Research Topics

Whales and climate

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Published in
Frontiers in Marine Science

ISSN 1664-8714
ISBN 978-2-8325-4244-6
DOI 10.3389/978-2-8325-4244-6

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Whales and climate

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Citation
Meynecke, J.-O., Guzman, H. M., Secchi, E., Derville, S., Richards, R., eds. (2024).
Whales and climate. Lausanne: Frontiers Media SA.
doi: 10.3389/978-2-8325-4244-6

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frontiers | Frontiers in Marine Science

TYPE Editorial
PUBLISHED 20 December 2023
DOI 10.3389/fmars.2023.1347360

OPEN ACCESS

EDITED AND REVIEWED BY
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RECEIVED 30 November 2023
ACCEPTED 12 December 2023
PUBLISHED 20 December 2023

CITATION
Meynecke J-O, Derville S and Richards R (2023) Editorial: Whales and climate. *Front. Mar. Sci.* 10:1347360.
doi: 10.3389/fmars.2023.1347360

Editorial: Whales and climate

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KEYWORDS

environmental change, cetacea, climate change adaptation, behaviour, marine protection

Editorial on the Research Topic
Whales and climate

Background

Baleen whales have exhibited alterations from their traditional migration, breeding, and feeding patterns in recent years (Ramp et al., 2015; Moore et al., 2019). Climate change is recognised as a key factor driving these shifts, leading to concerns about the recovery of whale populations. Whales face heightened vulnerability due to their extensive seasonal migrations, exposure to extreme climatic conditions from polar feeding grounds to tropical breeding grounds within a few months each year, low reproduction rates and long lifespans (Tyack, 1986; Corkeron and Connor, 1999). The future population recovery of all baleen whales is intricately tied to climate change and its impact on their feeding and breeding habitats (Thomas et al., 2016; Tulloch et al., 2019) (Figure 1).

The objective of the Whales and Climate topic was to contribute research that enhances the understanding of the intricate relationship between baleen whales and climate change. Climate impacts on the marine environment are inherently complex, marked by uncertainty, time lags, non-linearities, and a multitude of pathways, obscuring cause-and-effect relationships. The topic provided a platform to help quantify the interactions between climate change and mysticeti. It illuminated how past, present, and future climate conditions influence various aspects of the whales' life cycle, including breeding, feeding, and migration, as well as their overall recovery from whaling. Additionally, the Whales and Climate topic aimed to assess the relative vulnerability of different whale populations and species to the effects of climate change. By defining impacts and potential relationships with climate conditions, we aspired to advance modeling approaches and promote the integration of future climate projections into research on whales and climate.

The research of the 13 papers included in this Research Topic investigated body conditions, changes in migration timing, species distribution and abundance, relationships with environmental factors and the potential role of whales in carbon sequestration.

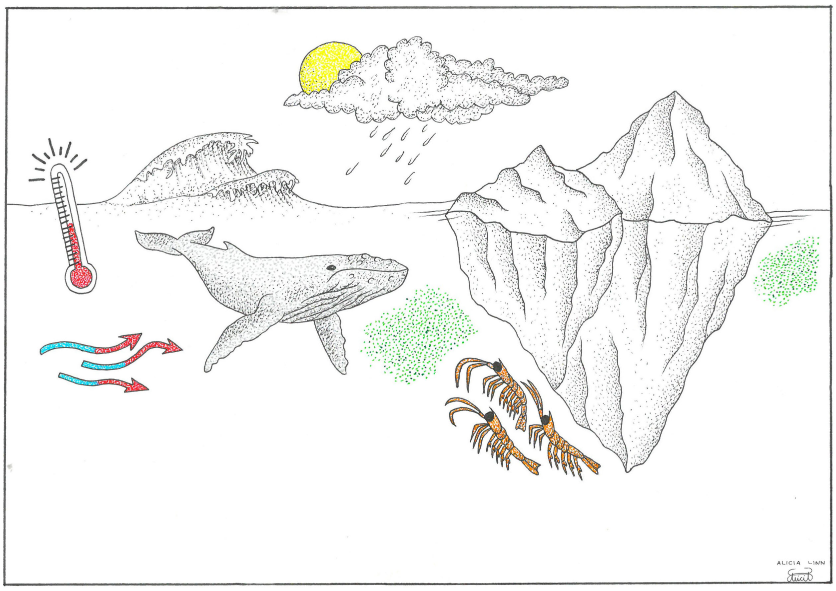

FIGURE 1
An artist impression of whales and climate change illustrating some of the factors influencing the whale´s life cycle such as volume of sea ice, phytoplankton blooms, krill abundance, wind directions and speed and ocean temperature.

Research output and findings

A review identified a number of key environmental drivers of the feeding, calving and migration areas of humpback whales (*Megaptera novaeangliae*) (Meynecke et al.). Feeding studies revealed a preference for upwelling areas with high chlorophyll-a and dynamic fronts, rich in prey (e.g., Fleming et al., 2016). Calving grounds were characterized by shallow, warm waters with gentle currents for better calf survival (e.g., Smith et al., 2012). Migration routes favoured shallow, near-shore waters with moderate temperature and chlorophyll-a levels (e.g., Zerbini et al., 2006). A review on contemporary distribution and abundance of humpback whales in the Southern Hemisphere provided a comprehensive overview of the species' current status, focusing on post-whaling trends in population growth, changes in distribution and migration patterns, and instances of supplementary feeding. These results were linked to environmental change (Seyboth et al.).

Habitat and migration shifts

The response of whales to changing climatic conditions have been documented in many regions worldwide (Simmonds and Eliott, 2009; Tulloch et al., 2019; Derville et al., 2023) and are likely reflecting adaption of baleen whales to their environment. Habitat and migration shifts were analysed in five studies. Findings from Costa Rican humpback whale breeding grounds from 2000 to 2020 suggested that intensified warming events may reduce migration to Costa Rica, possibly leading to the whales seeking more thermally suitable areas along the Mexican-Guatemalan coasts (Pelayo-González et al.). Changes in migration patterns were also reported for humpback whales in Western Australia. The study was based on 16 years of acoustic data from Western Australia's Perth Canyon and defined trends of earlier arrival by 1.4 days/year during the northward migration, and the possibility of earlier departure during the southward migration (Gosby et al.). Sea surface temperature (SST) was identified as the most significant predictor for whale presence, with an increase of 1°C in SST corresponding to a 4.4-hour decrease in daily acoustic presence.

A change in migration patterns and timing can lead to an overall habitat shift as detected in a study on cetaceans from the Northwest Atlantic. Habitat suitability was assessed for 16 species using generalized additive models based on data sets of SST, bottom temperature, distance to 1000m depth and other variables collected between 2010 and 2017 by NOAA. The outcomes suggested an average northward shift of habitats by 178 km (Chavez-Rosales et al.). In the Indian Ocean 18 years of acoustic recordings likely from pygmy blue whales (*Balaenoptera musculus brevicauda*) in relation to SST, chlorophyll-a concentration, El-Niño Southern Oscillation (ENSO), and Indian Ocean Dipole (IOD) showed that whale songs increased annually. The early arrival and greater duration of presence in Chagos Archipelago was correlated with higher chlorophyll-a concentration and positive IOD phases (Huang et al.). Similar shifts in call detections were presented in a study from the eastern Indian Ocean on pygmy blue whales (Truong and Rogers). Analysing 16 years of acoustic data from Cape Leeuwin, the authors correlated migration of pygmy blue whales in the eastern Indian Ocean with environmental drivers. They found increased whale calls during La Niña years, particularly linked to enhanced productivity in the Great Australian Bight and Indian Ocean feeding areas.

The warming of whale feeding grounds has profound effects on whales ranging from the establishment of new feeding areas, reduction of time spend in traditional feeding grounds and shifts in migration routes (Cabrera et al., 2022; Pendleton et al., 2022).

However, the warming of breeding areas also poses an additional challenge for whales. High-resolution SST projections, showed that by the end of the century, 35% of humpback whale breeding areas in Hawaii may surpass or approach current temperature thresholds under a moderate emission scenario, rising to 67% under intensive emissions (Hammerstein et al.).

Body conditions and feeding

Body condition of whales can serve as an environmental indicator that reflects changes in the marine ecosystem due to their position in food webs and sensitivity to alterations (e.g., George et al., 2015; Christiansen et al., 2020). Body conditions of blue whales (*Balaenoptera musculus*) were assessed on the west coast of the US from photographs collected from 2005-2018 (Wachtendonk et al.). This analysis revealed that better body conditions were associated with negative Pacific Decadal Oscillation (PDO). Poor body conditions were detected during a marine heat wave. More detailed assessment of body conditions can be undertaken using aerial photogrammetry (Christiansen et al., 2020). A study found declining body conditions from gray whales (*Eschrichtius robustus*) documented in the Arctic and sub-Arctic region and the Oregon coast vary greatly amongst sub-groups depending on the impact climate change has on their distinct feeding grounds.

Due to low population sizes, northern right whales (*Eubalaena glacialis*) are particularly vulnerable to environmental variability driven by climate change (Meyer-Gutbrod et al., 2021). Collection of long-term data sets such as photo identification of individual whales can serve as valuable tools to assess reproduction rates in relation to climate change. Right whales utilising the Gulf of St. Lawrence since 2015 exhibited increased birthing rates, with maternal behavior guiding offspring habitat use (Bishop et al.). This shift was attributed to increased water temperature and productivity in the region.

Shifts in feeding location can also be detected through stable isotopes (Best and Schell, 1996). Linking stable isotopes extracted from baleen from humpback whales and southern right whales (*Eubalaena australis*) (1963-2019) with large scale climate indices such as Southern Annular Mode (SAM) revealed Western Pacific humpback whales exhibited elevated isotopes during La Niña and positive SAM phases, possibly due to reduced feeding opportunities (Dedden and Rogers). In the Indian Ocean, the opposite occurred, suggesting improved feeding during positive SAM phases.

Whales play vital roles in marine ecosystems through the distribution of nutrients (Roman et al., 2014). Baleen whales may help remove carbon from the atmosphere but are unlikely to have the potential for sequestration sufficient to mitigate climate change, contrary to popular perception.

However, prioritising large-scale marine protection and addressing ecological gaps can enhance resilience and promote natural carbon capture in particular through phytoplankton (Flynn et al., 2023).

Perspectives

This Research Topic provided multidisciplinary investigations on whales and climate relations by applying state of the art methods. The findings shed light on the complex interplay of environmental and behavioral factors impacting on whale populations, emphasising the necessity of updating conservation measures amid climate-induced habitat shifts. For vulnerable species, the potential contraction or displacement of their habitats could exacerbate population declines (Stewart et al., 2023).

The following points are suggested for future research to assess impacts of climate change on whales.

1) Bridging multi-scale analysis to better understand the mechanisms behind ocean changes and whales.

2) Building large data sets based on standardised data collection and collaborations to create data-driven models for local and regional case studies with high-resolution climate data.

3) Seeking adaptive ecosystem management and urgent greenhouse gas reductions to preserve the whales' ecological integrity.

Author contributions

JM: Conceptualization, Methodology, Project administration, Resources, Writing – original draft, Writing – review & editing. SD: Conceptualization, Validation, Writing – review & editing. RR: Conceptualization, Validation, Writing – review & editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This study was supported by a private charitable trust under the Whales and Climate Program (www.whalesandclimate.org).

Acknowledgments

We like to thank all the authors and reviewers who have participated in this Research Topic to a lay a foundation in this important research field and supporters of the Whales and Climate Program.

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.

Publisher's note

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frontiers in Marine Science

REVIEW
published: 10 November 2021
doi: 10.3389/fmars.2021.720774

The Role of Environmental Drivers in Humpback Whale Distribution, Movement and Behavior: A Review

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

Received: 04 June 2021
Accepted: 22 October 2021
Published: 10 November 2021

Citation:
Meynecke J-O, de Bie J,
Barraqueta J-LM, Seyboth E, Dey SP,
Lee SB, Samanta S, Vichi M,
Findlay K, Roychoudhury A and
Mackey B (2021) The Role
of Environmental Drivers in Humpback
Whale Distribution, Movement
and Behavior: A Review.
Front. Mar. Sci. 8:720774.
doi: 10.3389/fmars.2021.720774

Humpback whales, *Megaptera novaeangliae*, are a highly migratory species exposed to a wide range of environmental factors during their lifetime. The spatial and temporal characteristics of such factors play a significant role in determining suitable habitats for breeding, feeding and resting. The existing studies of the relationship between oceanic conditions and humpback whale ecology provide the basis for understanding impacts on this species. Here we have determined the most relevant environmental drivers identified in peer-reviewed literature published over the last four decades, and assessed the methods used to identify relationships. A total of 148 studies were extracted through an online literature search. These studies used a combined estimated 105,000 humpback whale observations over 1,216 accumulated study years investigating the relationship between humpback whales and environmental drivers in both Northern and Southern Hemispheres. Studies focusing on humpback whales in feeding areas found preferences for areas of upwelling, high chlorophyll-a concentration and frontal areas with changes in temperature, depth and currents, where prey can be found in high concentration. Preferred calving grounds were identified as shallow, warm and with slow water movement to aid the survival of calves. The few studies of migration routes have found preferences for shallow waters close to shorelines with moderate temperature and chlorophyll-a concentration. Extracting information and understanding the influence of key drivers of humpback whale behavioral modes are important for conservation, particularly in regard to expected changes of environmental conditions under climate change.

