 1287–1291. doi: 10.1139/cjfas-2015-0136

Macdonald, C., Gallagher, A. J., Barnett, A., Brunnschweiler, J., Shiffman, D. S., and Hammerschlag, N. (2017). Conservation potential of apex predator tourism. *Biol. Conserv.* 215, 132–141. doi: 10.1016/j.biocon.2017.07.013

MacNeil, M. A., Chapman, D. D., Heupel, M., Simpfendorfer, C. A., Heithaus, M., Meekan, M., et al. (2020). Global status and conservation potential of reef sharks. *Nature* 583, 801–806. doi: 10.1038/s41586-020-2519-y

Mann, J., Connor, R. C., Barre, L. M., and Heithaus, M. R. (2000). Female reproductive success in bottlenose dolphins (*Tursiops sp.*): life history, habitat, provisioning, and group-size effects. *Behav. Ecol.* 11, 210–219. doi: 10.1093/beheco/11.2.210

Meyer, L., Barry, C., Araujo, G., Barnett, A., Brunnschweiler, J. M., Chin, A., et al. (2021). Redefining *provisioning* in marine wildlife tourism. *J. Ecotourism* 1–20. doi: 10.1080/14724049.2021.1931253

Mourier, J., Claudet, J., and Planes, S. (2020). Human-induced shifts in habitat use and behaviour of a marine predator: the effects of bait provisioning in the blacktip reef shark. *Anim. Conserv.* 24, 230–238. doi: 10.1111/acv.12630

Mourier, J., Lédée, E., Guttridge, T., and Jacoby, D. M. P. (2018). "Network analysis and theory in shark ecology–methods and applications," in *Shark Research: Emerging Technologies and Applications for the Field and Laboratory*, eds J. C. Carrier, M. R. Heithaus, and C. A. Simpfendorfer (Boca Raton, FL: CRC Press), 337–356.

Pacoureau, N., Rigby, C. L., Kyne, P. M., Sherley, R. B., Winker, H., Carlson, J. K., et al. (2021). Half a century of global decline in oceanic sharks and rays. *Nature* 589, 567–571. doi: 10.1038/s41586-020-03173-9

Papastamatiou, Y. P., Bodey, T. W., Caselle, J. E., Bradley, D., Freeman, R., Friedlander, A. M., et al. (2020). Multiyear social stability and social information use in reef sharks with diel fission-fusion dynamics. *Proc. Biol. Sci.* 287:20201063. doi: 10.1098/rspb.2020.1063

Perryman, R. J. Y., Venables, S. K., Tapilatu, R. F., Marshall, A. D., Brown, C., and Franks, D. W. (2019). Social preferences and network structure in a population of reef manta rays. *Behav. Ecol. Sociobiol.* 73:114. doi: 10.1007/s00265-019-2720-x

Psorakis, I., Voelkl, B., Garroway, C. J., Radersma, R., Aplin, L. M., Crates, R. A., et al. (2015). Inferring social structure from temporal data. *Behav. Ecol. Sociobiol.* 69, 857–866. doi: 10.1007/s00265-015-1906-0

Queiroz, N., Humphries, N. E., Couto, A., Vedor, M., da Costa, I., Sequeira, A. M. M., et al. (2019). Global spatial risk assessment of sharks under the footprint of fisheries. *Nature* 572, 461–466. doi: 10.1038/s41586-019-1444-4

Schilds, A., Mourier, J., Huveneers, C., Nazimi, L., Fox, A., and Leu, S. T. (2019). Evidence for non-random co-occurrences in a white shark aggregation. *Behav. Ecol. Sociobiol.* 73:138. doi: 10.1007/s00265-019-2745-1

Semeniuk, C. A. D., and Rothley, K. D. (2008). Costs of group-living for a normally solitary forager: effects of provisioning tourism on southern stingrays *Dasyatis americana*. *Mar. Ecol. Prog. Ser.* 357, 271–282. doi: 10.3354/meps07299

Simpfendorfer, C. A., Huveneers, C., Steckenreuter, A., Tattersall, K., Hoenner, X., Harcourt, R., et al. (2015). Ghosts in the data: False detections in VEMCO pulse position modulation acoustic telemetry monitoring equipment. *Anim. Biotelemetry* 3:55. doi: 10.1186/s40317-015-0094-z

Sims, D., Nash, J., and Morritt, D. (2001). Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. *Mar. Biol.* 139, 1165–1175. doi: 10.1007/s002270100666

Snijders, L., Blumstein, D. T., Stanley, C. R., and Franks, D. W. (2017). Animal social network theory can help wildlife conservation. *Trends Ecol. Evol.* 32, 567–577. doi: 10.1016/j.tree.2017.05.005

Sosa, S., Puga-Gonzalez, I., Hu, F., Pansanel, J., Xie, X., and Sueur, C. (2020). A multilevel statistical toolkit to study animal social networks: the animal network toolkit software (ANTs) R package. *Sci. Rep.* 10:12507 . doi: 10.1038/s41598-020-69265-8

Sulikowski, J. A., Wheeler, C. R., Gallagher, A. J., Prohaska, B. K., Langan, J. A., and Hammerschlag, N. (2016). Seasonal and life-stage variation in the reproductive ecology of a marine apex predator, the tiger shark *Galeocerdo cuvier*, at a protected female-dominated site. *Aquat. Biol.* 24, 175–184. doi: 10.3354/ab00648

Tinari, A. M., and Hammerschlag, N. (2021). An ecological assessment of large coastal shark communities in South Florida. *Ocean Coast. Manag.* 211:105772. doi: 10.1016/j.ocecoaman.2021.105772

Vianna, G. M. S., Meekan, M. G., Pannell, D. J., Marsh, S. P., and Meeuwig, J. J. (2012). Socio-economic value and community benefits from shark-diving tourism in Palau: a sustainable use of reef shark populations. *Biol. Conserv.* 145, 267–277. doi: 10.1016/j.biocon.2011.11.022

Wearmouth, V. J., and Sims, D. W. (2008). Chapter 2 sexual segregation in marine fish, reptiles, birds and mammals behaviour patterns, mechanisms and conservation implications. *Adv. Mar. Biol.* 54, 107–170. doi: 10.1016/S0065-2881(08)00002-3

Webber, Q. M. R., and Vander Wal, E. (2018). An evolutionary framework outlining the integration of individual social and spatial ecology. *J. Anim. Ecol.* 87, 113–127. doi: 10.1111/1365-2656.12773

Whitehead, H., and James, R. (2015). Generalized affiliation indices extract affiliations from social network data. *Methods Ecol. Evol.* 6, 836–844. doi: 10.1111/2041-210X.12383

Worm, B., Davis, B., Kettemer, L., Ward-Paige, C. A., Chapman, D., Heithaus, M. R., et al. (2013). Global catches, exploitation rates, and rebuilding options for sharks. *Mar. Policy* 40, 194–204. doi: 10.1016/j.marpol.2012.12.034

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 14 September 2021
doi: 10.3389/fmars.2021.688505

Non-random Co-occurrence of Juvenile White Sharks (*Carcharodon carcharias*) at Seasonal Aggregation Sites in Southern California

James M. Anderson[1]*, Alyssa J. Clevenstine[1,2], Brian S. Stirling[1], Echelle S. Burns[3,4,5], Emily N. Meese[6], Connor F. White[7], Ryan K. Logan[8], John O'Sullivan[9], Patrick T. Rex[1], Jack May (III)[1], Kady Lyons[1], Chuck Winkler[10], Emiliano García-Rodríguez[11], Oscar Sosa-Nishizaki[11] and Christopher G. Lowe[1]

[1] Department of Biological Sciences, California State University, Long Beach, Long Beach, CA, United States, [2] United States Fish and Wildlife Service, Fremont, CA, United States, [3] Marine Science Institute, University of California, Santa Barbara, Santa Barbara, CA, United States, [4] Bren School of Environmental Science and Management, University of California, Santa Barbara, Santa Barbara, CA, United States, [5] Environmental Market Solutions Lab, University of California, Santa Barbara, Santa Barbara, CA, United States, [6] Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX, United States, [7] Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, United States, [8] Guy Harvey Research Institute, Nova Southeastern University, Dania Beach, FL, United States, [9] Monterey Bay Aquarium, Monterey, CA, United States, [10] Aquatic Research Consultants, San Pedro, CA, United States, [11] Departamento de Oceanografía Biológica, Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), Ensenada, Mexico

Edited by:
David M. P. Jacoby,
Institute of Zoology, Zoological
Society of London, United Kingdom

Reviewed by:
Sara Andreotti,
Stellenbosch University, South Africa
Charlie Huveneers,
Flinders University, Australia
Robert Perryman,
Macquarie University, Australia

***Correspondence:**
James M. Anderson
james.anderson@csulb.edu

Specialty section:
This article was submitted to
Marine Megafauna,
a section of the journal
Frontiers in Marine Science

Received: *30 March 2021*
Accepted: *19 July 2021*
Published: *14 September 2021*

Citation:
Anderson JM, Clevenstine AJ, Stirling BS, Burns ES, Meese EN, White CF, Logan RK, O'Sullivan J, Rex PT, May J (III), Lyons K, Winkler C, García-Rodríguez E, Sosa-Nishizaki O and Lowe CG (2021) Non-random Co-occurrence of Juvenile White Sharks (Carcharodon carcharias) at Seasonal Aggregation Sites in Southern California. Front. Mar. Sci. 8:688505. doi: 10.3389/fmars.2021.688505

Many terrestrial and aquatic taxa are known to form periodic aggregations, whether across life history or solely during specific life stages, that are generally governed by the availability and distribution of resources. Associations between individuals during such aggregation events are considered random and not driven by social attraction or underlying community structure. White sharks (*Carcharodon carcharias*) have been described as a species that exhibits resource-driven aggregative behaviors across ontogenetic stages and juvenile white sharks are known to form aggregations at specific nursery sites where individuals may remain for extended periods of time in the presence of other individuals. We hypothesized juvenile white sharks form distinct communities during these critical early phases of ontogeny and discuss how a tendency to co-occur across life stages may be seeded by the formation of these communities in early ontogeny. We present results from a series of social network analyses of 86 juvenile white sharks derived from 6 years of passive acoustic telemetry data in southern California, demonstrating the likelihood of association of tagged juvenile white sharks is greater when sharks are of similar size-classes. Individuals in observed networks exhibited behaviors that best approximated fission-fusion dynamics with spatiotemporally unstable group membership. These results provide evidence of possible non-resource driven co-occurrence and community structure in juvenile white sharks during early life stages.

Keywords: social structure, acoustic telemetry, network analysis, sociality, juvenile white shark

INTRODUCTION

Sociality, or the propensity of individuals to form social groups (Merriam-Webster., 2021), is a trait exhibited across taxa and varies between loose temporary aggregations to life-long associations (Alexander, 1974; Sabol et al., 2020). Social interactions have been shown to reduce predation risk and increase foraging efficiency, navigational capability, and reproductive opportunities (Farine et al., 2015; Berdahl et al., 2018; Campbell et al., 2018; Diaz-Aguirre et al., 2019). Thus, animal social groups usually form when the associated benefits of group behavior outweigh the costs, while the influence of such associated costs upon the decision to engage in social behaviors is driven by extrinsic (e.g., prey availability) and intrinsic (e.g., competition) variability (Krause and Ruxton, 2002; Silk et al., 2014). Animal social groups are thus characterized by motivated cohesion and can be distinguished from aggregative behaviors, which are temporary assemblages of individuals in response to non-social forcing factors, such as seasonal resource availability (Jacoby et al., 2011; Meese and Lowe, 2019; Grueter et al., 2020).

White sharks (*Carcharodon carcharias*) are circumglobally distributed in both temperate and tropical waters (Compagno, 2002). In the sub-adult to adult ontogenetic stages, they are known to occur as solitary individuals but are also found in seasonal aggregations at feeding grounds such as pinniped haul outs (Bruce et al., 2006; Robbins, 2007; Domeier and Nasby-Lucas, 2008; Jorgensen et al., 2010; Duffy et al., 2012; Kock et al., 2013, 2018; Kanive et al., 2021). To date, the extent to which socially motivated factors play a role in co-occurrences of individual white sharks remains unresolved, with only two published studies on the subject arriving at different conclusions (Findlay et al., 2016; Schilds et al., 2019). Specifically, Findlay et al. (2016) reported that associations between white sharks in their study were random, although they exhibited weak structuring by sex and body size, whereas Schilds et al. (2019) reported non-random, sex-dependent associations with temporal variability. These studies drew upon observations of sub-adult and adult sharks co-occurring under baited and chummed (burleyed) conditions, at locations proximal to pinniped haul-outs, with very different time thresholds constituting co-occurrence. Juvenile white sharks use nearshore and beach habitat, where they have been observed to exhibit high degrees of residency and aggregation site fidelity (Weng et al., 2007; Bruce and Bradford, 2008; Werry et al., 2012; Dicken and Booth, 2013; Harasti et al., 2017; Oñate-González et al., 2017; Curtis et al., 2018; Tamburin et al., 2019; White et al., 2019; Spaet J. L. Y. et al., 2020; Anderson et al., 2021a,b). Such site fidelity is common among elasmobranchs in early ontogeny, as these habitats typically provide opportunities for optimal growth and foraging, and reduced predation risk (Simpfendorfer and Milward, 1993; Heupel et al., 2007; Chapman et al., 2009). Preliminary high-spatial-resolution movement data derived from hyperbolic positioning via a high density acoustic array off Carpinteria, California, indicate individual juvenile white sharks form aggregations (5–30 individuals of multiple size-classes) and use overlapping, spatially restricted areas (~8 km^2) continuously, for periods of weeks to months (Spurgeon et al., unpublished data; Anderson et al., 2021b).

It is unknown whether co-occurrence of individual sharks is random, driven by resource availability and/or environmental factors, or is a function of socially mediated behaviors. Co-occurrence may be a function of overlap in home ranges and exploited niches, or may be due to preferred associations between individuals of phenotypic characteristics. In network theory, this propensity for individuals with similar traits to co-occur is termed assortativity (Newman, 2002; Noldus and Van Mieghem, 2015). Co-occurrence of individual sharks may afford the opportunity for the transfer of information and the development of association preferences. Thus, seasonal resource-driven aggregations may seed the development of social groups and assortative interactions (Jacoby et al., 2011).

In this study, we applied a network analysis to passive acoustic telemetry data gathered from tagged juvenile white sharks [< 150–350 cm Total Length (TL)] in southern California over a 6-year period (2014–2019). This approach was designed to gather insight as to whether tagged shark co-occurrence at acoustically monitored sites was random, an artifact of resource-driven aggregation behavior, or may be driven by social preferences. We aimed to examine (1) whether apparent structure could be identified within generated networks, (2) the extent to which tagged sharks formed associations with other tagged individuals, (3) the extent of association stability across time, and (4) to characterize assortativity in association preferences.

MATERIALS AND METHODS

Tag Models and Tagging Procedures

A total of ninety sharks, of which detection data from eighty-six individuals used in the study were accessed via one of three ways (incidental catch, targeted catch, dart tagging), and were outfitted with either Vemco V16 or V13 coded acoustic transmitters (Vemco | Innovasea, Nova Scotia, Canada; transmitter family V13-1x-069k, V13-2x-069k, V16-4x-069k, V16-5x-069k. V16-6x-069k) (**Supplementary Table 1**).

Incidental Catch

Commercial gillnet fishers, working in collaboration with CSULB and CICESE researchers, brought incidentally captured juvenile white sharks to the nearest port in a large fish tote (1.2 × 1.2 × 1.2 m) with flowing seawater. Incidentally-caught sharks were caught offshore (>3 nm) outside of State waters. Researchers physically assessed, measured, and surgically implanted a plasma sterilized V16 transmitter into the abdominal cavity of the shark through a small incision (5 cm). The wound was closed with 2–3 interrupted sutures, before the animal was released approximately 2 km offshore. All individuals were visually monitored during release and behavior was recorded. A previous study demonstrated post-release survival rates of juvenile white sharks retrieved live from gillnets to be in the order of 93% (Lyons et al., 2013), while a more recent analysis indicated that minimizing handling and on-deck holding times may in turn minimize non-lethal post-release negative effects (Raoult et al., 2019). Approximate elapsed times from researchers taking possession of the shark to offshore release were < 30 min.

Targeted Catch

Juvenile white sharks were caught in shallow inshore waters either via a purse-seine, or via targeted quick-extraction with a gillnet. Sharks were transferred to a custom-made staging tank and ventilated, before being sexed, sized, and outfitted with a surgically implanted V16 transmitter as described above. Approximate handling times in all instances were < 20 min.

Dart Tagging

Juvenile white sharks swimming close to, or at the surface (at least 2 m visibility) were approached by either a small boat or personal watercraft from behind, with the aim of minimizing stress and flight response from the targeted animal and tagged with either a V13 or V16 acoustic tag using a 3 m modified pole-spear fitted with a tag applicator. Tags were inserted into the dorsal musculature at the base of the first dorsal fin using a titanium dart tethered to the tag. When possible, targeted sharks were visually checked for the presence of existing tags, and sex of individual was determined using a pole-mounted dip camera. Tagging effort via this method was largely directed at locations where sharks were known to seasonally aggregate. Shark size (TL cm) was estimated by comparison to an object of known size (the watercraft) from orthogonal aerial drone footage. Comparative methods such these have been shown to produce valid estimates of size (Sequeira et al., 2016; May et al., 2019). All tagged sharks were assigned a size-class based upon their measured or estimated size at time of tagging (**Table 1**). For sharks detected in more than one calendar year, a growth rate of 25 cm per year was assumed (Cailliet et al., 1985).

Spatial and Temporal Detection Analysis

Acoustic detection data were acquired from a wide-spread acoustic receiver array of up to 75 Vemco VR2 and VR2W receivers, deployed between Estero Bay (35.448, −120.952) and San Diego [32.876, −117.260 (**Figure 1**)], but also included offshore island monitoring sites at Santa Catalina Island (33.389, −118.359). From north to south, these included locations proximal to the following locations/landmarks: Estero Bay, Morro Bay, Pismo Beach, Santa Barbara, Ventura, Santa Catalina Island, Santa Monica Bay, Long Beach—Huntington Beach, Newport Beach—Laguna Beach, Dana Point—San Clemente, Oceanside, and San Diego (**Figure 1**). Receivers were largely installed and maintained by CSULB, but also included receivers of collaborators: University of California San Diego (UCSD), the Southern California Acoustic Telemetry Tracking Network (SCATTN), and the Ensenada Center for Scientific Research and Higher Education (CICESE). Acoustic receivers were deployed in shallow ($\sim$ 3–40 m depth) coastal waters within 1,000 m of the shoreline (50% within 400 m), across a range of environments, including calm protected habitats (e.g., embayments, harbors), exposed high energy sand substrata (e.g., beach habitat), rocky reef, and kelp forest habitats. Receiver detection range (nominal range 150–700 m) varied by site, habitat type, and transmitter power output (Heupel et al., 2006; Kessel et al., 2014; Huveneers et al., 2016). For example, range testing performed in waters off Santa Catalina Island and Long Beach Harbor revealed average detection ranges of 150 m to $\sim$ 200 m (V13 and V9 low power transmitters, respectively; Wolfe and Lowe, 2015; Clevenstine and Lowe, 2021), while mean detection ranges of high power output V16 transmitters in waters off San Clemente and Santa Barbara are estimated to be in the region of 500–700 m (Stirling et al., unpublished data). Thus, a nominal detection range of 500 m across the entire array was considered. To account for the possibility of false detections, raw receiver data were filtered to include only individuals that were detected two or more times per day (Simpfendorfer et al., 2015). Detection data were visually inspected to check for the possibility of double-tagged animals. Where double-tagged animals were identified, all data pertaining to the 2nd tag were removed from the analyses.

TABLE 1 | Allocated size-classes of juvenile white sharks detected.

Size (cm)	Size-class
<150	1
150–175	2
175–200	3
200–225	4
225–250	5
250–275	6
275–300	7
300–325	8
325–350	9
>350	10

Social Network Construction and Association Definition

A gambit-of-the-group approach (Cairns and Schwager, 1987; Franks et al., 2010) was used to build proximity-based social networks using individual tagged sharks as nodes and strength of association as edges, calculated via the simple ratio index (SRI) using the R packages *spatsoc* (version 0.1.14; Robitaille et al., 2019) and *igraph* (version 1.2.5; Csardi and Nepusz, 2006). The SRI score's an individual's strength of association between 0 and 1, with 0 indicating no co-occurrence while a score close to 1 indicates a high level of co-occurrence (Aplin et al., 2013). SRI was chosen over other indices (e.g., half-weight index) as the properties and nature of acoustic detection data render them unlikely to violate the assumptions required for SRI: recorded associations are accurate, the probability of identification is independent of whether an individual is associated or not (Stehfest et al., 2013; Lilly et al., 2020). To comply with formatting requirements, detections were rounded to the nearest hour (i.e., hourly presence) and any subsequent detections of the same animal at the same receiver within that hour removed. Animal detections and associated relocations were grouped according to a temporal threshold of 1-h bins (*time group*), before being spatially grouped according to a threshold of 1 km radius (*group*). Thus, animals were considered to co-occur in space and time if they were detected at the same receiver within an hour of each other, or at separate receivers within an hour of each other, provided the two receivers were $\leq$ 1 km from each other. A 1 km spatial threshold was chosen as this allowed for

FIGURE 1 | Study area (inset) and locations of all receivers used in the study (2014–2019). Receiver locations are colored according to latitude.

individuals to be considered as being within the same group in instances where they were detected on separate receivers that had overlapping detection ranges, although creating such a spatial buffer introduces the possibility that sharks may be grouped together, or regarded as associating, when in-fact they could be up to 2 km from each other (assuming a 500 m detection range).

Data were then subset by Julian year (2014–2019) before generating networks and associated graphs. Network communities were identified through weighted eigenvector community detection (Newman, 2006), and community modularity (*Q*, the extent to which communities within a network are distinct from each other) was calculated using the R package *igraph*. Homophilic propensity, the tendency of individuals to associate with others with similar traits, was examined by calculating assortment coefficients based on estimated shark size. Strength of associations were calculated as edge lists using a temporal based nearest neighbor approach, whereby the nearest neighbor to each individual within each time group was calculated, incorporating a distance threshold of 1 km radius.

Pre-network permutation tests based on mean values from 10,000 randomized networks generated in the R package *spatsoc* were used to examine whether the observed overall network structure (all years combined) differed from structure of randomized networks. Coefficients of variation (CV's) of SRI indices between vertices from observed networks were compared to those from the randomized networks using two-sample *t*-tests.

To further confirm the non-random nature of the observed structure, we used pre-network permutation tests (10,000) for each constructed network in each individual year of the study. CV's of SRI indices from observed and random networks were compared to examine observed and expected relationships (Bejder et al., 1998; Farine and Whitehead, 2015; Farine et al., 2015), whereby tagged sharks were assumed to exhibit preferred co-occurrences where coefficients of variation from observed networks were greater than 97.5% of coefficients of variations from randomized (permuted) networks (Findlay et al., 2016). It was not possible to replicate this same process for the overall (all years combined) network as it was not possible to account for phenotypic changes in those individuals that were as identified as nodes in networks across more than 1 year.

Association Preference Examination

We used multiple linear regression to examine structural predictors of association strength (*strength*) in observed networks, with separate models run for each annual network. Predictor variables included estimated shark size-class (*size-class*), number of detections (*detections*), detection period (*days*), and number of acoustic receiver stations visited (*statvis*). The inclusion of size-class allows for identification of homophilic association preferences, while the inclusion of the number of detections, detection period, and the number of stations visited allows for identification of possible structure inherent to the data. The sex of the shark was not included as a predictor variable due to the number of animals in the study with unconfirmed sex (**Supplementary Table 1**). The most parsimonious model for each year was identified from a global model via AICc values using the R package *glmulti* (Calcagno and de Mazancourt, 2010), and confirmed by individually comparing the final model to the next two most parsimonious model iterations. Final models were also compared against null models ($strength \sim 1$) to examine significance of predictors used (**Supplementary Table 1**). The global model was written as $strength \sim size\ class + statvis + detections + days + detections * days$.

A multiple regression quadratic assignment procedure with double-semi-partitioning (MRQAP-DSP; Farine, 2013) was used to further quantify the influence of specific structural factors (i.e., size-class) included in multiple regression models in each year. To examine whether association strength differed for sharks grouped in the same size-class, a binary matrix was constructed that encoded size-class and tested for correlation with a binary

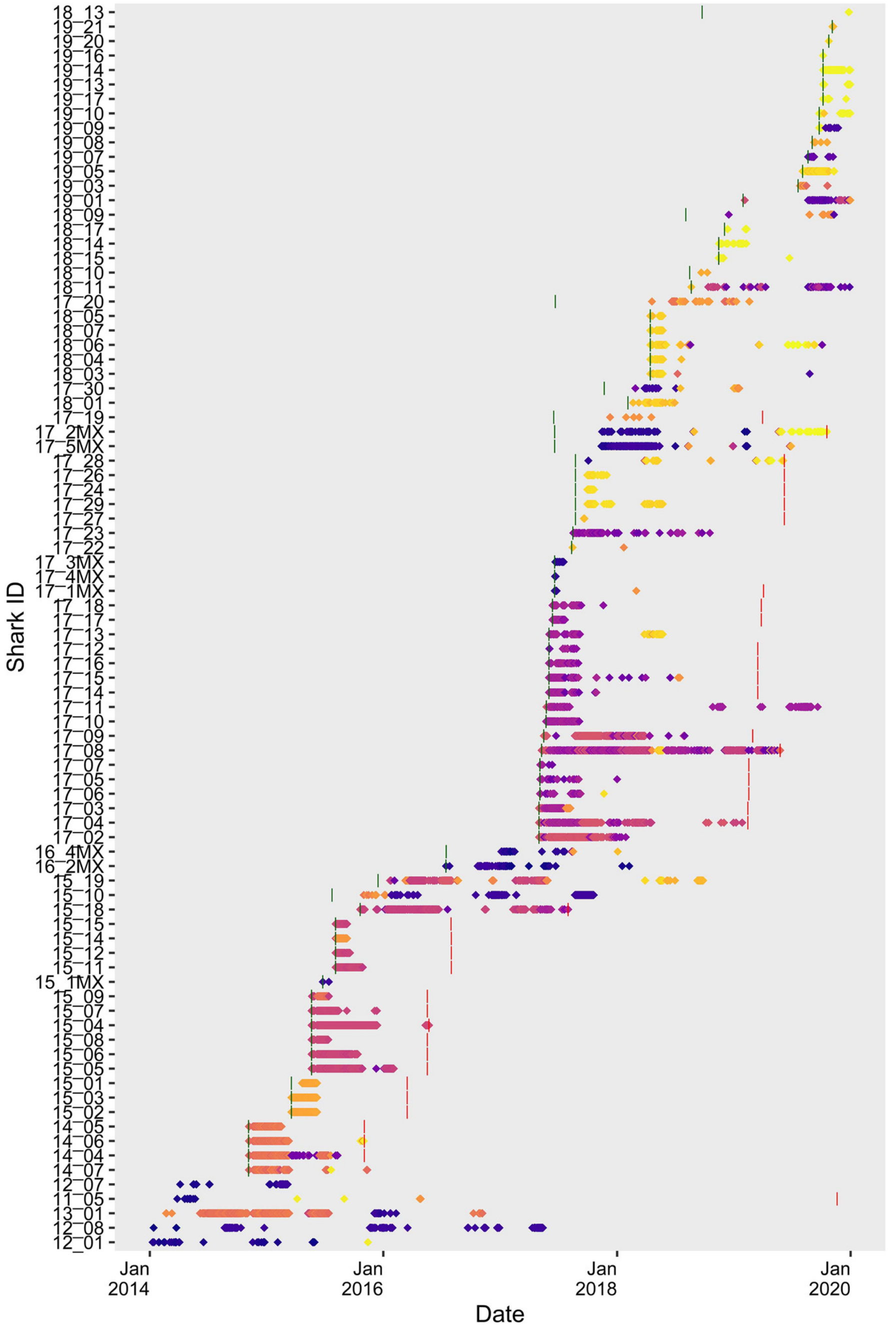


FIGURE 2 | Time series plot showing presence/absence of tagged juvenile white sharks at monitored locations. Points are colored according to individual receiver station latitude demonstrate co-occurrence. Latitudes corresponding to point color are shown in **Figure 1**. Green and red vertical lines show tagging date and tag-battery life, respectively. Sharks with bars missing were either tagged prior to 2014, or tag-battery life extends beyond 2019.

version of the SRI matrix using Mantel tests (999 permutations) following the method described by Farine and Whitehead (2015), using the R package *vegan* (Oksanen et al., 2011). This process was repeated for each yearly dataset (2014–2019).

RESULTS

A total of 86 tagged juvenile white sharks were detected on at least 1 day across the study period (2014–2019) and included in the overall analyses. Of these, 29 (34%) were outfitted with internal tags, while 57 (66%) were tagged externally. Total number of days detected on acoustic receivers and sum detection period varied by shark, ranging from 1 to 424 days detected [66 ± 75 (mean ± SD)], across a sum period of 1–1,216 (265 ± 277) days (**Figure 2**). A total of 26 sharks were detected in 2 or more calendar years (range 2–4 years, 2.42 ± 0.58). The number of returning tagged sharks showed an increasing trend across the study (**Figure 2**) and was positively correlated with the cumulative number of sharks tagged (Pearson's product-moment correlation; $r = 0.82$, $p = 0.048$). Only externally tagged sharks were observed to represent nodes in networks in more than 1 year (**Supplementary Table 2**). Tagged juvenile white sharks exhibited both temporal and spatial overlap in detection patterns, suggesting possible association preferences (**Figure 2**).

Social Organization and Association Preference

Overall observed network structure (**Figure 3**) was compared against a null network generated from 10,000 pre-network permutations based upon the CV's of individuals, accounting for years in which individual sharks were present in a network. Observed network strength values (mean = 0.36 ± 0.41) were significantly greater than expected values (0.27 ± 0.36; Welch Two Sample *t*-test; $t = -2.513$, $p = 0.012$), indicating there was apparent structure (i.e., association preferences) in juvenile white shark seasonal aggregations. Additionally, CV's of observed association strength indices vs. randomized networks for each individual year indicated that, with the exception of 2016, observed network structure was significantly stronger than expected from a randomly structured network (**Supplementary Figure 1**). Thus, co-occurrence of tagged juvenile white sharks at acoustically monitored locations was considered non-random. Community modularity for all detections across all years was high ($Q = 0.63$), which reflects that although communities appear to be connected, they were spatiotemporally distinct with limited individual connections to other communities. Fifty-five of the 86 sharks (64%) included in analyses formed associations with another shark. Thirty-nine of the 86 sharks (45%) were a part of a significant network (**Supplementary Table 2**), with nine sharks (10%) identified as being part of a significant network in more than 1 year. The number of associations formed by individuals within a single year ranged from 1 to 10 (2.21 ± 1.65). The total number of associations per shark varied both within and between years throughout the study period but showed no discernable trend across the study period (**Supplementary Table 1**). Mean number of associations per shark was highest in 2015, which is reflected by the associated mean SRI value of 0.7. Lowest mean SRI values were observed in 2016 and 2019 (0.03 and 0.05, respectively), suggesting tagged sharks had low likelihoods of spatiotemporal overlap within acoustically monitored locations in those years (**Table 2**).

The number of associations between sharks was not correlated with individual year (Pearson's product-moment correlation;

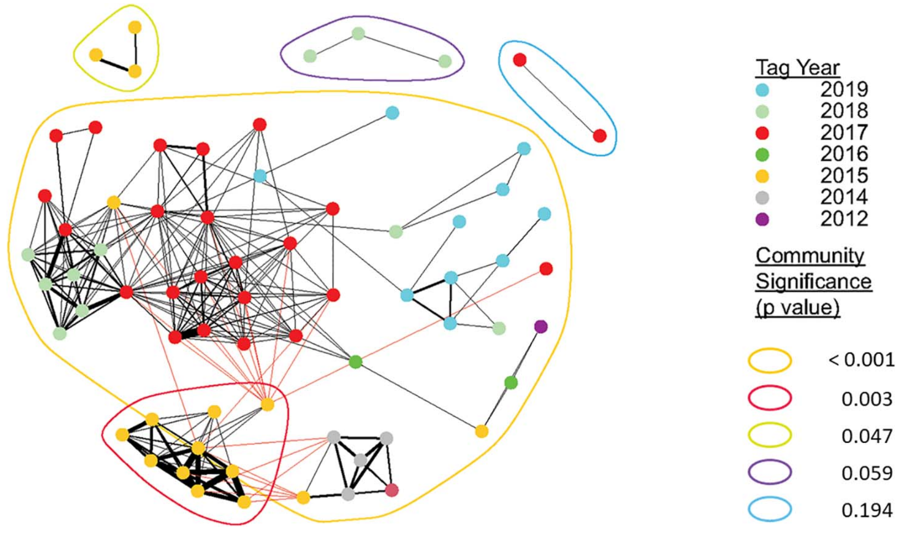


FIGURE 3 | Sociogram showing associations of all tagged juvenile white sharks across all years. Nodes represent individual sharks, node color indicates the year in which they were detected or formed strongest associations (in the case of sharks detected over more than year). Edge thickness indicates the relative number of connections (associations) between nodes. Colors encircling multiple nodes represent identified distinct communities. Detected sharks that did not form dyadic connections to at least one other tagged shark ($n = 31$) are not shown. Community modularity for all detections across all years was high ($Q = 0.63$), which reflects that although communities appear to be connected, they were spatiotemporally distinct with limited individual connections to other communities.

TABLE 2 | Summary table of characteristics of observed networks across individual years.

Year	Total active tags	Tag type ratio (internal : external)	Total detected	Total returning	Total in network(s)	Mean SRI ± SD	Modularity (Q)	Assortativity (r)	Mean dyads per Shark ± SD
2014	17	1:3	9	2	4	0.55 ± 0.23	8.8×10^{-16}	−0.25	2.5 ± 1.29
2015	36	0:12	25	6	12	0.70 ± 0.52	0.42	0.55	4 ± 3.10
2016	42	2:1	9	7	3	0.03 ± 0.04	0.28	−0.41	1 ± 0.0
2017	73	3:9	36	5	12	0.42 ± 0.42	0.28	0.08	3 ± 2.52
2018	92	4:5	33	12	8	0.27 ± 0.42	0.07	−0.06	2.88 ± 1.96
2019	110	2:6	29	10	8	0.05 ± 0.09	0.35	0.65	1.38 ± 0.52

$r = -0.240$, $p = 0.105$) or with the total number of available (i.e., detectable) tagged sharks (Pearson's product-moment correlation; $r = -0.214$, $p = 0.148$). Node degree, the number of connections an individual has with other sharks, was not found to correlate with the date of first detection, thus there was no relationship between how early in a calendar year a shark was tagged and the number of associations that shark had with other tagged sharks. The exception to this was in 2017, where a positive correlation was observed (Pearson's product-moment correlation; $r = -0.393$, $p = 0.018$), which was likely a function of six sharks with both the highest degree and SRI values being tagged within 1 month of each other (two on the same day, three within 3 days, four within 8 days, five within 22 days). With the exception of 2015, returning sharks were not observed to renew individual associations from the previous year. However, the exception in 2015 is a function of sharks aggregating and forming association preferences in 2014 continuing to do so through the change of year into 2015.

Network analyses based on weighted eigenvector community detection demonstrated that for all years combined (**Figure 3**), as well as each individual year, some aggregating sharks formed distinct, significant communities (**Table 2**). In years where spatiotemporally separate aggregations formed, relatively high community modularity was observed, as indicated by high calculated Q-values (**Table 2**, **Figure 4**, and **Supplementary Video 1**). Similarly, assortment coefficients were observed to be highest in years with higher Q-values (**Table 2**). Of the 39 tagged animals that were members of significant communities, 18 were detected in two or more spatially distinct locations (considered separate aggregations) across 2014 ($n = 4$), 2015 [$n = 8$ (three sharks from the significant network in 2014)], 2017 ($n = 3$), 2018 ($n = 1$), and 2019 ($n = 2$) (**Supplementary Table 2**). Sixteen sharks were identified as being members of significant communities across two or more years. Fourteen were sharks identified in communities in two separate years. Two sharks (Shark IDs 15_19 and 17_08) were part of significant communities in three separate years (2016, 2017, 2018 and 2017, 2018, 2019, respectively).

Observed Social Structure and Size Class

General linear models were run for each year in the dataset to examine potential predictors of association strength. For all years, the best fitting model was $strength \sim size\ class + detections^{*} days$ (**Figure 5** and **Supplementary Table 3**). The interaction term of $detections^{*} days$ was significant in all years for which it was included, except for 2018, where the interaction was not significant and these terms were removed, and the model re-run (Carey, 2013). Model correlation coefficients ranged from 0.19 to 0.83 (0.52 ± 0.23). The interaction term and response variable (association strength) were found to be strongly collinear across all models where included and is reflected by high associated variance inflation factors (**Figure 5**). Shark size-class was included in all final models, and was found to be a significant predictor of association for 3 of 6 final models [2017, 2018, and 2019 (**Figure 5**)]. The results from MRQAP-DSP regression indicated that shark size-class was a significant predictor of co-occurrence in 3 of 6 yearly datasets examined (2015, 2017, 2019; **Table 3**). Tagged shark co-occurrence was found to be significantly correlated with shark size-class in those same years [Mantel tests: (2015) $r = 0.332$, $p = 0.001$; (2017) $r = 0.08$, $p = 0.04$; (2019) $r = 0.144$, $p = 0.014$; **Table 4**].