Keywords: climate change, oceanography, cetacean, distribution drivers, environmental change, *Megaptera novaeangliae*, occurrence

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*, hereafter referred to as HWs) conduct one of the longest annual migrations of any mammal (Stone Florez-Gonzalez and Katona, 1990; Stevick et al., 2011). HWs are found in all oceans, migrating between high latitude feeding grounds in summer and tropical and sub-tropical breeding grounds in winter (Dawbin, 1966; Clapham and Mead, 1999). Many HW populations are generally showing marked increases to protection from last century's severe whaling pressure (Chittleborough, 1965; Findlay, 2001; Noad et al., 2019). Northern and Southern Hemisphere HW populations are generally distinct, but some genetic and photographic evidence suggest a small level of interchange (Baker et al., 1990; Stone Florez-Gonzalez and Katona, 1990; Garrigue et al., 2007; Rasmussen et al., 2007). Currently, at least 16 HW populations are recognized worldwide including some sub-populations (Jackson et al., 2015), with whales utilizing coastal and open ocean habitats in both hemispheres. In the Southern Hemisphere, the species is distributed in seven breeding populations including sub-populations, from A to G (IWC, 1998, 2011).

A wide range of environmental conditions are encountered in these habitats, and HWs are able to identify and adapt to preferred conditions for their most important life stages or behavioral 'modes' herein referred to as breeding, feeding, migrating, and resting. Given the different habitats used and their mobility, migratory species have spatially broad ecological niches (Guisan and Zimmermann, 2000). Underlying reasons behind HW habitat selection are still debated (Corkeron and Connor, 1999). Different habitats may be favored depending on whether migration occurs to optimize energy budgets and thermoregulation (Brodie, 1975), calf growth and survivorship (Clapham, 1996), protection from predation (Naessig and Lanyon, 2004; Steiger, 2008) or feeding (Andrews-Goff et al., 2018).

Large-scale spatial patterns are well documented for migration (Dawbin, 1966; Garrigue et al., 2000), feeding (Owen et al., 2017) and breeding grounds (Smith et al., 2012); however, smaller-scale patterns of habitat use, cues that induce a switch between behavioral modes and the factors influencing the choice for each of these areas, are not as well understood (Franklin, 2014; Valani et al., 2020). Some studies suggest little or no influence of changing oceanographic conditions (currents, temperature, and salinity) on large scale migrations (Horton et al., 2020), while others suggest that HWs shift the timing of migration in response to oceanographic conditions (Ramp et al., 2015; Avila et al., 2019; Kershaw et al., 2021).

Some of the drivers that have been identified to influence HW habitat selection include bathymetry (Dalla Rosa et al., 2012), sea surface temperature (SST) (Dransfield et al., 2014), distance to coast/offshore (Burrows et al., 2012), hydrodynamics (Tynan et al., 2005), variations in chlorophyll-a concentration as a proxy for prey (Fiedler et al., 1998), salinity (Gregr and Trites, 2001), tides (Chenoweth et al., 2011), and the extent of the sea ice (Bombosch et al., 2014; Andrews-Goff et al., 2018). Large scale climate phenomena such the El Niño-Southern Oscillation (ENSO) or Southern Annular Mode (SAM) were used in some studies as a proxy for changes in oceanographic variables such as SST (Derville et al., 2019; Groß et al., 2020). Some of these variables are highly dynamic and have been locally changing over time, as environmental conditions are being altered by climate change, affecting all parts of the ocean (Freer et al., 2017). A comprehensive understanding of the influence of environmental conditions on this highly mobile species is required to enable any prediction of climate change and other anthropogenic effects on HWs (Meynecke and Meager, 2016; Fournet et al., 2018; Bolin et al., 2019; Meynecke et al., 2020; Santora et al., 2020; Suryan et al., 2021), and to design effective management plans for their protection (Doniol-Valcroze et al., 2007; Azzellino et al., 2014), including the development of dynamic protected areas (Maxwell et al., 2020).

Previous research has shown that HWs and other cetaceans demonstrate sensitivity toward changes in oceanographic variables, whether natural or climate-change induced (van Weelden et al., 2021). This includes the arrival of HWs in the Gulf of Lawrence shifted by 1 day per year over a 25-year period (1984–2010), resulting in significant earlier arrival on that feeding ground (Ramp et al., 2015). Encounter rates of HW groups that contained at least one mother with calf dropped by 76.5% in the Hawaii breeding grounds between 2013 and 2018, a period that coincides with a marine heat-wave observed in the area (Cartwright et al., 2019). The species also shifted its distribution and diet (from krill to schooling fish) with varying oceanographic and ecological conditions (Fleming et al., 2016; Becker et al., 2019), when SST in the California Current System increased. In a study from Oceania (population E), HWs also showed local responses to SST anomalies in their distribution in breeding grounds in Oceania with a maximum temperature tolerance at 28°C (Derville et al., 2019). Recent changes in HW feeding patterns have been observed off the west coast of South Africa, with large aggregations of 20–200 individuals involved in a novel feeding behavior ('supergroups') during October–November in the southern Benguela Upwelling System, which is located well north of their expected Antarctic feeding grounds (Findlay et al., 2017; Cade et al., 2021).

Given climate-induced changes in the ecosystem, including consequences to prey availability for the HWs, their reproduction can also be affected, e.g., as lower numbers of calves are observed following years of decreased prey biomass (Seyboth et al., 2021). Observed and projected changes in climatic variables include increasing ocean temperatures, changing ocean currents, rising sea levels, reduction in sea ice, more frequent and intense unpredictable weather events, and changes to the distribution and abundance of species that are prey items for HWs (Flores et al., 2012; McBride et al., 2014). Such changes need to be understood in the context of other human ocean resource-use impacts, including noise, physical and chemical pollutants, unsustainable extraction and habitat modification (**Figure 1**). It is anticipated that climate change will lead to a decline in the large-scale supply of nutrients due to enhanced upper water stratification in polar waters and consequently reduce the marine primary productivity driving food availability for HWs (Tulloch et al., 2018). HWs require high concentrations of prey to maximize

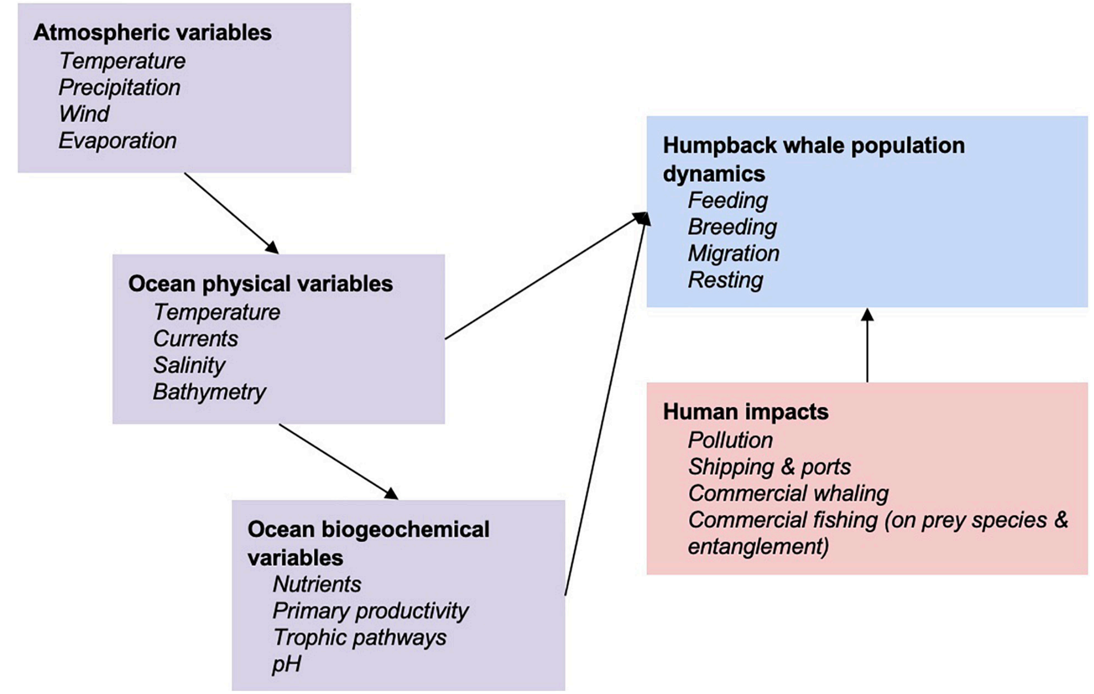

FIGURE 1 | Conceptual framework to a systems approach of understanding humpback whale responses to environmental variables and human impacts (adapted from Meynecke et al., 2020).

energy efficiency while feeding (Piatt et al., 1989; Goldbogen et al., 2008). Therefore, preferred feeding ground habitats (Nicol et al., 2000; Doniol-Valcroze et al., 2007; Ressler et al., 2015), and opportunistic feeding in other locations (Visser et al., 2011), would occur where environmental conditions increase marine productivity and aggregation of prey (e.g., prior high chlorophyll-a concentration, upwelling and fronts). HWs can exhibit substantial flexibility in behaviors and prey selection and are suspected to have historically adapted their foraging behavior to new prey species when environmental conditions were unfavorable to common target prey species (Benson et al., 2002; Fleming et al., 2016). Habitat use during feeding may be heavily driven by immediate ocean conditions (Rockwood et al., 2020). Disentangling feeding-related movements driven by changing environmental cues and intrinsic/learned behavior remains an ongoing challenge (e.g., Weinrich, 1998), compounded by the need to disentangle past exploitation and current environmental change drivers (Nicol et al., 2008). Movement patterns can also be influenced by a variety of intra-specific social interactions (Ersts and Rosenbaum, 2003; Craig et al., 2014) or by human activity in particular in breeding areas (Cartwright et al., 2012) making the disentanglement from environmental change drivers more complex. There is evidence of range expansion in breeding grounds as populations recover from decades of commercial whaling (Mobley et al., 1999; Johnston et al., 2007; Lammers et al., 2011) or maybe as a result of environmental changes (Torre-Williams et al., 2019).

In this review, we aim to extract combinations of environmental variables emphasizing on physical variables (with the addition of chlorophyll) that determine HW distribution and movements during behavioral modes of migration, breeding, feeding and resting by systematically analyzing accessible peer reviewed literature on the subject. Highlighting shared variables across populations using different habitats may provide insight into conservation efforts for understudied populations and assist with the modeling of species distribution. We also aim to identify commonly tested variables and how they influence HW behavioral modes, and outline the various methods applied to investigate the relationships. This synthesis in turn, highlights where further research is required.

METHODS

We set out to review the relationship between HWs and environmental drivers by compiling the literature from online databases. We consulted Web of Knowledge, Google Scholar and Scopus. Searches for scientific literature were conducted up until 1st January 2021. Searches included multiple combinations of keywords (**Table 1**), with qualifying publications containing at least one word from each of the following categories: target species, environmental parameters tested (predictor variables) and the type of effect/behavior observed (response variables).

All parameters describing physical environmental conditions were included, and those that were very similar but differently termed were grouped together (e.g., "distance to the coast" and "distance offshore"). If results were presented in a paper without specific details on the statistical analyses, these studies were still included. Studies that lacked clear descriptive information on relationships of whales with environmental factors or were

TABLE 1 | Combination of keywords used in online search for literature related to humpback whales and environmental variables.

Target	Predictor variable	Response variable
Whale	Temperature	Distribution
Humpback whale	Currents	Stranding
Megaptera	Bathymetry	Entanglement
Marine mammal	Chlorophyll-a	Abundance
	Salinity	Migrating
	Upwelling	Resting
	Physical	Feeding
	Hydrodynamics	

focused on prey only were excluded. We excluded studies focusing on prey only, because projections of prey availability are often spatially and temporally limited, whereas projections of SST or even chlorophyll are more readily available. Studies focusing on prey only often have different objectives to those investigating abiotic drivers and would benefit from an independent review.

The selection was based on inclusion of keywords in either, title, abstract or main text and if results on HW and environmental drivers were presented. The summary included details about the study publication (authors, year and journal of publication), timing (season and year), and location (hemisphere, country and hydrographic region) of research, the species studied (when other species besides HWs were included), method and platform of observation (whale watching boat, other type of vessel, photo ID, aerial, land-based, acoustic, tag, whaling records or stranding records), mode of behavior or effect observed (migrating, breeding, feeding, resting, stranding, entanglement), sample size (including the number of survey years per study), the range of environmental parameters investigated (including the methods of measurements used and the relationships observed), and finally whether climate change or global warming (considered as synonyms) was specifically mentioned or investigated. Publications did not necessarily include details for every category, and publications could have multiple features in some categories (e.g., both feeding and migrating behavior was observed). If the total sample size of HWs was not explicitly mentioned, then this was estimated based on the details provided and noted in the overview table.

Details about the location of fieldwork were recorded to allow comparisons between countries or regions and hemispheres, and between areas of similar/contrasting hydrography, such as eastern and western boundary currents, polar and tropical areas, or central oceanic waters. The environmental parameters investigated included temperature, hydrodynamics (this represented studies investigating the effects of currents, upwelling, etc.), chlorophyll concentration, salinity, bathymetry, distance offshore, tides and weather. As this review focuses mainly on abiotic parameters with the addition of chlorophyll concentration, prey was not included as a category in the database; however, if publications added prey as a variable or concluded that particular environmental parameters were indirectly related to cetacean distribution by concentrating prey, this was recorded and included in the review.

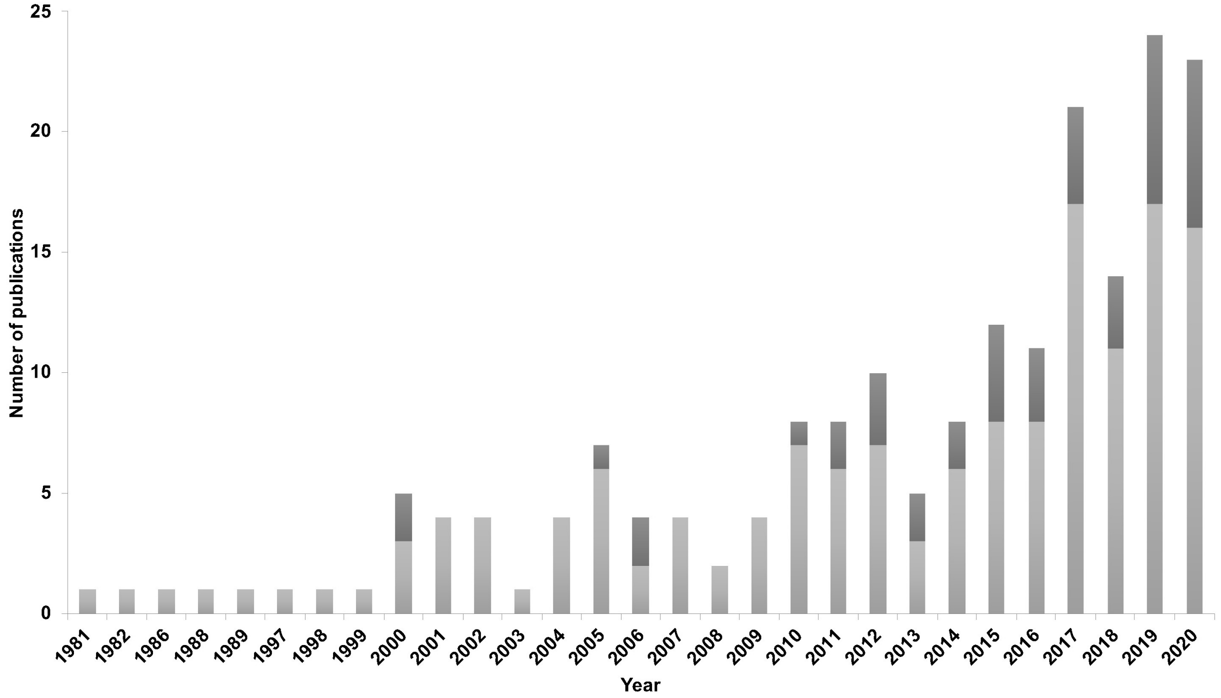

FIGURE 2 | Number of retrieved studies investigating humpback whales and environmental drivers between 1981 and 2020. Dark gray bars indicate mention of climate change or climate shift in the studies.

RESULTS

Overview of Studies and Summary of Findings

A total of 148 studies that investigated the relationships between HWs and their surrounding physical environmental conditions were extracted (**Supplementary Table 1**). An additional 31 studies were disregarded after detailed assessment; in these cases, environmental drivers were not explicitly defined, discussed, not the focus of the study or no analyses were performed to investigate relationships.

A trend over time (1981–2020) showed an increase in online accessible peer reviewed studies investigating HW relationships with environmental drivers. In particular, in the past 4 years between 10 and 18 studies have been published per year. Climate change has also been addressed more often in recent years proportionally to the total number of publications (**Figure 2**). Forty-three studies mentioned climate change, climate shift or global warming (e.g., Bassoi et al., 2019) and two studies used climate projections in their analysis (Thompson et al., 2012; Derville et al., 2019).

Most studies were conducted in regions attributed to the United States, followed by Australia, Antarctica and Brazil (**Figure 3**). This regional bias also reflects the bias of the populations studied. The North-eastern Pacific populations were subject to a high number of studies (39), followed by population G and the North Atlantic populations (both in 20 studies) and population A (14). In the Southern Hemisphere, population E was included in a higher number of studies (12) and all other populations less than 10 times. However, Southern and Northern Hemisphere populations have been equally represented in the selected studies (78 and 75 times, respectively, counting double the few studies conducted worldwide).

The most accessible regions for HW research occurred near the coast or in the vicinity of islands. Coastal habitats were therefore included in half (74) of the studies while open ocean habitats were only subject to investigation in 22 studies with 5 involving satellite tags or remote sensing. Overall, our review has stronger contributions from HWs populations in the North-East Pacific, North Atlantic and G population and from studies conducting data collection in coastal waters. This is important to note when ranking the environmental drivers in order of relative importance. Certain environmental drivers were tested more often simply because they were the most likely to be applicable for coastal habitats and the particular HW populations studied.

The majority of studies (91) used dedicated survey vessels to collect data. Less common were studies using photo ID and acoustics (12 studies each), land-based surveys (16) and aerial surveys (17). Citizen science or whale watch boats were used in 18 studies and satellite tagging in 26 studies. Some studies (34) used more than one source of data. The number of HW records used for each study varied greatly between 5 (satellite tagging, Curtice et al., 2015) and over 10,000 records (citizen science, Stack et al., 2019).

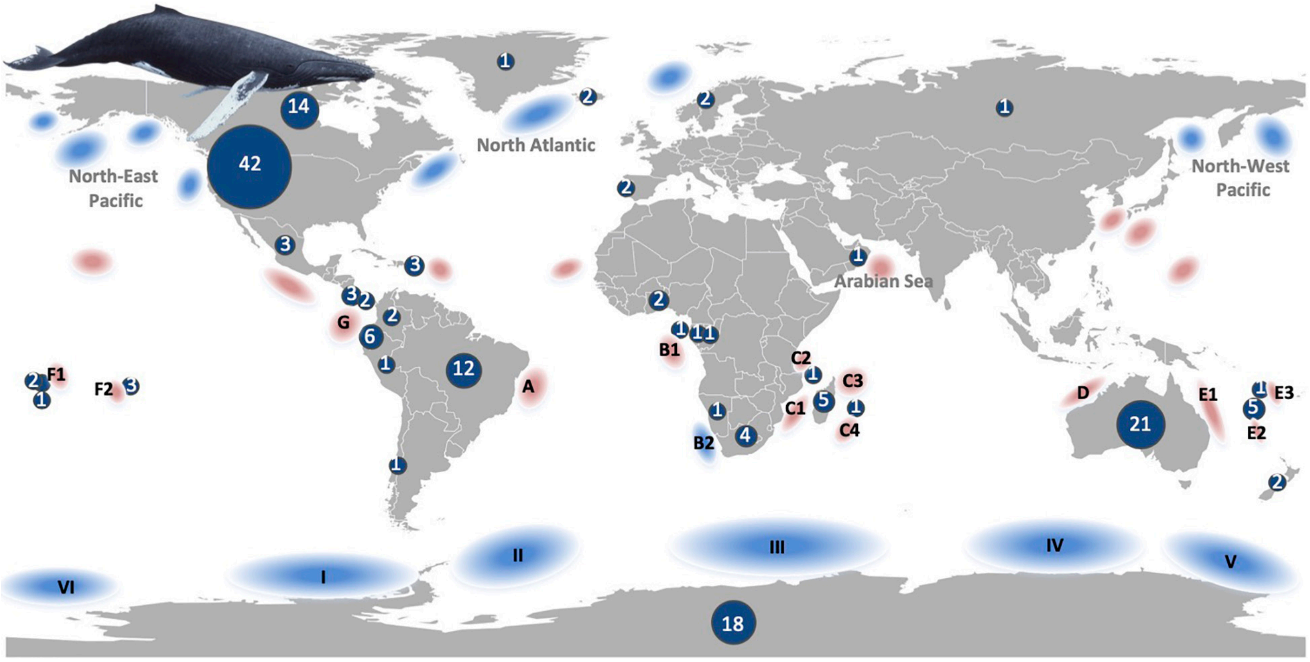

FIGURE 3 | Humpback whale populations (at least 16 distinct populations shown as combined North-East Pacific, North Atlantic, Arabian Sea, North-West Pacific for the Northern Hemisphere and A-G breeding populations for the Southern Hemisphere) with approximate breeding (red) and feeding (blue) areas (classification based on Jackson et al., 2015). The number of studies extracted from 148 publications that investigated environmental drivers and humpback whale distribution are shown by country and separately for Antarctica.

Feeding in relation to environmental variables was the focus of a high number of retrieved studies (63) and consequently investigations were carried out mostly during summer months (Northern or Southern Hemispheres) (84) followed by winter (78), spring (47) and autumn (35). Migration was explicitly mentioned in 55 studies and resting mentioned in 19 studies. Relationships between entanglements and strandings and environmental drivers were mentioned in 7 studies (e.g., Meynecke and Meager, 2016; Volep et al., 2017). In a number of studies (69) other cetaceans were included in the analyses with up to 35 other species of which fin whales (*Balaenoptera physalus*) and minke whales (*Balaenoptera acutorostrata* and *Balaenoptera bonaerensis*) were most often included (**Supplementary Figure 1**).

METHODS APPLIED RELATING ENVIRONMENTAL DRIVERS TO HUMPBACK WHALE DISTRIBUTION

The majority of studies included in this review used multivariate analyses whereas remaining studies adopted a range of other statistical approaches investigating single variable responses or described relationships based on field observations. Generalized Linear Models (GLMs) were most often applied (39), followed by General Additive Models (GAMs) (28), regression and correlation analyses (21), Maximum Entropy Models (MAXENT) (10), and other statistical approaches (7), such as Mann–Kendall trend test or Mann–Whitney *U* Test. Some studies have focused on a descriptive evaluation of the relationships, e.g., through visual representation showing the overlap of sightings with environmental variables (17) and others have focused on the analyses of density estimates that included variables as a function of sighting probability using Distance sampling (Thomas et al., 2010) (8) (**Figure 4**). Multivariate models have become increasingly popular with nearly half of all retrieved studies between 2010 and 2020 using GLMs, GAMs or MAXENT (Becker et al., 2010; De Rock et al., 2019). In general, multivariate models can capture complex interactions better than other statistical approaches, address auto- and cross-correlation of variables; and therefore, provide a more comprehensive representation of real-life ecosystems (Digby and Kempton, 2012). Such modeling approaches have become more attractive due to the availability of larger data sets and improved computational power allowing for faster processing.

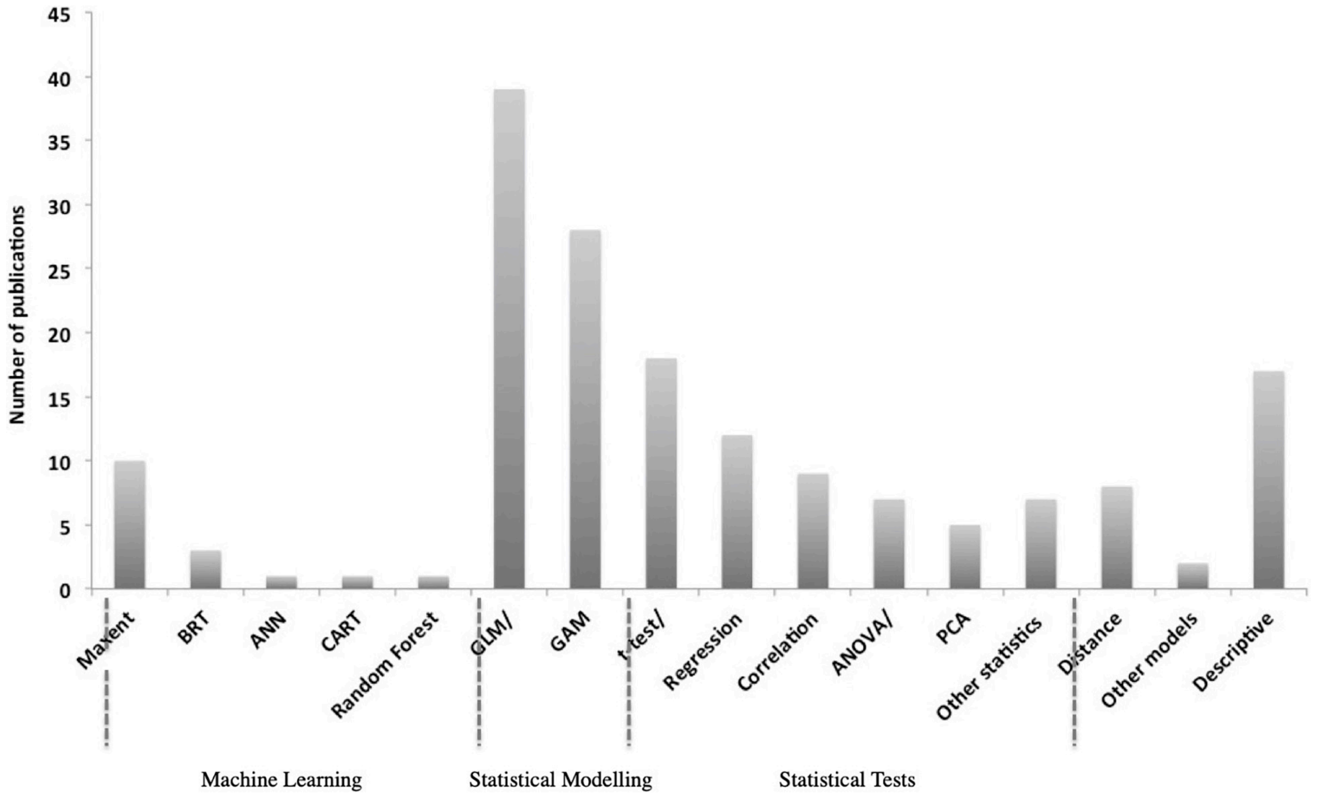

FIGURE 4 | Tendency in the use of methods in order of complexity applied to study humpback whale relationships with environmental drivers extracted from 148 publications. Only the most frequent used methods are presented here based on retrieved studies between 1981–2020 and divided into machine learning techniques, statistical models and tests, and a category that includes usage of Distance software, other seldomly applied models (e.g., occupancy model or relative environmental suitability models) and descriptive assessments.