DISCUSSION

Juvenile white sharks in southern California are known to seasonally aggregate in annually variable, spatially discrete nearshore locations (Lyons et al., 2013; White et al., 2019; Anderson et al., 2021a). The drivers behind these aggregation "hot spot" patterns, and the selection of specific habitat locations over an abundance of comparable available habitat remain unclear, and are not consistently explained by environmental correlates (Spaet J. et al., 2020; Anderson et al., 2021a). While the study included detection data from tagged juvenile white sharks at locations across southern California, a majority of annual detections and co-occurrences of tagged sharks occurred at seasonal aggregation hot spots, as indicated in **Figures 2**, **4**. It must be acknowledge that a majority of tagged sharks included in the study (65%) were tagged externally, and the majority of these sharks were tagged at known aggregation locations (see **Supplementary Table 1** for tagging locations). Thus, to some extent, detection patterns and observed network structures may be a function of tagging methodologies used. However, where this is the case, the patterns in the detection data also reflect that these sharks had already formed aggregations and may have also already formed preferential associations with individual conspecifics present within the aggregation. For instance, individuals caught offshore by commercial fishers were less likely to be found within nearshore aggregations. Individuals that spatiotemporally overlap each other are more likely to be associated with each other, due to inherently

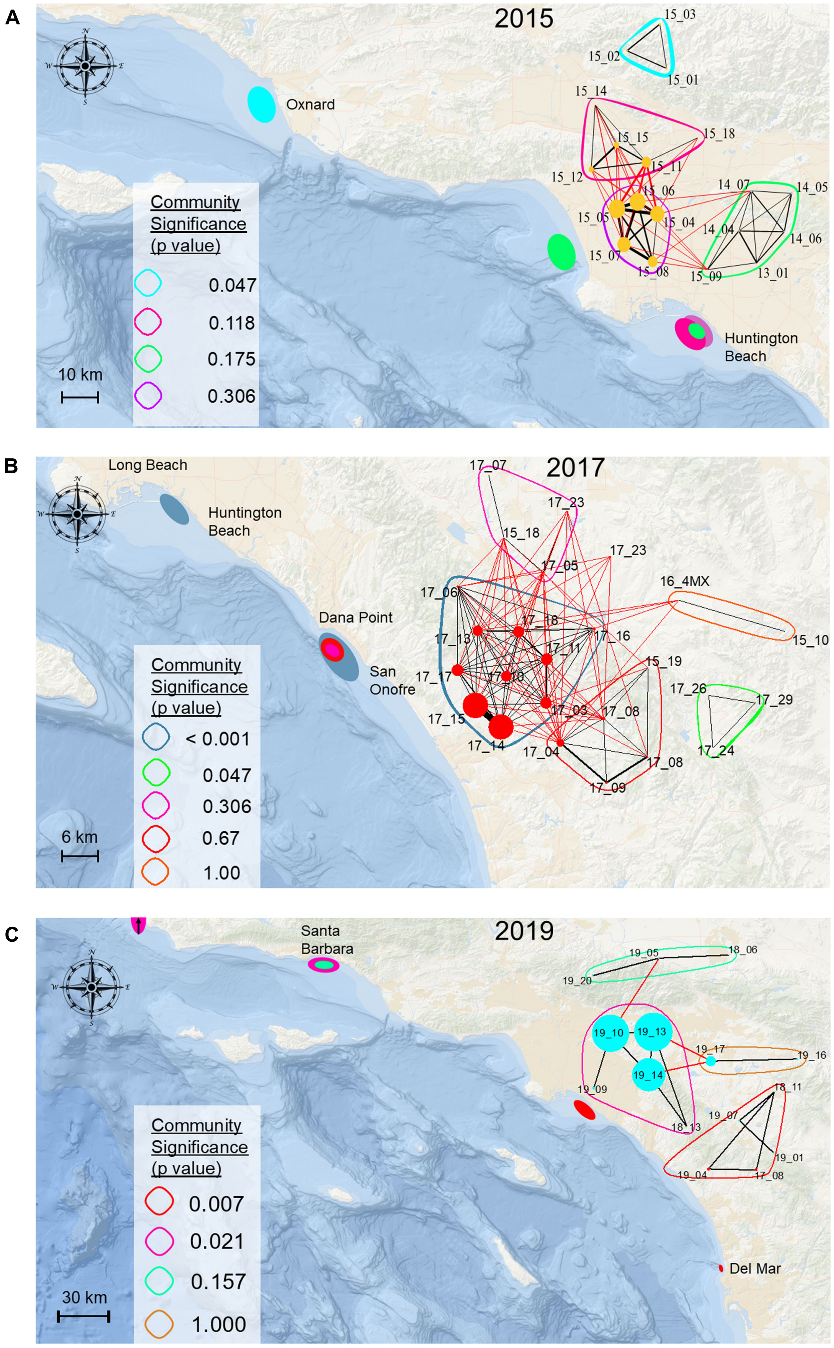
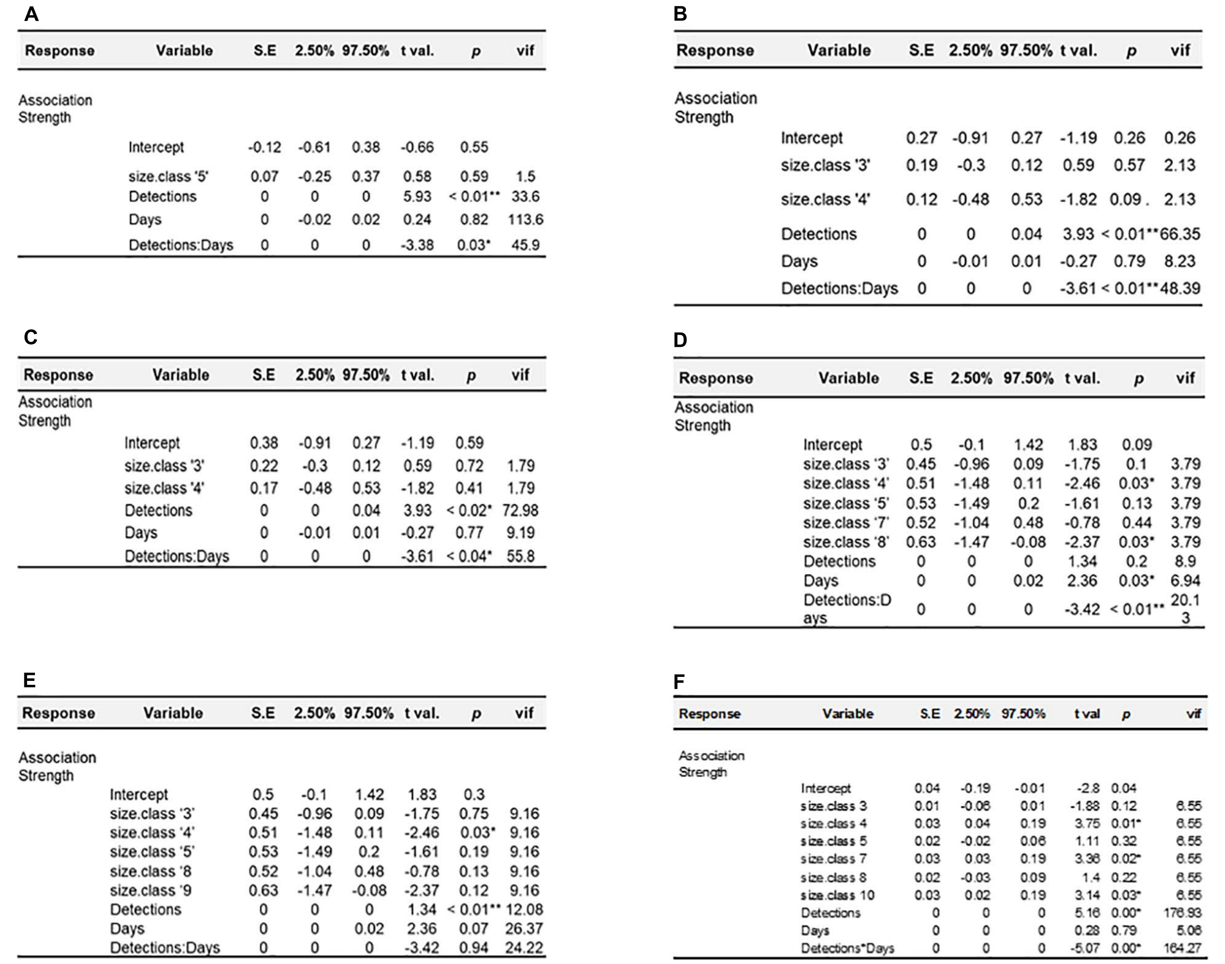


FIGURE 4 | Maps depicting community modularity in observed networks for 2015 **(A)**, 2017 **(B)**, and 2019 **(C)**. Community composition and corresponding discrete spatial locations of specific network communities are reflected in coloration of bands surrounding network nodes, and oval shaped markers within map coastal locations.

greater probability of co-occurrence. Pre-network (data stream) permutations can be used to examine whether a metric of interest (in this case observed association strength) differs to that which might occur at random. Our comparison of observed and permuted association strengths demonstrated that except for 2016 (a notably data deficient year) observed association preferences differed significantly to expected values, indicating apparent co-occurrence of individuals in space and time is non-random (**Supplementary Figure 1**). Observed relative association strengths in animal social networks may be a function of resource availability or site fidelity (Lusseau et al., 2006; Armansin et al., 2016). Thus, we incorporated methods that aimed to discern whether observed network structure could be explained by social factors, or were likely



A

Response	Variable	S.E	2.50%	97.50%	t val.	p	vif
Association Strength							
	Intercept	-0.12	-0.61	0.38	-0.66	0.55	
	size.class '5'	0.07	-0.25	0.37	0.58	0.59	1.5
	Detections	0	0	0	5.93	< 0.01**	33.6
	Days	0	-0.02	0.02	0.24	0.82	113.6
	Detections:Days	0	0	0	-3.38	0.03*	45.9

B

Response	Variable	S.E	2.50%	97.50%	t val.	p	vif
Association Strength							
	Intercept	0.27	-0.91	0.27	-1.19	0.26	0.26
	size.class '3'	0.19	-0.3	0.12	0.59	0.57	2.13
	size.class '4'	0.12	-0.48	0.53	-1.82	0.09 .	2.13
	Detections	0	0	0.04	3.93	< 0.01**	66.35
	Days	0	-0.01	0.01	-0.27	0.79	8.23
	Detections:Days	0	0	0	-3.61	< 0.01**	48.39

C

Response	Variable	S.E	2.50%	97.50%	t val.	p	vif
Association Strength							
	Intercept	0.38	-0.91	0.27	-1.19	0.59	
	size.class '3'	0.22	-0.3	0.12	0.59	0.72	1.79
	size.class '4'	0.17	-0.48	0.53	-1.82	0.41	1.79
	Detections	0	0	0.04	3.93	< 0.02*	72.98
	Days	0	-0.01	0.01	-0.27	0.77	9.19
	Detections:Days	0	0	0	-3.61	< 0.04*	55.8

D

Response	Variable	S.E	2.50%	97.50%	t val.	p	vif
Association Strength							
	Intercept	0.5	-0.1	1.42	1.83	0.09	
	size.class '3'	0.45	-0.96	0.09	-1.75	0.1	3.79
	size.class '4'	0.51	-1.48	0.11	-2.46	0.03*	3.79
	size.class '5'	0.53	-1.49	0.2	-1.61	0.13	3.79
	size.class '7'	0.52	-1.04	0.48	-0.78	0.44	3.79
	size.class '8'	0.63	-1.47	-0.08	-2.37	0.03*	3.79
	Detections	0	0	0	1.34	0.2	8.9
	Days	0	0	0.02	2.36	0.03*	6.94
	Detections:Days	0	0	0	-3.42	< 0.01**	20.13

E

Response	Variable	S.E	2.50%	97.50%	t val.	p	vif
Association Strength							
	Intercept	0.5	-0.1	1.42	1.83	0.3	
	size.class '3'	0.45	-0.96	0.09	-1.75	0.75	9.16
	size.class '4'	0.51	-1.48	0.11	-2.46	0.03*	9.16
	size.class '5'	0.53	-1.49	0.2	-1.61	0.19	9.16
	size.class '8	0.52	-1.04	0.48	-0.78	0.13	9.16
	size.class '9	0.63	-1.47	-0.08	-2.37	0.12	9.16
	Detections	0	0	0	1.34	< 0.01**	12.08
	Days	0	0	0.02	2.36	0.07	26.37
	Detections:Days	0	0	0	-3.42	0.94	24.22

F

Response	Variable	S.E	2.50%	97.50%	t val	p	vif
Association Strength							
	Intercept	0.04	-0.19	-0.01	-2.8	0.04	
	size.class 3	0.01	-0.06	0.01	-1.88	0.12	6.55
	size.class 4	0.03	0.04	0.19	3.75	0.01*	6.55
	size.class 5	0.02	-0.02	0.06	1.11	0.32	6.55
	size.class 7	0.03	0.03	0.19	3.36	0.02*	6.55
	size.class 8	0.02	-0.03	0.09	1.4	0.22	6.55
	size.class 10	0.03	0.02	0.19	3.14	0.03*	6.55
	Detections	0	0	0	5.16	0.00*	176.93
	Days	0	0	0	0.28	0.79	5.06
	Detections*Days	0	0	0	-5.07	0.00*	164.27

FIGURE 5 | Results of multiple linear regression analyses. Each panel shows model results for the corresponding year; **(A)** 2014, **(B)** 2015, **(C)** 2016, **(D)** 2017, **(E)** 2018, **(F)** 2019.

TABLE 3 | Results from MRQAP-DSP regression.

Predictor	2014		2015		2016		2017		2018		2019	
	Coefficient	***p***	**Coefficient**	***p***	**Coefficient**	***p***	**Coefficient**	***p***	**Coefficient**	***p***	**Coefficient**	***p***
Size class	4.9×10^{-2}	1.00	4.8×10^{-2}	**0.0007**	-5.3×10^{-3}	0.79	1.1×10^{-2}	**0.047**	-3.2×10^{-3}	0.65	9.1×10^{-3}	**0.006**
Stations visited	NA	NA	5.7×10^{-2}	**0.005**	-7.2×10^{-3}	0.65	4.5×10^{-3}	0.49	5.3×10^{-3}	0.8	4.2×10^{-4}	0.70
Total detections	NA	NA	-2.6×10^{-2}	0.99	NA	NA	-1.3×10^{-2}	0.87	-7.7×10^{-3}	0.83	-2.8×10^{-3}	0.61
Detection period (days)	NA	NA	-2.9×10^{-2}	0.002	NA	NA	8.7×10^{-3}	0.1	-6.5×10^{-3}	**0.07**	-1.4×10^{-4}	0.93

Table shows effects of four predictor variables upon association strength in tagged sharks between 2014 and 2019. Two of the years where size class was not significantly correlated with association strength were years where < 5 individuals formed at least one distinct community. With the exception of 2015, no other predictors were significant. Variance explained by all models was low (2014: $R^2 = 7.0 \times 10^{-2}$, 2015: $R^2 = 0.19$, 2016: $R^2 = 7.16 \times 10^{-3}$, 2017: $R^2 = 0.017$, 2018: $R^2 = 4.9 \times 10^{-3}$, 2019: $R^2 = 0.08$). Bold values denote a statistically significant predictor variable in a given year.

driven by other forcing (e.g., environmental conditions and/or resource availability).

Assortativity and Community Structure

Animals that exhibit homophilic association preferences may do so with respect to phenotypic characteristics such as species, sex, size, and kinship (Mourier and Planes, 2021). As animal size was the only phenotypic characteristic we were able to consistently gather, we were restricted to using size-class as a metric of assortment. Although the resulting assortativity coefficients were variable, our analyses suggest the likelihood of association of tagged juvenile white sharks is greater where sharks are of similar size-classes. A comparable relationship was described in a study of juvenile white sharks in South Africa (Findlay et al., 2016).

TABLE 4 | Results of Mantel tests for correlation between yearly simple ratio index (SRI) matrices and shark size-class.

Year	Estimate (*rho*)	*p*-value
2014	0.332	0.455
2015	0.332	**0.001**
2016	−0.021	0.662
2017	0.080	**0.040**
2018	−0.029	0.796
2019	0.144	**0.014**

Observed estimates were compared to 999 permuted estimates. Significant p-values and respective years are indicated in bold.

The low variance explained by our multiple regression and MRQAP analyses indicates community structure was also driven by other factors we were unable to quantify, which could include spatiotemporal overlap due to environmental factors and/or resource availability, as well as sampling effects. However, black tip reef sharks (*Carcharhinus melanopterus*) have been documented to exhibit preferential associations to conspecifics of similar size and sex regardless of prey availability (Mourier et al., 2012), which lends support to apparent preferential association toward conspecifics of similar size in the current study.

Shark Co-occurrence and Group Dynamics

Individuals in observed networks exhibit behaviors that best approximate fission-fusion dynamics (formation and dissolution of groups over time) with spatiotemporally unstable group membership. Fission-fusion dynamics are common in animal groups across taxa, including elasmobranchs (Haulsee et al., 2016; Perryman et al., 2019; Papastamatiou et al., 2020), and are regarded as being advantageous in the exploitation of heterogeneous environments (Ramos-Fernández and Morales, 2014; Silk et al., 2014; Farine et al., 2015). Dyadic relationships seen between individual juvenile white sharks in our study are not represented by predictable or stable co-occurrence (association) as might be expected by animals that exhibit central-place foraging behavioral characteristics. Rather, the dyadic patterns observed in our study suggest individuals co-occur (fusion) punctuated by variable spatiotemporal intervals (fission). Such behaviors may be a function of exploitation of shared resources (e.g., food). A recent study of Australasian gannets (*Morus* serrator) determined that social associations in the study population were context dependent, and were most prevalent during foraging (constituting local enhancement). These associations were also most prevalent in regions where resources were clustered (Jones et al., 2020). Southern California juvenile white shark aggregation hot spots have been largely associated with shallow, sandy beach habitat, although across southern California, such habitat constitutes < 30% of total available shore type (Anderson et al., 2021a). Although we were not able to quantify resource homogeneity at aggregation hot spots, hot spot locations themselves were annually spatially variable. If spatial locations of aggregation hot spots are resource driven, we can expect there to be a comparatively higher degree of resource clustering at hot spot locations with respect to ostensibly similar neighboring habitat. Juvenile white sharks in the study were observed to co-occur at different receivers both within the same spatiotemporal aggregation, as well as separate, spatially discrete locations and aggregations within the same year (**Supplementary Video 1**). Although this behavior, which linked nodes between network communities, could simply indicate individuals at similar ontogenetic stages were responding in similar ways to the same environmental cues, it may also be attributable to following behaviors and association borne from local enhancement, where individuals are attracted to actively foraging conspecifics (Poysa, 1992). Thus, the interplay of environmental drivers and context-specific social behaviors may govern co-occurrence and apparent association of individual juvenile white sharks in the study.

Although 10% of tagged sharks were identified at the same locations across more than 1 year, there was no evidence of stability in structure across multiple years, as returning sharks did not form repeated associations at monitored locations in subsequent years. Juvenile white sharks aggregating at nearshore locations, including those in this study, have been demonstrated to exhibit overlapping, restricted area use (Lyons et al., 2013; Anderson et al., 2021a). An individual's tendency toward association may be indicated by the propensity for spatiotemporal overlap and successive return to the same locations (Klimley and Holloway, 1999; Lilly et al., 2020), a trait exhibited in juvenile white sharks (Bruce et al., 2019; Spaet J. L. Y. et al., 2020; Anderson et al., 2021a). Observations of juvenile white shark interactions derived from drone surveys undertaken during the study period (Rex et al., unpublished data) indicate that individuals may often be within 10–20 m of each other while in these loose aggregations, and do not appear to be schooling in the manner seen in other aggregative shark species [e.g., scalloped hammerhead sharks (*Sphyrna lewini*), black tip reef sharks (*Carcharhinus melanopterus*)]. In addition, observations of these interactions suggest the presence of dominance hierarchies and conspecific aggression. Although tagged sharks generally exhibited low frequency of associations with other tagged conspecifics (**Supplementary Table 1**), the strength of those associations, as indicated by SRI indices, were relatively strong, with the exception of sharks in 2016 and 2019, which were both years with low mean and total associations (**Table 1** and **Supplementary Table 1**). Individuals within heterogeneous environments likely do not experience equal benefits from local enhancement and information derived from social behaviors and co-occurrence (Jones et al., 2020). Thus, fission may not be a singular synchronous event, but rather an ongoing social construct governed by intrinsic plasticity. Aggregation dynamics in juvenile white sharks may therefore be governed by the interplay of resource quality, environmental heterogeneity, and the continuous evaluation of the cost-benefit relationship of sociality. This can be likened to the hypothesis of the ecological loop that affects dispersal, proposed by Bowler and Benton (2005), whereby the size of a population (in this case at an aggregation site), which is mediated by the environment (which varies in space and time), governs interactions between individuals for resources.

Although sociality has been examined and described in a number of elasmobranch species (Sims et al., 2000; Jacoby et al., 2010, 2011, 2016; Guttridge et al., 2013; Wilson et al., 2014, 2015; Armansin et al., 2016; Mourier et al., 2019; Perryman et al., 2019; Schilds et al., 2019; Mourier and Planes, 2021; Papastamatiou et al., 2020), the extent to which co-occurrence in white sharks as a function of social forcing factors is unknown. The difficulty of interpreting the true level of association between animals is a function of the data collection method, and the spatiotemporal thresholds used. For example, Schilds et al. (2019) used photographic identification of individuals present at a baited location within the same day as a means of identifying co-occurrence, thus arrival of connected nodes at the monitored location could potentially be hours apart. In the present study, shark presence and associations at monitored aggregation locations may be under-estimates as they only reflect tagged sharks within spatially discrete locations and time thresholds (1 h), which may better represent natural co-occurrence. However, the potential for temporally co-occurring individuals to be up to 2 km apart from each other in some instances, due to the nature of acoustic telemetered data, may also represent over-estimates of spatio-temporal co-occurrence.

While the primary drivers behind co-occurrence in shark species may be extrinsic factors such as resource availability and use, additional adaptive benefits of social interactions beyond direct biological benefits (e.g., increased opportunity for reproduction) have been identified and described (e.g., Jacoby et al., 2010; Mourier et al., 2012, 2019; Armansin et al., 2016; Jacoby and Freeman, 2016; Mourier and Planes, 2021; Papastamatiou et al., 2020). Papastamatiou et al. (2020) concluded that for sharks exhibiting central place foraging life history characteristics, information transfer during social foraging increased foraging efficiency and may lead to temporally stable social groups across years. Other shark species that exhibit more solitary life histories but aggregate seasonally at feeding sites may also exhibit preferential associations based on phenotypic characteristics (Findlay et al., 2016; Haulsee et al., 2016).

For naïve individuals, information transfer facilitates exploitation of patchy resources already identified by others (Aplin et al., 2013). The specific drivers governing where and when juvenile white sharks aggregate in southern California have yet to be defined but are thought to include water temperature and resource availability (White et al., 2019; Anderson et al., 2021a), and decisions by individual sharks to remain within a specific aggregation location may therefore reflect resource quality. Thus, perceived habitat quality derived from cues generated by both con and hetero-specifics, as well as transfer of information (e.g., following of "experienced" individuals by naïve individuals) within aggregation locations may lead to increased likelihood of association at a given location.

CONCLUSION

Although individual presence at aggregation sites may be driven by environmental cues and resource availability, the tendency of individuals to remain within aggregations may be the result of conscious behaviors, potentially driven by sociality, which may stem from naïve individuals acquiring information and experiencing local enhancement. To better understand the dynamics of associations between individuals, far higher resolution data is required. This could be achieved through the use of high-density acoustic arrays across much smaller spatial scales, specifically centered at aggregation hot spots [e.g., VPS (Vemco Positioning System) arrays], where the movements of individuals in three-dimensional space throughout an array can be achieved via trilateration of acoustic tag transmissions or by using proximity-based tags. Such studies would provide a more objective means of quantifying co-occurrence, fusion, and fission between individuals and groups, and elucidate the potential social dynamics that may govern space use and niche exploitation at juvenile white shark aggregation locations.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by the CSULB Institutional Animal Care and Use Committee.

AUTHOR CONTRIBUTIONS

JA, AC, EB, and CL conceived the study. CL, EB, EM, CFW, RL, CW, PR, JM, KL, JA, AC, EG-R, and OS-N tagged the sharks and collected the data. CFW, EB, EM, BS, JA, PR, and JM organized the data. JA analyzed the data, created the main figures, and drafted the manuscript. All authors contributed equally to manuscript revisions.

FUNDING

Funding for tagging and acoustic monitoring was provided by Monterey Bay Aquarium and AltaSea. Funding for data maintenance and analysis was provided by State of California. In-kind support for tagging and monitoring was provided by Los Angeles and Orange County Lifeguards, Cities of Huntington Beach, Seal Beach, Ventura, Santa Barbara, Newport Beach, Laguna, Long Beach, and San Clemente.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.688505/full#supplementary-material

REFERENCES

Alexander, R. D. (1974). The evolution of social behavior. *Annu. Rev. Ecol. Syst.* 5, 325–383. doi: 10.1146/annurev.es.05.110174.001545

Anderson, J. M., Burns, E. S., Meese, E. N., Farrugia, T. J., Stirling, B. S., White, C. F., et al. (2021a). Interannual nearshore habitat use of young of the year white sharks off Southern California. *Front. Mar. Sci.* 8:645142. doi: 10.3389/fmars.2021.645142

Anderson, J. M., Spurgeon, E. A., Stirling, B. S., May, J. I., Rex, P. T., Hyla, B., et al. (2021b). High resolution acoustic telemetry reveals swim speeds and inferred field metabolic rates in juvenile white sharks (Carcharadon carcharias). *Commun. Biol.*

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., and Sheldon, B. C. (2013). Individual personalities predict social behaviour in wild networks of great tits (Parus major). *Ecol. Lett.* 16, 1365–1372. doi: 10.1111/ele.12181

Armansin, N. C., Lee, K. A., Huveneers, C., and Harcourt, R. G. (2016). Integrating social network analysis and fine-scale positioning to characterize the associations of a benthic shark. *Anim. Behav.* 115, 245–258. doi: 10.1016/j.anbehav.2016.02.014

Bejder, L., Fletcher, D., and Brager, S. (1998). A method for testing association patterns of social animals. *Anim. Behav.* 56, 719–725. doi: 10.1006/anbe.1998.0802

Berdahl, A. M., Kao, A. B., Biro, D., Flack, A., Westley, P. A. H., Codling, E. A., et al. (2018). Collective animal navigation and migratory culture: from theoretical models to empirical evidence. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 373:20170009. doi: 10.1098/rstb.2017.0009

Bruce, B. D., and Bradford, R. W. (2008). *Spatial dynamics and habitat preferences of juvenile white sharks – identifying critical habitat and options for monitoring recruitment*. Hobart, TAS: CSIRO Marine and Atmospheric Research.

Bruce, B. D., Harasti, D., Lee, K., Gallen, C., and Bradford, R. (2019). Broad-scale movements of juvenile white sharks *Carcharodon carcharias* in eastern Australia from acoustic and satellite telemetry. *Mar. Ecol. Prog. Ser*. 619, 1–5. doi: 10.3354/meps12969

Bruce, B. D., Stevens, J. D., and Malcolm, H. (2006). Movements and swimming behaviour of white sharks (Carcharodon carcharias) in Australian waters. *Mar. Biol.* 150, 161–172. doi: 10.1007/s00227-006-0325-1

Cailliet, G. M., Natanson, L. J., Weldon, B. A., and Ebert, D. (1985). Preliminary studies on the age and growth of the white shark Carcharodon carcharias, using vertebral bands. *Bull. South. Calif. Acad. Sci. Mem.* 9, 49–60.

Cairns, S. J., and Schwager, S. J. (1987). A comparison of association indices. *Anim. Behav.* 35, 1454–1469. doi: 10.1016/S0003-3472(87)80018-0

Calcagno, V., and de Mazancourt, C. (2010). glmulti: An R Package for easy automated model selection with (Generalized) Linear Models. *J. Stat. Software* 34:63083.

Campbell, L. A. D., Tkaczynski, P. J., Lehmann, J., Mouna, M., and Majolo, B. (2018). Social thermoregulation as a potential mechanism linking sociality and fitness: Barbary macaques with more social partners form larger huddles. *Sci. Rep.* 8:6074. doi: 10.1038/s41598-018-24373-4

Carey, G. (2013). *Quantitative Methods in Neuroscience*. Boulder, CO: University of Colorado, Boulder.

Chapman, D. D., Babcock, E. A., Gruber, S. H., Dibattista, J. D., Franks, B. R., Kessel, S. A., et al. (2009). Long-term natal site-fidelity by immature lemon sharks (Negaprion brevirostris) at a subtropical island. *Mol. Ecol.* 18, 3500–3507. doi: 10.1111/j.1365-294X.2009.04289.x

Clevenstine, A. J., and Lowe, C. G. (2021). Aggregation site fidelity and movement patterns of the protected marine predator giant sea bass (Stereolepis gigas). *Environ. Biol. Fishes* 104, 401–417. doi: 10.1007/s10641-021-01077-9

Compagno, L. (2002). *Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Bullhead, mackerel andcarpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes)*, Vol. 2. Rome: Food and Agriculture Organization of the United Nations.

Csardi, G., and Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal Complex Syst.* 1695, 1–9.

Curtis, T. H., Metzger, G., Fischer, C., McBride, B., McCallister, M., Winn, L. J., et al. (2018). First insights into the movements of young-of-the-year white sharks (Carcharodon carcharias) in the western North Atlantic Ocean. *Sci. Rep.* 8:10794. doi: 10.1038/s41598-018-29180-5

Diaz-Aguirre, F., Parra, G. J., Passadore, C., and Möller, L. (2019). Genetic relatedness delineates the social structure of southern Australian bottlenose dolphins. *Behav. Ecol.* 30, 948–959. doi: 10.1093/beheco/arz033

Dicken, M. L., and Booth, A. J. (2013). Surveys of white sharks (Carcharodon carcharias) off bathing beaches in Algoa Bay, South Africa. *Mar. Freshw. Res.* 64:530. doi: 10.1071/MF12336

Domeier, M., and Nasby-Lucas, N. (2008). Migration patterns of white sharks Carcharodon carcharias tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. *Mar. Ecol. Prog. Ser.* 370, 221–237. doi: 10.3354/meps07628

Duffy, C., Francis, M. P., and Bonfil, R. (2012). "Regional population connectivity, oceanic habitat, and return migration revealed by satellite tagging of white sharks,Carcharodon carcharias, at NewZealand aggregation sites," in *Global perspectiveson the biology and life history of the white shark*, ed. M. L. Domeier (Boca Raton, FL: CRC Press), 310–318.

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using asnipe. *Methods Ecol. Evol.* 4, 1187–1194. doi: 10.1111/2041-210X.12121

Farine, D. R., Firth, J. A., Aplin, L. M., Crates, R. A., Culina, A., Garroway, C. J., et al. (2015). The role of social and ecological processes in structuring animal populations: A case study from automated tracking of wild birds. *R. Soc. Open Sci.* 2:150057. doi: 10.1098/rsos.150057

Farine, D. R., and Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *J. Anim. Ecol.* 84, 1144–1163. doi: 10.1111/1365-2656.12418

Findlay, R., Gennari, E., Cantor, M., and Tittensor, D. P. (2016). How solitary are white sharks: social interactions or just spatial proximity? *Behav. Ecol. Sociobiol.* 70, 1735–1744. doi: 10.1007/s00265-016-2179-y

Franks, D. W., Ruxton, G. D., and James, R. (2010). Sampling animal association networks with the gambit of the group. *Behav. Ecol. Sociobiol.* 64, 493–503. doi: 10.1007/s00265-009-0865-8

Grueter, C. C., Qi, X., Zinner, D., Bergman, T., Li, M., Xiang, Z., et al. (2020). Multilevel organisation of animal sociality. *Trends Ecol. Evol.* 35:24. doi: 10.1016/j.tree.2020.05.003

Guttridge, T. L., van Dijk, S., Stamhuis, E. J., Krause, J., Gruber, S. H., and Brown, C. (2013). Social learning in juvenile lemon sharks, Negaprion brevirostris. *Anim. Cogn.* 16, 55–64. doi: 10.1007/s10071-012-0550-6

Harasti, D., Lee, K., Bruce, B., Gallen, C., and Bradford, R. (2017). Juvenile white sharks Carcharodon carcharias use estuarine environments in south-eastern Australia. *Mar. Biol.* 164, 1–14. doi: 10.1007/s00227-017-3087-z

Haulsee, D. E., Fox, D. A., Breece, M. W., Brown, L. M., Kneebone, J., Skomal, G. B., et al. (2016). Social network analysis reveals potential fission-fusion behavior in a shark. *Sci. Rep.* 6, 1–9. doi: 10.1038/srep34087

Heupel, M. R., Carlson, J. K., and Simpfendorfer, C. A. (2007). Shark nursery areas: Concepts, definition, characterization and assumptions. *Mar. Ecol. Prog. Ser.* 337, 287–297. doi: 10.3354/meps337287

Heupel, M. R., Semmens, J. M., and Hobday, A. J. (2006). Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Mar. Freshw. Res.* 57:91. doi: 10.1071/MF05091

Huveneers, C., Simpfendorfer, C. A., Kim, S., Semmens, J. M., Hobday, A. J., Pederson, H., et al. (2016). The influence of environmental parameters on the performance and detection range of acoustic receivers. *Methods Ecol. Evol.* 7, 825–835. doi: 10.1111/2041-210X.12520

Jacoby, D. M. P., Busawon, D. S., and Sims, D. W. (2010). Sex and social networking: the influence of male presence on social structure of female shark groups. *Behav. Ecol.* 21, 808–818. doi: 10.1093/beheco/arq061

Jacoby, D. M. P., Croft, D. P., and Sims, D. W. (2011). Social behaviour in sharks and rays: analysis, patterns and implications for conservation. *Fish Fish.* 13, 399–417. doi: 10.1111/j.1467-2979.2011.00436.x

Jacoby, D. M. P., and Freeman, R. (2016). Emerging network-based tools in movement ecology. *Trends Ecol. Evol.* 31, 301–314. doi: 10.1016/j.tree.2016.01.011

Jacoby, D. M. P., Papastamatiou, Y. P., and Freeman, R. (2016). Inferring animal social networks and leadership: Applications for passive monitoring arrays. *J. R. Soc. Interface* 13:20160676. doi: 10.1098/rsif.2016.0676

Jones, T. B., Green, J. A., Patrick, S. C., Evans, J. C., Wells, M. R., Rodr Iguez-Malag, M. A., et al. (2020). Consistent sociality but flexible social associations across temporal and spatial foraging contexts in a colonial breeder. *Ecol. Lett.* 23, 1085–1096. doi: 10.1111/ele.13507

Jorgensen, S. J., Chapple, T. K., Anderson, S., Hoyos, M., Reeb, C., and Block, B. A. (2010). "Connectivity among White Shark Coastal aggregation areas in the Northeastern pacific," in *Global Perspectives on the Biology and Life History of the White Shark*, ed. M. L. Domeier (Boca Raton, FL: CRC Press), 159–168.

Kanive, P. E., Rotella, J. J., Chapple, T. K., Anderson, S. D., White, T. D., Block, B. A., et al. (2021). Estimates of regional annual abundance and population growth rates of white sharks off central California. *Biol. Conserv.* 257:109104. doi: 10.1016/j.biocon.2021.109104

Kessel, S. T., Cooke, S. J., Heupel, M. R., Hussey, N. E., Simpfendorfer, C. A., Vagle, S., et al. (2014). A review of detection range testing in aquatic passive acoustic telemetry studies. *Rev. Fish. Biol. Fish.* 24, 199–218. doi: 10.1007/s11160-013-9328-4

Klimley, A. P., and Holloway, C. F. (1999). School fidelity and homing synchronicity of yellowfin tuna, *Thunnus* albacares. *Mar. Biol.* 133, 307–317. doi: 10.1007/s002270050469

Kock, A., O'Riain, M. J., Mauff, K., Meÿer, M., Kotze, D., and Griffiths, C. (2013). Residency, habitat use and sexual segregation of white sharks, carcharodon carcharias in False Bay, South Africa. *PLoS One* 8:e55048. doi: 10.1371/journal.pone.0055048

Kock, A. A., Photopoulou, T., Durbach, I., Mauff, K., Meÿer, M., Kotze, D., et al. (2018). Summer at the beach: Spatio-temporal patterns of white shark occurrence along the inshore areas of False Bay, South Africa. *Mov. Ecol.* 6, 1–13. doi: 10.1186/s40462-018-0125-5

Krause, J., and Ruxton, G. D. (2002). *Living in Groups*. Oxford: Oxford University Press.

Lilly, J., McLean, M. F., Dadswell, M. J., Wirgin, I., Comolli, P., and Stokesbury, M. J. W. (2020). Use of social network analysis to examine preferential co-occurrences in Atlantic Sturgeon Acipenser oxyrinchus oxyrinchus Mitchill, 1815. *Anim. Biotelemetry* 8:14. doi: 10.1186/s40317-020-00201-3

Lusseau, D., Wilson, B., Hammond, P. S., Grellier, K., Durban, J. W., Parsons, K. M., et al. (2006). Quantifying the influence of sociality on population structure in bottlenose dolphins. *J. Anim. Ecol.* 75, 14–24. doi: 10.1111/j.1365-2656.2005.01013.x

Lyons, K., Jarvis, E. T., Jorgensen, S. J., Weng, K., O'sullivan, J., Winkler, C., et al. (2013). The degree and result of gillnet fishery interactions with juvenile white sharks in southern California assessed by fishery-independent and-dependent methods. *Fish. Res.* 147, 370–380. doi: 10.1016/j.fishres.2013.07.009

May, C., Meyer, L., Whitmarsh, S., and Huveneers, C. (2019). Eyes on the size: Accuracy of visual length estimates of white sharks, Carcharodon carcharias. *R. Soc. Open Sci.* 6:190456. doi: 10.1098/rsos.190456

Merriam-Webster. (2021). *Sociality*. Available Online at: https://www.merriam-webster.com/dictionary/sociality [Accessed March 3, 2021]

Meese, E. N., and Lowe, C. G. (2019). Finding a resting place: How environmental conditions influence the habitat selection of resting batoids. *Bull. South. California Acad. Sci.* 118:87. doi: 10.3160/0038-3872-118.2.87

Mourier, J., Lédée, E. J. I., and Jacoby, D. M. P. (2019). A multilayer perspective for inferring spatial and social functioning in animal movement networks. *bioRxiv* 2019:749085. doi: 10.1101/749085

Mourier, J., and Planes, S. (2021). Kinship does not predict the structure of a shark social network. *Behav. Ecol.* 32, 211–222. doi: 10.1093/beheco/araa119

Mourier, J., Vercelloni, J., and Planes, S. (2012). Evidence of social communities in a spatially structured network of a free-ranging shark species. *Anim. Behav.* 83, 389–401. doi: 10.1016/j.anbehav.2011.11.008

Newman, M. E. J. (2002). Assortative mixing in networks. *Phys. Rev. Lett.* 89:208701. doi: 10.1103/PhysRevLett.89.208701

Newman, M. E. J. (2006). Finding community structure in networks using the eigenvectors of matrices. *Phys. Rev. E* 74:036104. doi: 10.1103/PhysRevE.74.036104

Noldus, R., and Van Mieghem, P. (2015). Assortativity in complex networks. *J. Complex Networks* 3, 507–542. doi: 10.1093/comnet/cnv005

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2011). *vegan: Community Ecology Package*. Available online at: https://CRAN.R-project.org/package=vegan

Oñate-González, E. C., Sosa-Nishizaki, O., Herzka, S. Z., Lowe, C. G., Lyons, K., Santana-Morales, O., et al. (2017). Importance of bahia sebastian vizcaino as a nursery area for white sharks (Carcharodon carcharias) in the Northeastern Pacific: A fishery dependent analysis. *Fish. Res.* 188, 125–137. doi: 10.1016/j.fishres.2016.12.014

Papastamatiou, Y. P., Bodey, T. W., Caselle, J. E., Bradley, D., Freeman, R., Friedlander, A. M., et al. (2020). Multiyear social stability and social information use in reef sharks with diel fission-fusion dynamics: Shark sociality and information use. *Proc. R. Soc. B Biol. Sci.* 287:9. doi: 10.1098/rspb.2020.1063

Perryman, R. J. Y., Venables, S. K., Tapilatu, R. F., Marshall, A. D., Brown, C., and Franks, D. W. (2019). Social preferences and network structure in a population of reef manta rays. *Behav. Ecol. Sociobiol.* 73, 1–18. doi: 10.1007/s00265-019-2720-x

Poysa, H. (1992). Group foraging in patchy environments: the importance of coarse- level local enhancement. *Ornis Scand.* 23, 159–166. doi: 10.2307/3676444

Ramos-Fernández, G., and Morales, J. M. (2014). Unraveling fission-fusion dynamics: how subgroup properties and dyadic interactions influence individual decisions. *Behav. Ecol. Sociobiol.* 68, 1225–1235. doi: 10.1007/s00265-014-1733-8

Raoult, V., Williamson, J. E., Smith, T. M., and Gaston, T. F. (2019). Effects of on-deck holding conditions and air exposure on post-release behaviours of sharks revealed by a remote operated vehicle. *J. Exp. Mar. Bio. Ecol.* 511, 10–18. doi: 10.1016/j.jembe.2018.11.003

Robbins, R. (2007). Environmental variables affecting the sexual segregation of great white sharks Carcharodon carcharias at the Neptune Islands South Australia. *J. Fish Biol.* 70, 1350–1364. doi: 10.1111/j.1095-8649.2007.01414.x

Robitaille, A. L., Webber, Q. M. R., and Vander Wal, E. (2019). Conducting social network analysis with animal telemetry data: Applications and methods using spatsoc. *Methods Ecol. Evol.* 10, 1203–1211. doi: 10.1111/2041-210X.13215

Sabol, A. C., Lambert, C. T., Keane, B., Solomon, N. G., and Dantzer, B. (2020). How does individual variation in sociality influence fitness in prairie voles? *Anim. Behav.* 163, 39–49. doi: 10.1016/j.anbehav.2020.02.009

Schilds, A., Mourier, J., Huveneers, C., Nazimi, L., Fox, A., and Leu, S. T. (2019). Evidence for non-random co-occurrences in a white shark aggregation. *Behav. Ecol. Sociobiol.* 73, 1–12. doi: 10.1007/s00265-019-2745-1

Sequeira, A. M. M., Thums, M., Brooks, K., and Meekan, M. G. (2016). Error and bias in size estimates of whale sharks: Implications for understanding demography. *R. Soc. Open Sci.* 3:150668. doi: 10.1098/rsos.150668

Silk, M. J., Croft, D. P., Tregenza, T., and Bearhop, S. (2014). The importance of fission-fusion social group dynamics in birds. *Ibis (Lond).* 156, 701–715. doi: 10.1111/ibi.12191

Simpfendorfer, C. A., Huveneers, C., Steckenreuter, A., Tattersall, K., Hoenner, X., Harcourt, R., et al. (2015). Ghosts in the data: False detections in VEMCO pulse position modulation acoustic telemetry monitoring equipment. *Anim. Biotelemetry* 3:55. doi: 10.1186/s40317-015-0094-z

Simpfendorfer, C. A., and Milward, N. E. (1993). Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. *Environ. Biol. Fishes* 37, 337–345. doi: 10.1007/bf00005200

Sims, D. W., Southall, E. J., Quayle, V. A., and Fox, A. M. (2000). Annual social behaviour of basking sharks associated with coastal front areas. *Proc. R. Soc. B Biol. Sci.* 267, 1897–1904. doi: 10.1098/rspb.2000.1227

Spaet, J. L. Y., Patterson, T. A., Bradford, R. W., and Butcher, P. A. (2020). Spatiotemporal distribution patterns of immature Australasian white sharks (Carcharodon carcharias). *Sci. Rep.* 10, 1–13. doi: 10.1038/s41598-020-66876-z

Spaet, J., Manica, A., Brand, C., Gallen, C., and Butcher, P. (2020). Environmental conditions are poor predictors of immature white shark Carcharodon carcharias occurrences on coastal beaches of Eastern Australia. *Mar. Ecol. Prog. Ser.* 653, 167–179. doi: 10.3354/meps13488

Stehfest, K. M., Patterson, T. A., Dagorn, L., Holland, K. N., Itano, D., and Semmens, J. M. (2013). Network analysis of acoustic tracking data reveals the structure and stability of fish aggregations in the ocean. *Anim. Behav.* 85, 839–848. doi: 10.1016/j.anbehav.2013.02.003

Tamburin, E., Hoyos-Padilla, M., Sánchez-González, A., Hernández-Herrera, A., Elorriaga-Verplancken, F. R., and Galván-Magaña, F. (2019). New nursery area for white sharks (Carcharodon carcharias) in the Eastern Pacific Ocean. *Turkish J. Fish. Aquat. Sci.* 20, 325–329. doi: 10.4194/1303-2712-v20_4_08

Weng, K. C., O'Sullivan, J. B., Lowe, C. G., Dewar, H., Winkler, C., and Block, B. A. (2007). Movements, behavior and habitat preferences of juvenile white sharks Carcharodon carcharias in the Eastern Pacific. *Mar. Ecol. Prog. Ser.* 338, 211–224. doi: 10.3354/meps338211

Werry, J., Bruce, B., Sumpton, W., Reid, D., and Mayer, D. (2012). ""Beach Areas Used by Juvenile White Shark, Carcharodon carcharias," in *Eastern Australia," in Global Perspectives on the Biology and Life History of the White Shark*, ed. M. L. Domeier (Boca Raton, FL: CRC Press), 271–286.