Overview of Environmental Data Sources and Whale Records in Reviewed Literature

A variety of open-source datasets e.g., through the National Oceanic and Atmospheric Administration (NOAA) Data Catalog[1] and other datasets have been frequently used to investigate environmental drivers of HW distributions (Shelden and Rugh, 2010; Guidino et al., 2014; Garrigue et al., 2015). Each approach has its benefits and their selection largely depends on suitability of the data and the purpose of the studies.

Temporal and spatial resolution of the environmental data determines what type of analysis may be possible. Availability of marine environmental data with a large temporal (decades) and spatial resolution (global) is still very limited. In terms of Earth Observations, satellite SST and sea ice concentration have been one of the few variables available for the past 40 years since 1979 (Merchant et al., 2019). SST can be obtained from remote sensing data from AVHRR (Advanced Very High-Resolution Radiometer Pathfinder) or MODIS (Moderate Resolution Imaging Spectroradiometer). For instance, resolution in the studies ranged from 1 km grids (e.g., Doniol-Valcroze et al., 2007) to 28 km grids (e.g., Derville et al., 2019) and from daily (e.g., Picanço et al., 2009) to annual averages (Kaschner et al., 2006).

Variables such as bathymetry, slope, distance to shore and in most cases terrain type are reliable measures to determine suitable habitats as they vary little over time. Typical units for these are measurements of length, angle or categorical values for terrain type (e.g., "rugged or smooth"). Bathymetry has predominantly been derived from bathymetric charts ranging in 50 m^2 to 1 km^2 resolution on predefined grids (Lindsay et al., 2016; Lodi et al., 2020). In some regions, topography data were available from government agencies (e.g., hydrographic services) and related variables such as slope were calculated from bathymetric charts. Distance to shore was usually calculated using coastline data (Tardin et al., 2019). The dynamic distance to sea ice edge on feeding grounds (can be defined by the border of minimum 50% sea ice coverage) was obtained from the United States National Snow and Ice Data Center (NSIDC). The majority of environmental variables change over timescales that range from days to years. Traditionally, biotic and abiotic measurements were taken during HW surveys at sea, only covering a small area and timeframe. Larger areas over longer periods were sampled, for example through the Array for Real-time Geostrophic Oceanography (ARGO) Program providing temperature, conductivity and pressure from floating data loggers as well as current velocities (Roemmich et al., 2019). Early on, SST data was measured either as point data or continuously from survey vessels (Smith et al., 1986) but in recent years *in situ* temperature data as well as its gradient over depth were generally obtained using CTDs (Conductivity, Temperature, and Depth logger), in some studies to 1 km depth (Hazen et al., 2009; Munger et al., 2009; Keen, 2017).

Chlorophyll concentration was typically obtained through on-board fluorometers (Keen, 2017) or from daily to monthly remote sensing data through MODIS Aqua (9 km grid resolution), SeaWiFS (Sea-viewing Wide Field-of-view Sensor) or MERIS (Medium Resolution Imaging Spectrometer; 4 km grids) (e.g., García-Morales et al., 2017). Generally, a finer temporal and spatial resolution is desirable for chlorophyll concentrations due to its fine scale variation in time (days) and space (Wernand et al., 2013). In some studies, prey density or species that were considered potential prey were included in the analyses (Nowacek et al., 2011). Associated data on these were region specific and either collected during surveys through netting or echo sounder or derived from commercial landings. While prey density is the most promising variable to define feeding events and feeding habitat, it is also not available over large spatial and temporal scales (Siegel and Watkins, 2016). This is complicated further as HWs have been known to shift prey species depending on prey availability (Fleming et al., 2016; Owen et al., 2017).

For information on surface currents, ARGO drifter buoys were used in more recent studies (Horton et al., 2011). Daily sea surface current velocity (m/s) data were typically obtained from the Copernicus Marine Environment Monitoring Service (CMEMS) or when available from regional models (e.g., Bluelink) (Bolin et al., 2019; Riekkola et al., 2019) or the regional oceanic modeling system (ROMS) (Shchepetkin and McWilliams, 2005). Upwelling indices provided by NOAA or derived *in situ* using AD (Acoustic Doppler Current Profiler) have also been used (Nicol et al., 2000; Shelden and Rugh, 2010). Tide charts or regional tidal models were utilized to derive tidal data, such as its range or constituent.

Weather related variables such as wind speed/direction, sea state, air pressure and visibility were in most cases collected during observation or derived from open-source databases. Riekkola et al. (2019) used SSH data in meters (55 km^2 or 27 km^2 grids) derived from Copernicus Marine Environment Monitoring Service (CMEMS). Large scale climate indices like SOI, PDO, ONI (Oceanic Niño Index), SAM and NPGO were available from meteorological services and applied on a monthly or annual temporal resolution (e.g., Dransfield et al., 2014; Avila et al., 2019; Cartwright et al., 2019; Groß et al., 2020).

Most (91) of the HW records in the studies presented here were derived from dedicated scientific surveys (e.g., Salden, 1988) that included some form of abundance estimations (as opposed to presence data only). However, scientific surveys are expensive and are often limited in time, space and effort. Deriving data from multiple sources can overcome data scarcity (Pacifici et al., 2017). Citizen science data has become increasingly relevant and has allowed studies to cover larger temporal scales often with presence only data (Tiago et al., 2017; Derville et al., 2019; Stack et al., 2019; Valani et al., 2020). Other solutions to gain higher spatial and temporal resolution of whale records were the use of multi-species data sets collected as part of reoccurring scientific surveys (Chenoweth et al., 2011).

Satellite tagging of HWs can provide many details of an individual over large areas and a good temporal resolution. However, the limited number of whales observed as presence only data (often under 20 per study) limits the extrapolation of

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[1] https://data.noaa.gov/datasetsearch/

observations to whole populations. On the other hand, datasets covering thousands of records lack detailed information on individuals and are often limited to a certain region.

Overview of Applied Methodologies in Reviewed Literature

A classical approach to study marine species distribution patterns is by applying types of linear regression (e.g., multiple linear regressions by least squares, ordinary least squares models or general linear models) (e.g., Baker and Herman, 1981). Linear regression is easy to apply fitting linearly separable datasets. However, linear regression and correlation analyses are limited by their assumption of linearity, use of dependent variables and sensitivity to outliers (Smith and Santos, 2020). Other used statistical approaches to test environmental variables with species presence are Paired *t*-tests, Mann–Whitney *U*-test, *G*-test, and ANOVAs. All have similar limitations as linear regression analyses. Some studies have used 'Distance sampling' that also allows for assessing the influence of habitat variables on abundance estimates (Thomas et al., 2010) but this technique is designed to overcome sampling constraints in surveys and not to analyze relationships of species distribution with environmental variables.

To overcome some of the above limitations, species distribution models (SDMs) have been used. Generally, they can be described as mathematical tools allowing the description and prediction of distribution patterns of species and comprise several modeling techniques/algorithms [e.g., GAMs, GLMs, boosted regression trees (BRTs), random forests (RFs) and MAXENT]. Various studies have provided insights in the different types of SDMs and their performance (Derville et al., 2018; Smith et al., 2020b).

The choice of a specific SDM varies greatly and depends upon the study goal, the availability of data (e.g., occurrence data, need to simulate pseudo-absence, functional traits) and the assumptions and constraints applied. Generally, the use of SDMs comprise the following four steps: (i) model selection, (ii) model implementation, (iii) model validation and (iv) model error and uncertainty estimation. The first step is model selection, which includes implementation of statistical procedures (e.g., cross-validation, stepwise selection) to select the set of predictor variables. In the second step, the selected model predicts a spatial pattern, which can include parametric models (e.g., GAMs and GLMs) or machine learning techniques (e.g., BRTs, RFs, and MAXENT). Validation involves the use of performance measures [e.g., Area under the Curve (AUC), specificity, goodness-of-fit, and regression] to estimate the validity of the model output. The last step quantifies the errors and uncertainties that may derive from insufficient data and model misspecification.

For example, the choice for parametric models (GLMs and GAMs) depends mainly on the type of input data, with GAMs capable of handling species data with a widespread distribution. This makes GAMs often more flexible as simulation models than GLMs. However, this has consequences for robustness, with GLMs being more robust than GAMs.

More recently, machine (e.g., MAXENT, BRTs, and RFs) and deep (Artificial Neural Networks, Purdon et al., 2020) learning techniques are being used for SDMs, which allow the testing and fitting of multiple interactions among predictors and are tolerant of outliers, collinearity, and irrelevant predictors. Importantly, these techniques do not require strong assumptions prior to model selection. Taking into account the benefits and constraints of different SDMs, some studies have compared their performance on cetacean distribution [e.g., GLMs vs. GAMs,; GAMs vs. MAXENT, Fiedler et al. (2018); BRTs vs. MAXENT vs. GLMs vs. GAMs, Derville et al. (2018)]. Machine learning techniques showed excellent explanatory performance when discriminating between presence and absence, but poorer performance when predicting on independent data (Oppel et al., 2012; Becker et al., 2020). The inferior predictive performance has been attributed to machine learning techniques overfitting to a greater degree than parametric models.

Boosted regression trees and ensemble approaches (e.g., Abrahms et al., 2019 on blue whales) have the ability to automatically fit interactions between predictor variables. On the contrary, in GAMs interactions between predictor variables must be explicitly defined when fitting. Different authors found contrary evidence between advantages and disadvantages of using BRTs and GAMs. Elith et al. (2008) suggested that an advantage of BRTs over GAMs is that they could handle sharp discontinuities when modeling species with distributions that occupied only a small proportion of the sample's environmental space. Becker et al. (2020) found the opposite, with GAMs performing well and BRTs exhibiting poor predictive ability. The study suggests that both models should be used and that caution should be taken when applying BRTs to anomalous novel data and when including spatial terms (latitude and longitude) in the suite of potential predictors.

Among presence-only data models, MAXENT is the most popular. This technique is capable of incorporating model complexity while preventing overfitting and is appropriate to predict areas of potential species occurrence based on comparison with automatically generated background data. An important limitation that affects the accuracy of presence-only modeling relates to biases in the occurrence localities. For instance, Fiedler et al. (2018) compared MAXENT vs. GAMs performances for four large cetaceans by applying presence-absence or presence only data. Both methods produced very similar predictions when background data points were selected from observed absences. However, when presence-only data was modeled with pseudo-absences the spatial pattern of predictions was considerably altered. Its output can thus be interpreted in one of two ways, depending on sampling assumptions. If the data are assumed to be a random sample in space, it can predict relative occurrence probability but not occurrence probability. And if the data are assumed to be a random sample of individuals, it can predict relative occurrence data. In light of the availability of larger data sets, machine and deep learning methods utilizing Artificial Intelligence are becoming more popular as powerful methods for analyzing complex ecological relationships (**Figure 4**).

MAIN ENVIRONMENTAL DRIVERS AND THEIR RELATIONSHIPS WITH HUMPBACK WHALES

We have identified some main environmental drivers from the reviewed studies which include: bathymetry, temperature, distance offshore, chlorophyll, hydrodynamics, weather, salinity, tide, ice, turbidity, terrain and magnetic fields (**Figure 5**). A number of other variables fall under these main drivers and have been grouped accordingly. Details on all variables used in the reviewed studies can be found in **Supplementary Table 1**.

Bathymetry, temperature, distance to shore and their associated variables were the most common parameters investigated, being included in 137 studies. Fewer publications have included the effects of variables such as chlorophyll concentration, hydrodynamics, weather, salinity, and tides. Out of the 148 studies, bathymetry and associated variables were investigated 98 times, SST 77 times and distance to shore or ice edge 60 times. The categories turbidity (8), terrain type (5) and magnetic fields (3) were the least tested and 18 studies included prey as an additional variable (**Figure 5**).

The same environmental drivers can play very different roles for HWs depending on the whale's behavioral mode and are related to the specific regional conditions. The regions used by HWs have contrasting characteristics (SST between −2 and 5°C in Arctic or Antarctic waters and 23–27°C along tropical coastlines and open ocean). Bathymetry has been a reliable predictor for the location of breeding grounds (Smith et al., 2012) but influences migration to a lesser degree (Horton et al., 2011). Hydrodynamics such as current speed and upwelling are more relevant for feeding activities. Environmental drivers are often correlated and overlap, which complicates analyses (**Figure 6**).

We have grouped together the 73 studies that claimed to isolate the impact of one single driver or that analyzed only one variable (**Figure 7**). In many of these, bathymetry and temperature and associated variables (e.g., slope, SST) were individually investigated and the majority found them to significantly influence parts of the HW behavioral modes and habitat selection. A detailed overview of each study and their investigated variables is presented in the **Supplementary Data**. In the following paragraphs we will provide an overview of the findings for each variable category.

ENVIRONMENTAL DRIVERS INFLUENCING HUMPBACK WHALES BEHAVIOR MODES

Feeding

The diet of HWs in general includes different types of prey (fish, krill, squid, and copepods) (Baker et al., 1985; Clapham and Palsboll, 1997; Clapham et al., 2009). Some populations have shown plasticity in their diet and adapting to prey availability (Gavrilchuk et al., 2014; Fleming et al., 2016) with different feeding techniques such as lunge feeding (Ware et al., 2011), bubble net feeding (Friedlaender et al., 2011), bottom feeding (Hain et al., 1995), pectoral herding (Kosma et al., 2019) and feeding in groups (Friedlaender et al., 2011; Findlay et al., 2017), or feeding individually (Ware et al., 2011). Such feeding at different trophic levels compounds investigation of environmental drivers, particularly with lags in environmental changes, primary and secondary productivity. The type and strength of relationships between physical variables and HW distribution in feeding areas depends on the type of selection and region, making the establishment and generalization of relationships with physical drivers challenging. There are also lag effects between drivers such as upwelling and prey availability and observed feeding events (or abundance in a feeding area), and synergistic effects from different variables. Measuring the relative importance of each for HWs distribution can be a difficult task. For example, HWs in the Southern Hemisphere predominantly feed on Antarctic krill (*Euphausia superba*) (Bettridge et al., 2015) whereas HWs in the Northern Hemisphere mostly feed on fish species (Evans, 1987).

Despite these challenging aspects, there are a number of variables that evidently are more reliable predictors for feeding grounds than others. For example, high relative abundance of HWs was observed in cooler waters (e.g., Orgeira et al., 2017) near the boundaries of major currents (Bestley et al., 2019) and regions of upwelling (e.g., Thompson et al., 2012) with high chlorophyll concentration (Tynan et al., 2005).

Some studies have found relationships between feeding activities and particular ranges of depths and temperature. In a multi-species study by Calambokidis et al. (2004) from the west coast of the United States, most whales, including HWs, were sighted between 100–200 m depth contours (8.4 km from shelf) in relatively colder areas (mean of 13.9°C) where upwelling occurred. This is similar to the findings of Dransfield et al. (2014) who showed that the highest HW counts were associated with an SST between 12 and 14°C on this coast. However, Burrows et al. (2016) found no significant relationship between depth and feeding in a multi-species study from California (United States) indicating contrasting results for depth and temperature variables. Further north in the Bering Sea, Zerbini et al. (2016) found that HW abundance was low in shallow depths, and generally high at intermediate and greater depths (200 m). Feeding dives of up to 200 m were also reported from Digital Acoustic Recording Tags (D-tags) attached to HWs near West Greenland (Bejder et al., 2019) and 300 m in the West Antarctic Peninsula (Nowacek et al., 2011). A study in Antarctica by Bombosch et al. (2014) found that SSH (Sea Surface Height Anomaly) (19.6% of deviation explained) and SST gradient (13%) were the best explanatory factors in the final distribution model. Independently of depth, temperature effects were investigated in most of these studies, with mixed results but generally a positive relationship with cooler waters was found (Nicol et al., 2000; Barendse et al., 2010).

Chlorophyll concentration was often included for investigation as a proxy for prey availability and was often more accessible than data on prey, by being accessed through remote sensed satellite data or measured *in situ* during surveys. Various studies have shown relationships between chlorophyll

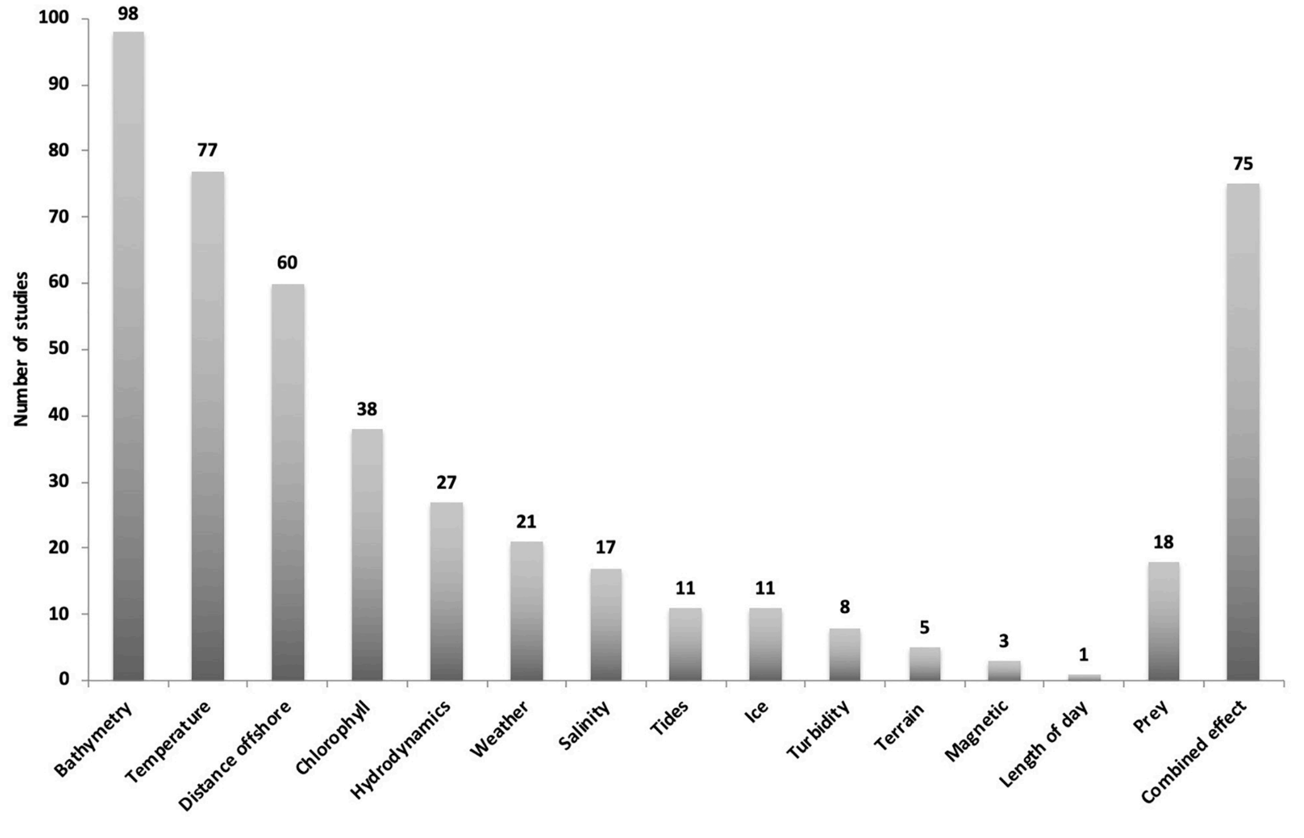

FIGURE 5 | Overview of environmental driver categories from 148 publications investigating humpback whales and relationships with environmental drivers. Most studies tested more than one variable with 75 studies testing combined effects.

concentration and potential HW prey species (Atkinson et al., 2008; Kershaw et al., 2021). Higher HW abundance was observed in conjunction with high chlorophyll concentrations in feeding areas such as fjords in Canada (Keen et al., 2018). Owen et al. (2019) showed that chlorophyll concentration was significantly correlated with the broad-scale foraging behavior of five tagged HWs in East Antarctica, similar to Bestley et al. (2019) indicating the role of persistent primary production in foraging behavior. A mixed species study from the west coast in South Africa showed higher abundance in waters with relative high chlorophyll-a concentrations in summer (around 4 mg/m^3) (Purdon et al., 2020). However, a study from Antarctica by Andrews-Goff et al. (2018) showed no direct relation between seasonal chlorophyll-a and HW foraging habitat when using chlorophyll climatology as a proxy for primary production. This is likely due in part to the inability of satellites to measure productivity of closely ice-associated habitats. Additionally, persistent cloud cover necessitates averaging of remotely sensed chlorophyll measurements (here across a 3-month period) and this has been leading to the loss of temporal information.

Among the least considered variables were ebb and flood tide, and internal waves, for which no significant relationship with feeding was found by Pineda et al. (2015), and dimethyl sulfide (DMS), a chemical released in areas of high marine productivity for which a relationship with HW behavior was found in Iceland and Madagascar, but not in Antarctica (Bouchard et al., 2019). Flood tide was a driver for feeding events of HWs in the Gulf of Maine (Hazen et al., 2009) and Alaska (Barlow et al., 2019) where feeding on fish occurs in tidal influenced bays and fjords.

Overall, environmental drivers for feeding behavior of HWs are region-specific and are best described as a combination of multiple factors. For instance, Riekkola et al. (2019) identified distance to the ice edge (with 2-months lag), SSH and the specific period of the year/region as relevant predictors of the behavioral state of HWs within their Southern Ocean feeding grounds. Similarly, large scale weather drivers such as the Southern Annular Mode (SAM) or Antarctic Oscillation were found to explain almost 24% of the variability of fatty acids (related to type and amount of food intake) in HWs over a 10-year period of the E1 population feeding in East Antarctica influencing migration patterns (Groß et al., 2020). In the Northern Hemisphere, at the feeding area at Cordell Bank north of San Francisco (United States), HW habitat use was associated with fluorescence, temperature and salinity. In addition, bathymetry, distance to the shelf break, distance to islands, coast and four climate indices (Upwelling Index – UI, Pacific Decadal Oscillation – PDO, North Pacific Gyre Oscillation – NPGO, and Southern Oscillation Index – SOI) also remained as significant covariates in the final GLM (Rockwood et al., 2020). In the Atlantic, Ramp et al. (2015) were able to determine a link with the North

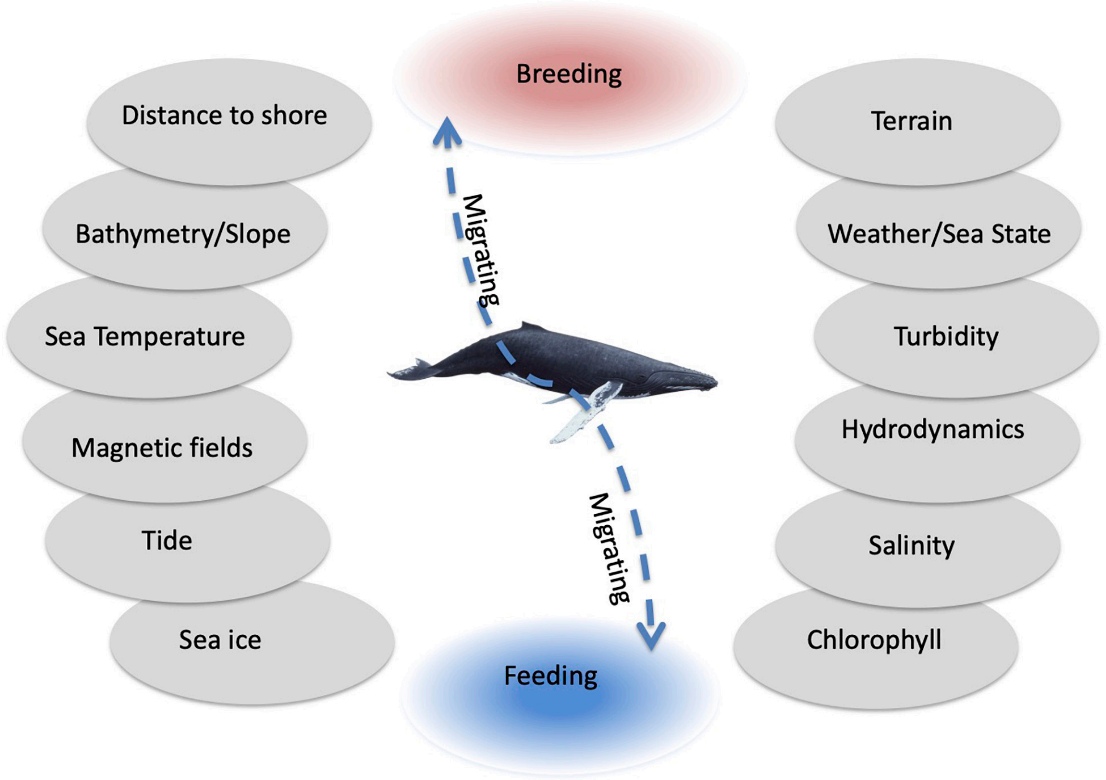

FIGURE 6 | The main environmental drivers in order of relevance to humpback whale breeding (red), migration (dashed line), and feeding (blue) from bottom to top (e.g., sea ice concentration and chlorophyll being more important for feeding and distance to shore and terrain being more important for breeding).

Atlantic Oscillation (NAO) index, reinforcing the overall role of the main climate patterns as significant variables in explaining feeding behavior.

A number of studies added prey abundance as variables to improve the predictive capacity of their models. This method, however, requires longer time series due to high variability in prey abundance and such times series are often difficult to obtain. For example, the best results from a GAM included SST and krill abundance for explaining isotopic signatures in HW sampled in the California Current (United States, Fleming et al., 2016) and a 40% contribution (in a second GLMM after some covariates were removed) of herring spawning and HW calving rate was determined for the Gulf of St Lawrence (United States) feeding area (Kershaw et al., 2021).