White, C. F., Lyons, K., Jorgensen, S. J., O'Sullivan, J., Winkler, C., Weng, K. C., et al. (2019). Quantifying habitat selection and variability in habitat suitability for juvenile white sharks. *PLoS One* 14:e0214642. doi: 10.1371/journal.pone.0214642

Wilson, A. D. M., Brownscombe, J. W., Krause, J., Krause, S., Gutowsky, L. F. G., Brooks, E. J., et al. (2015). Integrating network analysis, sensor tags, and observation to understand shark ecology and behavior. *Behav. Ecol.* 26, 1577–1586. doi: 10.1093/beheco/arv115

Wilson, A. D. M., Croft, D. P., and Krause, J. (2014). Social networks in elasmobranchs and teleost fishes. *Fish Fish.* 15, 676–689. doi: 10.1111/faf.12046

Wolfe, B. W., and Lowe, C. G. (2015). Movement patterns, habitat use and site fidelity of the white croaker (Genyonemus lineatus) in the palos verdes superfund site, Los Angeles, California. *Mar. Environ. Res.* 109, 69–80. doi: 10.1016/j.marenvres.2015.06.002

Conflict of Interest: CW was the Principal of the company Aquatic Research Consultants.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 17 September 2021
doi: 10.3389/fmars.2021.655595

Edited by:
Mourier Johann,
Institut de Recherche Pour le Développement (IRD), France

Reviewed by:
Fábio Daura-Jorge,
Federal University of Santa Catarina, Brazil
Bruno Díaz López,
Bottlenose Dolphin Research Institute (BDRI), Spain

***Correspondence:**
Songhai Li
lish@idsse.ac.cn

†ORCID:
Mingming Liu
orcid.org/0000-0003-3802-1002
Mingli Lin
orcid.org/0000-0002-9182-0519
Lijun Dong
orcid.org/0000-0003-4303-5513
Peijun Zhang
orcid.org/0000-0002-7047-7133
David Lusseau
orcid.org/0000-0003-1245-3747
Songhai Li
orcid.org/0000-0003-4977-1722

Specialty section:
This article was submitted to Marine Megafauna, a section of the journal Frontiers in Marine Science

Received: 19 January 2021
Accepted: 24 August 2021
Published: 17 September 2021

Citation:
Liu M, Lin M, Tang X, Dong L, Zhang P, Lusseau D and Li S (2021) Group Size of Indo-Pacific Humpback Dolphins (Sousa chinensis): An Examination of Methodological and Biogeographical Variances. Front. Mar. Sci. 8:655595. doi: 10.3389/fmars.2021.655595

Group Size of Indo-Pacific Humpback Dolphins (*Sousa chinensis*): An Examination of Methodological and Biogeographical Variances

Mingming Liu[1,2,3†], Mingli Lin[1†], Xiaoming Tang[1,2], Lijun Dong[1†], Peijun Zhang[1†], David Lusseau[3,4†] and Songhai Li[1,5†]*

[1] Marine Mammal and Marine Bioacoustics Laboratory, Institute of Deep-Sea Science and Engineering, Chinese Academy of Sciences, Sanya, China, [2] University of Chinese Academy of Sciences, Beijing, China, [3] School of Biological Sciences, University of Aberdeen, Aberdeen, United Kingdom, [4] National Institute of Aquatic Resources, Technical University of Denmark, Lyngby, Denmark, [5] Tropical Marine Science Institute, National University of Singapore, Singapore, Singapore

Observer-based counts and photo-identification are two well-established methods with an extensive use in cetacean studies. Using these two methods, group size has been widely reported, especially for small dolphins. Both methods may come with potential errors in estimating the group size, yet there is still a lack of comparison between both methods over a broad range of group size. Particularly, biogeographical variances in group size estimates were often mixed with methodological variances, making it difficult to compare estimates from different geographic regions. Here, group size estimates of a small, shallow-water, and near-shore delphinid species, Indo-Pacific humpback dolphins (*Sousa chinensis*), were simultaneously sampled using observer-based counts and photo-identification at three regions in the northern South China Sea. Data showed that dolphin group size from two methods were highly variable and associated with sampling regions. Generalized linear mixed models (GLMMs) indicated that dolphin group size significantly differed among regions. Statistical examinations further demonstrated dolphin group size could be affected by a complex combination of methodological and biogeographical variances. A common hurdle to examine potential factors influencing the estimation process is the inability to know the true group size at each sample. Therefore, other methods that could generate comparable estimates to represent true group size are warranted in future studies. To conclude, our findings present a better understanding of methodological and biogeographical variances in group size estimates of humpback dolphins, and help yield more robust abundance and density estimation for these vulnerable animals.

Keywords: humpback dolphins, group size, observer-based counts, photo-identification, methodology, biogeography

INTRODUCTION

Groups are a fundamental unit of gregarious animal species (Casari and Tagliapietra, 2018). Thus, the estimation of group size is crucial for research in animal ecology and behavior (Peña and Nöldeke, 2018; Kappeler, 2019). For example, in standard distance sampling protocols, a reliable estimate of animal abundance is highly dependent on whether group size of detected animals could be estimated as accurately as possible (Buckland et al., 1993; Barlow et al., 1998). Group size is also a prominent trait to indicate social characteristics for a wide range of animal taxa (Parrish and Edelstein-Keshet, 1999; Kappeler et al., 2019). However, it is difficult to generate accurate group size estimates for wild animals, since the estimation process may be affected by diverse factors (Walsh et al., 2009; Clement et al., 2017).

A fundamental approach to estimate group size of free-ranging dolphins is on-site counts by observers from vessels (Mann, 1999). However, dolphins are highly mobile, spend prolonged periods underwater, and are partially visible from the sea surface, all of which pose substantial difficulties to estimate group size (Gerrodette et al., 2002). Furthermore, social dynamics may differ among dolphin species (Gowans et al., 2007), which can greatly affect the estimation process of group size. Consequently, group size estimates from observer counts are often variable, especially for extremely large groups (referred to as "schools" in some studies), with non-trivial between-observer variance as well as within-observer between sample variance (Erwin, 1982; Gerrodette and Perrin, 1991; Bouveroux et al., 2018). Although observers' experience can be improved through training and practice, it is still hard to remove potential bias from observer-based counts (Gerrodette and Perrin, 1991; Clement et al., 2017), and the bias may increase with the group size (Gerrodette et al., 2019).

The photo-identification technique can be available in estimating the group size of those naturally marked cetacean species (Würsig and Würsig, 1977). Many delphinid species have distinctive natural markings on/around the dorsal fin, which allows the identification of individuals from photographs and further provides a mechanism for estimating their group size (Urian et al., 2015; Pawley et al., 2018). However, the use of photo-identification may bring potential errors due to misidentification. Dolphin group size may be underestimated, because no guarantee can ensure that all marked individuals present within an encounter could be captured, and some individuals, particularly younger ones, are often poorly marked or unmarked (Hupman et al., 2018; Wickman et al., 2021). Furthermore, photo-identification cannot always generate accurate group size estimates, as some dolphin species have poor nick/notch markings for matching the left and right sides of the same individuals (Auger-Méthé et al., 2010; Hupman et al., 2018).

In dolphin societies, group size, social structures, and dynamics differ among species, which is known as interspecific variability of sociality (Gygax, 2002b; Gowans et al., 2007). Additionally, a specific dolphin species can build different sizes of groups at various spatial and temporal scales (Gygax, 2002a; Liu et al., 2021a,b), which is so-called biogeographical or inter-population variability of sociality (Liu et al., 2021c). Although both observer-based counts and photo-identification have been widely applied in dolphin sociality studies, little attention, if anything at all, has been paid to compare the performance of these two methods in estimating group size. Intraspecific variability in dolphin group size is often confusing, since variances from methodology and biogeography were mixed in many studies, leading to substantial difficulties in comparing the estimates from different systems (Gygax, 2002a,b; Liu et al., 2020b, 2021c).

Thus far, it is well known that both observer-based counts and photo-identification might come with potential errors in estimating dolphin group size. However, scant is known at which bias in group size estimates might occur and how these methods have potential influences. A common hurdle to examine potential factors influencing the estimation process is the inability to know the true group size at each sample (Walsh et al., 2009; Hamilton et al., 2018). Moreover, the potential bias and variance in group size estimates might be of species specificity, and thus bias correction factors estimated in different ocean basins and for different species cannot guarantee to apply for all studies.

The Indo-Pacific humpback dolphins (*Sousa chinensis* Osbeck, 1765), hereafter referred to as "humpback dolphins," are small delphinid species inhabiting shallow and near-shore waters of the eastern Indian and western Pacific Oceans (Jefferson and Smith, 2016; Li, 2020). Group size estimates have been widely reported for this species across many known populations, and all studies have used either observer-based counts (Chen et al., 2010; Wang et al., 2015) or photo-identification (Chen et al., 2016; Wang et al., 2016). Humpback dolphins are often observed or photographically captured in groups with variable sizes (Würsig et al., 2016), from a single animal to small groups (mostly about ten or fewer), and sometimes to large aggregations (several tens or low hundred; Parsons, 2004; Liu et al., 2021c). Reducing errors in estimating group size is crucial to density and abundance estimate for this species (Marsh and Sinclair, 1989; Chen et al., 2010), but there is no a good grasp of how well traditional estimation methods (i.e., observer-based counts, and photo-identification) applied to this species.

In this study, observer-based counts and photo-identification were simultaneously used to sample group size estimates of three geographically isolated humpback dolphin populations in the northern South China Sea. Both methodological and biogeographical variances in group size estimates of humpback dolphins were assessed. This study aims (1) to better understand the bias and variance in group size estimates of humpback dolphins and (2) to reveal the intra- and inter-population variability in group size of this species.

MATERIALS AND METHODS

Sampling Regions

Three areas along the northern coast of the South China Sea were selected as sampling regions: the waters southwest off Hainan Island (SWH; Li et al., 2016; Liu et al., 2020b), Sanniang Bay

(SNB; Chen et al., 2016; Wu et al., 2017; Peng et al., 2020), and Leizhou Bay, China (LZB; Xu et al., 2012, 2015; Liu et al., 2021a,b; **Figures 1A,B**). All these regions have been well known to support critical habitats with resident humpback dolphins. In this manuscript, sampling regions were always depicted in the order of SWH, SNB, and LZB, unless otherwise stated. Based on line-transect sampling design, boat-based surveys were performed in each sampling region by evenly-spaced zigzag transects (Buckland et al., 1993; Dawson et al., 2008). Given that humpback dolphins strongly preferred inhabiting shallow and near-shore waters (Jefferson and Smith, 2016), similar fishing or speed boats (∼7-15 m in length) were used to investigate the waters at depth ≤30 m and offshore ≤20 km. Boat-based surveys were only conducted under satisfactory visual conditions (no rain/fog) and sea states (≤4 on the Beaufort scale; Li et al., 2016; Liu et al., 2020a,b, 2021a).

Observer-Based Counts

During the boat-based surveys, a minimum of two trained observers visually scanned 180° of the sea surface to search humpback dolphins, with naked eyes and/or 7 × 50 binoculars (Li et al., 2016; Liu et al., 2020a,b, 2021a). All observers were experienced with basic knowledge on humpback dolphin behavior, and had received observation training over than 30 days at sea prior to this study. To keep consistency, two primary observers were maintained throughout the survey period and across different sampling regions. Within an encounter, one primary observer would count the number of dolphins and the other would take photos (Liu et al., 2021b). In this study, the term "group" was referred to any aggregation of humpback dolphins (including solitary individual) in the observers' effective field of view, generally either socially (i.e., engaged in similar behaviors) or spatially associated (e.g., within 200 m of each other; Karczmarski, 1999; Jefferson, 2000). Once a group was encountered, the group was approached at a slow sailing speed (<8 km/h) and kept an appropriate distance (10–50 m) behind or off to the side of the group. To ensure the impendence of each group sample, our data collection procedures referred to the protocols described by Kinzey et al. (2000).

For each group, multiple counts were repeated several times to estimate the group size whenever possible (Karczmarski, 1999; Jefferson, 2000). Typically, the group size was recorded in the form of minimum/maximum/best counts on the standardized datasheet (e.g. 5/10/7; Kinzey et al., 2000). Sometimes, only one individual or a pair of individuals were observed, the group size was thus recorded as absolute best values (1 or 2). In some other cases, only a low estimate (e.g., ≥10) was possible to be recorded as a best count. Besides, the group size might also be recorded in the form of a range (e.g., 10-20), thus the best count was averaged by the upper and lower limits (e.g., 15 was average by 10 and 20). For the further analysis, only the best counts were used to indicate observer-based counts, i.e., G_{observer} (Gerrodette et al., 2002).

Photo-Identification

Once a group was encountered, high-quality digital photos were taken, using a Canon 7D Mark II camera (Canon, Tokyo, Japan) fitted with 100-400 mm lens and an Olympus EM-1 camera (Olympus, Fujifilm, Japan) with 150- or 300-mm lens (1.5 × amplifier). Whenever possible, both the right and left lateral sides of dolphin dorsal fins would be photographed (Tang et al., 2021). For each group, a scoring system was used to assess all original photos based on the visibility, size, focus, direction, and contrast (Liu et al., 2020b; Tang et al., 2021). Each of the five aspects accounted for 20 at most, and the total scores range from 20 to 100 on a 100-point scale. All original photos were classified into three classes: poor <60, 60 ≤good < 80, and excellent ≥80 (Fearnbach et al., 2012). Only qualified photos (i.e., good, and excellent) were used for establishing the photo-identification dataset. Dolphin individuals were manually identified according to natural or non-natural markings on/around their dorsal fin. Several identifiable features like nicks, notches, pigmentation, and/or permanent scars, were included for identification and cross-matching (Wang et al., 2015; Methion and López, 2018). Whenever possible, body color, dorsal fin shape, nicks, notches, and sometimes permanent scars would be used to match two lateral sides of an individual (López et al., 2018; Liu et al., 2020b).

In this study, three classes of individual distinctiveness were defined: highly distinctive (D1), medium distinctive (D2), and non-distinctive (D3) (Friday et al., 2000; Zanardo et al., 2016). For each group, the marked individuals included D1 and D2 individuals, while the unmarked individuals only consisted of D3 individuals. All dolphin groups were classified into three types: almost all captured (AAC), not all captured (NAC), or all not captured (ANC). Group size estimates were only generated for AAC or NAC groups while excluding ANC because of no available photos. A group was considered as AAC when G_{observer} was ≤10 individuals, indicating that all or almost all individuals were captured in the group (Tyne et al., 2014; Hupman et al., 2018). A threshold, i.e., 10 was selected because humpback dolphins were often observed in small groups with ≤10 individuals (Parsons, 2004; Würsig et al., 2016; Liu et al., 2021c). For AC groups, we calculated the photo-identification group size G_{photo} by counting the number of D1, D2, and D3 individuals present. We defined a group with $G_{\text{observer}} >$ 10 individuals as NAC group. For NAC groups, the photo-identification group size G_{photo} were estimated as using the formula:

$$G_{\text{photo}} = \frac{n_{(\text{marked, i})}}{\theta} = n_{\text{marked, i}} \cdot \frac{N_{(\text{marked } + \text{unmarked, i})}}{N_{(\text{marked, i})}}$$

where $n_{(\text{marked, i})}$ is number of marked individuals in the group *i*. The mark rate (θ) was calculated from the proportion of randomly selected photos that contained identifiable dolphins (Williams et al., 1993; López et al., 2018). Among given randomly selected photos, $N_{(\text{marked } + \text{unmarked, i})}$ and $N_{(\text{marked, i})}$ is number of photos with marked and unmarked individuals, number of photos with marked individuals (Tyne et al., 2014; Hupman et al., 2018).

Data Analysis

Using the ArcGIS 10.1 (ESRI, Redlands, CA, United States), all boat-based survey routes and sighting locations of humpback dolphin achieved in each sampling region were mapped. A matrix

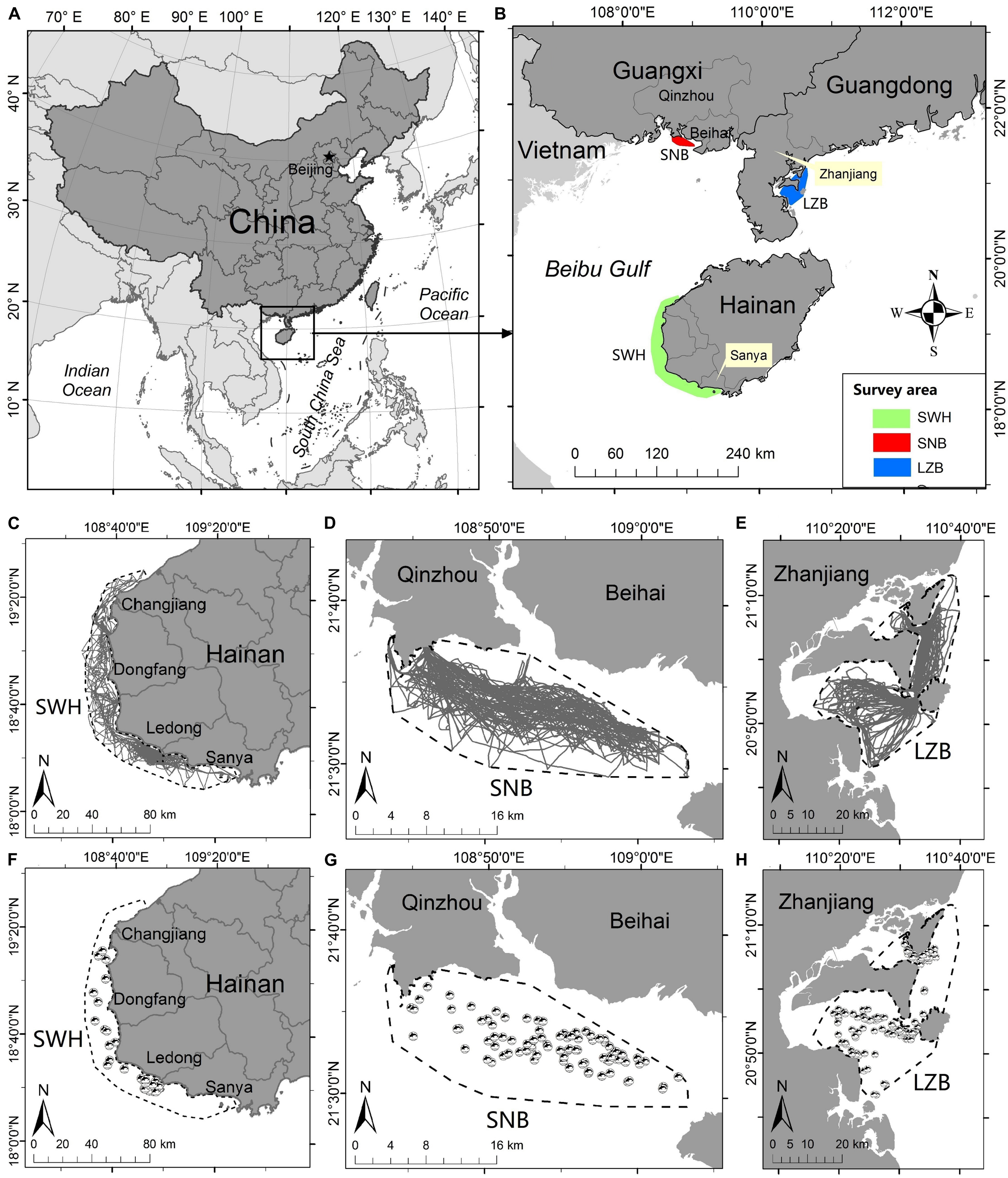


FIGURE 1 | Map of the study area: **(A)** the northern section of South China Sea, and **(B)** three sampling regions, i.e., the waters southwest off Hainan Island (SWH), Sanniang Bay (SNB), and Leizhou Bay (LZB). **(C-E)** Boat-based survey routes and **(F-H)** sighting locations of Indo-Pacific humpback dolphins (*Sousa chinensis*) achieved in each sampling region.

heatmap was illustrated to show the number of boat-based survey days and humpback dolphin sightings per month from 2013 to 2019 in three survey regions. Frequency histograms were illustrated to display group size patterns obtained from various methods in different regions (Bouveroux et al., 2018; Liu et al., 2021b). The skewness, kurtosis, and median value of group size data were calculated for each subset (Doane and Seward, 2011). For paired group size estimates, all groups were presented in a scatter plot to illustrate the ratio of $G_{observer}$ to G_{photo} (i.e., $R_{observer/photo}$) on a log-log scale with 1:1 reference line (Scott et al., 1985).

Generalized linear mixed models (GLMMs) were built to examine variances in group size of humpback dolphins, including fixed and random effects. In this study, the fixed effects were predicted by method ($G_{observer}$ or G_{photo}) and region (SWH, SNB, or LZB), and the random effects by year (2013–2019) and season (spring: March–May, summer: June–August; autumn: September–November; or winter: December–February; Liu et al., 2021b). In the R 4.0.5 (R Development Core Team, 2021), the package "lme4" was used (Bates et al., 2015) to construct GLMMs with a Poisson family and logit link function (Vargas-Fonseca et al., 2018; Dorning and Harris, 2019). According to Akaike's Information Criterion (AIC), the GLMMs were simplified sequentially to remove non-significant fixed and random effects. Once a significant effect was found, *Post hoc* Scheffe tests or Wilcoxon paired tests were used to compare mean values of estimated group size in different levels.

Based on relevant published literature (Zhou et al., 2007; Chen et al., 2009; Xu et al., 2012, 2015; Wang et al., 2013; Li et al., 2016; Liu et al., 2020a,b, 2021a; Peng et al., 2020), mean or median values of humpback dolphins previously collected in the sampling region were extracted from previous studies. Then, non-parametric one sample sign tests were used to compare the group size estimates in each sampling region collected from the present study and from the previous studies. All statistical analyses were conducted in the R 4.0.5, with a defined significance level of $p < 0.05$. All descriptive statistics were shown as mean ± SD, unless otherwise stated.

RESULTS

From 2013 to 2019, a total of 231, 58, and 101 surveys were carried out in the SWH, SNB, and LZB, respectively (**Figure 2**). In these three waters, boat-based surveys covered a survey area of 3,319, 329, and 939 km^2, respectively (**Figures 1C–E**). In total, 1,540, 299, and 714 h of survey effort (6.67, 5.16, and 7.07 h per survey day on average) were achieved, resulting in 15,548, 4,246, and 6,089 km of survey distance in each survey area. During these boat-based surveys, 47, 136, and 143 humpback dolphin groups were encountered (**Figures 1F–H**). The encounter rate (i.e., number of groups per 100 km) was 0.30, 3.20, and 2.35, respectively (**Table 1**). In each survey region, observer-based counts ($G_{observer}$) were recorded for 45, 117, and 139 dolphin groups, respectively (**Figure 2**). In addition, 11,354 (32.8% out of 34,615), 11,056 (42.4% out of 26,076), and 15,779 (34.5% out of 45,739) qualified photos were available for the photo-identification in each region (**Table 1**). The process of photo-identification generated group size estimates (G_{photo})for 30, 123, and 113 dolphin groups in the SWH, SNB, and LZB, respectively (**Table 1**).

Histograms of group size estimates were skewed with a long tail to the right (**Figures 3A–F**), since most groups (80-90% of the total observation) consisted of fewer than 20 members and only a few groups (<5%) were large with >30 members. The skewness and kurtosis of histograms varied between estimation methods, and also differed among sampling regions (**Figures 3A–F**). The median values of $G_{observer}$ were 10, 5, and 9 in the SWH, SNB, and LZB, respectively. The median values of G_{photo} were 12, 5, and 8 in each sampling region (**Figures 3A–F**). The scatter plot of $R_{observer/photo}$ i.e., the ratio of $G_{observer}$ to G_{photo} , showed that values of $R_{observer/photo}$ were randomly distributed on and near the 1:1 line (**Figure 4**).

The GLMM indicated that variances in dolphin group size were primarily affected by sampling region ($p < 0.001$) and interaction of region × method ($p = 0.035$; **Table 2**). In addition, the interaction of year × season had a significant random effect on influencing dolphin group size ($p < 0.001$). The interaction of method × year × season had a significant mixed effect on influencing dolphin group size ($p = 0.022$). *Post-hoc* Scheffe tests showed that $G_{observer}$ in the SWH were significantly larger than $G_{observer}$ in the SNB ($p < 0.001$), or LZB ($p < 0.001$), while $G_{observer}$ in the SNB were smaller than $G_{observer}$ in the LZB ($p < 0.001$; **Figure 5**). G_{photo} in the SWH were significantly larger than G_{photo} in the SNB ($p < 0.001$), or LZB ($p = 0.009$), but G_{photo} in the SNB were not statistically different from G_{photo} in the LZB ($p = 0.129$; **Figure 5**). Wilcoxon paired comparisons indicated that group size in the SWH ($p = 0.023$) and LZB ($p = 0.038$) varied between two estimation methods, but group size in the SNB ($p = 0.177$) did not vary between methods.

In total, 10 relevant publications were obtained with documenting group size estimates of humpback dolphins in the SWH ($n = 2$), SNB ($n = 3$), and LZB ($n = 5$; **Table 3**). In the SWH, statistical comparisons indicated significant differences between $G_{observer}$ or G_{photo} in this study and the mean group size estimated from Li et al. (2016): $G_{observer}$ vs. 21.6 ($p = 0.036$), G_{photo} vs. 21.6 ($p = 0.004$). In the SNB, there was no significant differences between $G_{observer}$ or G_{photo} in this study and the mean group size of 6.39 (Peng et al., 2020) or 5.63 (Chen et al., 2009): $G_{observer}$ vs. 6.39 ($p = 0.141$), G_{photo} vs. 6.39 ($p = 0.062$), $G_{observer}$ vs. 5.63 ($p = 0.922$), and G_{photo} vs. 5.63 ($p = 0.378$). In the LZB, no significant differences were detected between $G_{observer}$ or G_{photo} in this study and the median group size of 8 estimated from Zhou et al. (2007) or the mean group size of 8.12 estimated from Xu et al. (2015): $G_{observer}$ vs. 8.12 ($p = 0.087$), G_{photo} vs. 8.12 ($p = 0.057$), $G_{observer}$ vs. 8 ($p = 0.159$), G_{photo} vs. 8 ($p = 0.088$). However, significant differences were detected between our data and the mean or median group size of estimated from Xu et al. (2012, 2015): $G_{observer}$ vs. 7 ($p = 0.013$), G_{photo} vs. 7 ($p = 0.043$), $G_{observer}$ vs. 7.5 ($p = 0.013$), $G_{observer}$ vs. 6 ($p < 0.001$), G_{photo} vs. 7.5 ($p = 0.045$), and G_{photo} vs. 6 ($p = 0.036$).

DISCUSSION

In this study, several key findings were obtained. First, this study clearly illustrated that traditional estimation methods, i.e., observer-based counts and photo-identification could generate variable group size estimates for humpback dolphins. Second, this study demonstrated that group size of humpback dolphins

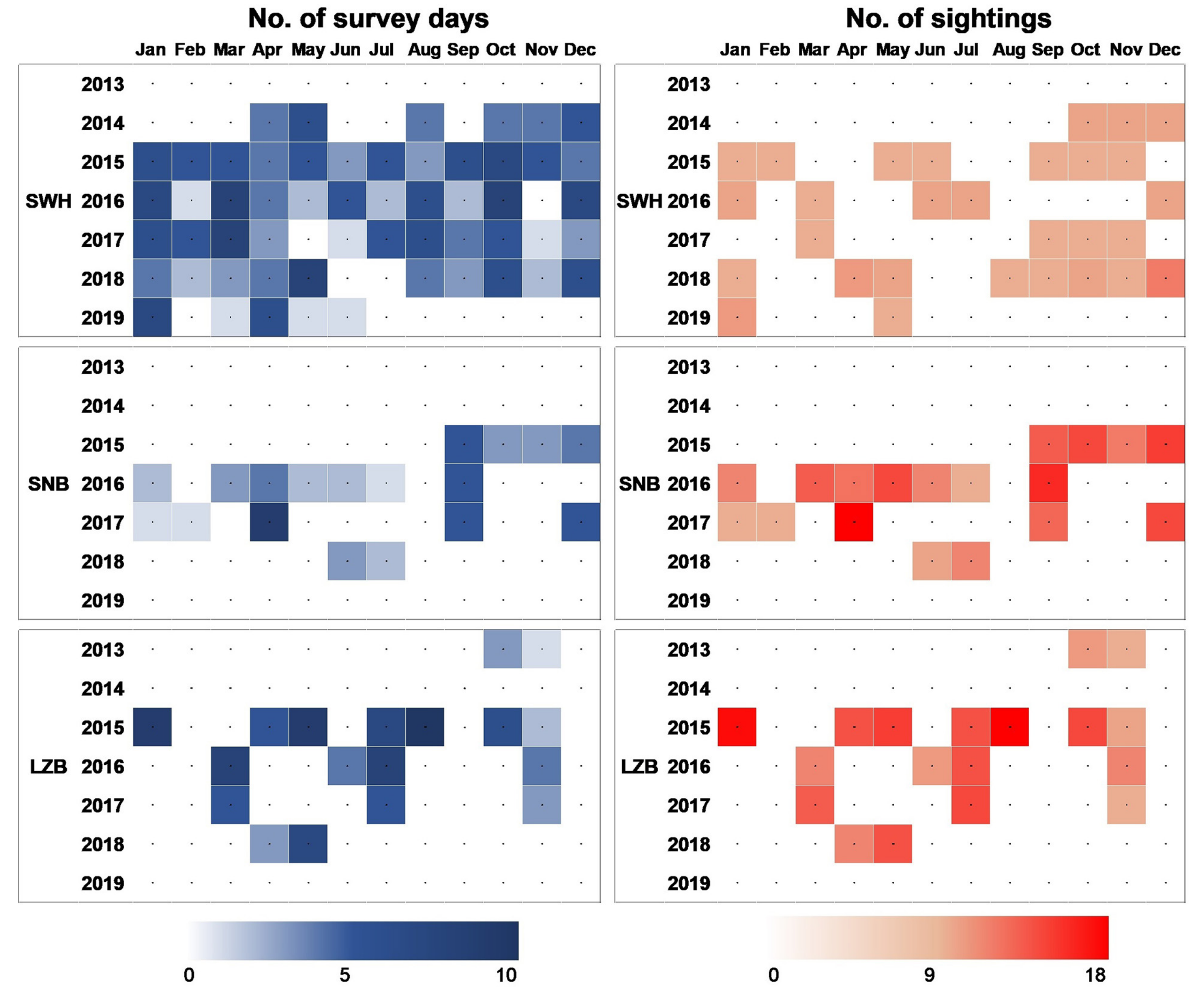


FIGURE 2 | A colorful matrix plot to show number of survey days and humpback dolphin sightings per month from 2013 to 2019 in three survey areas: SWH, SNB, and LZB.

TABLE 1 | Summary of survey information on Indo-Pacific humpback dolphins (*Sousa chinensis*) in the waters southwest off Hainan Island (SWH), Sanniang Bay (SNB), and Leizhou Bay (LZB).

Metrics	**Sampling region**			**Total**
	SWH	**SNB**	**LZB**	
Survey area (km^2)	3,319	329	939	4,587
No. of survey days	231	58	101	390
Survey hours	1,540	299	714	2,553
Survey effort (km)	15,548	4,246	6,089	25,883
No. of groups	47	136	143	326
Encounter rate (groups/100 km)	0.30	3.20	2.35	1.26
No. of observer-based counts	45	117	139	297
No. of dolphin photos	34,615	26,076	45,739	106,430
Observer-based counts ($G_{observer}$, mean ± SD)	12.9 ± 10.1	6.1 ± 4.4	9.4 ± 7.4	9.73 ± 7.5
No. of photo-identification group size estimates	30	123	113	266
Photo-identification estimates (G_{photo}, mean ± SD)	17.2 ± 18.2	7.0 ± 6.4	10.1 ± 8.1	9.32 ± 10.2

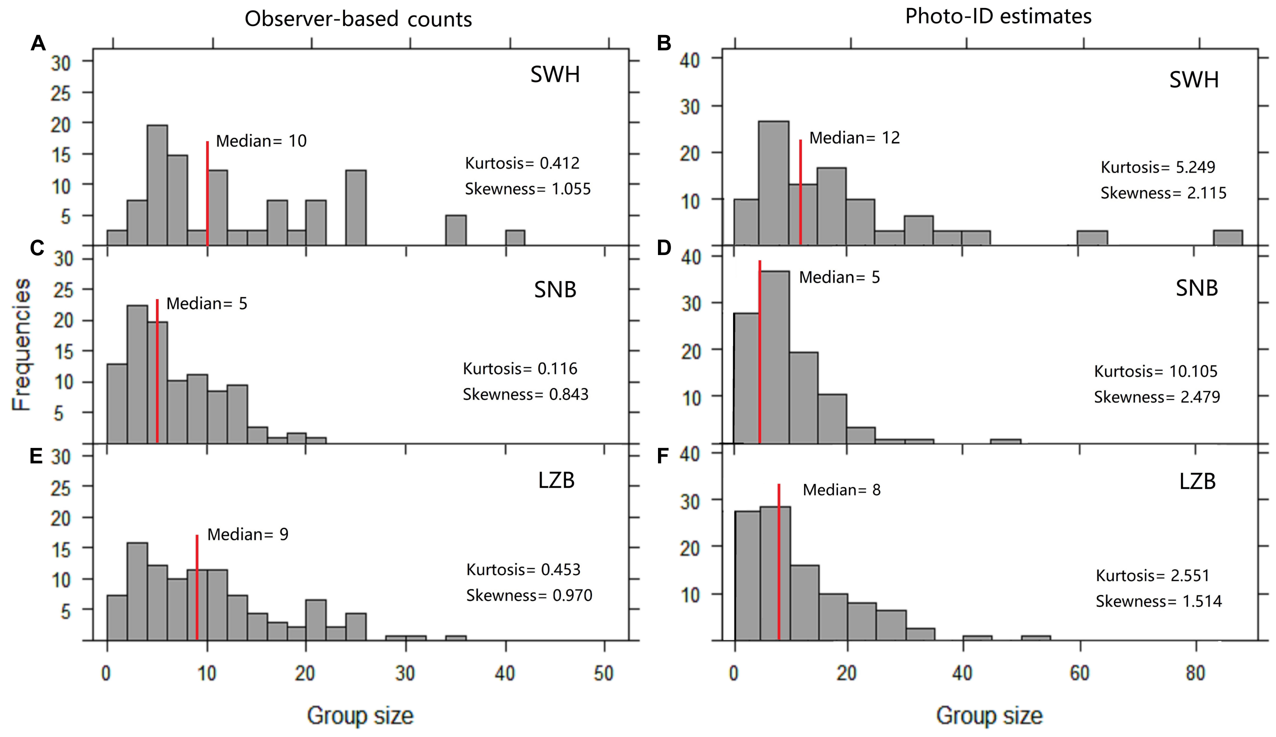


FIGURE 3 | Frequency histograms of humpback dolphin group size in the **(A,B)** SWH, **(C,D)** SNB, and **(E,F)** LZB.$G_{observer}$: observer-based counts, G_{photo} : photo-identification estimates.

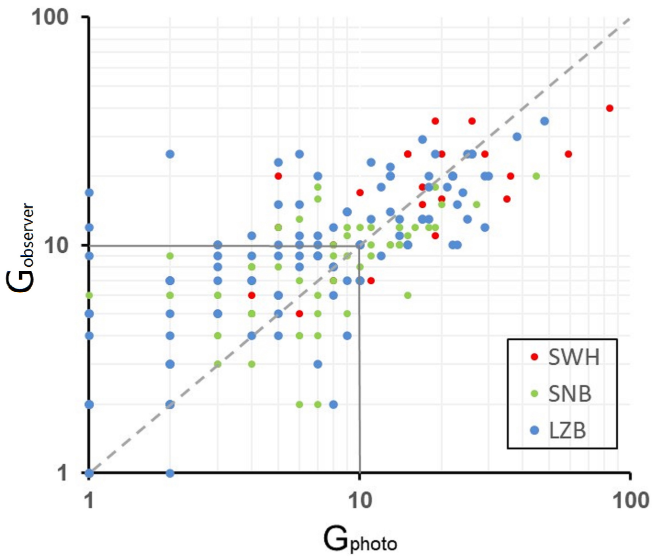


FIGURE 4 | $R_{observer/photo}$ of humpback dolphin group size on a log-log scale: observer-based counts ($G_{observer}$) against photo-identification estimates (G_{photo}). The grey dash line is the 1:1 line.

was significantly different among three sampling regions. Third, methodological variances in dolphin group size were found in some sampling regions, revealed by statistical comparisons between data in this study and in previous studies. These findings are beneficial to the use of different methods in estimating group size for humpback dolphins, and help clarify potential methodological and biogeographical variances in group size estimates.

This study made the first attempt to sample comparable group size of humpback dolphins from different geographic regions

TABLE 2 | A Poisson generalized linear mixed model (GLMM) investigating the fixed effects of method (observer-based counts and photo-identification) and region (SWH, SNB, and LZB), the random effects of survey year (2013-2019) and season (spring, summer, autumn, and winter), and the mixed effects of their interactions on group size of humpback dolphins.

Model parameter	Coefficient	Standard error (SE)	*Z*-value	*P*-value
Intercept	2.91	0.22	9.25	**<0.001**
Region	0.87	0.39	6.14	**<0.001**
Method × Region	0.62	0.13	5.68	**0.035**
Year × Season	−0.24	0.04	−4.18	**<0.001**
Method × Year × Season	−0.38	0.16	−6.98	**0.022**

Significant P values (<0.05) are shown in bold. The GLMM was simplified based on minimizing the value of Akaike's Information Criterion (AIC).

by using two methods simultaneously. Our data clearly revealed that dolphin group size across three sampling regions, no matter from observer-based counts or photo-identification, were highly variable, typically including single individual, small pairs, and rarely middle-to-large aggregations of several tens (Parsons, 2004; Würsig et al., 2016; Liu et al., 2021c). Notably, small groups with ≤ 10 members were the most frequently encountered (80-90%), while only a small proportion ($<5\%$) were large groups with >30 members. Such grouping pattern (i.e., living in small groups) has been considered a general social strategy of near-shore delphinid species inhabiting shallow and/or estuarine waters (Gygax, 2002a,b; Gowans et al., 2007), where the availability of prey is often predictable in space and time. Additionally, near-shore dolphins might prefer hosting small groups due to relatively low predation pressure compared with oceanic species (Bouveroux et al., 2018; Liu et al., 2021c).

This study confirmed that the inter-population variability of humpback dolphin group size was primarily explained by biogeographical differences. Dolphin group size manifested skewed distribution patterns with only a few groups much larger than the median, but the skewness and kurtosis of histograms varied among regions and between methods. This finding suggested possible biogeographical and methodological variances in group size estimates of humpback dolphins, which was further demonstrated by the GLMM and statistical comparisons. The GLMM indicated that variances in group size of humpback dolphins were primarily explained by the sampling region. Besides humpback dolphins, several other delphinid species, such as bottlenose dolphins *Tursiops* spp. (Connor, 2000; Bouveroux et al., 2018), Guiana dolphins *Sotalia guianensis* (Moura et al., 2019), and some river dolphins *Inia geoffrensis* and *Sotalia fluviatilis* (Gomez-Salazar et al., 2012), have been found to form different sizes of groups in various geographic habitats. Such inter-population variability in dolphin group size might reflect the adaptations of dolphin populations to different ecological constraints in fine-scale environments (Gygax, 2002a,b; Gowans et al., 2007; Peña and Nöldeke, 2018).

This study revealed that both inter- and intra-population variability of humpback dolphin group size might be influenced by different methods. Using either observer-based counts or photo-identification, group size data have been previously documented in the SWH (Li et al., 2016), SNB (Chen et al., 2009; Wang et al., 2013; Peng et al., 2020), LZB (Zhou et al., 2007; Xu et al., 2012, 2015), and elsewhere (Parsons, 2004; Würsig et al., 2016; Liu et al., 2021c). However, previous studies rarely provided comparable estimates that were simultaneously collected with these two methods, making it hard to compare estimates achieved in different study systems. Statistical comparisons between different studies clearly showed that the use of observer-based counts or photo-identification might result in complex variances in group size estimates of humpback dolphins (Liu et al., 2020b, 2021c). Furthermore, dolphin group size might also be influenced by sample size (Gerrodette et al., 2019; Liu et al., 2020b), survey period (Koper et al., 2016), observer experience (Boyd et al., 2019), and/or the process of photo-identification (Auger-Méthé et al., 2010; Hupman et al., 2018) to varying degrees.

Both experienced observers and photo-identification might give underestimated, overestimated, or unbiased group size for

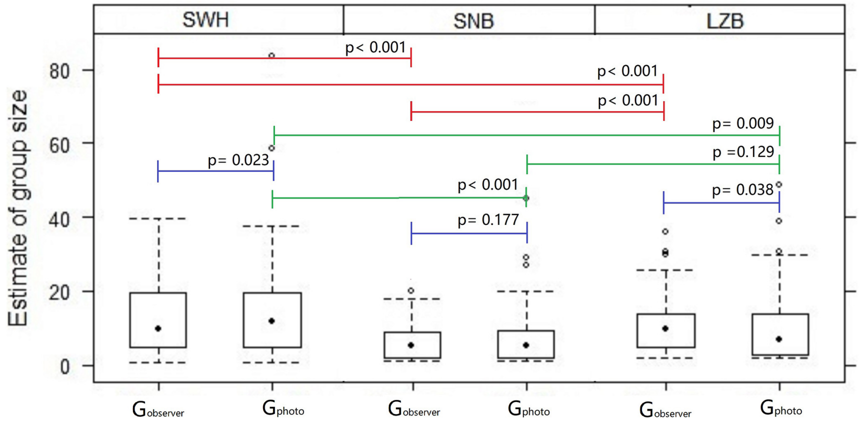


FIGURE 5 | Boxplot of humpback dolphin group size obtained from observer-based counts ($G_{observer}$) and photo-identification estimates (G_{photo}) in the SWH, SNB, and LZB. The median (black dots), lower (25%) and upper (75%) quartiles, and outlier values (black circles) are illustrated. *P*-values were indicated for the paired comparisons of group size between methods and geographic comparisons of group size between regions, with a significance level of <0.05.

TABLE 3 | Comparisons of humpback dolphin group size obtained from different studies in three sampling regions, i.e., SWH, SNB, and LZB.

Sampling region	Group size estimates					References	Comparison with means of $G_{observer}$ or G_{photo} in this study (*P* value)
	Mean ± SD	Median	No. of sampling groups	Range	Method$^{\#}$		
SWH	12.9 ± 10.1	NA	45	1-40	$G_{observer}$	Liu et al., 2020b	FSD
SWH	17.8 ± 18.2	NA	30	1-84	G_{photo}	Liu et al., 2020b	FSD
SWH	21.6 ± 8.8	NA	6	12-40	$G_{observer}$	Li et al., 2016	$G_{observer}$ vs. 21.6 **(p = 0.036*)** G_{photo} vs. 21.6 **(p = 0.004*)**
SNB	6.39 ± 4.43	NA	164	1-22	G_{photo}	Peng et al., 2020	$G_{observer}$ vs. 6.39 (p = 0.141) G_{photo} vs. 6.39 (p = 0.062)
SNB	NA	NA	13	2-15	$G_{observer}$	Wang et al., 2013	NA
SNB	5.63	NA	19	NA	G_{photo}	Chen et al., 2009	$G_{observer}$ vs. 5.63 (p = 0.922) G_{photo} vs. 5.63 (p = 0.378)
LZB	9.4 ± 7.2	NA	253	1-48	$G_{observer}$	Liu et al., 2020a, 2021a	FSD
LZB	8.12 ± 5.85	7	611	1-35	G_{photo}	Xu et al., 2015	$G_{observer}$ vs. 8.12 (p = 0.087) $G_{observer}$ vs. 7 **(p = 0.013*)** G_{photo} vs. 8.12 (p = 0.057) G_{photo} vs. 7 **(p = 0.043*)**
LZB	7.5 ± 5.45	6	118	1-23	G_{photo}	Xu et al., 2012	$G_{observer}$ vs. 7.5 **(p = 0.013*)** $G_{observer}$ vs. 6 **($p < 0.001$*)** G_{photo} vs. 7.5 **(p = 0.045*)** G_{photo} vs. 6 **(p = 0.036*)**
LZB	NA	8	96	1-27	G_{photo}	Zhou et al., 2007	$G_{observer}$ vs. 8 (p = 0.159) G_{photo} vs. 8 (p = 0.088)

NA, Not available; FSD, From the same dataset.
$^{\#}G_{observer}$ *: observer-based counts;*G_{photo} *: photo-identification estimation.*
**Statistically significant difference (<0.05) shown in bold.*

humpback dolphins, while the potential bias and variance in $G_{observer}$ and G_{photo} became unpredictable as the true group size was unknown for each sample (Scott et al., 1985; Gerrodette et al., 2002). Although primary observers in this study were experienced, there was still a high risk of underestimating group size due to various factors including visual conditions (i.e., sea state, sun glare; Barlow et al., 1998), dolphin behaviors (aerial behavior, underwater foraging, or boat-avoiding; Walsh et al., 2009), observers' perception (Erwin, 1982; Binda et al., 2011), and group dispersal (Clement et al., 2017; Hamilton et al., 2018).