Breeding

Breeding grounds include areas with activities such as calving, nursing and mating. Breeding grounds are typically identified by shallow (<50 m), warm (21–28°C) and calm waters, close to the coast where HWs spend several weeks to give birth and nurse their newborns (Jenner et al., 2001; Smith et al., 2012; Bruce et al., 2014; Irvine et al., 2018). They can extend along the expanse of the migratory corridor rather than in precise identified locations. In fact, a number of studies have demonstrated that breeding behaviors have occurred outside recognized breeding grounds for HW populations (Bruce et al., 2014; Lucena et al., 2015; Irvine et al., 2018). HWs can calf every 2 years depending on feeding success (Baker and Herman, 1987; Torre-Williams et al., 2019) and the gestation period is around 12 months (Chittleborough, 1958).

Bathymetry is the driver most often identified with HW calving, breeding and resting grounds. This includes associated variables such as bed slope (e.g., Sleeman et al., 2007; Chou et al., 2020). Generally, there is consistency of the findings throughout all populations. Most studies reported significant relationships with depth ranging between 20 and 50 m. Steep, continental slopes and deep waters are generally avoided by HWs when breeding. These patterns of habitat preferences were also reflected in individual movements recorded through satellite tracking (Garrigue et al., 2020). New Caledonia singletons and pods with calves preferred depths of less than 20 m (Derville et al., 2019) and in the Great Barrier Reef the preferred depth range was between 30 and 58 m (Smith et al., 2020a). These findings were similar for the population G in Costa Rica and Peru (20–50 m depth) (May-Collado et al., 2005; Guidino et al., 2014). Breeding areas in offshore reef environments appear to be slightly deeper with preferences found around 50 m (Garrigue et al., 2020) likely because deeper waters are close by compared to that of breeding areas on continental shelves.

Sea surface temperature preferences for breeding grounds generally ranged from 19 to 28°C. There are some regional differences with 21–23°C reported for the Great

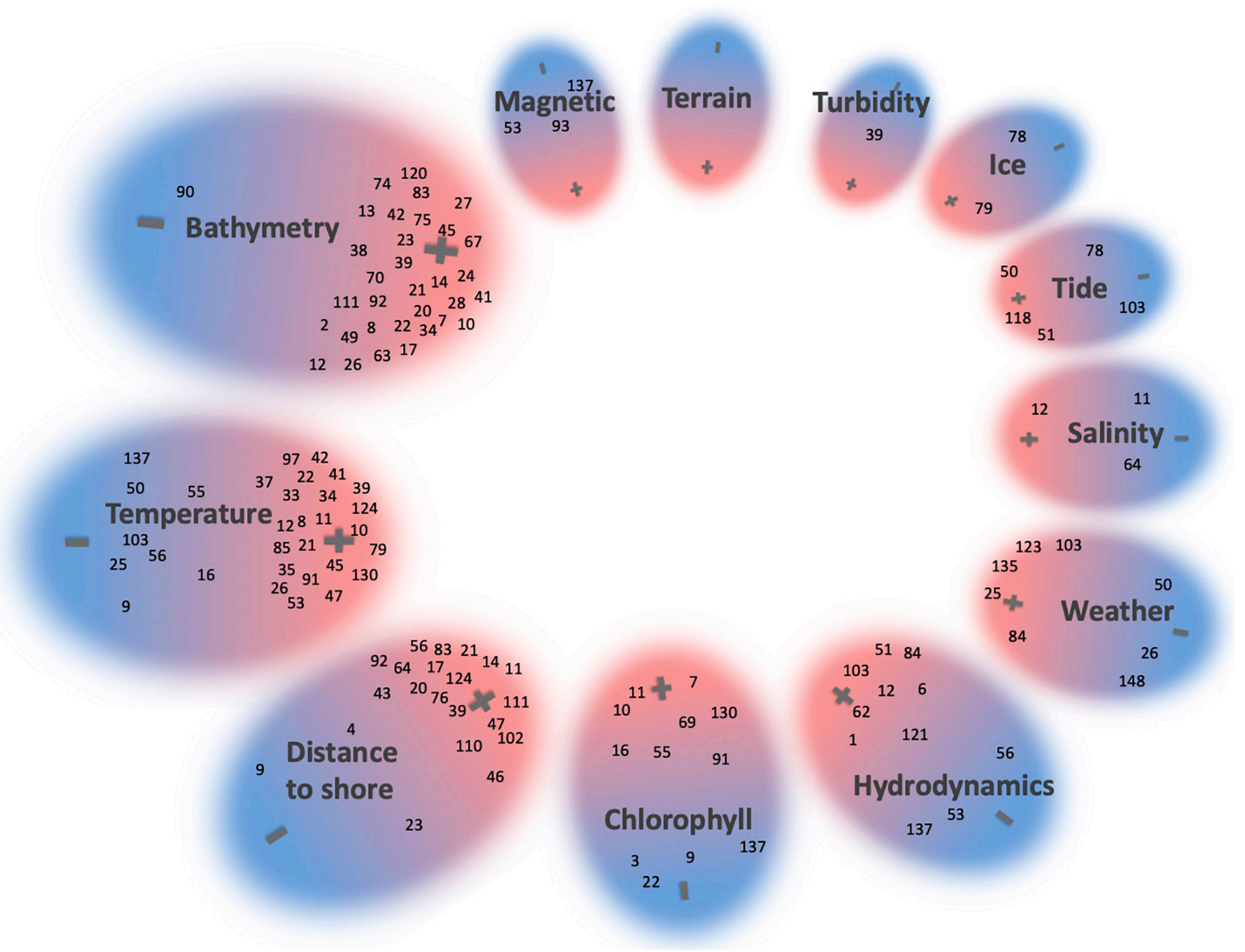

FIGURE 7 | A representation of 73 studies assessing HWs and single environmental drivers. A "+" indicates that an influence of the variable was found and a "–" that no influence of that particular variable was found. Studies identified a weak relationship were placed in the middle. If more than one variable was analyzed, studies were assigned to multiple variables (e.g., temperature, bathymetry, and distance). The size of circles is related to the number of studies testing that particular variable. Studies were indexed (see **Supplementary Data** for a list of references).

Barrier Reef (Smith et al., 2020a), 22.3–27.8°C for Oceania (Derville et al., 2019), 19.4–26°C for Brazil (Tardin et al., 2019), average 24.6°C for breeding grounds of population G (Rasmussen et al., 2007), any temperature above 20°C for population D on the west coast of Australia (Burton, 2001) and above 21°C for Hawaii (Johnston et al., 2007). The highest tolerated temperature is believed to be around 27.7°C (Derville et al., 2019). However, there may also be different temperature preferences both within and among breeding ground sites (Beaugrand and Kirby, 2016).

Given the identified shallow water preference for mother-calf pairs, it is not surprising that the related variable distance offshore (or for reef and island environments: distance to reef or island) showed significant relationships in a number of studies (e.g., Ersts and Rosenbaum, 2003; Lindsay et al., 2016). Breeding behavior and high HW abundance in breeding grounds generally occurs in close proximity of a few kilometers (<10 km) to continents, islands or reefs consistently throughout a number of regions and populations worldwide. Mothers and calves are found predominantly within 1–5 km to shore (Salden, 1988; Ersts and Rosenbaum, 2003). However, in shallow bays preferences for distance to shore can be much further from the shoreline (e.g., up to 70 km, Chou et al., 2020), indicating that shallow slopes and bathymetry are better variables to describe suitable breeding areas than coastal distance. Other variables considered when investigating breeding areas were SSH and wind speed, both indicators of mesoscale circulation and turbulence. Calmer conditions allow calves to remain close to their mothers and may assist with nursing and lower overall energy expenditure (Whitehead and Moore, 1982; Martins et al., 2001; Oviedo and Solís, 2008). An example is the Bay of Guinea (West Africa) which is a large open embayment where HWs exhibit breeding behavior in low wind speed (5.9 ± 1.3 m/s) over several months (Chou et al., 2020). Such conditions are expected in bays and areas protected by reefs and islands.

Resting

Resting occurs during breeding, feeding and migration [described as prolonged surfacing periods, logging, reduced swimming speed and permanence in the same area for days or even weeks (Franklin et al., 2011)]. Prolonged periods of resting mostly occur during migration by mother-calf pairs for nursing, and to reduce energetically expensive associations with competitive male groups (Ersts and Rosenbaum, 2003; Franklin et al., 2017). Calm, shallow (<50 m) waters are utilized as resting places by mothers and calves during their journey to summer grounds (Franklin et al., 2011; Valani et al., 2020). Only a handful of studies have focused on environmental preferences for resting behavior and resting areas, likely because they are not as easy to define as feeding or breeding grounds. Resting areas are found in protected waters with shallow depth and calm surface conditions (Meynecke et al., 2013). Water depths and distance to shore have therefore been significant variables to describe resting behavior (e.g., Stack et al., 2019). The preferences for resting areas are similar to those of breeding areas, with resting mother-calf pairs found in 30 m or less depth of water (Valani et al., 2020) and in close proximity to shore often in open or closed embayments (Franklin et al., 2011; Bruce et al., 2014). Short periods of resting may also occur during offshore migration and feeding but limited information is available, with information mainly coming from direct observation or tagging (Weinstein et al., 2017). Lower SST (relative to surrounding waters) may be preferred during resting along the migratory corridor (Reinke et al., 2016; Tardin et al., 2019). For example, differences between northern and southern migration characteristics along the Agulhas Current were identified in South Africa (Findlay and Best, 1996; Findlay et al., 2011).

Migrating

Migratory behavior can be defined as any direct movement over prolonged time in the same direction, at steady swimming speed and excluding breeding, feeding and resting (Andrews-Goff et al., 2018). Mother-calf pairs will travel significantly slower (e.g., in the range of 2–4 km/h) than other pods (e.g., in the range of 4–5 km/h) (Noad and Cato, 2007).

Migration is likely a result of energetic advantages, allowing whales to take advantage of seasonally abundant prey resources in cooler waters and maximize reproductive success in warmer waters (Clapham, 2000; Rasmussen et al., 2007). The timing of migration and breeding is separated by maturity, sex, and reproductive cycle (Chittleborough, 1965; Dawbin, 1966; Craig et al., 2003). Valsecchi et al. (2010) also identified the selection of different migratory routes and the potential for sub-structure within populations in Australia. Craig and Herman (1997) identified that the timing of migration has shown to vary due to different energy requirements within HW cohorts in that males are more likely to maximize movements during migration for mating opportunities. Genetic and photographic data, and historic whaling data have shown a higher abundance of males along migratory corridors and breeding grounds, which may also be related to catch selection and observation bias (Chittleborough, 1958, 1965; Clapham, 1992; Brown et al., 1995; Craig et al., 2003). In contrast, females minimize energetic costs during migration and may not migrate every year (Best et al., 1995) if not breeding.

Mother-calf pairs are found closer to shore during migration and have more stop overs and resting than singletons or pods without calves (Bejder et al., 2019). Generally, HWs stay in proximity to shore and within the continental shelf while migrating near continents (e.g., Best and Ross, 1996; Paton and Kniest, 2011). Calambokidis et al. (2019) estimated that HWs spend the majority of their migration time within 30 m of the sea surface (90% at night and 69% during daytime). However, deep dives (400 m) have been reported during offshore migration (Derville et al., 2020). Model analyses found a relationship with distance to coast in Brazil and Chile but not with bathymetry (Viddi et al., 2010; Tardin et al., 2019). Burton (2001) also reported an avoidance of hypersaline waters in the Western Australia migration route. Once HWs leave the coast or reefs, there are limited available data on their migratory behavior other than historic whaling data, satellite data from individuals or some observations from offshore surveys. During migration in offshore environments no particular preference for bathymetry has been found (Rosenbaum and Collins, 2006). However, seamounts may play an important role in navigation. Derville et al. (2020) reported spatially structured movements of satellite-tagged HW around shallow seamounts (<200 m). Residence time significantly increased with proximity to shallow seamounts, while dive depth increased in the vicinity of seafloor ridges. This is in line with another satellite-tagging study for population C, where mixed cohorts traveled significantly faster during deep-water transit than shallow-water transit over 1–71 day deployment duration (Dulau et al., 2017). Minimal or no contribution of SST or chlorophyll to migratory behavior was found (Tardin et al., 2019; Groß et al., 2020; Horton et al., 2020). Stephenson et al. (2020) found SST to be a third-degree model contributor (with mixed layer depth and slope being first and second contributor respectively) in a multi-species study from New Zealand, but current literature on HWs does not appear to support a strong influence of SST on migratory behavior.

Considering that HWs cover vast areas of open sea, they also cross various currents and are exposed to strong weather conditions. A direct influence of weather on HW migratory behavior has not been documented to the best of our knowledge, while currents are the most investigated drivers. HWs have shown evidence of utilizing currents flowing in the direction of travel (Baker and Herman, 1981) and avoiding those flowing in the opposite direction (Findlay and Best, 1996; Burton, 2001; Findlay et al., 2011), while larger scale studies (covering oceans) showed no effect of currents suggesting that HWs are able to compensate and remain on direct migration paths (Horton et al., 2011, 2020). The influence of currents could also be dependent on the cohort with mother-calf pairs needing more resting time than other cohorts. Increased entanglements in near shore shark nets (400–500 m from shore) by mother-calf pairs as a proxy for higher number of whales were related to the pathway of the East Australian Current (EAC), with entanglements significantly increasing when the EAC was closer to shore (Volep et al., 2017; Bolin et al., 2019). This is a similar response to what Burton

(2001) discovered off the west coast of Australia, where whales were resting outside major currents.