Humpback dolphins typically have higher mark rates than other cetacean species (Pawley et al., 2018), and within an encounter, most often, all photographically captured individuals can be identified at least temporarily (i.e., within the encounter) including young individuals sometimes (Liu et al., 2020b; Tang et al., 2021). Photo-identification is less likely to overestimate group size for a given group, since each individual is often identified by comparable markings, unless repeated counts or mismatch between two lateral sides happen (Stevick et al., 2001; Urian et al., 2015). Thus, the comparisons between $G_{observer}$ and G_{photo} in this study is a classic problem, in which there is a relatively accurate method, i.e., photo-identification to obtain conservative measurements (Scott et al., 1985; Gerrodette and Perrin, 1991), while another method, i.e., observer-based counts, to generate measurements without knowing the potential bias and variance (Gerrodette et al., 2002, 2019).

Across all three sampling regions, photo-identification, i.e., G_{photo} appeared to generate larger values of mean group size than observer-based counts, i.e., $G_{observer}$, suggesting a high risk of underestimation of $G_{observer}$. This finding was consistent with previous studies: even experienced observers still tend to underestimate dolphin group size (Scott et al., 1985), and such trend increased with the group size (Gerrodette et al., 2019). However, photo-identification could not always give larger values of median group size. This was mainly because that the mean group size could be enlarged by rare large groups (Gerrodette et al., 2002, 2019), while the median group size was less likely affected by large values (Doane and Seward, 2011; Meropi et al., 2018). For example, large groups with up to 84 members have been identified through photo-identification in the SWH (Liu et al., 2020b), which greatly contributed to enlarge the mean group size 17.2, but would not influence the median group size 12.

The Indo-Pacific humpback dolphin is currently listed as a "Vulnerable" (VU) species by the Red List of International Union for Conservation of Nature (Jefferson et al., 2017), with an inferred decrease in abundance but no global abundance estimates (Jefferson and Smith, 2016; Li, 2020). The findings in this study are essential to yield more accurate abundance and density estimation for this species. Nevertheless, the true size of dolphin group in the wild is often uncertain, no matter in this study or in previous studies. Consequently, the potential bias and variance in dolphin group size estimated from observer-based counts or photo-identification could not be removed. The main challenge is to compare these traditional methods with a third one on that could better represent the true group size (Boyd et al., 2019). Therefore, other methods, such as drones-based aerial photographic counts (Hartman et al., 2020; Giles et al., 2021) and acoustic estimation (Van Parijs et al., 2002; Wang et al., 2005), are warranted to be employed in future research for a wider comparison and calibration.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

This animal study was reviewed and approved by the Chinese Academy of Sciences under an Ethics Statement with the number of IDSSE-SYLL-MMMBL-01.

AUTHOR CONTRIBUTIONS

MLiu, MLin, XT, LD, and PZ: data collection. MLiu, MLin, and XT: photographic catalogue establishment. MLiu: formal analysis and writing—original draft. SL, ML, and MLiu: funding acquisition. MLiu, MLin, DL, and SL: methodology. MLin, DL, and SL: writing—review and editing. All authors contributed to the article and approved the submitted version.

FUNDING

National Natural Science Foundation of China (Nos. 41406182, 41306169, and 41422604; Funding to SL and MLin), Biodiversity Investigation, Observation and Assessment Program of Ministry of Ecology and Environment of China (No. 2019–2023; Funding to SL), Ocean Park Conservation Foundation of Hong Kong (MM02-1516, AW02-1920; Funding to SL and MLin), and UK-China Newton Fund Placement from China Scholarship Council and British Council (Funding to MLiu).

ACKNOWLEDGMENTS

We are grateful to all the colleagues and students of the Marine Mammal and Marine Bioacoustics Laboratory. Great thanks to Xiao Xu, Mingzhong Liu, Jianchen Dong, Kuan Li, and Francesco Caruso for their assistance and participation in the field work. Much appreciated to the handling editor and two reviewers for their constructive comments and helpful suggestions.

REFERENCES

Auger-Méthé, M., Marcoux, M., and Whitehead, H. (2010). Nicks and notches of the dorsal ridge: promising mark types for the photo-identification of narwhals. *Mar. Mamm. Sci.* 26, 663–678.

Barlow, J., Gerrodette, T., and Perryman, W. (1998). Calibrating group size estimates for cetaceans seen on ship surveys. Southwest Fisheries Science Center, National Marine Fisheries Service. *Administr. Rep. LJ* 1998, 98–11.

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Software* 67, 1–48. doi: 10.18637/jss.v067.i01

Binda, P., Morrone, M. C., Ross, J., and Burr, D. C. (2011). Underestimation of perceived number at the time of saccades. *Vision Res.* 51, 34–42. doi: 10.1016/j.visres.2010.09.028

Bouveroux, T. N., Caputo, M., Froneman, P. W., and Plön, S. (2018). Largest reported groups for the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) found in Algoa Bay, South Africa: Trends and potential drivers. *Mar. Mamm. Sci.* 34, 645–665. doi: 10.1111/mms.12471

Boyd, C., Hobbs, R. C., Punt, A. E., Shelden, K. E., Sims, C. L., and Wade, P. R. (2019). Bayesian estimation of group sizes for a coastal cetacean using aerial survey data. *Mar. Mamm. Sci.* 35, 1322–1346. doi: 10.1111/mms.12592

Buckland, S. T., Anderson, D. R., Burnham, K. P., and Laake, J. L. (1993). *Distance sampling: estimating abundance of biological populations*. London: Chapman and Hall.

Casari, M., and Tagliapietra, C. (2018). Group size in social-ecological systems. *Proc. Natl. Acad. Sci.* 115, 2728–2733. doi: 10.1073/pnas.1713496115

Chen, B., Xu, X., Jefferson, T. A., Olson, P. A., Qin, Q., Zhang, H., et al. (2016). Conservation status of the Indo-Pacific humpback dolphin (*Sousa chinensis*) in the northern Beibu Gulf, China. *Adv. Mar. Biol.* 73, 119–139. doi: 10.1016/bs.amb.2015.10.001

Chen, B., Zheng, D., Yang, G., Xu, X., and Zhou, K. (2009). Distribution and conservation of the Indo-Pacific humpback dolphin in China. *Integr. Zool.* 4, 240–247. doi: 10.1111/j.1749-4877.2009.00160.x

Chen, T., Hung, S., Qiu, Y., Jia, X., and Jefferson, T. A. (2010). Distribution, abundance, and individual movements of Indo-Pacific humpback dolphins (*Sousa chinensis*) in the Pearl River Estuary, China. *Mammalia* 74, 117–126.

Clement, M. J., Converse, S. J., and Royle, J. A. (2017). Accounting for imperfect detection of groups and individuals when estimating abundance. *Ecol. Evol.* 7, 7304–7310. doi: 10.1002/ece3.3284

Connor, R. C. (2000). "Group living in whales and dolphins," in *Cetacean Societies: Field Studies of Dolphins and Whales*, eds J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead (Chicago: University of Chicago Press), 199–218.

Dawson, S., Wade, P., Slooten, E., and Barlow, J. (2008). Design and field methods for sighting surveys of cetaceans in coastal and riverine habitats. *Mamm. Rev.* 38, 19–49. doi: 10.1111/j.1365-2907.2008.00119.x

Doane, D. P., and Seward, L. E. (2011). Measuring skewness: a forgotten statistic? *J. Stat. Educ.* 19:2.

Dorning, J., and Harris, S. (2019). Quantifying group size in the red fox: impacts of definition, season and intrusion by non-residents. *J. Zool.* 308, 37–46. doi: 10.1111/jzo.12650

Erwin, R. M. (1982). Observer variability in estimating numbers: an experiment. *J. Field Ornithol.* 53, 159–167.

Fearnbach, H., Durban, J., Parsons, K., and Claridge, D. (2012). Photographic mark-recapture analysis of local dynamics within an open population of dolphins. *Ecol. Applicat.* 22, 1689–1700. doi: 10.1890/12-0021.1

Friday, N., Smith, T. D., Stevick, P. T., and Allen, J. (2000). Measurement of photographic quality and individual distinctiveness for the photographic identification of humpback whales, *Megaptera novaeangliae*. *Mar. Mamm. Sci.* 16, 355–374. doi: 10.1111/j.1748-7692.2000.tb00930.x

Gerrodette, T., and Perrin, C. (1991). Calibration of shipboard estimates of dolphin school size from aerial photographs. Southwest Fisheries Science Center, National Marine Fisheries Service. *Administr. Rep. LJ* 1991, 91–36.

Gerrodette, T., Perryman, W., and Barlow, J. (2002). Calibrating group size estimates of dolphins in the eastern tropical Pacific Ocean. *Administr. Rep. LJ* 2002, 02–08.

Gerrodette, T., Perryman, W. L., and Oedekoven, C. S. (2019). Accuracy and precision of dolphin group size estimates. *Mar. Mamm. Sci.* 35, 22–39. doi: 10.1111/mms.12506

Giles, A. B., Butcher, P. A., Colefax, A. P., Pagendam, D. E., Mayjor, M., and Kelaher, B. P. (2021). Responses of bottlenose dolphins (*Tursiops* spp.) to small drones. *Aquat. Conserv.* 31, 677–684. doi: 10.1002/aqc.3440

Gomez-Salazar, C., Trujillo, F., and Whitehead, H. (2012). Ecological factors influencing group sizes of river dolphins (*Inia geoffrensis* and *Sotalia fluviatilis*). *Mar. Mamm. Sci.* 28, E124–E142.

Gowans, S., Würsig, B., and Karczmarski, L. (2007). The social structure and strategies of delphinids: predictions based on an ecological framework. *Adv. Mar. Biol.* 53, 195–294. doi: 10.1016/s0065-2881(07)53003-8

Gygax, L. (2002b). Evolution of group size in the superfamily Delphinoidea (Delphinidae, Phocoenidae and Monodontidae): a quantitative comparative analysis. *Mamm. Rev.* 32, 295–314. doi: 10.1046/j.1365-2907.2002.00114.x

Gygax, L. (2002a). Evolution of group size in the dolphins and porpoises: interspecific consistency of intraspecific patterns. *Behav. Ecol.* 13, 583–590. doi: 10.1093/beheco/13.5.583

Hamilton, O. N., Kincaid, S. E., Constantine, R., Kozmian-Ledward, L., Walker, C. G., and Fewster, R. M. (2018). Accounting for uncertainty in duplicate identification and group size judgements in mark-recapture distance sampling. *Methods Ecol. Evol.* 9, 354–362. doi: 10.1111/2041-210x.12895

Hartman, K., van der Harst, P., and Vilela, R. (2020). Continuous focal group follows operated by a drone enable analysis of the relation between sociality and position in a group of male Risso's dolphins (*Grampus griseus*). *Front. Mar. Sci.* 7:283. doi: 10.3389/fmars.2020.00283

Hupman, K., Stockin, K. A., Pollock, K., Pawley, M. D., Dwyer, S. L., Lea, C., et al. (2018). Challenges of implementing mark-recapture studies on poorly marked gregarious delphinids. *PLoS One* 13:e0198167. doi: 10.1371/journal.pone.0198167

Jefferson, T. A. (2000). Population biology of the Indo-Pacific hump-backed dolphin in Hong Kong waters. *Wildlife Monogr.* 2000, 1–65.

Jefferson, T. A., and Smith, B. D. (2016). Re-assessment of the conservation status of the Indo-Pacific humpback dolphin (*Sousa chinensis*) using the IUCN Red List Criteria. *Adv. Mar. Biol.* 73, 1–26. doi: 10.1016/bs.amb.2015.04.002

Jefferson, T. A., Smith, B. D., Braulik, G. T., and Perrin, W. (2017). *Sousa chinensis* (errata version published in 2018). The IUCN Red List of Threatened Species 2017: e.T82031425A123794774. Available online at: https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T82031425A50372332.en (accessed date on 1 March 2021).

Kappeler, P. M. (2019). A framework for studying social complexity. *Behav. Ecol. Sociobiol.* 73:13.

Kappeler, P. M., Clutton-Brock, T., Shultz, S., and Lukas, D. (2019). Social complexity: patterns, processes, and evolution. *Behav. Ecol. Sociobiol.* 73, 1–6.

Karczmarski, L. (1999). Group dynamics of humpback dolphins (*Sousa chinensis*) in the Algoa Bay region, South Africa. *J. Zool.* 249, 283–293. doi: 10.1111/j.1469-7998.1999.tb00765.x

Kinzey, D., Olson, P., and Gerrodette, T. (2000). Marine mammal data collection procedures on research ship line-transect surveys by the Southwest Fisheries Science Center. *SWFSC Administr. Rep. LJ* 2000, 00–08.

Koper, R. P., Karczmarski, L., du Preez, D., and Plön, S. (2016). Sixteen years later: Occurrence, group size, and habitat use of humpback dolphins (*Sousa plumbea*) in Algoa Bay, South Africa. *Mar. Mamm. Sci.* 32, 490–507. doi: 10.1111/mms.12279

Li, S. (2020). Humpback dolphins at risk of extinction. *Science* 367, 1313–1314.

Li, S., Lin, M., Xu, X., Xing, L., Zhang, P., Gozlan, R. E., et al. (2016). First record of the Indo-Pacific humpback dolphins (*Sousa chinensis*) southwest of Hainan Island, China. *Mar. Biodiv. Rec.* 9:3. doi: 10.1186/s41200-016-0005-x

Liu, M., Bejder, L., Lin, M., Zhang, P., Dong, L., and Li, S. (2020a). Determining spatial use of the world's second largest humpback dolphin population: Implications for place-based conservation and management. *Aquat. Conserv.* 30, 364–374. doi: 10.1002/aqc.3253

Liu, M., Lin, M., Dong, L., Xue, T., Zhang, P., Tang, X., et al. (2020b). Group sizes of Indo-Pacific humpback dolphins in waters Southwest of Hainan Island, China: Insights into rare records of large groups. *Aquat. Mamm.* 46, 259–266. doi: 10.1578/AM.46.3.2020.259

Liu, M., Lin, M., Dong, L., Zhang, P., and Li, S. (2021a). Spatiotemporal variations in fine-scale habitat use of the world's second largest population of humpback dolphins. *J. Mamm.* 102, 384–395. doi: 10.1093/jmammal/gyab001

Liu, M., Lin, M., Lusseau, D., and Li, S. (2021b). Intra-Population variability in group size of Indo-Pacific humpback dolphins (*Sousa chinensis*). *Front. Mar. Sci.* 8:671568. doi: 10.3389/fmars.2021.671568

Liu, M., Lin, M., Lusseau, D., and Li, S. (2021c). The biogeography of group sizes in humpback dolphins (*Sousa* spp.). *Integr. Zool.* 16, 527–537. doi: 10.1111/1749-4877.12542

López, B. D., Grandcourt, E., Methion, S., Das, H., Bugla, I., Al Hameli, M., et al. (2018). The distribution, abundance and group dynamics of Indian Ocean humpback dolphins (*Sousa plumbea*) in the Emirate of Abu Dhabi (UAE). *J. Mar. Biol. Assoc. U K* 98, 1119–1127. doi: 10.1017/S0025315417001205

Mann, J. (1999). Behavioral sampling methods for cetaceans: a review and critique. *Mar. Mamm. Sci.* 15, 102–122. doi: 10.1111/j.1748-7692.1999.tb00784.x

Marsh, H., and Sinclair, D. F. (1989). Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. *J. Wildlife Manag.* 1989, 1017–1024.

Meropi, P., Bikos, C., and George, Z. (2018). Outlier detection in skewed data. *Simulat. Model. Pract. Theory* 87, 191–209. doi: 10.1016/j.simpat.2018.05.010

Methion, S., and López, B. D. (2018). Abundance and demographic parameters of bottlenose dolphins in a highly affected coastal ecosystem. *Mar. Freshw. Res.* 69, 1355–1364. doi: 10.1071/MF17346

Moura, J. F., Pivari, D., and Pagliani, B. (2019). Environmental factors related to group size and habitat use of Guiana dolphins from São Marcos Bay, Amazon Coast. *Trop. Ecol.* 60, 426–432. doi: 10.1007/s42965-019-00041-0

Parrish, J. K., and Edelstein-Keshet, L. (1999). Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science* 284, 99–101. doi: 10.1126/science.284.5411.99

Parsons, E. (2004). The behavior and ecology of the Indo-Pacific humpback dolphin (*Sousa chinensis*). *Aquat. Mamm.* 30, 38–55. doi: 10.1578/AM.30.1.2004.38

Pawley, M. D. M., Hupman, K. E., Stockin, K. A., and Gilman, A. (2018). Examining the viability of dorsal fin pigmentation for individual identification of poorly-marked delphinids. *Sci. Rep.* 8, 1–12. doi: 10.1038/s41598-018-30842-7

Peña, J., and Nöldeke, G. (2018). Group size effects in social evolution. *J. Theor. Biol.* 457, 211–220. doi: 10.1016/j.jtbi.2018.08.004

Peng, C., Wu, H., Wang, X., Zhu, Q., Jefferson, T. A., Wang, C. C., et al. (2020). Abundance and residency dynamics of the Indo-Pacific humpback dolphin, *Sousa chinensis*, in the Dafengjiang River Estuary, China. *Mar. Mamm. Sci.* 36, 623–637. doi: 10.1111/mms.12663

R Development Core Team (2021). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available online at: http://www.R-project.org/

Scott, M. D., Perryman, W. L., and Clark, W. G. (1985). The use of aerial photographs for estimating school sizes of cetaceans. *Inter-Am. Trop. Tuna Comm. Bull.* 18, 381–419.

Stevick, P. T., Palsbøll, P. J., Smith, T. D., Bravington, M. V., and Hammond, P. S. (2001). Errors in identification using natural markings: rates, sources, and effects on capture recapture estimates of abundance. *Can. J. Fish. Aquat. Sci.* 58, 1861–1870. doi: 10.1139/f01-131

Tang, X., Lin, W., Karczmarski, L., Lin, M., Chan, S. C., Liu, M., et al. (2021). Photo-identification comparison of four Indo-Pacific humpback dolphin populations off southeast China. *Integr. Zool.* 16, 586–593. doi: 10.1111/1749-4877.12537

Tyne, J. A., Pollock, K. H., Johnston, D. W., and Bejder, L. (2014). Abundance and survival rates of the Hawai'i Island associated spinner dolphin (*Stenella longirostris*) stock. *PLoS One* 9:E86132. doi: 10.1371/journal.pone.0086132

Urian, K., Gorgone, A., Read, A., Balmer, B., Wells, R. S., Berggren, P., et al. (2015). Recommendations for photo-identification methods used in capture-recapture models with cetaceans. *Mar. Mamm. Sci.* 31, 298–321. doi: 10.1111/mms.12141

Van Parijs, S. M., Smith, J., and Corkeron, P. J. (2002). Using calls to estimate the abundance of inshore dolphins: a case study with Pacific humpback dolphins *Sousa chinensis*. *J. Appl. Ecol.* 39, 853–864. doi: 10.1046/j.1365-2664.2002.00756.x

Vargas-Fonseca, O. A., Kirkman, S. P., Conry, D., Rishworth, G. M., Cockcroft, V., and Pistorius, P. A. (2018). Distribution and habitat use of Indo-Pacific bottlenose dolphins *Tursiops aduncus* along the south coast of South Africa. *Afr. J. Mar. Sci.* 40, 439–450. doi: 10.2989/1814232X.2018.1547221

Walsh, D. P., Page, C. F., Campa, H. E. III, Winterstein, S. R., and Beyer, D. E. Jr. (2009). Incorporating estimates of group size in sightability models for wildlife. *J. Wildlife Manag.* 73, 136–143. doi: 10.2193/2008-054

Wang, K., Wang, D., Akamatsu, T., Li, S., and Xiao, J. (2005). A passive acoustic monitoring method applied to observation and group size estimation of finless porpoises. *J. Acoust. Soc. Am.* 118, 1180–1185. doi: 10.1121/1.1945487

Wang, X., Wu, F., Turvey, S. T., Rosso, M., Tao, C., Ding, X., et al. (2015). Social organization and distribution patterns inform conservation management of a threatened Indo-Pacific humpback dolphin population. *J. Mamm.* 96, 964–971. doi: 10.1093/jmammal/gyv097

Wang, X., Wu, F., Turvey, S. T., Rosso, M., and Zhu, Q. (2016). Seasonal group characteristics and occurrence patterns of Indo-Pacific humpback dolphins (*Sousa chinensis*) in Xiamen Bay, Fujian Province, China. *J. Mamm.* 97, 1026–1032. doi: 10.1093/jmammal/gyw002

Wang, Z., Fang, L., Shi, W., Wang, K., and Wang, D. (2013). Whistle characteristics of free-ranging Indo-Pacific humpback dolphins (*Sousa chinensis*) in Sanniang Bay, China. *J. Acoust. Soc. Am.* 133, 2479–2489. doi: 10.1121/1.4794390

Wickman, L., Rayment, W., Slooten, E., and Dawson, S. M. (2021). Recommendations for estimating mark rate of cetaceans in photo-ID research: A critique of field sampling protocols and variance estimation. *Mar. Mamm. Sci.* 37, 328–343. doi: 10.1111/mms.12723

Williams, J. A., Dawson, S. M., and Slooten, E. (1993). The abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. *Can. J. Zool.* 71, 2080–2088. doi: 10.1139/z93-293

Wu, H., Jefferson, T. A., Peng, C., Liao, Y., Huang, H., Lin, M., et al. (2017). Distribution and habitat characteristics of the Indo-Pacific humpback dolphin (*Sousa chinensis*) in the northern Beibu Gulf. China. *Aquat. Mamm.* 43:219. doi: 10.1578/AM.43.2.2017.219

Würsig, B., Parsons, E. C. M., Piwetz, S., and Porter, L. (2016). The behavioural ecology of Indo-Pacific humpback dolphins in Hong Kong. *Adv. Mar. Biol.* 73, 65–90. doi: 10.1016/bs.amb.2015.08.008

Würsig, B., and Würsig, M. (1977). The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science* 198, 755–756. doi: 10.1126/science.198.4318.755

Xu, X., Song, J., Zhang, Z., Li, P., Yang, G., and Zhou, K. (2015). The world's second largest population of humpback dolphins in the waters of Zhanjiang deserves the highest conservation priority. *Sci. Rep.* 5:8147. doi: 10.1038/srep08147

Xu, X., Zhang, Z., Ma, L., Li, P., Yang, G., and Zhou, K. (2012). Site fidelity and association patterns of Indo-Pacific humpback dolphins off the east coast of Zhanjiang, China. *Acta Theriol.* 57, 99–109. doi: 10.1007/s13364-011-0058-5

Zanardo, N., Parra, G. J., and Möller, L. M. (2016). Site fidelity, residency, and abundance of bottlenose dolphins (*Tursiops* sp.) in Adelaide's coastal waters, South Australia. *Mar. Mamm. Sci.* 32, 1381–1401. doi: 10.1111/mms.12335

Zhou, K., Xu, X., and Tian, C. (2007). Distribution and abundance of Indo-Pacific humpback dolphins in Leizhou Bay, China. *N.Z. J. Zool.* 34, 35–42. doi: 10.1080/03014220709510061

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

ORIGINAL RESEARCH
published: 03 December 2021
doi: 10.3389/fmars.2021.652147

Social Behaviour of Humpback Whales (*Megaptera novaeangliae*) in Hervey Bay, Eastern Australia, a Preferential Female Stopover During the Southern Migration

Trish Franklin[1,2]*, Wally Franklin[1,2], Lyndon Brooks[2,3], Peter Harrison[2], Adam A. Pack[4,5] and Phillip J. Clapham[6]

[1] The Oceania Project, Hervey Bay, QLD, Australia, [2] Marine Ecology Research Centre, School of Environment, Science and Engineering, Southern Cross University, Lismore, NSW, Australia, [3] StatPlan Consulting Pty., Ltd., Woodburn, NSW, Australia, [4] Department of Psychology, Department of Biology, University of Hawai'i at Hilo, Hilo, HI, United States, [5] The Dolphin Institute, Hilo, HI, United States, [6] Seastar Scientific Inc., Vashon Island, WA, United States

Edited by:
Janet Mann,
Georgetown University, United States

Reviewed by:
Ari Friedlaender,
University of California, Santa Cruz,
United States
Robert McCauley,
Curtin University, Australia

***Correspondence:**
Trish Franklin
trish@oceania.org.au

Specialty section:
This article was submitted to
Marine Megafauna,
a section of the journal
Frontiers in Marine Science

Received: 11 January 2021
Accepted: 03 November 2021
Published: 03 December 2021

Citation:
Franklin T, Franklin W, Brooks L,
Harrison P, Pack AA and Clapham PJ
(2021) Social Behaviour of Humpback
Whales (Megaptera novaeangliae)
in Hervey Bay, Eastern Australia,
a Preferential Female Stopover During
the Southern Migration.
Front. Mar. Sci. 8:652147.
doi: 10.3389/fmars.2021.652147

Agonistic competitive social behaviour in humpback whales [*Megaptera novaeangliae* (Borowski, 1781)] has been extensively studied and reported in previous research. However, non-agonistic social behaviour in humpback whale pods has not been systematically studied. We investigated the social behaviour of 3,949 humpback whale pods over a period of 14 years during August, September, and October in Hervey Bay (Queensland, eastern Australia), a preferential female stopover early in the southern migration. Modelling and analyses of the data examined the factors influencing the occurrence and timing of non-agonistic social behaviour pods, agonistic competitive pods and newly associated pods. Non-agonistic social behaviour was observed more frequently during August when mature females, including early pregnant and resting females, co-occur and socially interact with immature males and females. Overall, relatively few mature males visit Hervey Bay. Agonistic competitive behaviour was observed with increasing frequency during September and October when mother-calf pods, with few escorts predominated. Mother-calf pods in Hervey Bay spent most of their time alone involved in maternal care. Agonistic competitive behaviour is related to the decreasing numbers of potentially oestrous females toward the end of the season. Non-agonistic social behaviour and agonistic competitive behaviour were more frequently observed in larger and newly associated pods. Overall, non-agonistic social behaviour pods were more prevalent than agonistic competitive social behaviour pods. The results of this study substantiate that non-agonistic social behaviour may be more prevalent than aggressive agonistic social behaviour in site-specific locations and habitats, depending upon the classes and timings of humpback whales using such habitats.

Keywords: humpback whale, *Megaptera novaeangliae*, Hervey Bay, agonistic and non-agonistic social behaviour, pod associations, mate competition, migratory stopovers

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are a migratory species. Except for humpback whales in the Arabian Sea (Mikhalev, 1997), individual females and males, in all maturational classes, and different reproductive states, in all other populations, migrate from high-latitude summer/autumn feeding areas to low latitude winter/spring breeding grounds (Chittleborough, 1965; Dawbin, 1966; Clapham and Mead, 1999). Feeding is rare or absent in winter breeding grounds, when most behaviours are related to calving and mating. The latter includes singing of long, complex song by male humpbacks to either attract females and/or meditate intrasexual interactions with other males (Payne and McVay, 1971; Clapham, 1996; Darling et al., 2006; Herman, 2017).

Humpback whale social behaviour and demographics in the feeding areas and breeding grounds in the Northern Hemisphere, as well as along some migratory routes, have been well described (see summaries in Clapham, 1993, 2000; Herman, 2017). In contrast, there is relatively little understanding about the behaviours and demographics of humpback whales in so-called "stopover" habitats along migratory routes, to and from feeding areas and breeding grounds. The use of so-called "stopovers" for rest, refuelling and predator avoidance, is not uncommon in species that undergo relatively long migrations including insects (Kennedy, 1951; McCord and Davis, 2012), reptiles (Rice and Balazs, 2008; Baudouin et al., 2015; Dujon et al., 2017; Nivière et al., 2018), mammals (e.g., Sawyer and Kauffman, 2011), and numerous bird species (e.g., Alerstam and Hedenström, 1998; Weber et al., 1998; Schaub et al., 2001, 2008; Delmore et al., 2012; McCabe and Olsen, 2015; Zaynagutdinova et al., 2019).

Several recent studies have identified and investigated migratory stopovers of humpback whales involving shallow-water environments for resting mother-calf pods (Carvalho et al., 2011; Meynecke et al., 2013; Bruce et al., 2014; Franklin et al., 2018; Stack et al., 2020), coastal feeding areas (Gill et al., 1998; Stockin and Burgess, 2005; Stamation et al., 2007; Barendse et al., 2010, 2013; Owen et al., 2015), and sea mounts used for resting, early feeding and singing and as navigational aids (Garrigue et al., 2015; MacKay et al., 2016; Derville et al., 2020).

Social behaviour in humpback whales can be broadly characterised as either agonistic or non-agonistic. While physical agonistic behaviour has occasionally been observed from females apparently rejecting the advances of an escort (Clapham, 1996, 2000; Pack et al., 2002; Franklin, 2012), and between a singing male and a male joiner (Darling and Berube, 2001), most physical agonistic social behaviour in humpback whales occurs within "competitive groups" (Clapham et al., 1992). These groups consist of a single female with or without a calf and two or more male escorts competing through various displays and aggressive acts for position and presumably potential mating access to the female (Tyack and Whitehead, 1983; Baker and Herman, 1984b; Clapham et al., 1992). Most non-agonistic social behaviour (described in detail below) in humpback whales in the breeding grounds or along migratory routes occurs in lone mother-calf pairs, in mother-calf pairs accompanied by a single escort (e.g., Craig et al., 2002, 2014; Cartwright and Sullivan, 2009; Cartwright et al., 2012; Zoidis et al., 2014; Zoidis and Lomac-MacNair, 2017), in male-male dyads (Brown and Corkeron, 1995; Darling and Berube, 2001; Darling et al., 2006), in male-female dyads (Jones, 2010; Herman et al., 2011; Pack et al., 2012) and among singers and whales that join them (Darling et al., 2006; Herman, 2017).

Some types of associations of humpback whales are relatively long term. These include the relationship between a mother and calf, which typically lasts 11–12 months (Clapham, 1996), and the relationships of some individuals in cooperative feeding groups, which may continue for years (e.g., Weinrich and Kuhlberg, 1991; Sharpe, 2001; Sharpe et al., 2013). However, most associations are short lived and temporary (Mobley and Herman, 1985; Clapham, 1993, 2000). The modal size for pods involving a calf present in Hawaii was three, mother-calf and escort (Herman and Antinoja, 1977; Herman et al., 1980; Glockner and Venus, 1983). In contrast, in Hervey Bay in pods with calves present the modal size was two because of the significantly higher proportion of mothers alone with their calves (Franklin et al., 2011). In the Hawaiian breeding grounds, mother-calf pairs typically do not affiliate with each other, reflecting reports of a general trend of female avoidance of other females in Northern Hemisphere breeding grounds (Clapham, 2000; Darling, 2001; Pack et al., 2017).

Hervey Bay is a wide shallow coastal embayment (Ribbe, 2014), south of the presumed breeding grounds of eastern Australian humpback whales within the Great Barrier Reef (Simmons and Marsh, 1986; Paterson, 1991; Smith et al., 2012). Commercial industrial whaling during the 1950s and early 1960s, in Antarctica and along the east coast of Australia south of Hervey Bay (Clapham et al., 2009; Ivashchenko and Clapham, 2014), decimated to near extinction, the east Australian humpback whale population (Woinarski et al., 2014; Harrison and Woinarski, 2018). Historically there are no formal reports of whales in Hervey Bay prior to the late 1980s (see e.g., Chaloupka et al., 1999). Early research in Hervey Bay during the late-1980s and early 1990s established that humpback whales enter and leave the Bay from the north, aggregate in the shallow eastern part of the Bay along the western shore of Fraser Island and that mothers with calves are the last cohort to use the Bay (Corkeron, 1993; Corkeron et al., 1994; also see **Figure 2** below). However, there were insufficient data to determine the importance of Hervey Bay for particular classes of humpback whales.

Subsequently, a long-term vessel-based photo-identification study of humpback whales was undertaken between 1992 and 2009 (see Franklin, 2012, 2014). Humpback whales use Hervey Bay as a stopover early in the southern migration during August, September, and October (Franklin et al., 2011, 2018). The estimated mean residency of humpback whales in Hervey Bay is constant by week within season and over years (Mean = 1.53 weeks, SE = 0.22 weeks, LCI 1.09 weeks: UCI 1.96 weeks; Franklin, 2014). Pod characteristics differ significantly in August compared to September and October, related to the different classes of humpback whales using the Bay (Franklin et al., 2011). Hervey Bay is a female preferential habitat (2.9:1 females to males, Franklin et al., 2018). Mature females, including resting and early pregnant females, occur during August, co-temporal with the immature male and female cohort (Franklin et al., 2018). During August immature males and females are actively involved in complex social interactions with each other and with mature females (e.g., see Franklin, 2012). Unescorted mother-calf pods predominate in Hervey Bay during September and October (Franklin et al., 2011). Overall, only a few mature males are present in Hervey Bay during August, September, and October (Franklin et al., 2018).

In the current study, we systematically investigated non-agonistic and agonistic social behaviour in pods of humpback whales in Hervey Bay to better understand the pod types, pod associations and social behaviours occurring in an area used as a stopover. Data collected over a 14-year period were used to (a) analyse and model the occurrence and timing of pod associations, non-agonistic social behaviour and agonistic competitive behaviour in pods, within season and between years; (b) determine the relative proportions of non-agonistic versus agonistic social behaviour; (c) reveal significant factors influencing agonistic and non-agonistic social behaviour; and (d) compare these observed behaviours at this stopover with those observed in the breeding grounds, feeding areas, and along migratory corridors.

MATERIALS AND METHODS

Study Area and Timing of Vessel-Based Surveys

Hervey Bay, formed by Fraser Island and the mainland, is located at 25°S, 153°E on the east coast of Queensland (**Figure 1**). It is a wide shallow coastal embayment approximately 4,000 km^2 in area with a mean depth of 20 m (Ribbe, 2014). Fraser Island is 126 km long; it lies along a northeasterly axis and its northern end bridges the continental shelf (Ribbe, 2014, also see

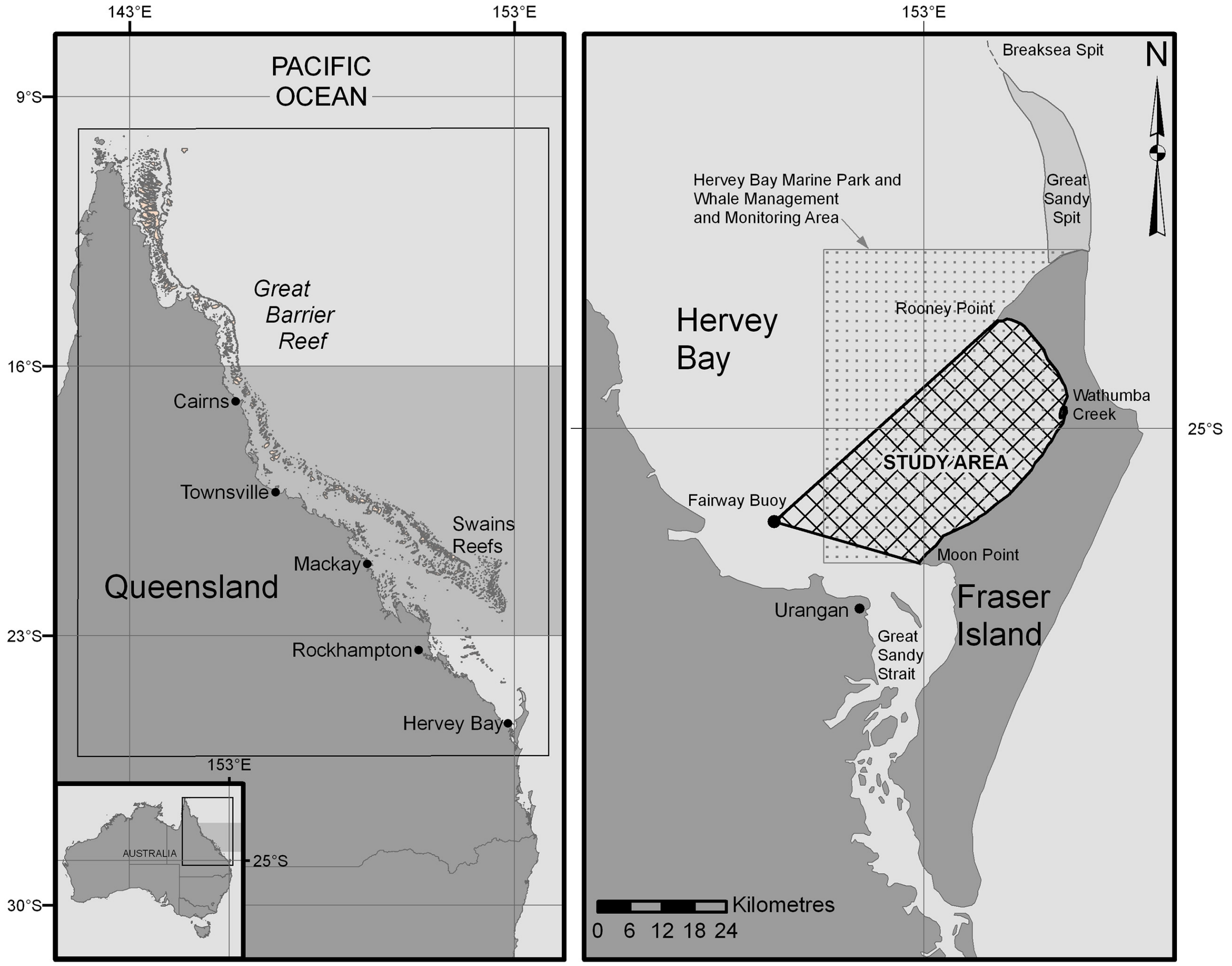


FIGURE 1 | The location of Hervey Bay on the eastern coast of Australia and its geographic relationship to the Great Barrier Reef and presumed breeding grounds (16°S–23°S; shaded area) of humpback whales is shown on the left-side map. The study area and the Hervey Bay Marine Park boundaries are shown on the eastern side of Hervey Bay. A primary feeding area for eastern Australian humpback whales is around the Balleny Islands, approximately 5,000 km south of Hervey Bay (Franklin et al., 2012; Constantine et al., 2014); although, the feeding range of Southern Ocean humpback whales spreads widely across Antarctica from the Balleny islands, east (Dalla Rosa et al., 2012) and west (Franklin et al., 2017).

Figure 2 below). The study area is in the eastern bay against the western shore of Fraser Island (**Figure 1**).

Paterson (1991) reported that the southern migration from the Great Barrier Reef began in late July, with humpback whales moving into and out of Hervey Bay from early August to mid-October. Consequently, we conducted vessel-based observations of humpback whale pods in the Hervey Bay study area from early August until mid-October each year between 1992 and 2005 with consistent annual effort.

Four different motorised vessels were utilised as dedicated research platforms between 1992 and 2005: two were monohulls and two were catamarans, ranging in length from 11 to 27 m. The study area is approximately 27.8 km from Urangan Boat Harbour, Hervey Bay (**Figure 1**). Fieldwork was planned

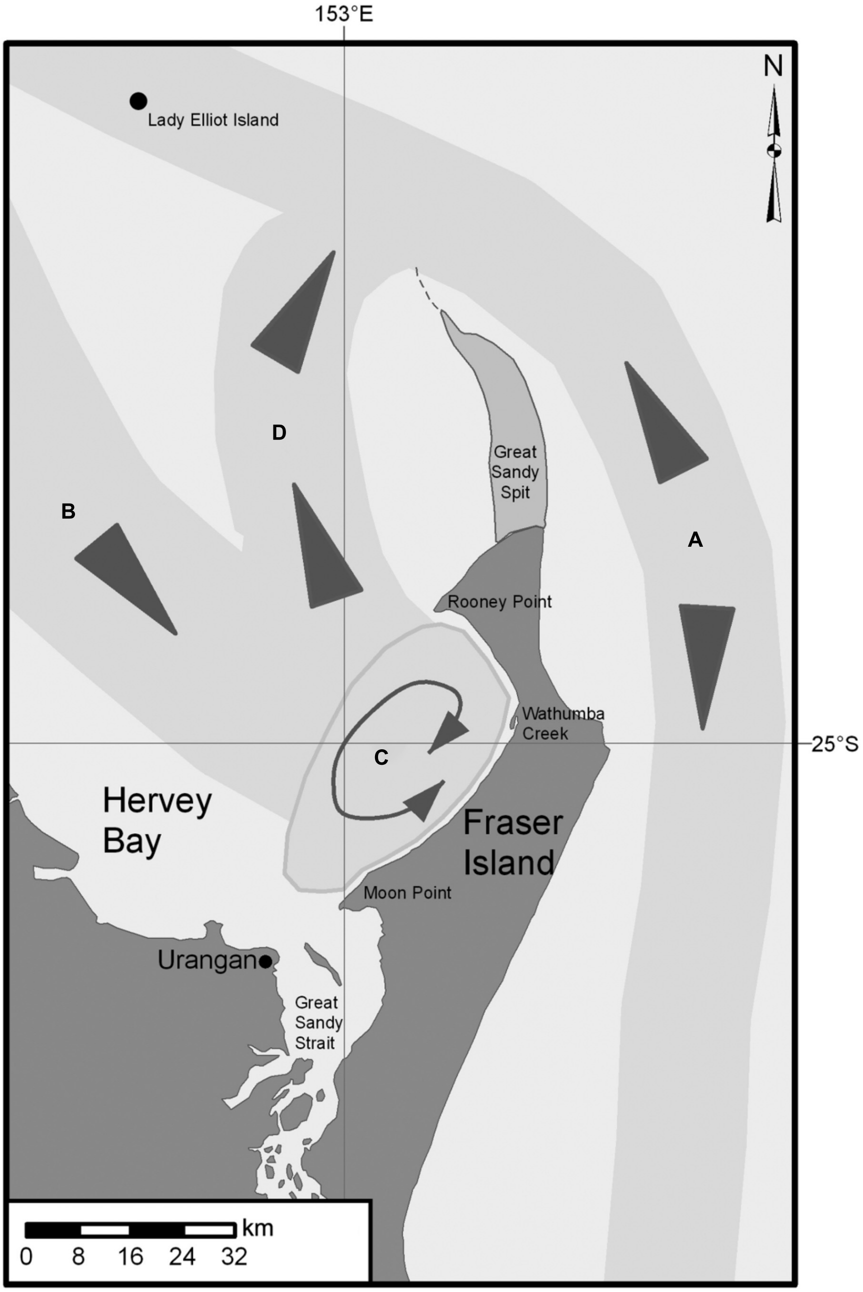


FIGURE 2 | Humpback whale migratory pathways into and out of Hervey Bay. Hervey Bay's northern entrance, east of the northern end of Great Sandy Spit, is 80 km wide with a mean depth of 20 m (Ribbe, 2014). Humpback whales enter **(B)** and leave Hervey Bay **(D)** to the north and aggregate in the eastern bay, off the western shore of Fraser Island **(C)** (Corkeron, 1993; Corkeron et al., 1994; Franklin et al., 2011, 2018). To enter Hervey Bay, humpback whales make a slight diversion from the primary north–south migratory pathway **(A)** (Paterson, 1991) and traverse shallow waters for approximately 40 km. They contend with 3 m tidal movements and do not return to deeper water until they pass north of Great Sandy Spit (Ribbe, 2014) and rejoin the primary southern migratory pathway **(A)**.

for 6 days each week, leaving Urangan harbour at 0800 each Sunday and returning at 1500 the following Friday. Planned daily operations were from 0930 to 1700 on Sunday, 0700 to 1700 Monday to Thursday, and from 0700 to 1330 on Friday.

Definitions of Terms in This Study

Given that a focus of this study is describing agonistic and non-agonistic social behaviour by pod types and pod associations, the following brief definitions of terms are provided here for clarity.

Singleton: a lone humpback whale.

Pod: is defined as either a singleton or two or more humpback whales within one to two body lengths of each other, generally moving in the same direction and at the same rate of travel (Whitehead, 1983; Clapham, 1993; Corkeron et al., 1994).

Initial pod: this is a pod as first encountered, prior to any change in pod size. If the initial pod joins, or is joined by, one or more pods during observation it is referred to as a ***newly associated pod***.

Calf: an individual whale was considered to be a calf if it appeared to be less than half the length of a particular adult with which it maintained a constant and close relationship (Clapham et al., 1999; Pack et al., 2009). The adult in close proximity to the calf was assumed to be its mother.

Escort: was defined as a whale accompanying a mother with calf (Herman and Antinoja, 1977). In the breeding grounds, escorts have been identified as males, and their association with mother-calf pairs has been proposed as a tactic while prospecting for potential mating opportunities (Glockner and Venus, 1983; Tyack and Whitehead, 1983; Baker and Herman, 1984a; Mobley and Herman, 1985; Clapham, 1996; Craig et al., 2002).

Competitive Pods: a group of three or more whales exhibiting agonistic "Competitive Group" surface behaviours, which typically consists of a single focal female, with or without a calf, and two or more male escorts, some of which compete with each other, presumably for access to the female (Tyack and Whitehead, 1983; Baker and Herman, 1984b; Clapham et al., 1992).

Non-Agonistic Pods: two or more whales, excluding unescorted mother-calf pairs, involved in spatially undirected surface activity and calm interactions with no high-energy actions, aggression or competitive behaviours occurring (Darling et al., 2006). Surface social behaviours involve slow coordinated movements (Herman and Antinoja, 1977; Tyack, 1981; Tyack and Whitehead, 1983). Surface social behaviours include head rising, spy-hops, rolling over ventral side up, pectoral fin extensions, tail fluke-extensions, breaching, pectoral fin slapping, lobtailing and milling.

Other Behaviour Pods: occurs with singletons and in pods that are neither a competitive pod nor a non-agonistic pod, as defined above. Surface behaviours in Hervey Bay may include surface travelling, resting (logging), or occasional surface activity, for example breaching, pectoral slapping, and/or lobtailing.

Field Procedures

Observations

A minimum of six research assistants, were rostered on morning and afternoon shifts. The roster duties were to scan and search for pods; take field notes, GPS positions, weather and environmental readings.

Pods were chosen for observation on a "first pod available" basis with no *a priori* selection of any particular pod class. During the weekly study period, a variable overnight anchorage within the study area was selected based on the location of the final pod observed, weather conditions, and tidal movements. Each morning, subject to weather and sea-state condition, travel was commenced in a direction that was different from the prior day, until a pod was sighted.

Each pod under observation was assigned an identification code that was recorded together with the date, time, and GPS location was taken at start and thereafter every 15 min until completion when a final GPS position was taken. The number of individuals and their sex (where possible, see below), pod composition, and surface behaviours within pods were also recorded throughout the duration of observation of each pod (continuous sampling; Altmann, 1974). All pod observations and behaviour data were recorded daily in field notes and entered into a FileMaker Pro database each evening. Behaviour that passes unobserved underwater or at night may be significantly different from that documented during the present study; we acknowledge this, but all observations reported here were necessarily made at the surface and during daylight.

Sex-Identification

To the extent possible, an individual whale's sex was determined using one of two methods: from direct observation of the genital area – female humpback whales have mammary slits and a hemispheric lobe just posterior to the genital slit (True, 1904; Glockner, 1983) or sex was inferred from the whale's previous sighting histories and/or its behavioural roles. For example, an adult-sized individual accompanying a calf consistently and providing it with nurturing behaviours has been verified to be female (Tyack and Whitehead, 1983; Pack et al., 2009), and escorts and singing whales have been verified to be males (Glockner and Venus, 1983; Tyack and Whitehead, 1983; Baker and Herman, 1984a; Clapham, 2000). Chu and Nieukirk (1988) verified that humpback whales with distinct vertical and horizontal dorsal fin and lateral body scars, resulting from competitive activity were male. Females never exhibit such marks (Franklin et al., 2020). With few exceptions (e.g., see Clapham et al., 1992), the whale designated from positioning and behaviour as the "focal whale" in competitive groups has been verified as female (Darling et al., 1983; Tyack and Whitehead, 1983; Baker and Herman, 1984b; Clapham et al., 1992, 1993; Clapham, 2000).

Pod Behaviour and Inter-Pod Association and Non-association Data

Each pod was surveyed until its composition, the number of whales present, individual sex (where possible), and the surface social activity and behaviours within pods throughout the period of observation were determined.

Upon commencement of observation of the initial pod (see Definitions above) a member of the observation team continually scanned for and reported on other pods within a radius of approximately a kilometre. If one or more of those pods were tracking toward the initial pod, or if the initial pod was tracking toward them, then the duration of observation was extended to observe and record associations as they occurred. The details of each associating pod, including time, GPS location, size, composition and surface social activity and behaviours were recorded. Each newly associated pod was designated as either a consecutive association (e.g., a mother-calf pod attracts one escort at time 1, time 2, time 3, etc.) or as a simultaneous association (e.g., three singletons approaching each other and associating at the same time).

Pods were firstly categorised into those that did not associate while under observation and those that did associate while under observation forming newly associated pods. All logged information on surface activity, behaviours and composition for each pod was reviewed and pods were categorised either as a non-agonistic pod, agonistic competitive pod or other behaviour pod, in accordance with the definitions above.

Statistical Analyses

The pod or singleton was used as the basic observational unit in analyses. The size of the newly associated pods by number of pods associating and size of the initial pod were reported. The duration of observations of competitive pods, non-agonistic pods and other behaviour pods were also reported.

The frequencies of competitive pods, non-agonistic pods and other behaviour pods, sorted by pods with no calves present and pods with calves present, by newly associated pods and pods that did not associate while under observation, and by number of whales (excluding calves) in pods (1, 2, and 3+) were reported. The data on non-agonistic pods, competitive pods, and newly associated pods, by week within season (1–10), together with the sub-set of pods used in statistical analysis and modelling were reported.

Variation in the proportion of newly associated pods by year, by week within year (1–10), by calf present or not present, and by pod size were assessed using chi-square analyses. The variation in the proportion of non-agonistic pods and competitive pods (independent analyses) by year, by week within year, by pods that did not associate while under observation and newly associated pods, and by pods with no calves present and pods with calves present were examined.

Chi-square analyses were used to document the univariate associations between the occurrence of non-agonistic pods and newly associated pods, year, week within year, number of whales (excluding calves) and presence of calf in the pod prior to fitting a binary logistic regression model to assess the joint effects of the above factors (explanatory variables) on the probability of occurrence of non-agonistic social behaviour in pods (response variable). Similarly, chi-square analyses were used to document the univariate associations between the occurrence of newly associated pods and agonistic competitive pods, year, week within year, number of whales (excluding calves) and presence of a calf in the pod prior to fitting a binary logistic regression model to assess the joint effects of the above factors (explanatory variable) on the probability of occurrence of agonistic competitive behaviour in pods (response variable).

The binary logistic regression models were fitted in SPSS (version 26; IBM Corporation, 2019) using the procedure Generalized Linear Models (GENLIN). Descriptions of the modelling process are included in the section "Results." Goodness of fit was assessed in terms of model deviance, its degrees of freedom and Chi squared tests, and AIC values. Multicollinearity was considered from the perspective of how the model effects should be interpreted in terms of the significance of the terms in the model relative to the raw, univariate tests and changes between raw, univariate proportions in the categories of explanatory factors and the real-scale estimates from the models.

RESULTS

Effort and Observations

A total of 139 6-day survey periods (Sunday to Friday) were conducted in the Hervey Bay study area (**Figure 1** above) between 1992 and 2005. Data on pods were obtained on 770 of the planned 834 survey days. Total survey time was 6,160 h and observations of humpback whale pods were conducted for a total of 2,760 h.

Data Set

Data were collected on 4,506 pods (see **Supplementary Appendix Data Sheet 1**), 1,022 (22.7%) of which were pods that associated while under observation, involving associations of from 2 to 5 pods, becoming 465 newly associated pods (**Supplementary Appendix Table 1**), and 3,484 (77.3%), which were pods that did not associate while under observation, making a total of 3,949 pods used in the analyses (see **Table 1** below and **Supplementary Appendix Table 3**).

TABLE 1 | Number of pods, week within year by pods (*n*), newly associated pods (NAP), non-agonistic pods (NP), the subset of pods used in analysis of non-agonistic social behaviour (Subset a), competitive pods (CP), the subset of pods used in analysis of agonistic competitive social behaviour (Subset b).

Week	Pods (*n*)	NAP	NP	Subset (a)[1]	%	CP	Subset (b)[2]	%
1	315	43	83	256	11.2	14	105	11.2
2	380	57	84	305	13.3	19	136	14.5
3	391	56	81	322	14.1	33	139	14.8
4	403	68	87	319	13.9	33	160	17.0
5	416	41	51	275	12.0	23	99	10.5
6	391	40	25	220	9.6	33	89	9.5
7	450	49	21	203	8.9	30	74	7.9
8	444	46	15	169	7.4	32	64	6.8
9	411	40	13	130	5.7	21	49	5.2
10	348	25	5	88	3.8	11	25	2.7
Total	3,949	465[3]	465[3]	2,287	100	249	940	100
%	100	11.78	11.78	57.91		6.31	23.80	

[1] *Subset (a): pods that included at least 2 whales (excluding a mother alone with her calf) (see NP definition above). This subset was used in the analysis of non-agonistic social behaviour.*

[2] *Subset (b): pods that included at least 3 whales of which at least 2 were non-mothers (see CP definition above). This subset was used in the analysis of agonistic competitive social behaviour.*

[3] *That the totals in newly associated pods (NAP) and non-agonistic pods (NP) are the same is a coincidence, these are discrete results. Note: the pods exhibiting NP and CP behaviour may or may not be newly associated pods (NAP). This is dealt with in analyses.*

Associations and Disassociations of Pods

Newly associated pods, formed by the consecutive or simultaneous association of up to five pods during the period of observation, with calves present versus those without calves present are reported in **Supplementary Appendix Table 1**.

Of the 465 newly associated pods, 295 (63.4%) contained no calf, and 170 (36.6%) contained one or more calves. Of the newly associated pods, 368 (79.1%) were formed from the association of two pods (of one or more whales each), 85 (18.3%) from the association of three pods, 10 (2.2%) from the association of four pods and two (0.4%) from the association of five pods. Of the newly associated pods, 341 (73.3%) were consecutive associations and 124 (26.7%) were simultaneous associations. Disassociations were recorded in 171 (36.8%) of the newly associated pods, but not used in analyses.

Non-agonistic Pods, Competitive Pods, and Other Behaviour Pods

Duration of Observation

The duration of observations of competitive pods, non-agonistic pods and other behaviour pods are reported in **Supplementary Appendix Table 2**. Competitive pods were observed for 0.07–2.50 h (median = 0.73 h, mean = 0.91 h, SD = 0.46 h, $n = 216$), non-agonistic pods for 0.05–5.07 h (median = 0.73 h, mean = 0.85 h, SD = 0.55 h, $n = 432$), and other behaviour pods for 0.02–3.72 h (median = 0.43 h, mean = 0.56 h, SD = 0.46 h, $n = 3268$). Observation durations of pods that did not associate while under study (PDNA, **Supplementary Appendix Table 3**) ranged from 0.02 to 3.72 h (median = 0.45 h, mean = 0.56 h, SD = 0.48 h, $n = 3{,}484$), and for newly associated pods (NAP, **Supplementary Appendix Table 3**) ranged from 0.02 to 5.07 h (median = 0.83 h, mean = 0.97 h, SD = 0.58 h, $n = 465$).

Frequencies, Proportions and Pod Sizes

The frequencies, proportions and pod sizes of non-agonistic pods, competitive pods, and other behaviour pods are reported for all pods, non-calf pods, pods containing one or more calves, and by newly associated pods and pods that did not associate (**Supplementary Appendix Table 3**). The pod data by week within season used in analyses and modelling is presented in **Table 1** above.

Avoidance and Repulsion Behaviour

There were instances in the "other behaviour pods" category (**Supplementary Appendix Table 2**) of agonistic behaviour that did not meet the definitions of a competitive pod. In 28 pods (0.71% of 3,949 pods), a mother actively repulsed or avoided the advances of a single escort (for description of these behaviours see Pack et al., 2002). All except one of these pods were trios, consisting of mother-calf and escort; the other pod was a mother in the company of two small calves repulsing an agonistic aggressive approach by a single escort. Between 1992 and 2005 there were only two sightings of a mother with two calves in Hervey Bay (Franklin et al., 2011). Of the 28 pods, 22 (78.6%) involved a mother avoiding the agonistic advances of a single escort and 6 pods (21.4%) involved her actively repulsing the agonistic advances of a single escort.

Non-agonistic Pods and Competitive Pods Within Season

The number of all observed pods, newly associated pods, non-agonistic pods and competitive pods are reported by week within season in **Table 1**.

Statistical Analysis and Modelling

Newly Associated Pods

The proportion of newly associated pods in Hervey Bay varied from 5.0 to 14.4% over the years, and from 16.9% to 7.2% over the weeks within year (**Figures 3A,B**, respectively). Although there was no systematic pattern to the variation over years, the proportion of newly associated pods over weeks within year was significantly greater in August compared to September and October (15.0%, 9.8%; Fisher's exact test, $P < 0.001$).

Newly associated pods on average, as expected, were significantly larger than pods that did not associate with other whales while under observation (Mann–Whitney test, $P < 0.001$). Newly associated pods ranged in size from 2 to 14 whales (mode = 4, median = 5, mean = 4.9, SD = 1.85, $n = 465$) while pods that did not associate with other whales while under observation, ranged from 1 to 9 whales (mode = 2, median = 2, mean = 2.3, SD = 0.98, $n = 3{,}484$) (**Figure 3C** and **Supplementary Appendix Table 3**).

The proportion of pods with calves present increased rapidly from the last week in August, to the end of the season in mid-October (3.6–92.8%, Franklin et al., 2011). Pods that included a calf were less likely to associate than pods that did not include a calf (9.9%: 13.2%, $\chi^2 = 10.57$, df = 1, $P < 0.001$). However, when pods that included a calf did associate, they were more likely to associate with pods that also included a calf, than with pods that did not include a calf (70.4%: 29.6%; $\chi^2 = 16.33$, df = 1, $P < 0.001$).

Non-agonistic Pods

As non-agonistic pods and newly associated pods were closely related (see results below), the following analyses were conducted on the dataset in **Table 1**, which includes the data on newly associated pods and pods that did not associate while under observation. Of the 3,949 pods in the data set, 2,287 [57.9%, Subset (a), **Table 1**] included at least 2 whales (excluding a mother alone with her calf), and it was this subset that was analysed.

Non-agonistic social behaviour was observed in 465 (20.3%) of the 2,287 pods. Non-agonistic social behaviour in pods was:

1. Observed with greater frequency in newly associated pods (139/435 = 32.0%) than in pods that did not associate (326/1,852 = 17.6%), ($\chi^2 = 44.79$, df = 1, $P < 0.001$);
2. Significantly variable over years ($\chi^2 = 44.79$, df = 13, $P < 0.001$);
3. Observed significantly more often in pods with no calf present (421/1,759 = 23.9%) than in pods with a calf or calves present (44/528 = 8.3%) ($\chi^2 = 61.02$, df = 1, $P < 0.001$);

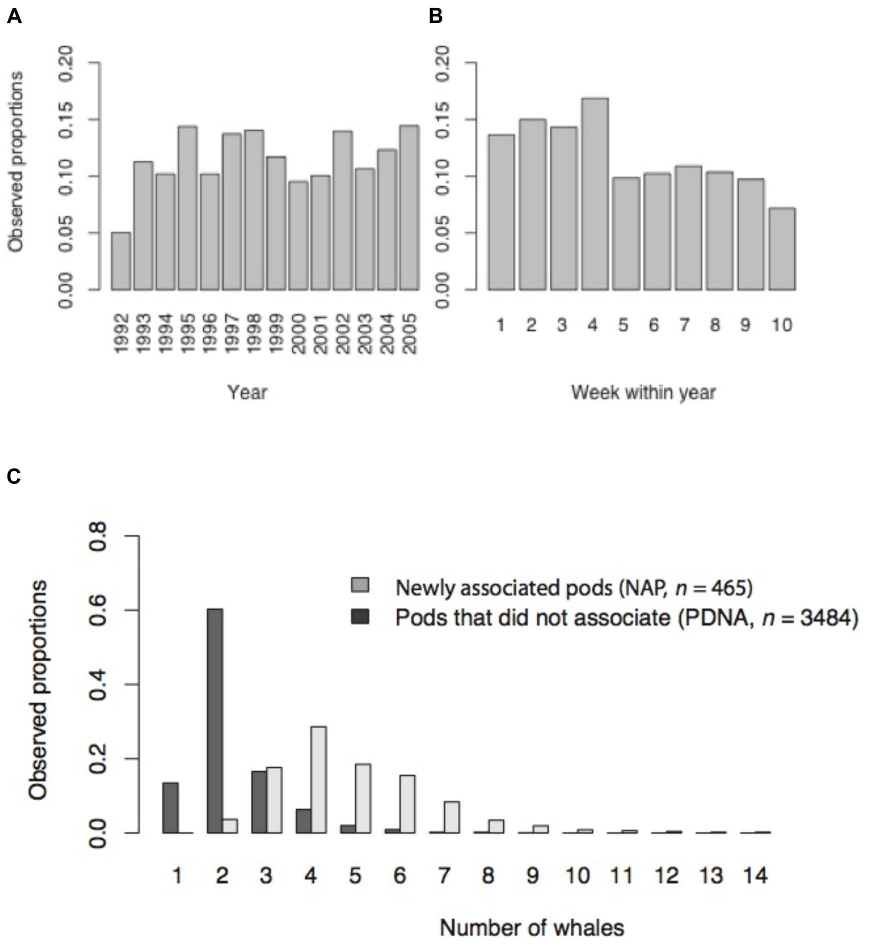


FIGURE 3 | Observed proportions: **(A)** newly associated pods by year, **(B)** newly associated pods by week within year, **(C)** pods by number of whales in pods for newly associated pods (NAP) and pods that did not associate while under observation (PDNA).

4. Observed to significantly increase in frequency with the number of whales in the pod (excluding calves) (176/1,319 = 13.3%, 125/446 = 28.0%, 76/276 = 27.5%, 88/246 = 35.8% in pods with 2, 3, 4, and 5+ whales, respectively, $\chi^2 = 101.12$, df = 3, $P < 0.001$);
5. Significantly variable by week within year ($\chi^2 = 104.88$, df = 9, $P < 0.001$).

However, these univariate effects were not independent. Consequently, a binary logistic regression model was fitted to assess the joint effects of newly associated pods (yes, no), presence of calf (present, not present), year, week within year and number of whales (excluding calves) (2, 3, 4, 5+) on the probability of observing non-agonistic social behaviour.

The five main effects were fitted as a block, which accounted for a significant proportion of variation (Likelihood ration $\chi^2 = 321.41$, df = 27, $P < 0.001$; AIC = 1217.846). None of the five predictors was redundant (All $p \leq 0.004$). Adding the two-way interaction effects individually to the model showed that only the newly associated pods by number of whales in the pod interaction effect was significant ($p < 0.05$).

The selected model included the five main effects and the newly associated pods by number of whales (excluding calves) interaction effect (Likelihood ratio $\chi^2 = 334.59$, df = 30, $P < 0.001$; AIC = 1210.661).

Goodness of fit was assessed as the ratio of the deviance to its degrees of freedom, which indicated significant deviation of the data from the binomial model (Deviance/df = 1.110, Chi squared $p = 0.021$). The significance of this, however, is largely a consequence of a very large number of degrees of freedom and adjustment of residual variances would not affect which variables were significant ($p < 0.05$) in the model. Bootstrapped estimates (2000 iterations) were obtained to check on this and their standard errors were found to be substantially unaffected. Moreover, Wedderburn (1974) provides theoretical considerations to justify the usual MLEs (Maximum Likelihood Estimations) as (asymptotically) optimal point estimators of the model parameters, even when there is overdispersion in the data. Given these considerations, the MLE estimates are reported here.

The only redundant effect ($p > 0.163$) was for the number of whales in the pod. This variable participates in the newly associated pods by number of whales (excluding calves) interaction effect and must be included in the model although it would not be independently interpreted. It is not unexpected that main effects underlying an interaction effect may be non-significant. That all main effects other than the number of whales in the pod remained significant (all $p < 0.001$) indicates that such multicollinearity as may be present among the explanatory variables does not deprive any of them from making an important contribution to the model. Moreover, the estimated proportions in the categories of each explanatory variable from the model and the raw percentages reported above correspond reasonably well indicating that multicollinearity has not strongly or adversely affected interpretation of the effects (see **Figure 4** below).

The parameter estimates (logistic scale) and their standard errors are not reported. The parameter estimates were used to calculate the estimated probabilities of observing non-agonistic social behaviour by the factors in the model.

The estimated probability of observing non-agonistic social behaviour by year, week within year and by number of whales (excluding calves), in newly associated pods (No, Yes) are plotted in **Figure 4**.

The variation over years in the probability of observing non-agonistic social behaviour (**Figure 4A**) includes a rapid decline over the period 1992–1995 followed by a sudden increase in 1996. This was followed by a decline to 2001 and an increase after that to 2005.

The probability of observing non-agonistic social behaviour was highest during the first 4 weeks of the season (August) and declined rapidly from week 5 (**Figure 4B**). Although the effect of the presence of a calf in a pod is not shown in **Figures 4A–C**, there was a significant main effect in the model with the rate of occurrence of non-agonistic social behaviour being significantly lower in pods that included calves (8.3% with calves, 23.9% without calves, see **Supplementary Appendix Table 3**). That the presence of calf and week within year effects were significant in the model indicates that the calf effect is not simply due to the rapidly increasing proportion of pods that included calves later in the season (3.6% in late August to 92.8% by mid-October, Franklin et al., 2011). This indicates that the calf effect is over and above the decline in the rate of non-agonistic social behaviour shown in **Figure 4B**.

The probability of observing non-agonistic social behaviour increased with the number of whales (excluding calves) in the pod and was higher for pods of two whales (excluding calves) that were newly associated, than for pods of two whales that did not associate while under observation (**Figure 4C**). This difference largely accounts for the pod size effect. Thus, the effect of newly associated pods is largely confined to the difference between newly associated pods of two (two singletons associating) rather than newly associated pods of larger size.

Competitive Pods

As competitive pods and newly associated pods were closely related (see results below), the following analyses were conducted on the data set in **Table 1**, which included the data on newly associated pods and pods that did not associate while under observation. Of the 3,949 pods in the data set, 940 [23.8%, Subset (b), **Table 1**] were pods that included at least three whales, of which at least two were non-mothers; it is this subset that was analysed. Competitive behaviour was observed in 249 (26.5%) of these 940 pods.

The factors; newly associated pod, year, presence of calf, number of whales in pod (excluding calves), and week within

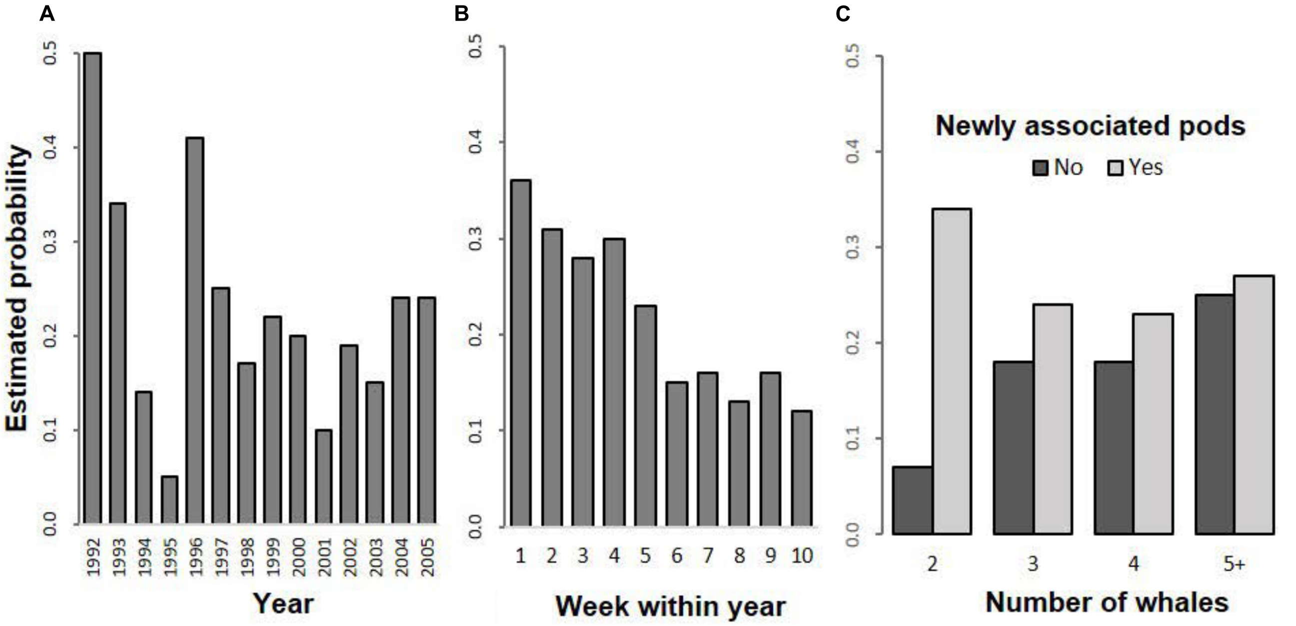


FIGURE 4 | Estimated probabilities of observing non-agonistic social behaviour: **(A)** by year; **(B)** by week within year; **(C)** by number of whales (excluding calves), in newly associated pods (No, Yes).

year were each assessed for effects on the probability of observing competitive social behaviour. Competitive social behaviour in pods was:

1. Observed in a greater proportion of newly associated pods (140/376 = 37.2%) than in pods that did not associate while under observation (109/564 = 19.3%) ($\chi^2 = 37.15$, df = 1, $P < 0.001$);
2. Not significantly variable over years ($\chi^2 = 13.55$, df = 13, $P = 0.406$);
3. Significantly more frequent in pods with calves present (87/191 = 45.5%) than in pods with no calf or calves present (162/749 = 21.6%), ($\chi^2 = 44.72$, df = 1, $P < 0.001$);
4. Observed to significantly increase in frequency with the number of whales in the pod (excluding calves) (70/425 = 16.5%, 72/270 = 26.7%, and 107/245 = 43.7% for 3, 4, and 5+ whales, respectively, $\chi^2 = 59.07$, df = 2, $P < 0.001$);
5. Observed to significantly increase in frequency over weeks within year (from ∼12 to ∼45%), $\chi^2 = 65.66$, df = 9, $P < 0.001$).

However, these univariate effects were not independent. Consequently, a binary logistic regression model was fitted to assess the joint effects of newly associated pods (yes, no), presence of calf (present, not present), number of whales (excluding calves) (3, 4, 5+), and week within year (1, 2, . . ., 10) on the probability of observing competitive social behaviour.

Together the four main effects accounted for a significant proportion of variation in the rate of observation of competitive pods (Likelihood ratio $\chi^2 = 137.23$, df = 13, $P < 0.001$). However, the marginal Wald tests showed the calf effect to be non-significant in the context of the other effects (Wald Chi squared = 2.993, df = 1, $P = 0.084$). The non-significance of the calf effect was largely due to the strength of the association between the increasing proportion of calf pods and week within season. The presence of calf effect was removed from the model at this point.

An attempt to fit interaction effects required considerable collapsing of categories and failed to produce useful results. Consequently, the selected model included only the three main effects for newly associated pods, number of whales (excluding calves) and week within year (Likelihood ratio $\chi^2 = 134.26$, df = 12, $P < 0.001$; AIC = 230.72). Goodness of fit was assessed as the ratio of the deviance to its degrees of freedom, which indicated no significant deviation of the data from the binomial model (Deviance/df = 1.103, Chi squared $p = 0.290$).

The parameter estimates (logistic scale) and their standard errors are not reported. The parameter estimates were used to calculate the estimated probabilities of observing competitive social behaviour by the explanatory factor levels.

Removal of the presence of calf from the model removed the most obvious cause of multicollinearity. All effects remaining in the model were significant ($p \leq 0.004$) and the estimated proportions in the categories of each explanatory variable from the model and the raw percentages reported above correspond reasonably well indicating that multicollinearity has not strongly or adversely affected interpretation of the effects (see **Figure 5** below).

The mean probabilities of observing competitive social behaviour by newly associated pods (yes, no), number of whales (excluding calves) (3, 4, 5+) and for week within year are plotted in **Figure 5**.

That the effects of increasing pod size and newly associated pods are jointly significant indicates that the rate of competitive social behaviour is greater in newly associated pods than in pods

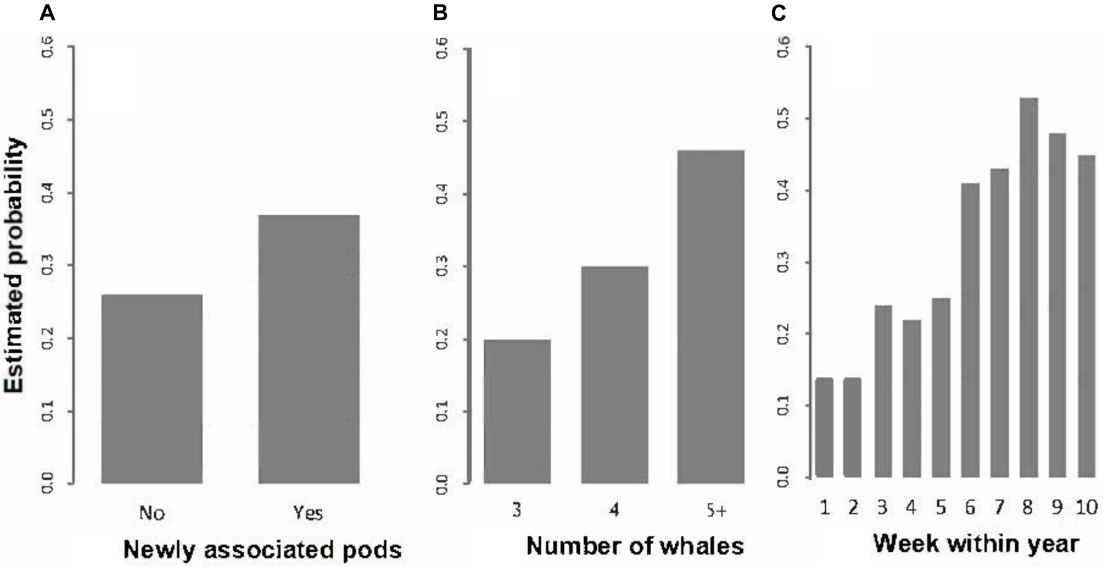


FIGURE 5 | Estimated probabilities of observing competitive social behaviour: **(A)** by newly associated pods (No, Yes); **(B)** by number of whales (excluding calves); and **(C)** by week within year.

that did not associate and is not simply a function of the increase in pod size following the formation of a newly associated pod. As shown in **Figure 5B**, larger pods were more likely to be competitive, with a larger increase in the frequency of competitive social behaviour between 4 and 5+ whales than between 3 and 4 whales. However, as shown in **Figure 5A**, if those pods have just associated, there is an approximately 11% increase in the frequency of competitive social behaviour compared to (i.e., over and above) pods of the same sizes that did not associate while under observation.

The calf effect was likely non-significant in the context of the other effects because the presence of calf and week within year were very strongly associated ($\chi^2 = 349.76$, df = 9, $P < 0.001$).

DISCUSSION

Our results provide the first systematic seasonal study of non-agonistic social behaviour and agonistic competitive social behaviour in humpback whale pods in a site-specific female-biassed stopover along the southern migratory route from the eastern Australian breeding grounds. Behaviour in Hervey Bay is related to maternally directed philopatry, pod associations and the occurrence and timing of classes of humpback whales using the Bay. There are important differences and similarities with humpback whale behaviour in Hervey Bay compared with behaviour reported in Northern Hemisphere breeding grounds and feeding areas (see review in Clapham, 2000), and along some migratory corridors in the Southern Hemisphere.

A major contrast in humpback behaviour presented in this study, compared to reports of female avoidance from traditional breeding grounds and feeding areas (Clapham, 2000), is that mature females in Hervey Bay, non-lactating and lactating, are involved in multiple non-agonistic pod associations and complex social interactions with immature males and females and new season's calves. The results presented in this study indicate that non-agonistic social behaviour may be more prevalent in humpback whale social organisation than previously reported (see Darling et al., 2006).

Differences and Similarities Between the Behaviour and the Social Interactions of Humpback Whales in Hervey Bay Compared to Northern Hemisphere Breeding and Feeding Grounds

Hervey Bay is neither a breeding nor a feeding ground, but a stopover early in the southern migration (Franklin et al., 2018), after humpback whales leave the putative breeding grounds north of Hervey Bay (Simmons and Marsh, 1986; Paterson, 1991; Chaloupka and Osmond, 1999; Smith et al., 2012). Burns et al. (2014) reported that eastern Australian humpback whales spend an average of 4 weeks in the breeding grounds, and the peak-breeding month in eastern Australia is August (Chittleborough, 1965). Calves are rarely seen in Hervey Bay during August (Franklin et al., 2011). Consequently, the calves entering Hervey Bay during September and October are likely to be larger, older and more robust than calves occurring in the breeding grounds and likely to be aged anywhere from 4 to 12 weeks.

It has been suggested that in feeding and breeding grounds a rarity of female-female associations may reflect avoidance and/or competition between females (Clapham, 2000). Furthermore, in the Hawaiian breeding ground mother-calf pods actively avoid encounters with other mother-calf pairs (Darling, 2001) and the modal size for pods having a calf present was three, mother-calf and escort (Herman and Antinoja, 1977; Herman et al., 1980, 2011; Glockner and Venus, 1983; Mobley and Herman, 1985). In Hervey Bay the modal size for pods was two, because of the significantly higher proportion of mothers alone with their calf (Franklin et al., 2011). In contrast to the above reports of female and mother-calf avoidance in feeding areas and breeding grounds, when pods that included a calf did associate in Hervey Bay, they were significantly more likely to associate with pods in which one or more mother-calf pairs were present than with pods not containing mother-calf pairs. Approximately 64% of "Other Behaviour" pods were mothers alone with their calves, while 29% involved associations of from two to seven mother-calf pods (see **Supplementary Appendix Table 3**).

The typical behaviour in these multiple mother-calf pod associations, usually involved highly surface-active calves, socially interacting with each other and with mothers carefully keeping the calves apart and possibly avoiding injury during these social interactions (Franklin, 2012). Moreover, last season's calves and mature females were often involved in these multiple mother-calf pod associations (Franklin, 2012), with mothers constantly engaged in ensuring the safety of the calves by maintaining separation amongst calves during these extended social interactions. Calf surface activity involves early social opportunities and experience for older calves. The largest association of mother-calf pods observed in Hervey Bay consisted of seven mother-calf pairs, involving fourteen individual whales in which, all calves were involved in surface-active behaviours and ongoing social interactions. We suggest that the opportunity for multiple mother-calf pod associations and social interactions among those mother-calf pods, occurring in Hervey Bay during September and October, may contribute to preparing the calves for their return journey to join the cohort of new-seasons yearlings in Hervey Bay during August the following year.

It is well established that the association between a new calf and its mother endures for most, if not all, of the first year of the calf's life (Clapham, 2000), and that calves learn from their mothers the migratory routes which will take them each season between breeding and feeding grounds (Baker and Herman, 1984a; Clapham, 2000; Franklin et al., 2018). Clapham (1993) reported that mothers spend 77% of their time alone with their calves in the feeding grounds, as the calves complete the weaning process to independent feeding. Similarly, during the stopover in Hervey Bay, prior to leaving for Antarctic feeding grounds, lactating females spend 69% of their time alone with their calves nursing, resting and engaging their offspring in surface behaviours (Franklin et al., 2011), the latter of which may assist in the development of muscular myoglobin (Cartwright et al., 2016).

Weinrich and Kuhlberg (1991) reported stable social associations among female humpback whales feeding in the southern Gulf of Maine and hypothesised that stable associations allow adult females to maximise their net energy gain through cooperative feeding. The structure of the annual migration with mature, resting and early pregnant, females leading the migration south from the breeding grounds, co-temporal with immature males and females and then lactating females with new calves being the last cohort to move south has been shown to be a constant feature of the social organisation of humpback whales (Dawbin, 1966, 1997; Franklin et al., 2018). As reported in this study, when mother-calf pods in Hervey Bay do associate, they are significantly more likely to associate with other mother-calf pods. We suggest that the behaviour of mature females in Hervey Bay involves cooperative social interactions with immature whales during August to maximise social development (Franklin, 2012) and as well, cooperative behaviour through separation among lactating females, during September and October (69% alone with calf, Franklin et al., 2011) which, may minimise the energetics of lactation (Lockyer, 1981, 1984).

In contrast to reports of female avoidance from breeding and feeding grounds in the Northern Hemisphere, when mature non-lactating and lactating females were observed interacting with each other during the Hervey Bay stopover, they were involved in non-agonistic social interactions and multiple pod associations. Overall, mature females in Hervey Bay are involved in non-agonistic cooperative social interactions.

Differences and Similarities Between the Behaviour and Social Interactions of Humpback Whales in Hervey Bay Compared to Other Site-Specific Migratory Corridor Locations

Baker et al. (1990) reported a marked segregation of mitochondrial DNA haplotypes among subpopulations of humpback whales on different feeding and wintering grounds and interpreted this segregation to be the consequence of maternally directed fidelity to migratory breeding and feeding destinations. Photo-identification of individual humpback whales over long periods of time has documented maternally directed fidelity to feeding destinations (Martin et al., 1984; Clapham and Mayo, 1987; Katona and Beard, 1990; Clapham et al., 1993; Palsbøll et al., 1997).

In the Southern Hemisphere, humpback whales predominantly migrate along the extensive continental coastlines and nearshore islands of eastern and western Australia, Africa, and South America, en route to and from tropical breeding grounds (Chittleborough, 1965; Dawbin, 1966, 1997). Franklin et al. (2018) reported that the site-specific female-biassed sex ratio occurring in Hervey Bay (25°S) involved female philopatry and high levels of survival and site fidelity, of all classes of humpback whales using Hervey Bay. They suggested that Hervey Bay was a socially and ecologically important habitat for mature females, accompanying and socially interacting with immature males and females in August and lactating females with older calves involved in maternal and social activities during September and October. The behaviour in Hervey Bay reported in this study is consistent with previous observations of the occurrence and timing of classes of humpback whales using Hervey Bay as a stopover early in the southern migration.

Several studies have reported site-specific behaviour along Southern Hemisphere coastal migratory corridors, including resting, nursing and early feeding locations. In contrast to Hervey Bay, Brown et al. (1995) reported a male-biassed sex ratio in the migratory corridor off Stradbroke Island, southeast Queensland (27°S), Australia, during the northern and southern winter migration. Brown and Corkeron (1995) investigated pod size on the northern migration from late-May to mid-August and reported that most pods travel north in pods of one to two whales with pod sizes ranging up to nine whales. Whereas in Hervey Bay on the southern migration, pod size range between two and fourteen whales, with the larger average pod sizes reflecting the high rates of pod associations in the Bay. Overall, 12.7% of pods biopsied off Stradbroke were classified as competitive (Brown and Corkeron, 1995), almost double the 6.3% of competitive pods observed in Hervey Bay. Furthermore, Brown and Corkeron (1995) reported that during the southern migration the social relationship between most males was characterised by non-agonistic and occasionally cooperative interactions. Franklin et al. (2018) suggested that habitat preferences and differential migration of females and males provides a plausible explanation for site-specific sex-bias in breeding grounds, migratory stopovers, and along migratory corridors.

The only other female-biassed sex ratio reported in a migratory corridor, other than Hervey Bay, was in an early feeding area off the southwestern coast of Africa (33°S), (Barendse et al., 2010). Barendse et al. (2013) also reported a female-dominated presence in the same area including non-nursing (possibly pregnant) females and yearlings, which suggested female-derived site fidelity, likely involving culturally transferred fidelity to a feeding area.

Meynecke et al. (2013) studied humpback whales using the Gold Coast Bay, southeast Queensland (28°S) as a temporary stopover during the northern and southern migration and reported resting behaviour during the southern migration. They reported similar patterns in pod sizes and timing of classes of whales during the southern migration to those recorded in Hervey Bay in this study. Consistent with Hervey Bay data, sightings of mothers with calves were highest in October with fewer sightings in August and September. Bruce et al. (2014) investigated the spatial use of Jervis Bay (35°S) off the coast of southern NSW by humpback whales during the late-2000s. They suggested that, associated with increases in the population, calf and non-calf pods were using Jervis Bay as a resting area with mother-calf pods preferring shallower waters.