DISCUSSION

This review synthesized 148 studies investigating HWs and their relationships with environmental variables. From these studies we determined the most frequently tested drivers and extracted relationships that are most related to each of the HW's behavioral modes considered here (feeding, breeding, resting, and migrating). Information provided in this review allows for a more comprehensive understanding on how these drivers determine HW behavior across regions and populations. It also provides important information for modeling HW movements.

Bathymetry and distance to shore were consistently determined throughout the literature as the most important variables for HW breeding in both hemispheres (e.g., Ersts and Rosenbaum, 2003; Félix and Botero-Acosta, 2011; Garrigue et al., 2011) with nursing groups found in shallower waters close to shore with gentle bed slopes (Whitehead and Moore, 1982; Mignucci-Giannoni, 1998; Oviedo and Solís, 2008; Cartwright et al., 2012; Craig et al., 2014). Preferred values for SST were less important than bathymetry in areas ranging from subtropical to tropical waters (19–28°C) (Rasmussen et al., 2012; Tardin et al., 2019). The role of weather-related variables such as SSH and sea state were not often investigated and further studies on these variables are recommended (Chou et al., 2020).

While resting areas have some similarities with breeding areas (bathymetry range, proximity to coast, reduced wind and wave forces, and degree of bed slope) questions remain if preferred conditions for resting areas are similar throughout all populations and whether HWs can shift their resting locations without compromising their energy budgets. There is evidence that resting areas in semi-enclosed bays facing the migration stream are used by population sub-groups and for short (days) or long (weeks) periods of time (Franklin, 2014).

Research in feeding areas has revealed a preference for strong gradients of temperature and currents (frontal zones) (Hamazaki, 2002; Bassoi et al., 2019). Environments with high chlorophyll concentration and steeper bed slopes were further preferred while feeding (Laidre et al., 2010; Santora et al., 2010; Friedlaender et al., 2011). High prey concentrations are often associated with these conditions (Schweigert et al., 2013) and other cetaceans have been observed feeding in regions with similar conditions (Griffin, 1999; Gannier and Praca, 2007). The successful use of chlorophyll concentration as a predictor variable for feeding varies spatially and relies on an interpretation of the complex relationship and lagged effect with HW prey at multiple trophic levels, as previously mentioned.

Only a few studies tested relationships with salinity and these generally suggested a preference for more saline waters during feeding (Smith et al., 1986; Gregr and Trites, 2001; Tynan et al., 2005; Dalla Rosa et al., 2012; Dransfield et al., 2014). This may be explained by the presence of cold, saline, nutrient-rich water rising to the surface during upwelling, and increasing productivity (Fiedler et al., 1998; Calambokidis and Barlow, 2004; Thompson et al., 2012). Cetaceans are believed to sense salt concentration through taste (Feng et al., 2014) and may be able to use it as a cue when searching for food (Bouchard et al., 2019). Opportunistic feeding has also been documented during migration (Stockin and Burgess, 2005; Danilewicz et al., 2008), indicating that certain environmental cues, such as high levels of DMS, can lead to feeding events (Bouchard et al., 2019). The importance of drivers is highly dependent on prey preferences and reflects the regional differences of HW populations. However, further research into hydrodynamics and biogeochemical processes can provide some of the missing links (e.g., time lag effects) to predict feeding events (Fiedler et al., 1998; Calambokidis and Barlow, 2004; Thompson et al., 2012). Such research will also assist in linking prey dynamics with fine-scale responses of HWs to environmental conditions (Tulloch et al., 2019; Meynecke et al., 2020).

The majority of studies reviewed here have focused on feeding and breeding areas, while migration and resting received less attention. However, HWs spend up to half of their life migrating (Dawbin, 1966), and many migration routes pass alongside highly developed coastlines risking negative human interaction. The cues or triggers for migration are not well understood and it remains speculative as to whether environmental factors drive HWs to leave feeding and breeding grounds at a particular time. It will likely be a combination of environmental triggers, physiology and behavior (social and learned). Other species such as blue whales showed earlier arrival in feeding grounds related to colder sea surface temperature anomalies from the previous season that correlated with greater krill biomass the following year (Szesciorka et al., 2020).

It is worth further investigating the importance of distinct oceanographic features (e.g., canyons and seamounts), fine scale oceanographic processes and the soundscape to determine relevant environmental drivers or human impacts on migration behavior. As technology advances, data of known relevant drivers including SST, salinity and chlorophyll will become available in higher resolution for open ocean environments which in turn will allow for more fine scale analyses.

The role of magnetic and gravitational field variables in combination with the position of the sun has shown limited evidence for determining migration routes but deserves further attention (Horton et al., 2011, 2020). As shown in other migrating animals, the main course and direction are likely a learned behavior (maternally directed site fidelity). However, diversions from this learned behavior have also been documented frequently and will be more evident in the future through automated fluke matching (Felix et al., 2020).

Challenges and Future Directions

As outlined in this review, a multifaceted approach will provide the best understanding of the relationships between HWs and a suite of environmental drivers. This includes the use of multi-species studies which are suitable to provide an overview of feeding aggregations, and help to define large-scale patterns and regions of high cetacean abundance (Ingman et al., 2021) but are limited in terms of extracting relevant relationships at the species level. The often very-detailed satellite tagging studies help with specific preferences of cohorts and individuals and give insights into unknowns, e.g., navigation during migration or maximum depths for feeding as well as fine scale habitat preferences. The less common studies on strandings and environmental drivers showing relationships of wind patterns and cooler waters with higher number of strandings can give insights into long-term trends of migration patterns in coastal waters (Evans et al., 2005; Meager and Limpus, 2014; Meynecke and Meager, 2016).

Our review identified that preferred conditions vary between populations (e.g., due to different prey preferences, varying temperature preferences for breeding areas). Other factors such as learned behavior may play an important role and can or could be more relevant in habitat selection than environmental drivers (Barendse et al., 2013). The importance of early experience and maternal influence on the return of HWs to traditional feeding grounds have been documented through individual return rates and population genetics (Baker et al., 2013; Whitehead and Rendell, 2021). Hence, HWs might not disperse to areas with suitable environmental conditions that may have been erased from the cultural memory of individuals due to whaling (Clapham et al., 2009) or that may be too remote or are emerging. Disentangling the effect of learned behavior from the effect of environmental drivers is challenging but may be achieved in future studies through fluke matching and individual records of thousands of HWs. Promising platforms using A.I. to train algorithms (e.g., Flukebook and Happy Whale) and dataset assembly through citizen science open new possibilities in this field of research. Further genetic (Apprill et al., 2014; Schmitt et al., 2014), isotope (Fleming et al., 2016) and fatty acid (Groß et al., 2020) studies related to environmental drivers will add to a better understanding of environmental drivers and relationships with HWs. Further testing and use of SDMs based on machine learning will improve predictive capacity and allow for constant as well as fast-changing variables over time to be included. However, a careful fitting and validation is important and requires extensive datasets (Reisinger et al., 2021).

Improving predictive capacity is particularly relevant for understanding the role of human impacts that might change HW behavior, forcing them to move to alternative, potentially less suitable, habitats (Corkeron, 1995) or altering recovery rates of populations. An area suitable for breeding, feeding or migration may be avoided or is degraded due to vessel traffic (Guzman et al., 2013), noise pollution (Au and Green, 2000; Laist et al., 2001; Weilgart, 2007), dredging (Todd et al., 2015), fishing (Gribble et al., 1998; Clapham and Mead, 1999), chemical inputs (Remili et al., 2020) and climate change (Jackson et al., 2001; Chilvers et al., 2005). These kinds of impacts need to be considered when undertaking habitat suitability studies or studies investigating predictive capacity of environmental drivers. A good understanding of the influence of environmental drivers is required to enable modeling of future impacts including climate change (**Figure 1**). Considering the variabilities that the marine ecosystem is currently subjected to and other factors as the HW populations recovery, such modeling is complex.

Disentangling the natural variability of distribution patterns from climate change is not straightforward. Combining long-term data sets spanning several decades and big data set analyses will make this more feasible in the future. Although there is some recognition of the impacts of climate change on HWs (e.g., Ramp et al., 2015), there are many knowledge gaps in the influence of climate variability on HW feeding, breeding and migration distributions. Given the temperature tolerance for HWs, small changes in SST due to climate change are likely not going to have major impacts on breeding grounds as long as suitable habitats below 28°C are accessible (Derville et al., 2019). Significant changes in ocean circulation patterns and sea ice are predicted as a result of climate change in feeding areas, which may result in changes to the timing of prey availability as well as the size, density and locations of important foraging areas (Nicol et al., 2000, 2008; Ramp et al., 2015). In the rapidly warming Western Antarctica Peninsula, there is evidence that krill are being replaced by salps, which are not a suitable diet for whales (Plum et al., 2020). Less predictable occurrence of prey and reduced densities would increase the time and energy cost of feeding. A possible adaptive response could be feeding outside traditional feeding grounds (Findlay et al., 2017) or reducing length and time of migration by shifting calving grounds closer to feeding grounds (Torre-Williams et al., 2019). A separate review of HW relationships with prey for different regions is recommended to provide a more in-depth overview of available studies.

Most of the responses of HWs to climate change are still unknown. In order to tackle the complex impacts of climate change on environmental variables and consequently on HWs, a multi- and transdisciplinary research approach is needed (Meynecke et al., 2020). With new time series of previously unavailable or limited data for environmental drivers (such as data from autonomous devices), we are also likely to see an increase of new variables in the future studies. It raises the question of whether environmental drivers have been selected because they were the most likely to relate with a HW's behavioral mode or because they were the most accessible and promising at the time. Some variables included here (e.g., DMS proxies for feeding areas) are still undertested and need to be further investigated regarding their influence on the distribution of the species populations and/or on the species behavior in specific regions. Other environmental drivers that will hopefully be subject to increased research in the future include nutrient and links to food abundance in the ice-covered ocean (Meyer et al., 2020) given the anticipated changes in polar regions (Turner and Marshall, 2011).

CONCLUSION

Determining the type and strength of relationships between environmental drivers and HWs continues to be of great relevance. Despite increasing research in this field over recent years, a number of unknowns remain in terms of both the physical and biological domains of this inter-disciplinary issue. However, increasing availability of multi-variate data streams, and analytical advancements for parametrization of models and in particular for predicting anthropogenic impacts have started to provide much-needed contexts for comprehensive assessments of environmental drivers. The findings highlighted in this review can provide the basis for future research by addressing the identified gaps. Determining environmental conditions that increase the risk of entanglements (Santora et al., 2020), vessel strikes (Redfern et al., 2017; Smith et al., 2020a), noise pollution (Erbe et al., 2019), impacts from whale tourism (Sprogis et al., 2020), climate change impacts (Meynecke et al., 2020), identifying where new habitats could arise and when currently used habitats might become unsuitable, would enable better protection of this iconic species. Elevated protection of current and future critical habitat and a plan for flexible protection zones are needed in light of the many challenges ahead.

AUTHOR CONTRIBUTIONS

J-OM, JdB, and J-LB contributed to conception and design of the study and organized the database. JdB and ES wrote sections of the manuscript. BM, KF, MV, AR, and J-OM contributed funding. All authors contributed to manuscript revision, read, and approved the submitted version.

FUNDING

This work was supported by a grant to Griffith University from a private charitable trust as part of the Whales & Climate Research Program.

ACKNOWLEDGMENTS

The authors like to thank the many colleagues who contributed to the ongoing discussion of this research.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.720774/full#supplementary-material

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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: 21 March 2022
doi: 10.3389/fmars.2022.832075

Stable Isotope Oscillations in Whale Baleen Are Linked to Climate Cycles, Which May Reflect Changes in Feeding for Humpback and Southern Right Whales in the Southern Hemisphere

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

Received: *09 December 2021*
Accepted: *22 February 2022*
Published: *21 March 2022*

Citation:
Dedden AV and Rogers TL (2022)
Stable Isotope Oscillations in Whale
Baleen Are Linked to Climate Cycles,
Which May Reflect Changes
in Feeding for Humpback
and Southern Right Whales
in the Southern Hemisphere.
Front. Mar. Sci. 9:832075.
doi: 10.3389/fmars.2022.832075

Baleen whales that undertake extensive long-distance migrations away from reliable food sources must depend on body reserves acquired prior to migration. Prey abundance fluctuates, which has been linked in some regions with climate cycles. However, where historically these cycles have been predictable, due to climate change they are occurring at higher frequencies and intensities. We tested if there were links between variability in whale feeding patterns and changes in climate cycles including the El Niño-Southern Oscillation (ENSO), Southern Annular Mode (SAM), and Indian Ocean Dipole (IOD). To reconstruct feeding patterns we used the values of bulk stable isotopes of nitrogen (δ^{15}N) and carbon (δ^{13}C) assimilated within the baleen plates of 18 humpback and 4 southern right whales between 1963 and 2019, then matched them with climate anomalies from the time in which the section of baleen grew. We show that variability in stable isotope values within baleen for both humpback and southern right whales is linked with shifts in climate cycles and may imply changes in feeding patterns due to resource availability. However, these relationships differed depending on the oceanic region in which the whales feed. In the western Pacific, Southern Ocean feeding humpback whales had elevated nitrogen and carbon stable isotope values during La Niña and positive SAM phases when lagged 4 years, potentially reflecting reduced feeding opportunities. On the other hand, in the Indian Ocean the opposite occurs, where lower nitrogen and carbon stable isotope values were found during positive SAM phases at 2–4-year lag periods for both Southern Ocean feeding humpback and southern right whales, which may indicate improved feeding opportunities. Identifying links between stable isotope values and changes in climate cycles may contribute to our understanding of how complex oscillation patterns in baleen are formed. As projections of future climate scenarios emphasise there will be greater variability in climate cycles and thus the primary food source of baleen whales, we can then use these links to investigate how long-term feeding patterns may change in the future.