Site-specific early feeding locations early in the southern migration have been reported within the migratory corridor off eastern Australia at Cape Morton, southeastern Queensland (27°S, Stockin and Burgess, 2005), Eden, off the coast of southern NSW (37°S, Stamation et al., 2007; Owen et al., 2015), and off the eastern coast of Tasmania (43°S, Gill et al., 1998). Garrigue et al. (2015) investigated the migratory movement of humpback whales in the southern waters of New Caledonia using satellite-monitored tags deployed between 21°S and 23°S. In contrast to Hervey Bay, they suggested that seamounts probably serve multiple and important roles as breeding locations, resting areas, navigational landmarks or even supplemental feeding grounds [also see MacKay et al. (2016) and Derville et al. (2020) for reports on use of seamounts by humpback whales]. Together these data suggest that site-specific stopover habitats in the Southern Hemisphere migratory corridors along the extensive coastlines of eastern and western Australia, South Africa, and South America; may enhance reproductive success (e.g., see Franklin, 2014; Noad et al., 2019) and therefore recovery of humpback whale populations using these habitats. Moreover, observed behaviour at these site-specific locations will be related to the occurrence and timing of classes of humpback whales using these locations.

Pod Associations and Non-agonistic Behaviour in August

While there was no systematic pattern in the frequency of newly associated pods over years in Hervey Bay, the rate of formation of newly associated pods within season was significantly higher during August compared to September and October (see **Figures 3A,B**). This result, together with the significant differences in pod characteristics and composition within season reported in Franklin et al. (2011), confirm that there are differences in the maturational and reproductive classes of humpback whales present in Hervey Bay in August compared to September and October (also see Franklin et al., 2018).

In Hervey Bay, 52% of singleton pods occurred in August when calves were rarely seen and 69% of 3 and 4+ larger pods with no calves present also occurred in August (Franklin et al., 2011). Overall, in Hervey Bay singletons and pairs predominated in the formation of newly associated pods (**Supplementary Appendix Table 1**). The social interactions occurring among singletons, involved in non-agonistic social behaviour in August, is reflected in the markedly higher probability of observing two singletons forming pairs in newly associated pods (**Figure 3C**). Consequently, the presence of socially active immature males and females, involved in increasing social interactions with each other and with mature females (e.g., see Franklin, 2012; Franklin et al., 2018) are likely to contribute to the higher rate of newly associated pods and the occurrence of non-agonistic pods during August.

There was significant variability in the occurrence of non-agonistic social behaviour over years and within season (see **Figure 4** above). Franklin et al. (2011) reported a significant increase in pods with 3+ whales over years in Hervey Bay. They suggested that as the population increased, larger groups became more common and were likely to have generated a skewed distribution in the population toward younger whales. Therefore, the variability of non-agonistic social behaviour over years may be related to the relative proportions of age, sex, reproductive and maturational classes of humpback whales entering Hervey Bay in any given year.

Franklin (2012) reported the social interactions of known-age individuals from calves to maturity and the complex social interactions between immature males and females, with non-lactating and lactating mature females. Pack et al. (2012) found that many male-female dyads were comprised of immature whales and suggested that these pairings were important for social learning and development. The social behaviour of mature females and immature males and females is reflected in the higher frequency of non-agonistic pods in newly associated pods and as pod size increases during August.

The probability of observing non-agonistic social behaviour increased with the number of whales in the pod (**Figure 3C**). Franklin et al. (2011) suggested that because whales enter and leave Hervey Bay from the north, the density and movements of whales increased the likelihood of interactions among pods, contributing to the formation of larger pods or to the probability of encountering recently aggregated pods. Consequently, the higher levels of non-agonistic social behaviour pods observed during August is related to pod associations and the complex social interactions occurring among immature males and females and mature females (Franklin, 2012).

Average residency of humpback whales in Hervey Bay is from 1.5 to 2 weeks (Franklin, 2014). Hervey Bay offers mature females an important habitat for social activity conducive to social development (Franklin, 2012; Franklin et al., 2018), and for physical development of immature male and female whales and calves (Cartwright et al., 2016). We suggest that Hervey Bay is an area of aggregation early in the southern migration, for mature females travelling with the new season's yearlings and the immature cohort during August.

Competitive Behaviour and Males Maximising Mating Opportunities

Only a low proportion of pods in Hervey Bay were involved in agonistic competitive behaviour. The probability of observing competitive pods in Hervey Bay was at its lowest during August and increased significantly throughout the season. Franklin et al. (2011) reported that pod characteristics early in the season in Hervey Bay were consistent with the presence of immature males and females, while Franklin et al. (2018) confirmed that mature, resting or early pregnant, females use Hervey Bay during August, co-temporal with immature male and female humpback whales with few mature males present. The absence of mature males relative to mature and immature females in August may contribute to the observed lower levels of competitive pods during August.

Although the probability of observing competitive pods was highest from mid-September onward, the number of pods available to engage in competitive behaviour was relatively small, as most pods were composed of mothers alone with their calves (Franklin et al., 2011). Chittleborough (1958, 1965) reported that post-partum oestrous may occur in a minority of cases and this would likely occur 1 month after parturition, and that August is the peak-birthing month. However, mothers with calves are rarely present in Hervey Bay during August and begin moving into the bay with older calves in early September (Franklin et al., 2011, 2018). Consequently, the occurrence of competitive pods from September onward in Hervey Bay, is likely to be related to some males seeking to maximise mating opportunities due to the presence of potentially oestrous mature, and the possibility of post-partum oestrous lactating females (e.g., see Franklin et al., 2018; Pallin et al., 2018). Baker and Herman (1984a) and Craig et al. (2002) reported increased competitive activity of males toward females with a calf at the end of the season in the Hawaiian breeding grounds, related to the declining numbers of non-lactating oestrous females. Consequently, the potential decline in availability of non-lactating oestrous females in Hervey Bay as the season progresses, may be a major factor influencing male behaviour leading to an increased rate of occurrence of competitive pods involving mother-calf pairs toward the end of the season.

Craig et al. (2014) reported that females with calves in the Hawaiian breeding grounds favoured shallow waters to avoid energetically costly male harassment. Overall, few mature male humpback whales use Hervey Bay (Franklin et al., 2018), and the relatively shallow waters of Hervey Bay (Ribbe, 2014) may be beneficial in minimising harassment of mature females from mature males prospecting for mating opportunities among mature females.

It has been reported that the reproductive success of long-lived mammals occurs over many breeding seasons and individual male humpback whales may behave to maximise their reproductive success over a lifetime (Clapham, 1996; Boness et al., 2002). Although Hervey Bay is south of the presumed breeding ground of eastern Australian humpback whales (Simmons and Marsh, 1986; Paterson, 1991; Chaloupka and Osmond, 1999; Smith et al., 2012), it is a habitat where predictable aggregations of females occur (Franklin et al., 2011, 2018). The proportion of competitive pods in Hervey Bay compared to other pod types was low (i.e., 6.3% of pods). However, the presence of some escorting behaviour combined with the occurrence of singing day and night (Mark Francis Franklin, unpublished data) indicates that some mature males are prospecting for mating opportunities in Hervey Bay with late, or post-partum, ovulating females.

Relative Proportions of Non-agonistic and Agonistic Behaviour

Competitive group behaviour has been well documented in the Northern Hemisphere predominantly in breeding grounds (Darling et al., 1983; Tyack and Whitehead, 1983; Baker and Herman, 1984b; Clapham et al., 1992; Clapham, 2000) and within a migratory corridor in the Southern Hemisphere (Brown and Corkeron, 1995). Darling et al. (2006) noted that competitive behaviour is more conspicuous than cooperative relationships, which are more difficult to identify and confirm. Non-agonistic and cooperative behaviour has been reported in various earlier studies (Herman and Antinoja, 1977; Tyack and Whitehead, 1983; Clapham et al., 1992; Brown and Corkeron, 1995). Darling et al. (2006) suggested that non-agonistic behaviour may be more prevalent in humpback whale interactions than has previously been reported, and that while competitive and non-agonistic relations do occur, the relative proportion of each type of behaviour in a humpback population is not known.

This current study provides a measure of the relative proportion of agonistic competitive behaviour and non-agonistic behaviour of humpback whales within season, in a preferential female stopover in Hervey Bay. Overall, agonistic behaviour (7.0%) occurred in competitive groups (6.3%), with only a very small proportion of repulsion or avoidance behaviour by mothers toward escorts (0.7%) occurring outside of competitive groups. However, it is important to note that 82.8% of pods in Hervey Bay were "other behaviour" pods, of which a third (1107 of 3268, 33.9% of pods; see **Supplementary Appendix Table 3**) were mothers alone with their calf, involved in non-agonistic social behaviour. Consequently, the results of this study substantiate that non-agonistic social behaviour may be more prevalent than aggressive agonistic social behaviour in site-specific locations and habitats, depending upon the classes and timing of humpback whales using such locations and habitats.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by the Animal Research Authorities issued by the Southern Cross University Animal Care and Ethics Committee.

AUTHOR CONTRIBUTIONS

TF and WF conceived the fieldwork, designed the study, collected the data, and wrote the manuscript. LB analysed the data and undertook modelling, assisted by TF and WF with data curation and interpretation of results. All authors contributed critically to the manuscript drafts and gave final approval for publication.

FUNDING

The long-term study of humpback whales in Hervey Bay, being conducted by TF and WF, were supported by The Oceania Project's paying internship program aboard the annual Whale Research Expeditions, and in part by an Australian Research Council Linkage grant with the Southern Cross University, Marine Ecology Research Centre (MERC) and International Fund for Animal Welfare (IFAW). This research in Hervey Bay was conducted under Scientific and Marine Park Permits issued by the Queensland Parks and Wildlife Service (permit numbers WISP03749806 and MP2006/020), and annual Animal Research Authorities issued by the Southern Cross University Animal Care and Ethics Committee.

ACKNOWLEDGMENTS

We thank Tim Stevens for assistance in the implementation of the long-term study in Hervey Bay and Emeritus Peter

Baverstock and Phil Clapham for their support of the research over many years, and the Research Assistants and the participants in The Oceania Project's Internship program for their assistance and financial contribution to the study. We particularly thank Mark Cornish for his long-term involvement as a Research Assistant and for his financial support of The Oceania Project. We also thank Greg Luker and Daniele Cagnazzi from Southern Cross University, Marine Ecology Research Centre for assistance with figures. Finally, we thank the reviewers for their constructive comments and suggestions which, enhanced and strengthened the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.652147/full#supplementary-material

REFERENCES

Alerstam, T., and Hedenström, A. (1998). The development of bird migration theory. *J. Avian Biol.* 29, 343–369. doi: 10.2307/3677155

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* 49, 227–267. doi: 10.1163/156853974x00534

Baker, C. S., and Herman, L. M. (1984b). Aggressive behaviour between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Can. J. Zool.* 62, 1922–1937. doi: 10.1139/z84-282

Baker, C. S., and Herman, L. M. (1984a). Seasonal contrasts in the social behavior of humpback whales. *Cetus* 5, 14–16.

Baker, C. S., Palumbi, S. R., Lambertsen, R. H., Weinrich, M. T., Calambokidis, J., and O Brien, S. J. (1990). Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. *Nature* 344, 238–240. doi: 10.1038/344238a0

Barendse, J., Best, P. B., Carvalho, I., and Pomilla, C. (2013). Mother knows best: occurrence and associations of Resighted humpback whales suggest maternally derived fidelity to a Southern hemisphere coastal feeding ground. *PLoS One* 8:e81238. doi: 10.1371/journal.pone.0081238

Barendse, J., Best, P. B., Thornton, M., Pomilla, C., Carvalho, I., and Rosenbaum, H. C. (2010). Migration redefined? Seasonality, movements and group composition of humpback whales *Megaptera novaeangliae* off the west coast of South Africa. *Afr. J. Mar. Sci.* 32, 1–22. doi: 10.3354/meps118001

Baudouin, M., de Thoisy, B., Chambault, P., Berzins, R., Entraygues, M., Kelle, L., et al. (2015). Identification of key marine areas for conservation based on satellite tracking of post-nesting migrating green turtles (*Chelonia mydas*). *Biol. Conserv.* 184, 36–41. doi: 10.1016/j.biocon.2014.12.021

Boness, D. J., Clapham, P. J., and Mesnick, S. L. (2002). "Life history and reproductive strategies," in *Marine Mammal Biology: An Evolutionary Approach*, ed. A. R. Hoelzel (Oxford: Blackwell Science Ltd), 278–324.

Brown, M. R., Corkeron, P. J., Hale, P. T., Schultz, K. W., and Bryden, M. M. (1995). Evidence for a sex-segregated migration in the humpback whale (*Megaptera novaeangliae*). *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 259, 229–234. doi: 10.1098/rspb.1995.0034

Brown, M., and Corkeron, P. (1995). Pod characteristics of migrating humpback whales (*Megaptera novaeangliae*) off the east Australian coast. *Behaviour* 132, 163–179. doi: 10.1163/156853995x00676

Bruce, E., Albright, L., Sheehan, S., and Blewitt, M. (2014). Distribution patterns of migrating humpback whales (*Megaptera novaeangliae*) in Jervis Bay, Australia: a spatial analysis using geographical citizen science data. *Appl. Geogr.* 54, 83–95.

Burns, D., Brooks, L., Harrison, P., Franklin, T., Franklin, W., Paton, D., et al. (2014). Migratory movements of individual humpback whales photographed off the eastern coast of Australia. *Mar. Mamm. Sci.* 30, 562–578. doi: 10.1111/mms.12057

Cartwright, R., and Sullivan, M. (2009). Associations with multiple male groups increase the energy expenditure of humpback whale (*Megaptera novaeangliae*) female and calf pairs on the breeding grounds. *Behaviour* 146, 1573–1600. doi: 10.1163/156853909x458377

Cartwright, R., Gillespie, B., Labonte, K., Mangold, T., Venema, A., Eden, K., et al. (2012). Between a rock and a hard place: habitat selection in female-calf humpback whale (*Megaptera novaeangliae*) Pairs on the Hawaiian Breeding Grounds. *PLoS One* 7:e38004. doi: 10.1371/journal.pone.0038004

Cartwright, R., Newton, C., West, K. M., Rice, J., Niemeyer, M., Burek, K., et al. (2016). Tracking the development of muscular myoglobin stores in mysticete calves. *PLoS One* 11:e0145893. doi: 10.1371/journal.pone.0145893

Carvalho, I., Brito, C., Dos Santos, M. E., and Rosenbaum, H. C. (2011). The waters of São Tomé: a calving ground for West African humpback whales? *Afr. J. Mar. Sci.* 33, 91–97.

Chaloupka, M., and Osmond, M. (1999). "Spatial and seasonal distribution of humpback whales in the Great Barrier Reef region," in *Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals. American Fisheries Society symposium No. 23*, ed. J. A. Musick (Bethesda MD: American Fisheries Society), 89–106.

Chaloupka, M., Osmond, M., and Kaufman, G. (1999). Estimating seasonal abundance trends and survival probabilities of humpback whales in Hervey Bay (east coast Australia). *Mar. Ecol. Prog. Ser.* 184, 291–301. doi: 10.3354/meps184291

Chittleborough, R. G. (1958). The breeding cycle of the female humpback whale, *Megaptera nodosa*, (Bonnaterre). *Aust. J. Mar. Freshw. Res.* 9, 1–18. doi: 10.1071/MF9580001

Chittleborough, R. G. (1965). Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Aust. J. Mar. Freshw. Res.* 16, 33–128. doi: 10.1071/mf9650033

Chu, K., and Nieukirk, S. (1988). Dorsal fin scars as indicators of age, sex, and social status in humpback whales (*Megaptera novaeangliae*). *Can. J. Zool.* 66, 416–420. doi: 10.1139/z88-059

Clapham, P. J. (1993). Social organization of humpback whales on a North Atlantic feeding ground. *Symp. Zool. Soc. Lond.* 66, 131–145. doi: 10.1093/oxfordjournals.jhered.a111340

Clapham, P. J. (1996). The social and reproductive biology of humpback whales – an ecological perspective. *Mamm. Rev.* 26, 27–49.

Clapham, P. J. (2000). "The humpback whale – Seasonal feeding and breeding in a baleen whale," in *Cetacean Societies: Field Studies of Dolphins And Whales*, eds J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead (Chicago, IL: The University of Chicago), 173–196.

Clapham, P. J., and Mayo, C. A. (1987). Reproduction and recruitment of individually identified humpback whales, *Megaptera novaeangliae*, observed in Massachusetts Bay 1979-1985. *Can. J. Zool.* 65, 2853–2863. doi: 10.1139/z87-434

Clapham, P. J., and Mead, J. G. (1999). *Megaptera novaeangliae. Mamm. Species* 604, 1–9. doi: 10.2307/3504352

Clapham, P. J., Baraff, L. S., Carlson, C. A., Christian, M. A., Mattila, D. K., Mayo, C. A., et al. (1993). Seasonal occurrence and annual return of humpback whales, *Megaptera novaeangliae*, in the Southern Gulf of Maine. *Can. J. Zool.* 71, 440–443. doi: 10.1139/z93-063

Clapham, P. J., Palsboll, P. J., Mattila, D. K., and Oswaldo, V. (1992). Composition and dynamics of humpback whale competitive groups in the West Indies. *Behaviour* 122, 182–194.

Clapham, P. J., Wetmore, S. E., Smith, T. D., and Mead, J. G. (1999). Length at birth and at independence in humpback whales. *J. Cetacean Res. Manag.* 1, 141–146.

Clapham, P., Mikhalev, Y., Franklin, W., Paton, D., Baker, S., Ivashchenko, Y. V., et al. (2009). Catches of humpback whales, *Megaptera novaeangliae*, by the soviet union and other nations in the Southern Ocean, 1947-1973. *Mar. Fish. Rev.* 71, 39–43.

Constantine, R., Steel, D., Allen, J., Anderson, M., Andrews, O., Baker, C. S., et al. (2014). Remote Antarctic feeding ground important for east Australian humpback whales. *Mar. Biol.* 161, 1087–1093. doi: 10.1007/s00227-014-2401-2

Corkeron, P. (1993). *Aerial Survey Methodology for Hervey Bay Marine Park Queensland – A Review. Report to the Queensland Department of Environment and Heritage*, Brisbane, QLD: Queensland Department of Environment and Heritage, 1–33.

Corkeron, P. J., Brown, M., Slade, R. W., and Bryden, M. M. (1994). Humpback Whales, *Megaptera novaeangliae* (Cetacea: balaenopteridae), in Hervey Bay, Queensland. *Wildl. Res.* 21, 293–305. doi: 10.1071/wr9940293

Craig, A. S., Herman, L. M., and Pack, A. A. (2002). Male mate choice and male-male competition coexist in the humpback whale (*Megaptera novaeangliae*). *Can. J. Zool. Revue Can. Zool.* 80, 745–755.

Craig, A. S., Herman, L. M., Pack, A. A., and Waterman, J. O. (2014). Habitat segregation by female humpback whales in Hawaiian waters: avoidance of males? *Behaviour* 151, 613–631.

Dalla Rosa, L., Félix, F., Stevick, P. T., Secchi, E. R., Allen, J. M., Chater, K., et al. (2012). Feeding grounds of the eastern South Pacific humpback whale population include the South Orkney Islands. *Pol. Res.* 31:17324. doi: 10.3402/polar.v31i0.17324

Darling, J. D. (2001). *Characterization of Behaviour of Humpback Whales in Hawaiian Waters*. Honolulu, HI: Hawaiian Islands Humpback Whale National Marine Sanctuary, Division of Aquatic Resources, Department of Land and Natural Resources, 61.

Darling, J. D., and Berube, M. (2001). Interactions of singing humpback whales with other males. *Mar. Mamm. Sci.* 17, 570–584. doi: 10.1111/j.1748-7692.2001.tb01005.x

Darling, J. D., Gibson, K. M., and Silber, G. K. (1983). "Observations on the abundance and behavior of humpback whales (*Megaptera novaeangliae*) off West Maui Hawaii 1977-1979," in *Communication and Behavior of Whales*, ed. R. Payne (Boulder, CO: Westview Press), 201–222.

Darling, J. D., Jones, M. E., and Nicklin, C. P. (2006). Humpback whale songs: do they organize males during the breeding season? *Behaviour* 143, 1051–1101.

Dawbin, W. H. (1966). "The seasonal migratory cycle of humpback whales," in *Whales, Dolphins and Porpoises*, ed. K. S. Norris (Berkeley, CA: University of California Press), 145–170. doi: 10.1525/9780520321373-011

Dawbin, W. H. (1997). Temporal segregation of humpback whales during migration in southern hemisphere waters. *Mem. Qld. Mus.* 42, 105–138.

Delmore, K. E., Fox, J. W., and Irwin, D. E. (2012). Dramatic intraspecific differences in migratory routes, stopover sties and wintering areas, revealed using light-level geolocators. *Proc. R. Soc. B* 279, 4582–4589. doi: 10.1098/rspb.2012.1229

Derville, S., Torres, L. G., Zerbini, A. N., Oremus, M., and Garrigue, C. (2020). Horizontal and vertical movements of humpback whales inform the use of critical pelagic habitats in the western South Pacific. *Sci. Rep.* 10:4871. doi: 10.1038/s41598-020-61771-z

Dujon, A. M., Schofield, G., Lester, R. E., Esteban, N., and Graeme, C. H. (2017). Fatloc-GPS reveals daytime departure and arrival during long-distance migration and the use of different resting strategies in sea turtles. *Mar. Biol.* 164:187. doi: 10.1007/s00227-017-3216-8

Franklin, T. (2012). *The Social and Ecological Significance of Hervey Bay Queensland for Eastern Australian Humpback Whales (Megaptera novaeangliae).* Ph.D. thesis. Lismore, NSW: School of Environmental Science and Management, Southern Cross University, 245.

Franklin, T., Franklin, W., Brooks, L., and Harrison, P. (2018). Site-specific female-biased sex ratio of humpback whales (*Megaptera novaeangliae*) during a stopover early in the southern migration. *Can. J. Zool.* 96, 533–544. doi: 10.1139/cjz-2017-0086

Franklin, T., Franklin, W., Brooks, L., Harrison, P. L., Burns, D., Holmberg, J., et al. (2020). Photo-identification of individual Southern Hemisphere humpback whales (*Megaptera novaeangliae*) using all available natural marks: implications for misidentification & automated algorithm matching technology. *J. Cetacean Res. Manag.* 21, 71–83.

Franklin, T., Franklin, W., Brooks, L., Harrison, P., Baverstock, P., and Clapham, P. (2011). Seasonal changes in pod characteristics of eastern Australian humpback whales (*Megaptera novaeangliae*), Hervey Bay 1992-2005. *Mar. Mamm. Sci.* 27, E134–E152. doi: 10.1111/j.1748-7692.2010.00430.x

Franklin, W. (2014). *Abundance, Population Dynamics, Reproduction, Rates of Population Increase and Migration Linkages of Eastern Australian Humpback Whales (Megaptera novaeangliae) Utilising Hervey Bay, Queensland.* Ph.D. thesis. Lismore, NSW: School of Environmental Science and Management, Southern Cross University, 396.

Franklin, W., Franklin, T., Andrews-Goff, V., Paton, D. A., and Double, M. (2017). Movement of two Humpback whales (*Megaptera novaeangliae*) satellite-radio tagged off Eden, NSW and matched by photo-identification with the Hervey Bay catalogue. *J. Cetacean Res. Manag.* 17, 29–33.

Franklin, W., Franklin, T., Brooks, L., Gibbs, N., Childerhouse, S., Smith, F., et al. (2012). Antarctic waters (Area V) near the Balleny Islands are a summer feeding area for some Eastern Australian (E (i) breeding group) Humpback whales (*Megaptera novaeangliae*). *J. Cetacean Res. Manag.* 12, 321–327.

Garrigue, C., Clapham, P. J., Geyer, Y., Kennedy, A. S., and Zerbini, A. N. (2015). Satellite tracking reveals novel migratory patterns and the importance of seamounts for endangered South Pacific humpback whales. *R. Soc. Open Sci.* 2:150489. doi: 10.1098/rsos.150489

Gill, P. C., Evans, K. J., and Wapstra, H. (1998). *Feeding by Humpback Whales in Tasmanian Waters. Records of the Queen Victoria Museum Launceston 107*. Launceston, TAS: Queen Victoria Museum and Art Gallery, 1–5.

Glockner, D. (1983). "Determining the sex of humpback whales (*Megaptera novaeangliae*) in their natural environment," in *Communication and Behavior of Whales*, ed. R. Payne (Boulder, CO: Westview Press Inc), 447–464.

Glockner, D. A., and Venus, S. C. (1983). "Identification, growth rate and behavior of humpback whale (*Megaptera novaeangliae*) cows and calves in the waters off Maui, Hawaii, 1977-1979," in *Communication and Behavior of Whales*, ed. R. S. Payne (Boulder, CO: Westview Press), 223–258.

Harrison, P. L., and Woinarski, J. C. Z. (2018). "Recovery of Australian subpopulations of humpback whale. Chapter 2," in *Recovering Australian Threatened Species*, eds S. Garnett, P. Latch, D. Lindemeyer, and J. Woinarski (Clayton, VIC: CSIRO Publishing), 5–12.

Herman, L. M. (2017). The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: review, evaluation, and synthesis. *Biol. Rev.* 92, 1795–1818. doi: 10.1111/brv.12309

Herman, L. M., and Antinoja, R. C. (1977). Humpback whales in Hawaiian breeding waters: population and pod characteristics. *Sci. Rep. Whales Res. Inst.* 29, 59–85.

Herman, L. M., Forestell, P. H., and Antinoja, R. C. (1980). "The 1976/77 migration of humpback whales into Hawaiian waters: composite description," in *Final Report to the U.S. Marine Mammal Commission, Report # MMC-77/19. National Technical Information Service PBSO-162332*. Arlington, VA: United States National Technical Information Services, 55.

Herman, L. M., Pack, A. A., Rose, K., Craig, A., Herman, E. Y. K., Hakala, S., et al. (2011). Resightings of humpback whales in Hawaiian waters over spans of 10-32 years: site fidelity, sex ratios, calving rates, female demographics, and the dynamics of social and behavioral roles of individuals. *Mar. Mamm. Sci.* 27, 736–768.

IBM Corporation (2019). *IBM Corp. Released 2019. IBM SPSS Statistics for Windows, Version 26.0.* Armonk, NY: IBM Corporation.

Ivashchenko, Y. V., and Clapham, P. J. (2014). Too much is never enough: the cautionary tale of soviet illegal whaling. *Mar. Fish. Rev.* 76, 1–21. doi: 10.7755/mfr.76.1_2.1

Jones, M. E. (2010). *Female Humpback Whale (Megaptera novaeangliae) Reproductive Class and Male–Female Interactions During the Breeding Season.* Ph.D. thesis. Keene, NH: Antioch University, 202.

Katona, S. K., and Beard, J. A. (1990). Population size, migrations and feeding aggregations of the Humpback whale (*Megaptera novaeangliae*) in the Western North Atlantic Ocean. *Rep. Int. Whaling Comm. Spec. Issue* 12, 295–305.

Kennedy, J. S. (1951). The migration of the Desert Locust (*Schistocerca gregaria* Forsk.) I. The behaviour of swarms. II. A theory of long-range migrations. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 235, 163–290. doi: 10.1098/rstb.1951.0003

Lockyer, C. (1981). Growth and energy budgets of large baleen whales from the Southern Hemisphere. *FAO Fish. Ser.* 5, 379–487.

Lockyer, C. (1984). Review of baleen whale reproduction and implications for management. *Rep. Int. Whaling Comm. Spec. Issue* 6, 27–50. doi: 10.1016/0048-9697(94)90087-6

MacKay, M. M., Würsig, B., Bacon, C. E., and Selwyn, J. D. (2016). North Atlantic humpback whale (*Megaptera novaeangliae*) hotspots defined by bathymetric features off western Puerto Rico. *Can. J. Zool.* 94, 517–527. doi: 10.1139/cjz-2015-0198

Martin, A. R., Katona, S. K., Matilla, D., Hembree, D., and Waters, T. D. (1984). Migration of humpback whales between the Caribbean and Iceland. *J. Mammal.* 65, 330–333.

McCabe, J. D., and Olsen, B. J. (2015). Landscape-scale habitat availability, and not local geography, predicts migratory landbird stopover across the Gulf of Maine. *J. Avian Biol.* 46, 395–405. doi: 10.1111/jav.00598

McCord, J., and Davis, A. (2012). Characteristics of monarch butterflies (*Danaus plexippus*) that stopover at a site in coastal South Carolina during fall migration. *J. Res. Lepid.* 45, 1–8.

Meynecke, J.-O., Vindenes, S., and Teixeira, D. (2013). "Monitoring humpback whale (*Megaptera novaeangliae*) behaviour in a highly urbanised coastline: gold Coast, Australia," in *Global Challenges in Integrated Coastal Zone Management*, 2nd Edn, eds E. Moksness, E. Dahl, and J. Støttrup (Chichester: Wiley-Blackwell Ltd), 101–113. doi: 10.1002/9781118496480.ch8

Mikhalev, Y. A. (1997). Humpback whales *Megaptera novaeangliae* in the Arabian Sea. *Mar. Ecol. Prog. Ser.* 149, 13–21.

Mobley, J. R., and Herman, L. M. (1985). Transience of social affiliations among humpback whales in Hawaiian breeding waters. *Can. J. Zool.* 63, 762–772. doi: 10.1139/z85-111

Nivière, M., Chambault, P., Pérez, T., Etienne, D., Bonola, M., Martin, J., et al. (2018). Identification of marine key areas across the Caribbean to ensure the conservation of the critically endangered hawksbill turtle. *Biol. Conserv.* 223, 170–180. doi: 10.1016/j.biocon.2018.05.002

Noad, M. J., Kniest, E., and Dunlop, R. A. (2019). Boom to bust? Implications for the continued rapid growth of the eastern Australian humpback whale population despite recovery. *Popul. Ecol.* 61, 198–209. doi: 10.1002/1438-390X.1014

Owen, K., Warren, J. D., Noad, M. J., Donnelly, D., Goldizen, A. W., and Dunlop, R. A. (2015). Effect of prey type on the fine-scale feeding behaviour of migrating east Australian humpback whales. *Mar. Ecol. Prog. Ser.* 541, 231–244. doi: 10.3354/meps11551

Pack, A. A., Herman, L. M., Craig, A. S., Spitz, S. S., and Deakos, M. H. (2002). Penis extrusions by humpback whales (*Megaptera novaeangliae*). *Aquat. Mamm.* 28, 131–146.

Pack, A. A., Herman, L. M., Craig, A. S., Spitz, S. S., Waterman, J. O., Herman, E. Y. K., et al. (2017). Habitat preferences by individual humpback whale mothers in the Hawaiian breeding grounds vary with the age and size of their calves. *Anim. Behav.* 133, 131–144. doi: 10.1016/j.anbehav.2017.09.012

Pack, A. A., Herman, L. M., Spitz, S. S., Craig, A. S., Hakala, S., Deakos, M. H., et al. (2012). Size-assortative pairing and discrimination of potential mates by humpback whales in the Hawaiian breeding grounds. *Anim. Behav.* 84, 983–993.

Pack, A. A., Herman, L. M., Spitz, S. S., Hakala, S., Deakos, M. H., and Herman, E. Y. K. (2009). Male humpback whales in the Hawaiian breeding grounds preferentially associate with larger females. *Anim. Behav.* 77, 653–662. doi: 10.1016/j.anbehav.2008.11.015

Pallin, L. J., Baker, C. S., Steel, D., Kellar, N. M., Robbins, J., Johnston, D. W., et al. (2018). High pregnancy rates in humpback whales (*Megaptera novaeangliae*) around the Western Antarctic Peninsula, evidence of a rapidly growing population. *R. Soc. Open Sci.* 5:180017. doi: 10.1098/rsos.180017

Palsbøll, P. J., Allen, J., Berube, M., Clapham, P. J., Feddersen, T. P., Hammond, P. S., et al. (1997). Genetic tagging of humpback whales. *Nature* 388, 767–769.

Paterson, R. A. (1991). The migration of Humpback Whales *Megaptera novaeangliae* in east Australian waters. *Mem. Qld. Museum* 30, 333–341.

Payne, R., and McVay, S. (1971). Songs of humpback whales. *Science* 173, 585–597. doi: 10.1126/science.173.3997.585

Ribbe, J. (2014). "Hervey bay and its estuaries," in *Estuaries of Australia in 2050 and Beyond, Estuaries of the World*, ed. E. Wolanski (Dordrecht: Springer Science+Business Media),

Rice, M. R., and Balazs, G. H. (2008). Diving behavior of the Hawaiian green turtle (*Chelonia mydas*) during oceanic migrations. *J. Exp. Mar. Biol. Ecol.* 356, 121–127. doi: 10.1016/j.jembe.2007.12.010

Sawyer, H., and Kauffman, M. J. (2011). Stopover ecology of a migratory ungulate. *J. Anim. Ecol.* 80, 1078–1087. doi: 10.1111/j.1365-2656.2011.01845.x

Schaub, M., Jenni, L., and Bairlein, F. (2008). Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. *Behav. Ecol.* 19, 657–666. doi: 10.1093/beheco/arn023

Schaub, M., Pradel, R., Jenni, L., and Lebreton, J.-D. (2001). Migrating birds stopover longer than usually thought: an improved capture-recapture analysis. *Ecology* 82, 852–859. doi: 10.2307/2680203

Sharpe, F. A. (2001). *Social Foraging of the Southeast Alaskan Humpback Whale (Megaptera novaeangliae).* Ph.D. dissertation. Vancouver, BC: Simon Fraser University, 129.

Sharpe, F., Szabo, A., Pack, A. A., and Nahmens, J. (2013). "The social structure of bubble net feeding whales in SE Alaska. Oral presentation," in *Proceedings of the 20th Biennial Conference on the Biology of Marine Mammals*, Dunedin.

Simmons, M. L., and Marsh, H. E. (1986). Sightings of humpback whales in Great Barrier Reef waters. *Sci. Rep. Whales Res. Inst.* 37, 31–46. doi: 10.1002/eap.2214

Smith, J. N., Grantham, H. S., Gales, N., Double, M. C., Noad, M. J., and Paton, D. (2012). Identification of humpback whale breeding and calving habitat in the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 447, 259–272. doi: 10.3354/meps09462

Stack, S. H., Currie, J. J., McCordic, J. A., Machernis, A. F., and Olson, G. L. (2020). Distribution patterns of east Australian humpback whales (*Megaptera novaeangliae*) in Hervey Bay, Queensland: a historical perspective. *Aust. Mammal.* 42, 16–27. doi: 10.1071/am18029

Stamation, K. A., Croft, D. B., Shaughnessy, P. D., and Waples, K. A. (2007). Observations of humpback whales (*Megaptera novaeangliae*) feeding during their southward migration along the coast of south-eastern New South Wales, Australia: identification of a possible supplemental feeding ground. *Aquat. Mamm.* 33, 165–174.

Stockin, K. A., and Burgess, E. A. (2005). Opportunistic feeding of an adult humpback whale (*Megaptera novaeangliae*) migrating along the coast of Southeastern Queensland, Australia. *Aquat. Mamm.* 31, 120–123. doi: 10.1578/am.31.1.2005.120

True, F. W. (1904). *The Whalebone Whales of the Western North Atlantic Compared with Those Occurring in European Waters; With Some Observations on the Species of the North Pacific*, Vol. 33. Washington, DC: Smithsonian Institution Press, 1–318.

Tyack, P. (1981). Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behav. Ecol. Sociobiol.* 8, 105–116. doi: 10.1007/bf00300822

Tyack, P., and Whitehead, H. (1983). Male competition in large groups of wintering humpback whales. *Behaviour* 83, 132–154. doi: 10.1163/156853982x00067

Weber, T. P., Alerstam, T., and Hedenström, A. (1998). Stopover decisions under wind influence. *J. Avian Biol.* 29, 552–560. doi: 10.2307/3677175

Wedderburn, R. W. M. (1974). Quasi-likelihood functions, generalized linear models, and the Gauss—Newton method. *Biometrika* 61, 439–447. doi: 10.2307/2334725

Weinrich, M. T., and Kuhlberg, A. K. (1991). Short-term association patterns of humpback whale (*Megaptera novaeangliae*) groups on their feeding grounds in the southern Gulf of Maine. *Can. J. Zool.* 69, 3005–3011. doi: 10.1139/z91-424

Whitehead, H. (1983). Structure and stability of humpback whale groups off Newfoundland. *Can. J. Zool.* 61, 1391–1397. doi: 10.1139/z83-186

Woinarski, J. C. Z., Burbidge, A. A., and Harrison, P. L. (2014). *The Action Plan for Australian Mammals 2012*. Clayton, VIC: CSIRO Publishing, 1038.

Zaynagutdinova, E. M., Kouzov, S. A., Batova, P. R., Mikhailov, Y. M., and Kravchuk, A. V. (2019). Spring migration stopovers of swans *Cygnus* sp. In the Russian part of the Gulf of Finland. *Wildfowl* 5, 123–138.

Zoidis, A. M., Lomac-Macnair, K. S., Chomos-Betz, A. E., Day, A. J., and MacFarland, A. S. (2014). Effects of sex, seasonal period, and sea state on calf behavior in Hawaiian humpback whales (*Megaptera novaeangliae*). *Aquat. Mamm.* 40, 44–58.

Zoidis, M. A., and Lomac-MacNair, S. K. (2017). A note on suckling behavior and laterality in nursing humpback whale calves from underwater observations. *Animals* 7:51.

Conflict of Interest: LB was employed by StatPlan Consulting Pty. Ltd. PC was employed by Seastar Scientific Inc.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Marine Science

ORIGINAL RESEARCH
published: 03 December 2021
doi: 10.3389/fmars.2021.665186

Socially Complex Breeding Interactions in Humpback Whales Are Mediated Using a Complex Acoustic Repertoire

Dana A. Cusano[1]*†, David Paton[2], Michael J. Noad[1] and Rebecca A. Dunlop[1]

[1] Cetacean Ecology and Acoustics Laboratories, School of Veterinary Science, The University of Queensland, Gatton, QLD, Australia, [2] Blue Planet Marine, Canberra, ACT, Australia

Edited by:
Janet Mann,
Georgetown University, United States

Reviewed by:
Vivienne Foroughirad,
Georgetown University, United States
Ellen Jacobs,
Georgetown University, United States,
in collaboration with reviewer VF
Marc Lammers,
Hawaiian Islands Humpback Whale
National Marine Sanctuary,
United States

***Correspondence:**
Dana A. Cusano
danacusano@gmail.com

†Present address:
Dana A. Cusano,
JASCO Applied Sciences, Capalaba,
QLD, Australia

Specialty section:
This article was submitted to
Marine Megafauna,
a section of the journal
Frontiers in Marine Science

Received: 08 February 2021
Accepted: 07 October 2021
Published: 03 December 2021

Citation:
Cusano DA, Paton D, Noad MJ
and Dunlop RA (2021) Socially
Complex Breeding Interactions
in Humpback Whales Are Mediated
Using a Complex Acoustic Repertoire.
Front. Mar. Sci. 8:665186.
doi: 10.3389/fmars.2021.665186

Intraspecific conflict can be costly; therefore, many species engage in ritualized contests composed of several stages. Each stage is typically characterized by different levels of aggression, arousal, and physical conflict. During these different levels of "intensity," animals benefit from communicating potential information related to features such as resource holding potential, relative fighting ability, level of aggression, intent (i.e., fight or flight), and whether or not the competitor currently holds the resource (e.g., a receptive female). This information may be conveyed using both visual displays and a complex acoustic repertoire containing fixed (e.g., age, sex, and body size) and flexible information (e.g., motivation or arousal). Calls that contain fixed information are generally considered "discrete" or stereotyped, while calls that convey flexible information are more "graded," existing along an acoustic continuum. The use of displays and calls, and the potential information they convey, is likely dependent on factors like intensity level. The breeding system of humpback whales (*Megaptera novaeangliae*) involves intense male competition for access to a relatively limited number of breeding females (the resource). Here, we investigated the behavior and acoustic repertoire of competitive groups of humpback whales to determine if an increase in intensity level of the group was correlated with an increase in the complexity of the vocal repertoire. We categorized the behavior of humpback whales in competitive groups into three mutually exclusive stages from low to high intensity. While discrete calls were infrequent compared to graded calls overall, their use was highest in "low" and "moderate" intensity groups, which may indicate that this stage of contest is important for assessing the relative resource holding potential of competitors. In contrast, visual displays, call rates, and the use of graded call types, were highest during "high intensity" competitive groups. This suggests that flexible information may be more important in "high intensity" levels as males continue to assess the motivation and intent of competitors while actively engaged in costly conflict. We have shown that the relatively complex social call repertoire and visual displays of humpback whales in competitive groups likely functions to mediate frequently changing within-group relationships.

Keywords: competition, discrete calls, graded calls, intraspecific conflict, resource holding potential, social system

INTRODUCTION

Intraspecific conflict arises when critical resources are limited, such as food, territory, or access to breeding opportunities (Campagna, 2009; Bradbury and Vehrencamp, 2011; Hardy and Briffa, 2013). Arguably the most common source of agonistic interaction involves the latter, particularly competition between males for access to reproductive females (Campagna, 2009). Conflict can be costly, requiring high energy expenditure and possibly injury or death (Campagna, 2009). In order to prevent serious injury, many species employ the strategy of "ritualized fighting," where competition escalates in successive stages that provide potential information on the contestants (Smith and Price, 1973; Maynard-Smith, 1974). This includes each individual's relative resource holding potential (RHP), which are the physiological and morphological traits (e.g., fitness and fighting ability) that primarily determine the outcome of a contest (Parker, 1974). Additional factors may also contribute to deciding the outcome of a conflict, including motivation, aggressiveness, and ownership status of the resource (Parker, 1974; Allen and Krofel, 2017). Individuals benefit from conveying this information continuously to facilitate decisions on whether to retreat or to engage. Males that produce honest signals indicative of strength and large body size, therefore, should persuade inferior opponents to avoid or disengage from combative situations they will likely lose, with fewer serious conflicts and injuries for both parties (Maynard-Smith and Harper, 2003). If competitors choose to proceed and aggression escalates, signaling behavior often reflects this escalation (Bradbury and Vehrencamp, 2011; Hof and Podos, 2013).

In an acoustic signaling system, this breadth of potential information requires a complex communicative repertoire, including calls that convey both fixed and flexible information. Acoustic cues related to fitness or fighting ability are typically correlated with fixed attributes which do not change over time or change slowly (Marler, 1961, 1977; Green and Marler, 1979). This includes features related to RHP, such as sex, body size, or age class. These calls tend to be highly stereotyped ("discrete") in that the call structure has little variability in acoustic features between- and within-contexts in order to reliably encode these traits. For example, the discrete "groans" of fallow deer (*Dama dama*) are displays produced during the breeding season to convey information on body size (Vannoni and McElligott, 2008; Charlton and Reby, 2011). As large body size in these animals is generally associated with higher rank, RHP, and mating success (McElligott et al., 2001), these acoustic features can be used by potential competitors to assess the odds of successfully winning an agonistic encounter (McElligott and Hayden, 1999). Red deer stags (*Cervus elaphus*), another species in which males defend harems, engage in "roaring contests" during the breeding season (Clutton-Brock and Albon, 1979; Reby et al., 2005). Males use the acoustic features of "roars" to remotely assess the fighting ability of their opponents. If neither male withdraws, the rate of roaring increases. Males also move closer together to signal RHP using visual displays. If males are evenly matched, or neither backs down, the interaction may then escalate to physical combat (Clutton-Brock and Albon, 1979).

Considering that factors other than RHP help to determine the outcome of a conflict, it may also be beneficial to convey information such as intent (i.e., willingness to fight, disengage, or not engage) or level of aggression during a contest (Morton, 1982; Enquist, 1985). This information is considered flexible, and is related to internal factors such as physiological or motivational state, as well as external factors such as social context (Marler, 1961, 1975, 1976; Morton, 1977; Hauser, 1996; Manser, 2010). Unlike discrete calls, those that contain flexible information tend to be variable, or "graded," both within and between calls. It is this gradation that provides listeners with information on the subtle variations in the signaler's internal attributes at the time of the call (Marler, 1961, 1976; Morton, 1977, 1982; Owings and Morton, 1998; Briefer, 2012). As escalation progresses beyond threats and displays, it may become increasingly more important to communicate flexible information (e.g., intent) rather than fixed information (e.g., body size or condition), especially considering that smaller animals with higher motivation are sometimes able to dominate larger opponents (Wagner, 1989; Kotiaho et al., 1999; Hofmann and Schildberger, 2001). For example, changes in the dominant frequency and temporal features of a graded call found in cricket frogs (*Acris crepitans*) provides accurate information regarding the intent of an individual, or how willing it is to progress in a conflict, independent of its body size. Males that attacked an opponent produced longer duration calls with more pulses per call than those that tolerated an opponent. Additionally, males that fled an opponent significantly lowered the dominant frequency of their call, while those that attacked lowered this frequency even further (Burmeister et al., 2002).

The frequency of intraspecific conflict and its intensity are partially dependent on the complexity of the social system (Campagna, 2009). Socially complex species that live in dense societies and have a polygamous mating system have more opportunities and motives to engage in conflict, particularly during the breeding season. Most baleen whales (i.e., the filter-feeding whales) have a relatively simple social system (Berta and Sumich, 1999; May-Collado et al., 2007), with little evidence of permanent groups, kin recognition, and long-term associations (but see Weinrich, 1991; Clapham, 1993; Ramp et al., 2010). There is also a tendency toward mating strategies that do not include overt aggressive male competition for mates (Boness et al., 2002). While some baleen species do engage in agonistic or competitive behaviors associated with breeding, the level and intensity of aggression is lower in species which engage primarily in sperm competition [e.g., North Atlantic right whales, *Eubalaena glacialis* (Kraus and Hatch, 2001; Parks, 2003; Parks and Tyack, 2005; Parks et al., 2007); southern right whales, *Eubalaena australis* (Clark, 1983, 1990; Payne and Dorsey, 1983); bowhead whales, *Eubalaena mysticetus* (Würsig et al., 1993; Rugh and Shelden, 2009)]. Humpback whales (*Megaptera novaeangliae*) do not utilize sperm competition and instead males have two main strategies; displaying using complex patterned songs (Payne and McVay, 1971), and more direct, physical competition for access to females (Brownell and Ralls, 1986; Clapham, 1996; Mesnick and Ralls, 2009). While song is well described, its function is not yet fully understood. Physical competition between males, however, is clear and results in the formation of large assemblages termed "competitive groups" (Tyack and Whitehead, 1983; Baker and Herman, 1984; Silber, 1986; Mattila et al., 1989; Clapham et al., 1992; Clapham, 1996; Pack et al., 1998; Darling and Bérubé, 2001; Herman et al., 2007; Félix and Novillo, 2015).

Competitive groups appear to function in intrasexual competition between males for access to a relatively limited number of breeding females (the resource) (Tyack and Whitehead, 1983). There is a definitive structure to groups, with multiple male escorts centered around a nuclear female (Tyack and Whitehead, 1983; Clapham et al., 1992; Brown and Corkeron, 1995). The escort that maintains the closest position to the female is the "principal," or "primary," escort. Primary escorts are challenged by other "secondary" escorts and will defend their close proximity to the female. Secondary escorts not only compete with the primary escort for this position, but also compete amongst themselves. In large and active groups, the composition and dynamic changes often, with principal escorts and secondary escorts changing positions and roles frequently (Tyack and Whitehead, 1983; Clapham et al., 1992). In addition, there are sometimes animals on the periphery of the group, typically smaller (i.e., juveniles or sub-adults), that appear to play a more observational role (Spitz et al., 2002). Competitive groups can vary in intensity, progressing from low to high levels of aggression and arousal (Baker and Herman, 1984). Usually, all males within the main group behave in a similar way, therefore intensity level can be classified at the group level. Low intensity (i.e., low aggression and arousal) groups are characterized by animals which have no direct physical contact and instead rely on displays and chasing behavior (Darling, 2001). Other "non-contact" agonistic display behaviors include blowing streams of bubbles, jaw clapping, and extending the throat pleats. Moderate intensity levels are indicated by more "intermediate" levels of aggression, with "head lunging" one of the most common behaviors observed (Baker and Herman, 1984). In contrast, higher intensity competitive groups tend to move more erratically and have elevated respiration rates (Tyack and Whitehead, 1983; Silber, 1986; Clapham et al., 1993). They also exhibit more aggressive behaviors, which can include "body thrashes," "tail lashes," collisions, injuries, and in one documented extreme case, death (Tyack, 1981; Tyack and Whitehead, 1983; Baker and Herman, 1984; Silber, 1986; Pack et al., 1998; Darling, 2001).

The dynamics of competitive groups likely depend on each competitor's relative RHP, based on attributes such as its size and position within the group, as well as levels of aggression and stamina. However, competitive groups are temporary and unstable, with new animals frequently splitting and joining (Tyack and Whitehead, 1983; Clapham et al., 1992). As each individual's relative RHP will change with changing group membership, this requires relationships to be quickly established and continuously re-established over the course of a conflict and throughout the breeding season. The number, diversity, and instability of relationships, and the frequently changing relative RHP of individuals in competitive groups would seemingly require a complex communication system. Humpbacks have the most variable, complex, and well-studied vocal repertoire of any of the large whales (Edds-Walton, 1997). Males produce stereotyped songs during the breeding season (Payne and McVay, 1971), and all humpback whales produce a large repertoire of social calls. These calls are produced by all age and sex classes (Winn et al., 1979; Zoidis et al., 2008; Indeck et al., 2021), and in all habitats [e.g., breeding grounds (Tyack and Whitehead, 1983; Silber, 1986), feeding grounds (Jurasz and Jurasz, 1979; D'Vincent et al., 1985; Thompson et al., 1986; Stimpert et al., 2007, 2011; Parks et al., 2014; Fournet et al., 2015), and on migration (Dunlop et al., 2007, 2008; Cusano et al., 2020)]. The number of calls within the repertoire is variable, depending on the population, habitat area, and behavioral context (Dunlop et al., 2007; Stimpert et al., 2008; Fournet et al., 2015; Rekdahl et al., 2017; Cusano et al., 2020). These social calls can be highly flexible in structure, ranging from low-frequency "grumbles" to high-frequency "chirps." Further, the acoustic repertoire of humpback calls includes both discrete and graded call types (Cusano et al., 2021), which may be related to the complexity of the social interaction (Cusano, 2021).

Here, we collected dedicated acoustic and behavioral data from competitive groups of humpback whales in order to test the hypothesis that their complex social call repertoire functions to mediate complex social interactions. We predicted that discrete and graded calls perform different functions during agonistic competitive interactions, and this will be reflected in differential use of these calls as intensity changes. Following trends evident in terrestrial species like deer, we hypothesized that discrete calls would be used more often in groups with lower levels of perceived group aggression (i.e., during agonistic displays) where it is more important to convey fixed information on RHP. In contrast, graded calls would increase with the perceived level of aggression (i.e., overt aggression) in order to convey flexible information regarding intent and motivation to escalate or continue conflict. Additionally, we hypothesized that call rates would increase linearly with group size and intensity, as increased call production is known to be correlated with high arousal in humpback whales (Cusano et al., 2020). The results from this study can ultimately increase our understanding of discrete and graded call use within an animal that engages heavily in male competition during the breeding season and provide a foundation for making comparisons between vocal behavior, mating strategies, and sociality in other baleen whales.

MATERIALS AND METHODS

Behavioral and acoustic data were collected on competitive groups of humpback whales on the breeding grounds in the Great Barrier Reef (**Figure 1**). Effort focused on the Whitsunday Island group which has high densities of humpback whales during the breeding season (Smith et al., 2012). Data collection was conducted in four consecutive years between July and September, 2016–2019. Data were collected from 6 to 7 m rigid-hulled inflatable boats on days with winds less than 15 knots and a sea state less than Beaufort 4. Competitive groups were located opportunistically, and were defined as two or more adults centered around a nuclear animal (assumed to be female)

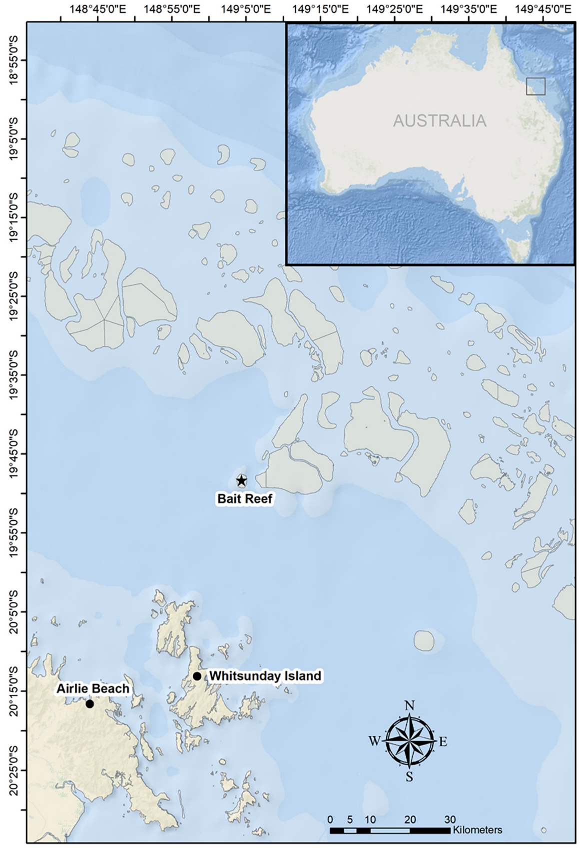


FIGURE 1 | Map of the study area in the Great Barrier Reef, indicating the primary survey area around Whitsunday Island. The majority of competitive groups were found to the northeast, between Whitsunday Island and Bait Reef.

and demonstrating agonistic surface-active or chasing behavior (Tyack and Whitehead, 1983; Clapham et al., 1992). Due to the challenges of obtaining biopsy samples in competitive groups, no information was available on the sex of most individuals, so it was impossible to say with certainty whether the nuclear animal was always female. Although all male competitive groups have been observed, these are relatively uncommon (Clapham et al., 1992; Brown and Corkeron, 1995). They are thought to function in dominance sorting, which would only be useful if individuals encounter each other frequently (Clapham, 1993), unlikely in a population this size (2015 absolute abundance estimate 24,545; Noad et al., 2019). Therefore, all competitive groups in the present study likely contain at least one female.

Behavioral Data

After sighting a competitive group, a behavioral focal follow was initiated using continuous focal animal sampling methods (Altmann, 1974). Recorded data included the number of animals in the group, approximate group speed based on the vessel speed, and the frequency of occurrence of specified behaviors. These behaviors were selected based on previous research on humpback competitive groups in other areas (Tyack and Whitehead, 1983; Baker and Herman, 1984; Silber, 1986; Mattila et al., 1989; Clapham et al., 1992; Clapham, 1996; Pack et al., 1998; Darling and Bérubé, 2001; Herman et al., 2007; Félix and Novillo, 2015) and formed the behavioral ethogram for the study (**Table 1**).

An intensity scale was established based on the estimated speed of the group, an estimate of the number of breaths per whale during each surfacing (given that animals performing high intensity behaviors tend to have elevated respiration rates, Helweg and Herman, 1994), and the presence and frequency of aggressive behaviors. The designation of an aggressive or highly aggressive behavior was primarily based on whether or not there was direct physical contact, or perceived attempted physical contact, between group members. For example, a "tail slap" is a behavior in which the fluke is raised out of the water and forcibly slapped against either the surface (aggressive) or another whale (highly aggressive) (Tyack, 1981; Tyack and Whitehead, 1983). Identification photographs were also taken of all animals in the group during the focal follow. Humpback whales may be individually identified using distinct markings on the tail (flukes) and the shape of the dorsal fin (Katona and Whitehead, 1981). Due to the size and continued rapid growth of the east Australian humpback whale population, the resighting of individuals is rare (Burns et al., 2014). Therefore, individuals could only be identified for the duration of the follow. Photos were used to corroborate the number of animals present, confirm the roles of individuals (e.g., the leading animal was presumed to be the nuclear female), and determine if individuals maintained consistent roles (e.g., displacement of the presumed primary or secondary escorts based on position to the nuclear female).

Each follow was assigned an intensity level by a trained observer using the behavioral ethogram. Intensity level was based on the behavior of the group as a whole. A new intensity level was assigned if the behavior of the group changed during the follow with no break in data collection. Three group intensity levels were determined from the behavioral focal follow data (**Table 2**). Level one ("low intensity") was characterized by the fastest swim speeds (>10 kts) and few course changes. It often appeared as if one animal was consistently leading (as identified using dorsal fin and fluke identification markings and shape), with the remaining animals following behind or chasing. Level two ("moderate intensity") was associated with slower speeds (<10 kts), more time spent at the surface, and a more erratic course (i.e., more course changes), and more surface-active behaviors (e.g., flipper slapping and tail slapping) compared with low intensity level groups. Many of these behaviors were identified as aggressive, but not highly aggressive, because of the lack of direct body contact (**Tables 1**, **2**). Lastly, level three ("high intensity") groups were similar in speed and time spent at the surface to moderate intensity level groups, but characterized by a higher frequency of highly aggressive behaviors such as tail slashing, and chin or head slaps on other group members (**Tables 1**, **2**). Animals during these follows would periodically surface with blood on their dorsal fins, indicative of this direct physical contact.

Acoustic Data

Acoustic recordings were collected using a Zoom H4n Pro Handy Recorder (Zoom North America, 44.1 kHz sampling rate,

TABLE 1 | Behavioral ethogram for humpback whale competitive groups.

Behavior	Description
Body slam **	The collision of two or more whales.
Breach **	Leap in which the entire, or part of, the whale body (up to the tail stock) exits the water. The whale twists in the air and lands on its dorsal or lateral side. Includes half breaches and other variations. Considered highly aggressive in this context as it was typically aimed at other individuals.
Bubble streaming *	Blowing bubble streams underwater.
Chin/Head Slap * or **	The head is raised out of the water and slapped against the water's surface (aggressive) or another whale (body contact—highly aggressive)
Open/Distended Pleats *	The distension of the ventral grooves or pleats to make the animal appear bigger in size.
Head Lunge **	Energetic forward motion with a forward lunge of the head, with less than 40% of the body leaving the water with an angle to the water $< 45°$.
Jaw Clap *	Forceful opening and closing of the mouth.
Pec Slap * or **	The left or right pectoral or both pectorals are raised out of the water and forcibly slapped against the water's surface (aggressive) or another whale (body contact—highly aggressive).
Roll	Surface or underwater roll in any direction or plane. Includes belly up.
Peduncle Throw/Rear body thrash * or **	The throwing of the entire fluke and peduncle in a lateral motion out of the water (aggressive) or at/on another whale (body contact—highly aggressive). No initial lifting from the water as in a peduncle or tail slap, just a single scything motion.
Tail Slap/Lobtail * or **	The fluke is raised out of the water and forcibly slapped against the water's surface (aggressive) or another whale (body contact—highly aggressive)
Tail Slash/Flick * or **	Movement of tail in a sideways motion through water (aggressive) or at/on another whale (body contact—highly aggressive)
Tonal Blow/Trumpet *	Blow accompanied by a loud vocalization, usually low frequency.
Underwater blow *	A forceful, audible release of breath underwater

**Indicates aggressive behavior, **indicates highly aggressive behavior, and * or ** indicates level of aggression is determined by whether body contact is made or presumed to be attempted.*

TABLE 2 | Intensity scale developed for competitive groups based on the behaviors outlined in the ethogram and observations of speed and breathing rates.

Intensity level	Est. avg. speed (kts)	Key behaviors
1 (Low)	10+	Fast travel in a steady direction, long down times, ∼ 3 blows/surfacing; chasing behavior, often with a consistent animal leading; limited presence of aggressive behaviors like head lunges, pec slaps, tail slaps (1–2 displays per surfacing).
2 (Moderate)	5–10	Slower travel in no clear direction, with shorter down times and longer surface times, ∼ 4 blows/surfacing; increased presence of aggressive behaviors, but limited or no heightened aggressive behaviors.
3 (High)	<5	Even slower travel, although with similar down times and surface times as 2; increased presence of aggressive behaviors (more than 10 displays per surfacing); addition of heightened aggressive behaviors like direct body contact and breaches; evidence of blood on tubercles and dorsal fins.

16 bit) and an HTI-96-MIN hydrophone with built in + 40 dB pre-amplifier dropped over the side of the boat (High-Tech, Inc.). The engine was shut down during recordings to minimize background noise. Although humpback whale calls are reported to have an estimated active space of up to 4 km in wind-dominated noise (Dunlop, 2018b), and up 2.5 km in vessel noise (Dunlop, 2018a), the acoustic environment in the study area was dominated by additional biotic noise (i.e., snapping shrimp, humpback whale song chorusing). Therefore, data were only collected when whales were within 400 m of the boat in order to ensure that all calls from the group were detected. Any whales within this distance were either involved in the competitive group or alone. As lone humpback whales rarely vocalize (Silber, 1986; personal observation), it is unlikely that calls were detected from animals outside the focal group. Due to the high speeds and often erratic behavior of competitive groups, the duration of acoustic recordings was limited to short periods (average duration 6 min 15 s, range 1–10 recordings per follow).

Spectrograms of recordings were visually and aurally browsed in Raven Pro 1.5 (Center for Conservation Bioacoustics [CCB], 2014, RRID:SCR_016190) using a Hann window, Fast Fourier Transform size of 4,096 samples, and 90% overlap. All humpback whale social calls were marked and extracted for further analysis. The nearly constant background song from singing males in the area meant that most calls detected from competitive groups had overlapping song units of varying amplitude. This precluded any analysis of acoustic features (e.g., frequency and bandwidth). The overlapping song also prevented any automated classification techniques like those used in previous social call analyses (Stimpert et al., 2011; Fournet et al., 2015; Rekdahl et al., 2017; Cusano et al., 2020, 2021; Indeck et al., 2021). Therefore, in order to determine call types, the results from a previous humpback social call analysis were used (Cusano et al., 2021) that applied fuzzy k-means (FKM) clustering to humpback calls from the same population (Ferraro and Giordani, 2015; Wadewitz et al., 2015; Fischer et al., 2017). Similar to other clustering methods, an FKM partitions data-points (individual calls) into clusters based on a set of user-defined features. In contrast to other clustering methods, however, fuzzy clustering assigns each data-point a membership value to each of the clusters while allowing intermediate membership between clusters (Bezdek, 1981). Based on cluster membership values, a typicality coefficient can then be calculated to define a threshold above or below which a call type could be considered discrete or graded, respectively (Wadewitz et al., 2015; Fischer et al., 2017; Cusano et al., 2021).

The FKM was run on a dataset of calls collected from the same population of humpback whales during their southward migration from the breeding ground in 2010, 2011, 2015, and 2017 (see Dunlop et al., 2015, 2016, for detailed data collection methodology). Using the FKM, calls were partitioned into clusters based on a set of 25 acoustic features, including temporal (e.g., duration), frequency (e.g., peak and center frequency), and bandwidth measurements. The FKM identified six discrete and seven graded call types (Cusano et al., 2021). A further thirteen were considered intermediate call types as they had average typicality coefficients that fell between the thresholds for discrete and graded calls. Following the results of the analysis, six call types were determined to be discrete, five of which were detected in the current study: "paired croak," "chirp," "harmonic squeak," "thwop," and "whup" (previously called "wop," Dunlop et al., 2007). In addition, individual song units are sometimes used as social calls in this population (Dunlop et al., 2007, 2008; Rekdahl et al., 2013). Although song units may have subtle variations in acoustic structure (Hafner et al., 1979), most males within a population follow the same song pattern at any given time, creating highly stereotyped songs (Winn and Winn, 1978; Payne et al., 1983; Payne and Payne, 1985; Garland et al., 2015; Allen et al., 2019). Song units were thus classified as discrete sounds in the present study. Calls detected from competitive groups that visually and aurally matched these discrete call types were assigned as that call. Calls that did not visually or aurally match one of the easily distinguishable discrete call types or that matched a graded or intermediate call type from the FKM were assigned as graded. Spectrograms of the discrete call types and an exemplar graded call are in **Figures 2**, **3**. Sound clips can be found in **Supplementary Material**.

Graded call types often fall along an acoustic continuum (Marler, 1961, 1976; Marler et al., 1992), rendering them difficult to classify based on visual or aural characteristics alone. However, three measurements could be obtained directly from the spectrograms and were thus not influenced by background song: minimum frequency, maximum frequency, and call duration. To determine whether there were differences in the use of graded sounds at different intensity levels, a cluster analysis was run to objectively group graded sounds into broad call classes. Analyses were run using the R programming language (R Core Team, 2020; RRID:SR_003005) with the partitioning around medoids (PAM) method in the package *cluster* (Maechler et al., 2019). This method is considered to be more robust than traditional k-means clustering, representing cluster centers as medoids that are less sensitive to outliers than means. The pairwise distances between all of the data points were computed to obtain a matrix of the sum of dissimilarities using the Gower coefficient (Gower, 1971; Maechler et al., 2019). The resulting dissimilarity matrix was used to run the cluster analysis. Using the silhouette method (Kaufman and Rousseeuw, 2009), the recommended number of clusters was determined to be either two or five. The two-cluster solution resulted in one cluster with a low silhouette width, indicating poor data structure (Kaufman and Rousseeuw, 2009), so the five-cluster solution was chosen. This resulted in five graded call classes: (1) low frequency, moderate duration; (2) mid-frequency, long duration; (3) broadband (i.e., spans a broad frequency range), very long duration; (4) high-frequency, short duration; and (5) very high-frequency, short duration.

Statistical Analysis

Call rates, the proportion of discrete and graded calls used, and the proportion of specific call types/classes used were modeled as a function of group intensity level to assess the differences in the communicative behavior within groups. Separate models were run for call rates and call proportions. Call rates were first standardized for varying group sizes by dividing the number of calls by the total number of animals. Then, rates were compared using generalized linear mixed models (GLMMs) with a negative binomial error distribution to model a quadratic relationship between the variance and mean (Brooks et al., 2017b). This allows for small counts (here, low call rates) to have similar weights to high counts (high call rates; Ver Hoef and Boveng, 2007). Models were run in R using the package *glmmTMB* (Brooks et al., 2017a). A log offset was applied to the fixed effect of "time" to provide rates (calls per time of deployment) rather than counts (number of calls). The number of animals in the group and group ID were included as random effects.

Next, a GLMM with a binomial error distribution for proportions was used to compare the use of discrete and graded calls between the intensity levels. The internally calculated proportion of discrete versus graded calls was the response variable, with the number of animals in the group and group ID added as random effects. Binomial GLMMs were run using the package *lme4* (Bates et al., 2015). Additionally, separate models were run for each of the six discrete call types and the five graded call classes to investigate differences between group intensity levels. However, due to the low effect size for group ID for some call types/classes, no random effects could be included, and general linear models (GLMs) were used for the individual call type/class models. *Post hoc* analyses for all models were run using the *emmeans* package (Lenth, 2021) with the "mvt" method for exact Dunnett style contrasts between intensity levels.

RESULTS

A total of 43 competitive groups were observed and recorded in 2016 (*n* = 5), 2017 (*n* = 12), 2018 (*n* = 12), and 2019 (*n* = 14) with 20 h and 38 min of acoustic and behavioral data (**Supplementary**

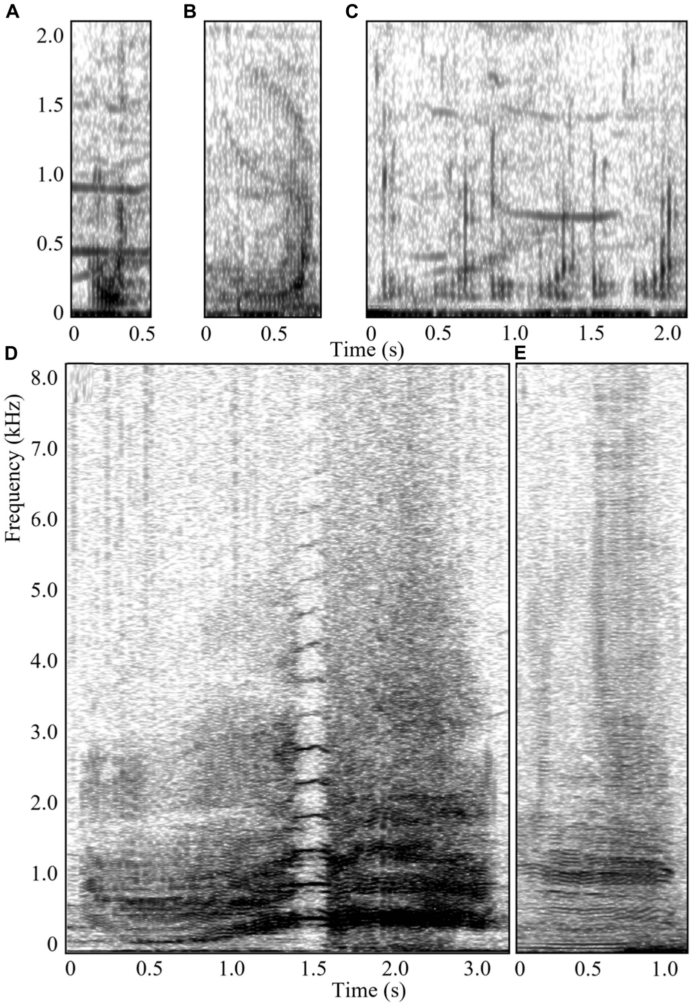


FIGURE 2 | Spectrograms (Hann window, Fast Fourier Transform 4096 samples, overlap 90%) of the relatively low frequency call types detected in competitive groups during this study: **(A)** "thwop," **(B)** "whup," **(C)** a series of "paired croaks," **(D)** a graded call, and **(E)** a low frequency "song unit social call." Sound clips can be found in **Supplementary Material**.

Material). In order to maintain a workable distance of <400 m (see section "Materials and Methods"), observations were broken up into 198 recordings from 59 focal follows. A large proportion of sightings of competitive groups (>75%) were to the northeast of the major island groups, particularly between Whitsunday Island and Bait Reef (**Figure 1**). As per previous studies, the number of whales in competitive groups was highly variable (average 5.8 ± 2.4 SD, range 3–16).

Intensity Level

Low intensity groups were encountered during 23 focal follows (39% of focal follows) for a total acoustic recording time of 05:18:57 from 67 recordings. The average group size was 5.7 animals (range 3–9). Moderate intensity groups were the most commonly observed, with a total of 29 focal follows (49% of focal follows) and 11:59:50 total recording time from 108 recordings. The average group size for moderate intensity groups was 5.4 (range 3–11). Lastly, high intensity groups were the least common, encountered during 7 focal follows (12% of focal follows) for a total recording time of 03:19:16 from 23 recordings. The average group size for level three was 8.9 animals (range 3–16). Intensity level was not correlated with the number of animals in the group (Fisher's exact test $p = 0.3304$).

Acoustic Behavior

A total of 6,414 calls were detected over the study period: 971 during low intensity follows, 4,033 during moderate intensity follows, and 1,410 during high intensity follows. As expected, call rates (per whale per hour) increased with intensity level. Groups that were classified as being within the lowest intensity level had the lowest call rate (GLMM estimate 4.49 ± 1.3 SE calls/whale/h) compared to moderate (12.5 ± 3.0 calls/whale/h), and high intensity groups (18.2 ± 6.8 calls/whale/h). Though there was an increase in call rate per whale between moderate and high intensity level groups, these results were not significantly different, possibly due to differences in sample size (GLMM odds

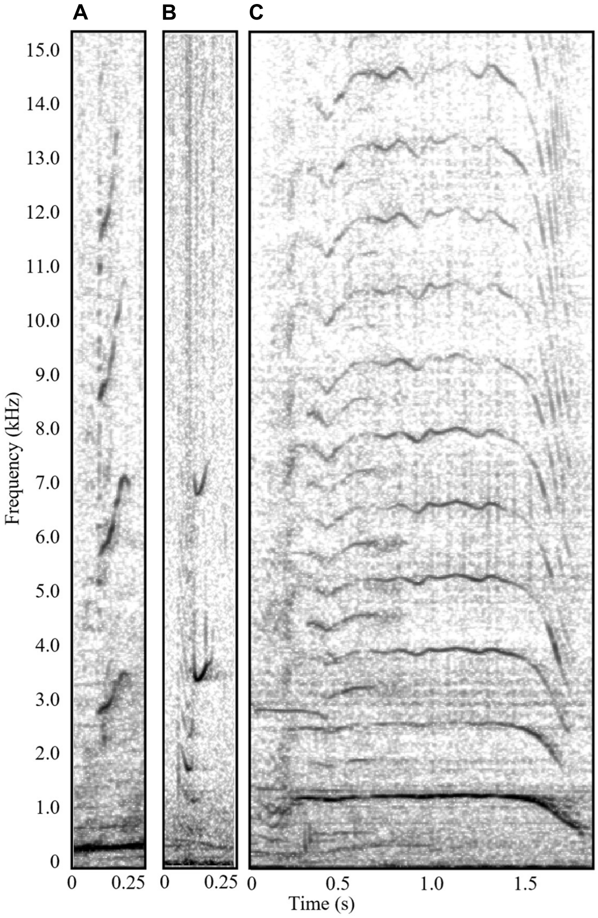


FIGURE 3 | Spectrograms (Hann window, Fast Fourier Transform 4096 samples, overlap 90%) of the relatively high frequency call types detected in competitive groups during this study: **(A)** "harmonic squeak," **(B)** "chirp," and **(C)** a high frequency "song unit social call." Sound clips can be found in **Supplementary Material**.

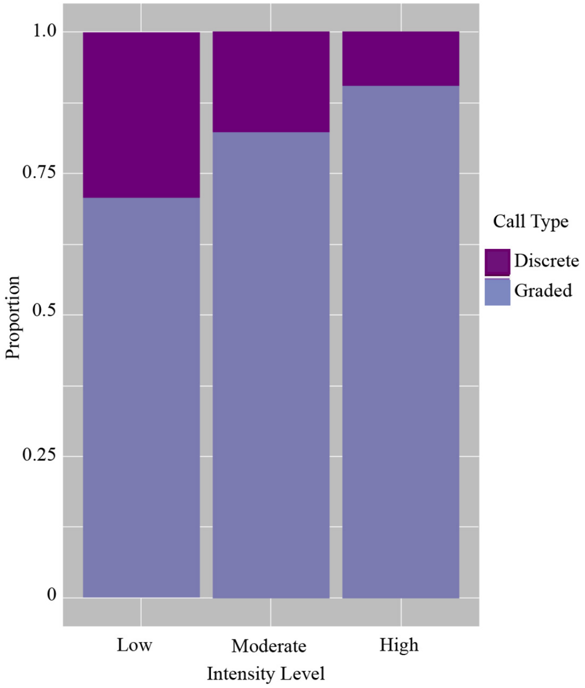


FIGURE 4 | Probability of detecting discrete and graded call types in the three intensity levels.

ratio 0.69 ± 0.24, t ratio = -1.08, *p* = 0.5207). The significant difference between low and moderate intensity levels (odds ratio 0.36 ± 0.10, t ratio = −3.62, *p* = 0.0019), and low and high intensity levels (GLMM odds ratio 0.25 ± 0.11, t ratio = −3.26, *p* = 0.0051) suggests there was a significant increase in the need for individuals to communicate in moderate and high intensity levels.

Of the total calls analyzed, 2,064 were classified as discrete calls (i.e., one of the five pre-defined call types) and 4,350 as graded calls (i.e., calls that did not fit into a discrete call type or were identified as graded or intermediate from the FKM). Vocalizing whales within all groups tended to use more graded calls than discrete calls regardless of intensity level (**Figure 4** and **Table 3**). However, when comparing the use of discrete and graded calls between intensity levels, the probability of detecting graded calls was lower in low (GLMM average probability 0.71 ± 0.07 SE) and moderate intensity levels (0.82 ± 0.05) compared with the high intensity level (0.91 ± 0.03, **Figure 4** and **Table 3**). The results of the GLMM indicated this difference was significant between all groups (**Table 3**). The highest probability of detecting graded calls was thus from groups in the highest intensity level, while the highest probability of detecting discrete calls was from groups in the lowest intensity level (**Figure 4**). This indicates that low intensity groups, where non-contact threats and displays are more common than overt contact aggression, may benefit more from communicating fixed information (e.g., body size) than moderate and high intensity groups. Additionally, these results suggest that graded calls are used more in escalated contests where contact aggression between whales is common, and these groups may benefit more from communicating flexible information (e.g., motivation and arousal).

When comparing the use of the six discrete call types, the GLM showed that groups that were low in intensity had a significantly higher probability of using certain discrete calls compared with moderate and high intensity levels (**Figure 5** and **Table 4**). This included paired croaks (GLM average probability 0.21 ± 0.03 SE), which are low-frequency, discrete calls produced in sequence and are only detected in groups containing one or more escorts (Cusano et al., 2020). Additionally, this call type is associated with an increase in arousal and social complexity, although the exact function is unknown (Cusano et al., 2020; Cusano, 2021). Whups and thwops, two additional low-frequency, discrete calls, also had a higher probability of detection in low intensity groups (0.64 ± 0.03 and 0.03 ± 0.01) compared with the other intensity levels (**Figure 5** and **Table 4**), although the difference in the use of thwops between low and moderate intensity groups was not statistically significant.

TABLE 3 | Results from the generalized linear mixed models with the probability of detecting discrete and graded calls in each intensity level in the first three columns, and the odds ratios in the last three columns.

Call type	Low (prob. ± SE)	Moderate (prob. ± SE)	High (prob. ± SE)	Low-mod (odds ± SE)	Low-high (odds ± SE)	Mod-high (odds ± SE)
Discrete	0.29 ± 0.08	0.18 ± 0.05	0.09 ± 0.03	1.92 ± 0.44	3.94 ± 1.16	2.06 ± 0.38
Graded	0.71 ± 0.07	0.82 ± 0.05	0.91 ± 0.03	z ratio = 2.85	z ratio = 4.69	z ratio = 3.94
				$p = 0.0111^{*}$	$p < 0.0001^{**}$	$p = 0.0003^{**}$

*Odds ratios indicate the odds of detecting discrete calls over graded calls in the first intensity level listed. *Indicates statistical significance at the p < 0.05 level; ** indicates statistical significance at the p < 0.001 level.*

The GLM showed that moderate intensity groups modified their acoustic repertoire to include a larger proportion of "chirps" (GLM average probability 0.18 ± 0.01 SE) compared to the other intensity levels, and "harmonic squeaks" (0.07 ± 0.01) compared to high intensity level groups (**Figure 5** and **Table 4**). In addition, there was a greater probability of detecting song unit social calls in moderate intensity groups (0.50 ± 0.01) compared to low intensity level groups. The probability of detecting song unit social calls was increased further in high intensity groups (0.78 ± 0.02) (**Figure 5** and **Table 4**). However, in contrast to low and moderate intensity levels, the song unit social calls primarily used in high intensity groups were low frequency, long duration units (**Figures 2E**, **3C**).

Lastly, the use of the five graded call classes differed between the three intensity levels in several ways. All three intensity levels had the highest probability of using low-frequency, moderate duration graded calls (**Figure 6** and **Table 5**). The most pronounced differences were in the use of certain graded call classes in the moderate intensity groups. There was a significantly higher probability of detecting broadband, very long-duration calls (Cluster 3) in moderate intensity groups (GLM average probability 0.16 ± 0.01 SE) compared to low (0.09 ± 0.01) and high intensity groups (0.05 ± 0.01). In addition, high-frequency, short duration calls (Cluster 4) had the highest probability of detection in moderate intensity groups (0.14 ± 0.01), and this was significantly higher than low intensity groups (0.09 ± 0.01). The very-high frequency, short duration graded calls (Cluster 5) also had a higher probability of detection in moderate intensity groups (0.05 ± 0.004), which was significant compared to high intensity groups (0.02 ± 0.01) (**Figure 6** and **Table 5**).

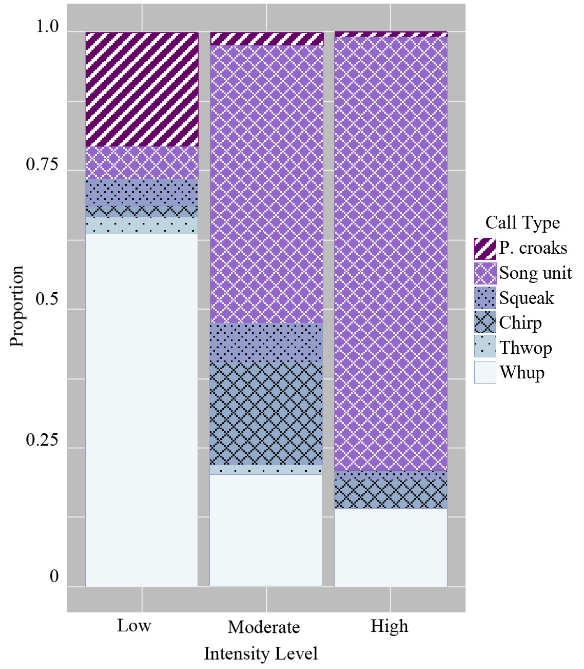


FIGURE 5 | Probability of detecting the six discrete call types in the three intensity levels.

DISCUSSION

In terrestrial animals, intraspecific conflict often progresses from low-intensity threats and displays to escalated conflicts. As the conflict escalates, animals are provided with an opportunity to constantly reassess their opponents and avoid conflicts they are unlikely to win (Zahavi, 1982). This can be carried out using acoustic signals, which may convey aspects of the conflict such as the local strategy used by an opponent, their relative fighting ability, and properties of the resource (e.g., the breeding female) (Enquist, 1985). Here, we have shown that humpback whales appear to behave in a similar way during competitive behavior. As the intensity level of these competitive interactions increased, from low-level non-contact displays to high-level overt aggression, the calling behavior of these whales also changed. Low intensity groups were more likely to use discrete calls, and this probability decreased with intensity. In other species, discrete call types typically contain fixed information related to features like body size which may be important information to convey to opponents, particularly at the start of a conflict in an attempt to avoid escalation (Maynard-Smith and Harper, 2003). In contrast, higher intensity groups used more aggressive behaviors, had significantly higher call rates per animal, and used more graded calls within their repertoire. Therefore, for these whales, graded calls may provide more information on the intent of the caller, or their willingness to engage or continue to conflict. While no conclusion can be made about the intent of the caller, these results show that in humpback whales, the use of graded and discrete calls, as well as call rates, are clearly correlated with the level of intensity. These findings demonstrate possible similarities in mating strategies between a marine mammal and terrestrial species (particularly ungulates, Clapham, 1996), and

TABLE 4 | Results of the generalized linear models, with the model calculated probability of each call type in each intensity level in the first three columns and the odds ratios in the last three columns.

Discrete call type	Low (prob. ± SE)	Moderate (prob. ± SE)	High (prob. ± SE)	Low-mod (odds ± SE)	Low-high (odds ± SE)	Mod-high (odds ± SE)
Chirp	0.02 ± 0.01	0.18 ± 0.01	0.06 ± 0.01	0.09 ± 0.04	0.36 ± 0.18	4.04 ± 0.80
				z ratio = −5.27	z ratio = −2.08	z ratio = 7.02
				$p < 0.0001^{**}$	$p = 0.0857$	$p < 0.0001^{**}$
Harmonic squeak	0.05 ± 0.01	0.07 ± 0.01	0.02 ± 0.01	0.70 ± 0.21	3.14 ± 1.34	4.49 ± 1.52
				z ratio = −1.18	z ratio = 2.67	z ratio = 4.45
				$p = 0.4579$	$p = 0.0196^{*}$	$p < 0.0001^{**}$
Paired croaks	0.21 ± 0.03	0.02 ± 0.004	0.01 ± 0.004	10.64 ± 2.60	25.14 ± 11.03	2.36 ± 1.07
				z ratio = 9.69	z ratio = 7.35	z ratio = 1.90
				$p < 0.0001^{**}$	$p < 0.0001^{**}$	$p = 0.1306$
Song unit	0.06 ± 0.01	0.50 ± 0.01	0.78 ± 0.02	0.06 ± 0.02	0.02 ± 0.005	0.28 ± 0.03
				z ratio = −10.11	z ratio = −14.02	z ratio = −10.98
				$p < 0.0001^{**}$	$p < 0.0001^{**}$	$p < 0.0001^{**}$
Thwop	0.03 ± 0.01	0.02 ± 0.004	0.002 ± 0.002	1.78 ± 0.75	19.20 ± 20.42	10.78 ± 11.04
				z ratio = 1.38	z ratio = 2.28	z ratio = 2.32
				$p = 0.3333$	$p = 0.0136^{*}$	$p = 0.0471^{*}$
Whup	0.64 ± 0.03	0.20 ± 0.01	0.14 ± 0.01	6.91 ± 1.03	10.82 ± 1.91	1.57 ± 0.22
				z ratio = 12.98	z ratio = 13.47	z ratio = 3.24
				$p < 0.0001^{**}$	$p < 0.0001^{**}$	$p = 0.0034^{*}$

*Odds ratios indicate the odds of detecting that call type in the first intensity level listed compared with the second intensity level listed. *Indicates statistical significance at the $p < 0.05$ level; ** indicates statistical significance at the $p < 0.001$ level.*

provide a basis for investigating what information content is actively conveyed in these contexts.

In this study, low intensity competitive groups were described as exhibiting little surface activity, and few overtly aggressive behaviors. Coupled with the low call rates and higher relative use of discrete calls (29% probability of detection), we propose that communication during low intensity competitive groups potentially functions as a way for males to assess each other remotely without resorting to physical contact. This is further supported by the relatively fast speeds of these groups, which would make visual displays less functional since they require individuals to be in closer proximity (Silber, 1986). There is ample evidence in terrestrial species to suggest that discrete calls function to convey information to potential competitors, which could include resource holding potential (RHP), sex, age class, and body size (Reby and McComb, 2003b). For example, the discrete roars of red deer during the breeding season contain information regarding the age and weight of the sender (Clutton-Brock and Albon, 1979; Reby and McComb, 2003a; Reby et al., 2005). These roars are relatively long in duration and are often produced in series. Roars are produced during the early stages of conflict, before escalation to physical fighting (Clutton-Brock and Albon, 1979). Here, whales within low intensity groups tended to use long duration, relatively low-frequency discrete call types such as paired croaks, which are always produced in a series to create relatively long duration sequences (Cusano et al., 2020). Further, this call type was used primarily in these lower intensity groups. Thus, it is possible that paired croaks function in a similar way to the roars of red deer, allowing individuals to gain valuable information on opponents in the early stages of intraspecific agonistic conflict.

Moderate and high intensity groups were considerably slower than intensity level one groups, and displayed more surface-active behavior. This included an increased number of aggressive behaviors like tail slashes and breaches (**Tables 1**, **2**). In high intensity groups, there was evidence of direct body contact including open wounds and blood. There was also a linear increase in call rate from low intensity level groups. Here, we propose that whales are progressing to using more conspicuous displays, both visual and acoustic. In both moderate and high intensity groups, there was also a larger proportion of graded calls, signals that are potentially more indicative of motivation or intent (Morton, 1982; Enquist, 1985). As suggested by Silber (1986), these vocalizations may be used in conjunction with visual threats to convey aggression level more effectively than using only one signal modality (Smith, 1977). This is also seen in some seals and sea lions during agonistic interactions, where graded calls that convey level of threat and/or intensity are associated with visual displays (Insley et al., 2003).

There were significant differences in the use of higher-frequency calls between intensity levels, both in terms of discrete call types and graded call classes. This included discrete "chirps" and "harmonic squeaks," as well as high- and very high-frequency graded calls. In terrestrial species, calls that are high in frequency, harmonic, tonal, and have a simple pattern of frequency modulation have been associated with fear or appeasement contexts (Morton, 1977; August and Anderson, 1987; Briefer, 2012), or with distress (Lingle et al., 2012; Briefer, 2018). In distress situations, these sounds are thought to attract the attention or even alter the arousal level of conspecifics. As such, it could be expected that these relatively high frequency calls would have a higher probability of use in the highest

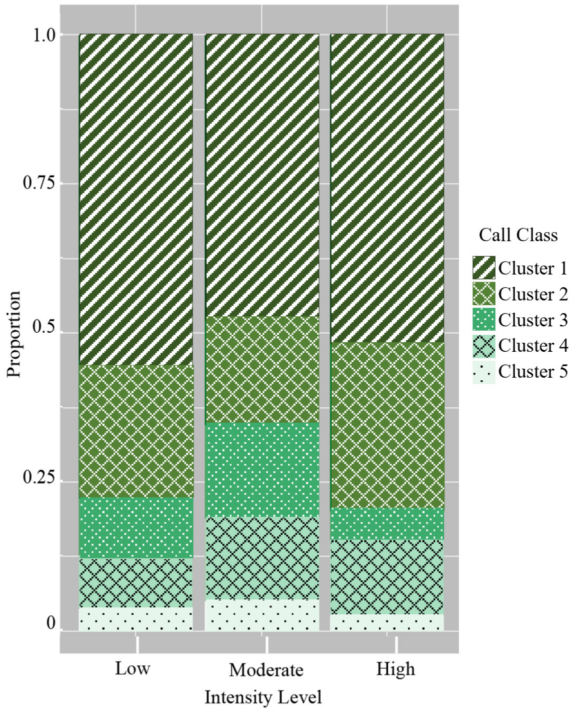


FIGURE 6 | Probability of detecting the five graded call classes in the three intensity levels. Cluster 1: Low-frequency/moderate duration; Cluster 2: Mid-frequency/long duration; Cluster 3: Broadband/very long duration; Cluster 4: High-frequency/short duration; and Cluster 5: Very high-frequency/short duration.

intensity competitive groups. Somewhat surprisingly, relatively high-frequency calls had a higher probability of detection in moderate intensity level groups. Of the high-frequency graded calls, and discrete "chirps" and "harmonic squeaks" produced in moderate intensity groups, roughly half occurred during focal follows with splits and joins. Previous research has shown that humpback whales use high-frequency calls often during the splitting and joining of group members, where changing hierarchies may occur (Dunlop et al., 2008; Cusano, 2021). Further research will be needed to determine if there is in fact a correlation between the stability of competitive groups and the use of relatively high frequency calls. However, combined with the results from previous studies, the results presented here provide preliminary evidence that high frequency calls may be particularly important during changing group dynamics, where information on intent and/or willingness to engage or disengage from competition could be beneficial to prevent further conflict.

Whales in aggressive, high-intensity groups emitted fewer discrete calls but interestingly the proportional use of song unit social calls increased. Song unit social calls are detected most often in lone males and groups of multiple animals, and are likely only used by males (Dunlop et al., 2008; Rekdahl et al., 2013). Song itself is a reproductive display, although its primary function has not been established (Tyack, 1981; Darling and Bérubé, 2001; Herman, 2017; Murray et al., 2018). It has been proposed to possibly function in female attraction, whether to an individual or to an area, and/or by facilitating male-male interactions (Herman, 2017). In either case, information contained in the song is likely available to both sexes (Murray et al., 2018) and could be used by eavesdroppers as well as intended recipients (Dunlop and Noad, 2016). The greatly increased use of song units as unpatterned social calls in the current study, particularly in more aggressive groups suggests that, at least as social calls, they are likely aimed at other males rather than females. The fact that song units have a lower source level when used in social contexts than when produced in song (Dunlop et al., 2013), and are produced at higher rates when males join groups of multiple adults, provides

TABLE 5 | Results of the generalized linear models for graded call classes, with the model calculated probability of each call class in each intensity level in the first three columns and the odds ratios in the last three columns.

Graded call class	**Low (prob. ± SE)**	**Moderate (prob. ± SE)**	**High (prob. ± SE)**	**Low-mod (odds ± SE)**	**Low-high (odds ± SE)**	**Mod-high (odds ± SE)**
Low-frequency/moderate duration	0.55 ± 0.02	0.48 ± 0.01	0.52 ± 0.02	1.30 ± 0.11 z ratio = 3.16 $p = 0.0045$*	1.12 ± 0.11 z ratio = 1.06 $p = 0.5327$	0.86 ± 0.07 z ratio = −1.97 $p = 0.1184$
Mid-frequency/long duration	0.23 ± 0.02	0.18 ± 0.01	0.28 ± 0.02	1.43 ± 0.14 z ratio = 3.52 $p = 0.0012$*	0.78 ± 0.09 z ratio = −2.13 $p = 0.0834$	0.55 ± 0.05 z ratio = −6.58 $p < 0.0001$**
Broadband/very long duration	0.09 ± 0.01	0.16 ± 0.01	0.05 ± 0.01	0.56 ± 0.08 z ratio = −4.23 $p = 0.0001$**	1.99 ± 0.41 z ratio = 3.36 $p = 0.0022$*	3.56 ± 0.60 z ratio = 7.54 $p < 0.0001$**
High-frequency/short duration	0.09 ± 0.01	0.14 ± 0.01	0.13 ± 0.01	0.62 ± 0.08 z ratio = −3.43 $p = 0.0018$*	0.68 ± 0.11 z ratio = −2.35 $p = 0.0481$*	1.10 ± 0.13 z ratio = 0.79 $p = 0.7069$
Very high-frequency/short duration	0.04 ± 0.01	0.05 ± 0.004	0.02 ± 0.01	0.74 ± 0.16 z ratio = -1.41 $p = 0.3305$	1.56 ± 0.47 z ratio = 1.50 $p = 0.2860$	2.12 ± 0.51 z ratio = 3.09 $p = 0.0054$*

*Odds ratios indicate the odds of detecting that call type in the first intensity level listed compared with the second intensity level listed. *Indicates statistical significance at the $p < 0.05$ level; ** indicates statistical significance at the $p < 0.001$ level.*

further evidence that they are an intragroup signal aimed at other males (Dunlop and Noad, 2016). Most of the song unit social calls used in the current study were low-frequency, pulsive sounds (**Figure 2E**). Low frequency pulsed sounds are thought to function in conveying information regarding dominance status, primarily to other males, in some terrestrial mammals (e.g., male rock hyraxes, *Procavia capensis*; Koren and Geffen, 2009; Demartsev et al., 2016; Weissman et al., 2019) and birds (e.g., male barn swallows, *Hirundo rustica* (Galeotti et al., 1997). These sounds could contain similar information in whales during humpback whale competitive behavior. However, as low frequency, pulsive song units are also produced while singing, they may also be used to convey the same information (e.g., RHP) but in a different context, supporting the theory that song may serve multiple functions (Herman, 2017; Murray et al., 2018).

Unfortunately, in the present study, the continuous background song precluded automated measurement of any acoustic features of the calls, or any quantitative classification of call types. Using data from the same population reduced the likelihood that a discrete call type was present in the current dataset that was not detected by the previous FKM analysis. However, it is possible that some discrete call types were missed here. Future studies should therefore attempt to perform a quantitative FKM analysis on data directly from competitive groups to identify potential call types that, although not detected in previous studies, are relatively discrete. Using data from other breeding grounds where population sizes are smaller (e.g., Tonga or New Caledonia) may help as there is likely less background chorusing from singing males (Allen, pers. comm.) due to lower numbers on these breeding grounds (Constantine et al., 2012). In the current study, we were also limited to making assumptions about the behavior of the animals based on surface observations. This might not be an accurate representation of their underwater behavior, especially as humpbacks in competitive groups are known to use the entire water column (Herman et al., 2007). However, we carefully determined intensity levels that were discrete and mutually exclusive, providing what is likely a conservative view of the variety of intensity levels observed in competitive groups. Incorporating underwater video will help to validate the correlation between surface and underwater behavior, as well as their relationship with calling behavior.

Overall, we have provided evidence that humpback whales follow similar trends to terrestrial species that engage heavily in male competition during the breeding season. As theories regarding male-male competition predict, humpback whale competitive groups progressed from low intensity displays to higher intensity contests, but with escalated contests being relatively uncommon. Further, we have shown that humpback whales use acoustic signals in concordance with visual displays and threats during this progression. Calls within humpback whale groups classified as low and moderate intensity likely function to convey more fixed information such as body size, while calls in the higher intensity levels likely function to convey flexible information on motivation and arousal. Future research can build from this to compare baleen whale species with drastically different mating strategies, social systems, and vocal repertoires in order to shed light on the link between high communicative complexity and sociality in baleen whales.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by The University of Queensland Office of Research Ethics.

AUTHOR CONTRIBUTIONS

DC, MN, RD, and DP conceived the study and assisted with data collection, and edited the final manuscript. DC and DP were responsible for obtaining funding for field data collection. DC oversaw data collection, processed and analyzed all data, interpreted the results, and prepared the final manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

Great Barrier Reef fieldwork (2017–2019) was funded by the Holsworth Wildlife Research Endowment and the Ecological Society of Australia (#2017001004), as well as substantial in-kind support from Blue Planet Marine, the Cetacean Ecology and Acoustic Laboratory Group, and the University of Queensland. Additional support was provided to the primary author from an American Australian Association Scholarship and a University of Queensland International Scholarship.

ACKNOWLEDGMENTS

We would like to thank the many people involved in the Great Barrier Reef Whale and Dolphin Research Programme, especially the numerous volunteers, K. Indeck for creating the map in **Figure 1**, J. Allen for her helpful comments on drafts, the three reviewers for their constructive feedback during review, and the Moreton Bay Research Station for hosting the Cetacean Ecology and Acoustics Laboratories Group. Finally, we wish to acknowledge the Quandamooka people, the traditional owners of the land on which the Moreton Bay Research Station was built, and the Ngaro, the traditional owners of the sea country where field work was conducted.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.665186/full#supplementary-material

REFERENCES

Allen, J. A., Garland, E. C., Dunlop, R. A., and Noad, M. J. (2019). Network analysis reveals underlying syntactic features in a vocally learnt mammalian display, humpback whale song. *Proc. R. Soc. B* 286:20192014. doi: 10.1098/rspb.2019.2014

Allen, M. L., and Krofel, M. (2017). "Resource holding potential," in *Encyclopedia of Animal Cognition and Behavior*, eds J. Vonk and T. K. Shackleford (New York, NY: Springer), 1–3. . doi: 10.1007/978-3-319-47829-6_444-1

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* 49, 227–266. doi: 10.1163/156853974X00534

August, P. V., and Anderson, J. G. (1987). Mammal sounds and motivation-structural rules: a test of the hypothesis. *J. Mammal* 68, 1–9. doi: 10.2307/1381039

Baker, C. S., and Herman, L. M. (1984). Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Can. J. Zool.* 62, 1922–1937. doi: 10.1139/z84-282

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Statist. Software* 67, 1–48. doi: 10.18637/jss.v067.i01

Berta, A., and Sumich, J. L. (1999). "Mating, breeding, and social organization," in *Marine Mammals: Evolutionary Biology*, 1st Edn, (San Diego, CA: Academic Press), 335–359.

Bezdek, J. C. (1981). "Objective function clustering," in *Pattern Recognition with Fuzzy Objective Function Algorithms*, (Boston, MA: Springer), 43–93. doi: 10.1007/978-1-4757-0450-1_3

Boness, D., Clapham, P. J., and Mesnick, S. L. (2002). "Life history and reproductive strategies," in *Marine Mammal Biology: an Evolutionary Approach*, ed. R. Hoelzel (Hoboken, NJ: Blackwell Science Ltd).

Bradbury, J., and Vehrencamp, S. (2011). *Principles of Animal Communication*. Sunderland, MA: Sinauer Associates.

Briefer, E. F. (2012). Vocal expression of emotions in mammals: mechanisms of production and evidence. *J. Zool.* 288, 1–20. doi: 10.1111/j.1469-7998.2012.00920.x

Briefer, E. F. (2018). Vocal contagion of emotions in non-human animals. *Proc. R. Soc. B: Biol. Sci.* 285:20172783. doi: 10.1098/rspb.2017.2783

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., et al. (2017b). Modeling zero-inflated count data with glmmTMB. *BioRxiv [preprint]* doi: 10.1101/132753

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., et al. (2017a). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9, 378–400. doi: 10.32614/RJ-2017-066

Brown, M., and Corkeron, P. (1995). Pod characteristics of migrating humpback whales (*Megaptera novaeangliae*) off the east Australian coast. *Behaviour* 132, 163–179. doi: 10.1163/156853995X00676

Brownell, R., and Ralls, K. (1986). Potential for sperm competition in baleen whales. *Rep. Int. Whaling Comm.* 8, 97–112.

Burmeister, S. S., Ophir, A. G., Ryan, M. J., and Wilczynski, W. (2002). Information transfer during cricket frog contests. *Anim. Behav.* 64, 715–725. doi: 10.1006/anbe.2002.4012

Burns, D., Brooks, L., Harrison, P., Franklin, T., Franklin, W., Paton, D., et al. (2014). Migratory movements of individual humpback whales photographed off the eastern coast of Australia. *Mar. Mamm. Sci.* 30, 562–578. doi: 10.1111/mms.12057

Campagna, C. (2009). "Aggressive behavior, intraspecific," in *Encyclopedia of Marine Mammals*, eds W. F. Perrin, B. Wursig, and J. G. M. Thewissen (Amsterdam: Elsevier). doi: 10.1016/B978-0-12-373553-9.00005-5

Center for Conservation Bioacoustics [CCB] (2014). *Raven Pro: Interactive Sound Analysis Software (Version 1.5)*. Ithaca, NY: The Cornell Lab of Ornithology.

Charlton, B. D., and Reby, D. (2011). Context-related acoustic variation in male fallow deer (Dama dama) groans. *PLoS One* 6:e21066. doi: 10.1371/journal.pone.0021066

Clapham, P. J. (1993). Social organization of humpback whales on a North Atlantic feeding ground. *Symp. Zool. Soc. Lond.* 65, 131–145.

Clapham, P. J. (1996). The social and reproductive biology of humpback whales: an ecological perspective. *Mammal Rev.* 26, 27–49. doi: 10.1111/j.1365-2907.1996.tb00145.x

Clapham, P. J., Mattila, D. K., and Palsbøll, P. J. (1993). High-latitude-area composition of humpback whale competitive groups in Samana Bay: further evidence for panmixis in the North Atlantic population. *Can. J. Zool.* 71, 1065–1066. doi: 10.1139/z93-142

Clapham, P. J., Palsbøll, P. J., Mattila, D. K., and Vasquez, O. (1992). Composition and dynamics of humpback whale competitive groups in the West Indies. *Behaviour*. 122, 182–194. doi: 10.1163/156853992X00507

Clark, C. W. (1983). "Acoustic communication and behavior of the southern right whale," in *Communication and Behavior of Whales*, ed. R. S. Payne (Boulder, CO: Westview Press), 163–198.

Clark, C. W. (1990). "Acoustic behaviour of mysticete whales," in *Sensory Abilities of Cetaceans*, eds J. A. Thomas and R. A. Kastelein (Boston, MA: Springer), 571–583. doi: 10.1007/978-1-4899-0858-2_40

Clutton-Brock, T. H., and Albon, S. D. (1979). The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69, 145–170. doi: 10.1163/156853979X00449

Constantine, R., Jackson, J. A., Steel, D., Baker, C. S., Brooks, L., Burns, D., et al. (2012). Abundance of humpback whales in Oceania using photo-identification and microsatellite genotyping. *Mar. Ecol. Prog. Ser.* 453, 249–261. doi: 10.3354/meps09613

Cusano, D. (2021). *Flexible Information in the Social Sounds of Humpback Whales*. Ph.D. thesis, Queensland, QLD: University of Queensland. doi: 10.1121/10.0005111

Cusano, D. A., Noad, M. J., and Dunlop, R. A. (2021). Fuzzy clustering as a tool to differentiate between discrete and graded call types. *JASA Exp. Lett.* 1:061201. doi: 10.1080/09524622.2020.1858450

Cusano, D. A., Indeck, K. L., Noad, M. J., and Dunlop, R. A. (2020). Humpback whale (*Megaptera novaeangliae*) social call production reflects both motivational state and arousal. *Bioacoustics*. 1–24. doi: 10.1080/09524622.2020.1858450

Darling, J. D. (2001). *Characterization of Behavior of Humpback Whales in Hawaiian Waters*. Honolulu, HI: Hawaiian Islands Humpback Whale National Marine Sanctuary.

Darling, J. D., and Bérubé, M. (2001). Interactions of singing humpback whales with other males. *Mar. Mamm. Sci.* 17, 570–584. doi: 10.1111/j.1748-7692.2001.tb01005.x

Demartsev, V., Bar Ziv, E., Shani, U., Goll, Y., Koren, L., and Geffen, E. (2016). Harsh vocal elements affect counter-singing dynamics in male rock hyrax. *Behav. Ecol.* 27, 1397–1404. doi: 10.1093/beheco/arw063

Dunlop, R. A. (2018b). The communication space of humpback whale social sounds in wind-dominated noise. *J. Acoust. Soc. Am.* 144, 540–551. doi: 10.1121/1.5047744

Dunlop, R. (2018a). "The communication space of humpback whale social sounds in vessel noise," in *Proceedings of the Meetings on Acoustics 176ASA*, (Illinois, ILL: Acoustical Society of America). doi: 10.1121/2.0000935

Dunlop, R. A., Cato, D. H., and Noad, M. J. (2008). Non-song acoustic communication in migrating humpback whales (*Megaptera novaeangliae*). *Mar. Mamm Sci.* 24, 613–629. doi: 10.1111/j.1748-7692.2008.00208.x

Dunlop, R. A., Cato, D. H., Noad, M. J., and Stokes, D. M. (2013). Source levels of social sounds in migrating humpback whales (*Megaptera novaeangliae*). *J. Acoust. Soc. Am.* 134, 706–714. doi: 10.1121/1.4807828

Dunlop, R. A., and Noad, M. J. (2016). The "risky" business of singing: tactical use of song during joining by male humpback whales. *Behav. Ecol. Sociobiol.* 70, 2149–2160. doi: 10.1007/s00265-016-2218-2218

Dunlop, R. A., Noad, M. J., Cato, D. H., and Stokes, D. (2007). The social vocalization repertoire of east Australian migrating humpback whales (*Megaptera novaeangliae*). *J. Acoust. Soc. Am.* 122, 2893–2905. doi: 10.1121/1.2783115

Dunlop, R. A., Noad, M. J., McCauley, R. D., Kniest, E., Paton, D., and Cato, D. H. (2015). The behavioural response of humpback whales (*Megaptera novaeangliae*) to a 20 cubic inch air gun. *Aquat. Mamm.* 41, 412–433. doi: 10.1578/AM.41.4.2015.412

Dunlop, R. A., Noad, M. J., McCauley, R. D., Kniest, E., Slade, R., Paton, D., et al. (2016). Response of humpback whales (*Megaptera novaeangliae*) to ramp-up of a small experimental air gun array. *Mar. Pollut. Bull.* 103, 72–83. doi: 10.1016/j.marpolbul.2015.12.044

D'Vincent, C. G., Nilson, R. M., and Hanna, R. E. (1985). Vocalization and coordinated feeding behavior of the humpback whale in southeastern Alaska. *Sci. Rep. Whales Res. Institute* 36, 41–47.

Edds-Walton, P. L. (1997). Acoustic communication signals of mysticete whales. *Bioacoustics* 8, 47–60. doi: 10.1080/09524622.1997.9753353

Enquist, M. (1985). Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Anim. Behav.* 33, 1152–1161. doi: 10.1016/S0003-3472(85)80175-5

Félix, F., and Novillo, J. (2015). Structure and dynamics of humpback whales competitive groups in Ecuador. *Anim. Behav. Cogn.* 2, 56–70. doi: 10.12966/abc.02.05.2015

Ferraro, M. B., and Giordani, P. (2015). A toolbox for fuzzy clustering using the R programming language. *Fuzzy Sets Systems* 279, 1–16. doi: 10.1016/j.fss.2015.05.001

Fischer, J., Wadewitz, P., and Hammerschmidt, K. (2017). Structural variability and communicative complexity in acoustic communication. *Anim. Behav.* 134, 229–237. doi: 10.1016/j.anbehav.2016.06.012

Fournet, M. E. H., Szabo, A., and Mellinger, D. K. (2015). Repertoire and classification of non-song calls in Southeast Alaskan humpback whales (*Megaptera novaeangliae*). *J. Acoust. Soc. Am.* 137, 1–10. doi: 10.1121/1.4904504

Galeotti, P., Saino, N., Sacchi, R., and Møller, A. P. (1997). Song correlates with social context, testosterone and body condition in male barn swallows. *Anim. Behav.* 53, 687–700. doi: 10.1006/anbe.1996.0304

Garland, E. C., Goldizen, A. W., Lilley, M. S., Rekdahl, M. L., Garrigue, C., Constantine, R., et al. (2015). Population structure of humpback whales in the western and central South Pacific Ocean as determined by vocal exchange among populations. *Conserv. Biol.* 29, 1198–1207. doi: 10.1111/cobi.12492

Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics* 27, 857–871. doi: 10.2307/2528823

Green, S., and Marler, P. (1979). "The analysis of animal communication," in *Social Behavior and Communication*, eds P. Marler and J. G. Vandenbergh (Boston, MA: Springer), 73–158. doi: 10.1007/978-1-4615-9116-0_3

Hafner, G. W., Hamilton, C. L., Steiner, W. W., Thompson, T. J., and Winn, H. E. (1979). Signature information in the song of the humpback whale. *J. Acoust. Soc. Am.* 66, 1–6. doi: 10.1121/1.383072

Hardy, I. C., and Briffa, M. (2013). *Animal Contests*. Cambridge: Cambridge University Press. doi: 10.1017/CBO9781139051248

Hauser, M. D. (1996). *The Evolution of Communication*. Cambridge, MA: MIT press.

Helweg, D. A., and Herman, L. M. (1994). Diurnal patterns of behaviour and group membership of humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Ethology* 98, 298–311. doi: 10.1111/j.1439-0310.1994.tb01078.x

Herman, E. Y., Herman, L. M., Pack, A. A., Marshall, G., Shepard, M. C., and Bakhtiari, M. (2007). When whales collide: crittercam offers insight into the competitive behavior of humpback whales on their Hawaiian wintering grounds. *Mar. Technol. Soc. J.* 41, 35–43. doi: 10.4031/002533207787441971

Herman, L. M. (2017). The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: review, evaluation, and synthesis. *Biol. Rev.* 92, 1795–1818. doi: 10.1111/brv.12309

Hof, D., and Podos, J. (2013). Escalation of aggressive vocal signals: a sequential playback study. *Proc. R. Soc. B: Biol. Sci.* 280:20131553. doi: 10.1098/rspb.2013.1553

Hofmann, H. A., and Schildberger, K. (2001). Assessment of strength and willingness to fight during aggressive encounters in crickets. *Anim. Behav.* 62, 337–348. doi: 10.1006/anbe.2001.1746

Indeck, K. L., Girola, E., Torterotot, M., Noad, M. J., and Dunlop, R. A. (2021). Adult female-calf acoustic communication signals in migrating east Australian humpback whales. *Bioacoustics* 30, 341–365. doi: 10.1080/09524622.2020.1742204

Insley, S., Phillips, A. V., and Charrier, I. (2003). A review of social recognition in pinnipeds. *Aquat. Mamm.* 29, 181–201. doi: 10.1578/016754203101024149

Jurasz, C. M., and Jurasz, V. P. (1979). Feeding modes of the humpback whale, *Megaptera novaeangliae*, in Southeast Alaska. *Sci. Rep. Whales Res. Institute* 31, 69–83.

Katona, S., and Whitehead, H. (1981). Identifying humpback whales using their natural markings. *Polar Rec.* 20, 439–444. doi: 10.1017/S003224740000365X

Kaufman, L., and Rousseeuw, P. J. (2009). *Finding Groups in Data: an Introduction to Cluster Analysis*. Hoboken, NJ: John Wiley & Sons.

Koren, L., and Geffen, E. (2009). Complex call in male rock hyrax (*Procavia capensis*): a multi-information distributing channel. *Behav. Ecol. Sociobiol.* 63, 581–590. doi: 10.1007/s00265-008-0693-2

Kotiaho, J. S., Alatalo, R. V., Mappes, J., and Parri, S. (1999). Honesty of agonistic signalling and effects of size and motivation asymmetry in contests. *Acta Ethol.* 2, 13–21. doi: 10.1007/PL00012227

Kraus, S. D., and Hatch, J. J. (2001). Mating strategies in the North Atlantic right whale (*Eubalaena glacialis*). *J. Cetacean Res. Manag. Special Issue* 2, 237–244.

Lenth, R. (2021). *Emmeans: Estimated Marginal Means, Aka Least-Squares Means. R Package Version 1.6.2-1*. Available online at: https://cran.r-project.org/package=emmeans (accessed September 5, 2021).

Lingle, S., Wyman, M. T., Kotrba, R., Teichroeb, L. J., and Romanow, C. A. (2012). What makes a cry a cry? a review of infant distress vocalizations. *Curr. Zool.* 58, 698–726. doi: 10.1093/czoolo/58.5.698

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., and Hornik, K. (2019). *Cluster: Cluster Analysis Basics and Extensions. 2.1.0*. Available online at: https://cran.r-project.org/package=cluster (accessed September 5, 2021).

Manser, M. B. (2010). "The generation of functionally referential and motivational vocal signals in mammals," in *Handbook of Behavioral Neuroscience*, ed. S. M. Brudzynski (London: Academic Press), 477–486. doi: 10.1016/B978-0-12-374593-4.00043-7

Marler, P. (1961). The logical analysis of animal communication. *J. Theor. Biol.* 1, 295–317. doi: 10.1016/0022-5193(61)90032-7

Marler, P. (1975). On the origin of speech from animal sounds. *Role Speech Lang.* 11:37.

Marler, P. (1976). "Social organization, communication and graded signals: the chimpanzee and the gorilla," in *Growing Points Ethology*, eds P. P. G. Bateson and R. A. Hinde (Cambridge: Cambridge University Press).

Marler, P. (1977). "The structure of animal communication sounds," in *Recognition of Complex Acoustic Signals*, eds T. Bullock and E. Evans (Berlin: Dahlem Konferenzen), 17–35.

Marler, P., Evans, C. S., and Hauser, M. D. (1992). "Animal signals: motivational, referential, or both?" in *Nonverbal Vocal Communication: Comparative and Developmental Approaches,* eds H. Papousek, U. Jurgens, and M. Papousek (Cambridge: Cambridge University Press), 66–86.

Mattila, D. K., Clapham, P. J., Katona, S. K., and Stone, G. S. (1989). Population composition of humpback whales, *Megaptera novaeangliae*, on Silver Bank, 1984. *Can. J. Zool.* 67, 281–285. doi: 10.1139/z89-041

May-Collado, L. J., Agnarsson, I., and Wartzok, D. (2007). Reexamining the relationship between body size and tonal signals frequency in whales: a comparative approach using a novel phylogeny. *Mar. Mamm. Sci.* 23, 524–552. doi: 10.1111/j.1748-7692.2007.02250.x

Maynard-Smith, J. (1974). The theory of games and the evolution of animal conflicts. *J. Theor. Biol.* 47, 209–221. doi: 10.1016/0022-5193(74)90110-6

Maynard-Smith, J., and Harper, D. (2003). *Animal Signals*. Oxford: Oxford University Press.

McElligott, A. G., Gammell, M. P., Harty, H. C., Paini, D. R., Murphy, D. T., Walsh, J. T., et al. (2001). Sexual size dimorphism in fallow deer (Dama dama): do larger, heavier males gain greater mating success? *Behav. Ecol. Sociobiol.* 49, 266–272. doi: 10.1007/s002650000293

McElligott, A. G., and Hayden, T. J. (1999). Context-related vocalization rates of fallow bucks. Dama dama. *Anim. Behav.* 58, 1095–1104. doi: 10.1006/anbe.1999.1237

Mesnick, S. L., and Ralls, K. (2009). "Mating systems," in *Encyclopedia of Marine Mammals*, eds W. F. Perrin, B. Wursig, and J. G. M. Thewissen (Amsterdam: Academic Press), 712–719. doi: 10.1016/B978-0-12-373553-9.00165-6

Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *Am. Nat.* 111, 855–869. doi: 10.1086/283219

Morton, E. S. (1982). "Grading, discreteness, redundancy, and motivation-structural rules," in *Acoustic Communication in Birds*, eds D. E. Kroodsma and M. H. Miller (New York, NY: Academic Press), 183–212. doi: 10.1016/B978-0-08-092416-8.50015-2

Murray, A., Dunlop, R. A., Noad, M. J., and Goldizen, A. W. (2018). Stereotypic and complex phrase types provide structural evidence for a multi-message display in humpback whales (*Megaptera novaeangliae*). *J. Acoust. Soc. Am.* 143, 980–994. doi: 10.1121/1.5023680

Noad, M. J., Kniest, E., and Dunlop, R. A. (2019). Boom to bust? Implications for the continued rapid growth of the eastern Australian humpback whale population despite recovery. *Popul. Ecol.* 61, 198–209. doi: 10.1002/1438-390X.1014

Owings, D. H., and Morton, E. S. (1998). *Animal Vocal Communication: a New Approach*. Cambridge: Cambridge University Press. doi: 10.1017/CBO9781139167901

Pack, A. A., Salden, D. R., Ferrari, M. J., Glockner-Ferrari, D. A., Herman, L. M., Stubbs, H. A., et al. (1998). Male humpback whale dies in competitive group. *Mar. Mamm. Sci.* 14, 861–873. doi: 10.1111/j.1748-7692.1998.tb00771.x

Parker, G. A. (1974). Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol.* 47, 223–243. doi: 10.1016/0022-5193(74)90111-8

Parks, S. E. (2003). Response of north Atlantic right whales (*Eubalaena glacialis*) to playback of calls recorded from surface active groups in both the north and South Atlantic. *Mar. Mamm. Sci.* 19, 563–580. doi: 10.1111/j.1748-7692.2003.tb01321.x

Parks, S. E., Brown, M. W., Conger, L. A., Hamilton, P. K., Knowlton, A. R., Kraus, S. D., et al. (2007). Occurrence, composition, and potential functions of North Atlantic right whale (*Eubalaena glacialis*) surface active groups. *Mar. Mamm. Sci.* 23, 868–887. doi: 10.1111/j.1748-7692.2007.00154.x

Parks, S. E., Cusano, D. A., Stimpert, A. K., Weinrich, M. T., Friedlaender, A. S., and Wiley, D. N. (2014). Evidence for acoustic communication among bottom foraging humpback whales. *Sci. Rep.* 4:7508. doi: 10.1038/srep07508

Parks, S. E., and Tyack, P. L. (2005). Sound production by North Atlantic right whales (*Eubalaena glacialis*) in surface active groups. *J. Acoust. Soc. Am.* 117, 3297–3306. doi: 10.1121/1.1882946

Payne, K., Tyack, P. L., and Payne, R. (1983). "Progressive changes in the songs of humpback whales (*Megaptera novaeangliae*): a detailed analysis of two seasons in Hawaii," in *Communication and Behavior of Whales*, ed. R. Payne (Boulder, CO: Westview Press).

Payne, K. B., and Payne, R. S. (1985). Large scale changes over 19 years in songs of humpback whales in Bermuda. *Zeitschrift für Tierpsychologie* 68, 89–114. doi: 10.1111/j.1439-0310.1985.tb00118.x

Payne, R., and Dorsey, E. (1983). "Sexual dimorphism and aggressive use of callosities in right whales (*Eubalaena australis*)," in *Communication and Behavior of Whales*, ed. R. S. Payne (Boulder, CO: Westview Press), 295–329.

Payne, R. S., and McVay, S. (1971). Songs of humpback whales. *Science* 173, 585–597. doi: 10.1126/science.173.3997.585

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ramp, C., Hagen, W., Palsbøll, P., Bérubé, M., and Sears, R. (2010). Age-related multi-year associations in female humpback whales (*Megaptera novaeangliae*). *Behav. Ecol. Sociobiol.* 64, 1563–1576. doi: 10.1007/s00265-010-0970-978

Reby, D., and McComb, K. (2003b). Vocal communication and reproduction in deer. *Adv. Study Behav.* 33, 231–264. doi: 10.1016/S0065-3454(03)33005-0

Reby, D., and McComb, K. (2003a). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Anim. Behav.* 65, 519–530. doi: 10.1006/anbe.2003.2078

Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W. T., and Clutton-Brock, T. (2005). Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proc. R. Soc. B: Biol. Sci.* 272, 941–947. doi: 10.1098/rspb.2004.2954

Rekdahl, M., Tisch, C., Cerchio, S., and Rosenbaum, H. (2017). Common nonsong social calls of humpback whales (*Megaptera novaeangliae*) recorded off northern Angola, southern Africa. *Mar. Mamm. Sci.* 33, 365–375. doi: 10.1111/mms.12355

Rekdahl, M. L., Dunlop, R. A., Noad, M. J., and Goldizen, A. W. (2013). Temporal stability and change in the social call repertoire of migrating humpback whales. *J. Acoust. Soc. Am.* 133, 1785–1795. doi: 10.1121/1.4789941

Rugh, D. J., and Shelden, K. E. (2009). "Bowhead whale: *Balaena mysticetus*," in *Encyclopedia of Marine Mammals*, eds W. F. Perrin, B. Wursig, and J. G. M. Thewissen (Amsterdam: Academic Press), 131–133. doi: 10.1016/B978-0-12-373553-9.00036-5

Silber, G. K. (1986). The relationship of social vocalizations to surface behavior and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*). *Can. J. Zool.* 64, 2075–2080. doi: 10.1139/z86-316

Smith, J. M., and Price, G. R. (1973). The logic of animal conflict. *Nature* 246, 15–18. doi: 10.1038/246015a0

Smith, J. N., Grantham, H. S., Gales, N., Double, M. C., Noad, M. J., and Paton, D. (2012). Identification of humpback whale breeding and calving habitat in the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 447, 259–272. doi: 10.3354/meps09462

Smith, W. (1977). *The Behavior of Communicating: An Ethological Approach*. Cambridge: Harvard University Press. doi: 10.4159/9780674043794

Spitz, S. S., Herman, L. M., Pack, A. A., and Deakos, M. H. (2002). The relation of body size of male humpback whales to their social roles on the Hawaiian winter grounds. *Can. J. Zool.* 80, 1938–1947. doi: 10.1139/z02-177

Stimpert, A. K., Au, W. W., Wiley, D. N., and Mattila, D. (2008). Contextual sound production by tagged humpback whales (*Megaptera novaeangliae*) on a feeding and breeding ground. *J. Acoust. Soc. Am.* 124, 2484–2484. doi: 10.1121/1.4782751

Stimpert, A. K., Au, W. W. L., Parks, S. E., Hurst, T., and Wiley, D. N. (2011). Common humpback whale (*Megaptera novaeangliae*) sound types for passive acoustic monitoring. *J. Acoust. Soc. Am.* 129, 476–482. doi: 10.1121/1.3504708

Stimpert, A. K., Wiley, D. N., Au, W. W. L., Johnson, M. P., and Arsenault, R. (2007). 'Megapclicks': acoustic click trains and buzzes produced during night-time foraging of humpback whales (*Megaptera novaeangliae*). *Biol. Lett.* 3, 467–470. doi: 10.1098/rsbl.2007.0281

Thompson, P. O., Cummings, W. C., and Ha, S. J. (1986). Sounds, source levels, and associated behavior of humpback whales, Southeast Alaska. *J. Acoust. Soc. Am.* 80, 735–740. doi: 10.1121/1.393947

Tyack, P. L. (1981). Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behav. Ecol. Sociobiol.* 8, 105–116. doi: 10.1007/BF00300822

Tyack, P. L., and Whitehead, H. (1983). Male competition in large groups of wintering humpback whales. *Behaviour* 83, 132–154. doi: 10.1163/156853982X00067

Vannoni, E., and McElligott, A. G. (2008). Low frequency groans indicate larger and more dominant fallow deer (Dama dama) males. *PLoS One* 3:e3113. doi: 10.1371/journal.pone.0003113

Ver Hoef, J. M., and Boveng, P. L. (2007). Quasi-Poisson vs. negative binomial regression: how should we model overdispersed count data? *Ecology* 88, 2766–2772. doi: 10.1890/07-0043.1

Wadewitz, P., Hammerschmidt, K., Battaglia, D., Witt, A., Wolf, F., and Fischer, J. (2015). Characterizing vocal repertoires—Hard vs. soft classification approaches. *PLoS One* 10:e0125785. doi: 10.1371/journal.pone.0125785

Wagner, W. E. Jr. (1989). Graded aggressive signals in Blanchard's cricket frog: vocal responses to opponent proximity and size. *Anim. Behav.* 38, 1025–1038. doi: 10.1016/S0003-3472(89)80141-1

Weinrich, M. T. (1991). Stable social associations among humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine. *Can. J. Zool.* 69, 3012–3019. doi: 10.1139/z91-425

Weissman, Y. A., Demartsev, V., Ilany, A., Barocas, A., Bar-Ziv, E., Shnitzer, I., et al. (2019). Acoustic stability in hyrax snorts: vocal tightrope-walkers or wrathful verbal assailants? *Behav. Ecol.* 30, 223–230. doi: 10.1093/beheco/ary141

Winn, H. E., Beamish, P., and Perkins, P. J. (1979). Sounds of two entrapped humpback whales (*Megaptera novaeangliae*) in Newfoundland. *Mar. Biol.* 55, 151–155. doi: 10.1007/BF00397311

Winn, H. E., and Winn, L. K. (1978). The song of the humpback whale *Megaptera novaeangliae* in the West Indies. *Mar. Biol.* 47, 97–114. doi: 10.1007/BF00395631

Würsig, B., Guerrero, J., and Silber, G. K. (1993). Social and sexual behavior of bowhead whales in fall in the western arctic: a re-examination of seasonal trends. *Mar. Mamm. Sci.* 9, 103–115. doi: 10.1111/j.1748-7692.1993.tb00434.x

Zahavi, A. (1982). The pattern of vocal signals and the information they convey. *Behaviour* 80, 1–8. doi: 10.1163/156853982X00409

Zoidis, A. M., Smultea, M. A., Frankel, A. S., Hopkins, J. L., Day, A., McFarland, A. S., et al. (2008). Vocalizations produced by humpback whale (*Megaptera novaeangliae*) calves recorded in Hawaii. *J. Acoust. Soc. Am.* 123, 1737–1746. doi: 10.1121/1.2836750

Conflict of Interest: DC was employed by the company JASCO Applied Sciences. This affiliation began after the presented research took place.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Advantages of publishing in Frontiers

OPEN ACCESS
Articles are free to read
for greatest visibility
and readership

FAST PUBLICATION
Around 90 days
from submission
to decision

HIGH QUALITY PEER-REVIEW
Rigorous, collaborative,
and constructive
peer-review

TRANSPARENT PEER-REVIEW
Editors and reviewers
acknowledged by name
on published articles

Frontiers
Avenue du Tribunal-Fédéral 34
1005 Lausanne | Switzerland

Visit us: www.frontiersin.org
Contact us: frontiersin.org/about/contact

REPRODUCIBILITY OF RESEARCH
Support open data
and methods to enhance
research reproducibility

DIGITAL PUBLISHING
Articles designed
for optimal readership
across devices

FOLLOW US
@frontiersin

IMPACT METRICS
Advanced article metrics
track visibility across
digital media

EXTENSIVE PROMOTION
Marketing
and promotion
of impactful research

LOOP RESEARCH NETWORK
Our network
increases your
article's readership