Keywords: stable isotopes, baleen whales, climate cycles, environmental drivers, long-term patters, El Niño-Southern Oscillation, Southern Annular Mode, Indian Ocean Dipole

INTRODUCTION

High-latitude ecosystems experience rapid changes driven by large-scale climate cycles. In the Southern Ocean, these cycles include interannual trends of the El Niño-Southern Oscillation (ENSO) index, shifts in the Southern Annular Mode (SAM) and Indian Ocean Dipole (IOD) cycles. Historically, climate oscillations (in particular ENSO) have been relatively predictable, occurring approximately every 2–7 years (Torrence and Webster, 1999). However, there is growing evidence to suggest these cycles are becoming harder to predict, with phases occurring more frequently and with greater intensity under future climate change projections (Trenberth and Hoar, 1997; Marshall, 2003; Yeh et al., 2009; Cai et al., 2014, 2015). In the Southern Ocean, these climate cycles drive changes in resource availability, in particular the abundance of lower trophic organisms that rely on certain environmental conditions for survival. For example, the timing of sea ice advance and retreat is not only influenced seasonally, but also by climate oscillations, in turn affecting Antarctic krill (*Euphausia superba*) that rely on sea ice as both a physical form of protection and a provider of algae, a critical food source under pack ice encouraging survival of larvae over winter (Siegel and Loeb, 1995; Loeb et al., 1997; Atkinson et al., 2004; Schmidt et al., 2018; Cotte and Guinet, 2020). Secondly, Atkinson et al. (2019) found that a reduction in sea ice following positive anomalies of SAM hindered egg production and the survival of larval krill, leading to a reduction in juvenile krill density in the Southwest Atlantic. At the same time, increased light availability due to sea ice reduction drives higher densities of phytoplankton (Arrigo and van Dijken, 2004), promoting adult krill growth (Atkinson et al., 2019). While areas in the Southwest Atlantic and southern Bellingshausen Sea regions experience shorter sea ice durations during positive SAM and La Niña events, the Ross Sea within the Pacific Ocean experiences extended sea ice duration (Stammerjohn et al., 2008). In other regions around the Antarctic shelf, SAM and ENSO effects are less consistent through time (e.g., areas along East Antarctica) (Stammerjohn et al., 2008). It is clear that climate signals drive environmental conditions and resource availability within the Southern Ocean, though these trends are not the same across different ocean regions. Climate cycles can therefore be used as a proxy for resource availability, especially where data on direct ice measurements and krill abundance are lacking. We expect that climate-induced changes in resource availability will impact consumers differently, depending on their feeding location within the Southern Ocean. Variability in resources is problematic for consumers within these regions, like baleen whales who are reliant on large aggregations of food sources, particularly as recent findings suggest the amount of prey they consume has been underestimated (Savoca et al., 2021).

Baleen whale populations throughout the Southern Ocean undertake extensive long-distance migrations from the high-latitude regions where they feed to their low-latitude breeding grounds where they are required to fast during austral winter (Corkeron and Connor, 1999). They are capital breeders, meaning they require enormous amounts of krill over the summer feeding periods to store lipid and protein reserves for later mobilisation to support the physiological costs associated with migration and reproduction (Stearns, 1989; Jönsson, 1997). There is growing evidence that Southern Hemisphere humpback whales (*Megaptera novaeangliae*) supplement their feeding throughout their southern migration, this is shown for the southwestern Pacific humpback whales, referred to as the E1 breeding stock (Paterson, 1987; Stamation et al., 2007; Gales et al., 2009; Pirotta et al., 2021). However, the potential environmental drivers behind this behaviour are largely unknown. With future climate projections emphasising greater variability in climate cycles (Cai et al., 2018) and therefore resource availability, it is important to understand how the long-term feeding patterns of baleen whales relate to changes within the environment. To do this successfully decadal biological data is required to capture patterns across climate cycles that may naturally occur anywhere between 2 and 7 years. Stable isotope compositions of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) assimilate within the tissues of consumers and provide insight into potential feeding patterns and spatial movements over time (DeNiro and Epstein, 1981; Hobson, 1999). Unlike short-term signals like satellite tags, blubber or skin, whale baleen grows continuously throughout life and remains metabolically inert, providing long-term isotopic data that assimilates over approximately 3–16 years, depending on the species (Schell et al., 1989; Best and Schell, 1996; Schell, 2000; Lee et al., 2005; Mitani et al., 2006; Bentaleb et al., 2011; Aguilar et al., 2014; Matthews and Ferguson, 2015; Eisenmann et al., 2016; Busquets-Vass et al., 2017; Lysiak et al., 2018; Trueman et al., 2019). This growing body of research on whale baleen all show that nitrogen and carbon isotopic signatures assimilate longitudinally along the growth axis of baleen plates, forming predictable annual oscillations which are suggested to reflect the timing of their yearly migrations by indicating physiological changes driven by feeding and fasting patterns. However, high variation and complex processes influencing assimilation through time mean that large uncertainties remain in our interpretation of stable isotope ratios within whale baleen (Trueman et al., 2019).

To identify whether stable isotope values (as a proxy for feeding patterns) reflect changes in climate cycles (as a proxy for resource availability) we utilised data available from existing literature on humpback and southern right whales (*Eubalaena australis*) that feed within the Pacific and Indian Ocean sectors of the Southern Ocean. To test whether there was a relationship between nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) stable isotope values in baleen and climate cycles, first we identified the time that each section of baleen grew to assign a date to each isotope value. Then, to account for changes in the baseline of oceanic stable isotopes across years (e.g., the influence of the Suess effect) and intra-individual variability in the diets of whales, we used an index that identifies this variability in nitrogen and carbon stable isotope values. By selecting breeding populations that feed in different sectors within the Southern Ocean, we aimed to identify regional differences in climate cycle trends. We analysed large-scale climate cycles that influence the Pacific and Indian Ocean sectors of the Southern Ocean including ENSO, SAM, and IOD as proxies for resource availability.

MATERIALS AND METHODS

Data Collection

Bulk stable isotope values of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) from the baleen of Southern Hemisphere humpback and southern right whales were extracted from available literature (**Table 1**). These baleen plates were originally obtained from stranded and necropsied whales (apart from individual "63/6" which was killed in error by whalers in 1963) along the Australian and South African coast and stored as part of either museum collections or internal laboratories until analysis by Best and Schell (1996) and Eisenmann et al. (2016). Only adult individuals with a known stranding date (dd/mm/yyyy) were included in this study to ensure accurate time sectioning along baleen plates and also avoid artificially high values from young individuals who may still be suckling (Borrell et al., 2016). Additionally, by excluding juveniles that have shorter baleen lengths (e.g., Best and Schell, 1996), we aim to capture long-term trends in adults, especially in the years prior to their stranding. By doing this, we avoid isotopic values that may be associated with and/or biased by individual physiology due to its potential compromised state prior to stranding. Humpbacks from Eisenmann et al. (2016) were kept within feeding groups for analysis. These included humpbacks that primarily fed within the Southwest Pacific Ocean sector of the Southern Ocean (known as classical feeders of the E1 breeding stock); humpbacks from the E1 breeding stock that supplemented their feeding in temperate regions as well as feeding in the Southern Ocean (known as supplementary feeders); humpbacks from the E1 breeding stock that remained in temperate regions year-round (known as temperate feeders); and humpbacks that primarily fed within the Indian Ocean sector of the Southern Ocean (known as classical feeders from the D breeding stock). Eisenmann et al. (2016) also show evidence for supplementary feeding from the D breeding stock, however, due to a very low sample size (*n* = 1) for this feeding group, it was excluded from this study. Associated biological information was extracted for each individual where available, alongside stranding circumstances to control external influences that may affect isotopic signatures, e.g., entanglement or ship strike causing death. Data points were extracted using software ImageJ based on their x and y axis, where x refers to the position of each point along the baleen; 0 cm = proximal and ∼200 cm = distal, and y being the bulk stable isotope values of $\delta^{15}N$ and $\delta^{13}C$, respectively.

Additionally, we sampled a single baleen plate that was opportunistically collected from a dead adult male humpback stranded on the 24/7/2019 at Stockton beach, Newcastle, Australia and loaned to us for stable isotope analyses from the collection at the Australian Museum (individual identification: "M.51091.001"). This plate had been taken from between the middle to back of the whale's mouth, representing the longest plates, i.e., to obtain the longest record. The plate was removed from within the gum to ensure the unerupted section beneath the gum was included.

TABLE 1 | Biological information for individuals within this study, and source identifying where data was extracted (all but one individual that was opportunistically sampled by the Australian Museum).

Species	Individual	Feeding category	Sex	Ocean	Stranding date	Source
HUMPBACKS	D11	Classical D	F	SE Indian	16/10/2013	Eisenmann et al., 2016
	D12	Classical D	F	SE Indian	18/08/2013	
	D13	Classical D	M	SE Indian	12/04/2014	
	D15	Classical D	F	SE Indian	29/07/2014	
	D01	Classical D	–	SE Indian	30/07/2007	
	D14	Classical D	–	SE Indian	12/07/2014	
	E27	Supplementary	M	SW Pacific	10/03/1989	
	E14	Supplementary	M	SW Pacific	5/06/2012	
	E13	Supplementary	M	SW Pacific	7/11/2011	
	E12	Supplementary	M	SW Pacific	6/11/2011	
	E23	Supplementary	–	SW Pacific	7/07/2014	
	E10	Classical E1	M	SW Pacific	1/10/2011	
	E08	Classical E1	–	SW Pacific	7/06/2010	
	E24	Classical E1	–	SW Pacific	31/08/2010	
	E26	Classical E1	–	SW Pacific	1/11/2010	
	E05	Temperate zone	F	SW Pacific	22/10/1998	
	E18	Temperate zone	–	SW Pacific	1/12/2012	
	M.51091.001	Classical E1	M	SW Pacific	24/07/2019	This study
SOUTHERN RIGHTS	63/6	–	M	SW Indian	14/08/1963	Best and Schell, 1996
	87/27	–	F	SW Indian	27/08/1987	
	N961	–	F	SW Indian	27/07/1983	
	N1645	–	M	SW Indian	27/10/1989	

Individual refers to their identification number, feeding category refers to the group/feeding behaviour as defined in Eisenmann et al. (2016). Ocean corresponds to the ocean sector within the Southern Ocean where they feed. All data (except M.51091.00) was extracted from source papers as shown.

Stable Isotope Analysis

The baleen plate was first cleaned with Milli-Q water, followed by a 2:1 chloroform:methanol solution using steel wool. This was repeated twice to ensure surface lipids and contaminants were removed before sampling. Using a Dremel engraving tool with a flexible shaft, approximately 0.5 mg of baleen powder was collected every 1 cm along the longitudinal growth axis, 0.5 cm from the outer edge, starting at the proximal end (most recent growth). Powdered samples were loaded into tin capsules and compressed airtight for processing and analysis using the Flash 2,000 organic elemental analyser, interfaced with a Delta V Advantage Isotope Ratio Mass Spectrometer *via* a ConFlo IV interface (Bioanalytical Mass Spectrometry Facility, Mark Wainwright Analytical Centre, UNSW Sydney). δ^{15}N and δ^{13}C values are expressed as a deviation from standards in parts per thousand (‰):

$$\delta X = \left[\left(\frac{Rsample}{Rstandard}\right) - 1\right] \times 1,000$$

where X = ^{13}C or ^{15}N, R = the ratio of respective heavier and lighter stable isotopes of nitrogen (N^{15}/N^{14}) and carbon (C^{13}/C^{12}). Reference standards of nitrogen and carbon USGS40 and USGS41A were used to correct potential drift caused by the instrument prior to isotope abundance calculation. C:N ratios ranged from (3.4 ± 0.1) which were within the range of pure keratin (3.4 ± 0.5) (Hobson and Schell, 1998; Trueman et al., 2019).

Time Sectioning Baleen

To establish the time that the stable isotope values represent, we estimated the time over which the section of baleen grew. We used three values: (1) the baleen plate growth rate; (2) the date the baleen stopped growing (when the whale died); and (3) the interval between samples taken along the baleen plate.

We used baleen growth rates reported by Best and Schell (1996) for their southern right whale specimens and those reported by Eisenmann et al. (2016) for their humpback whale specimens with the exception of the Australian Museum collection specimen "M.51091.001" where we calculated the growth rate using the technique described by Eisenmann et al. (2016). This technique is based on the assumption that the oscillations in stable isotope values along the baleen plate reflect annual physiological changes as the whales move from feeding to fasting (Best and Schell, 1996; Eisenmann et al., 2016). Specifically, for the whales in this study lower δ^{15}N values reflect times when the animal is feeding and higher δ^{15}N values are associated with fasting during migration. Therefore, to calculate the growth rate of baleen the length between two adjacent δ^{15}N minima were used to identify 1 year of growth. This is based on the assumption that baleen growth is linear and constant through time and between individuals of the same species, which may not always be true.

The stranding date (per individual) was used as the date when the baleen stopped growing. We assume that the baleen plates were collected from within the gum of the whale, meaning the entire plate (including the unerupted section containing the most recent growth) was included.

We calculated the number of days between each data point using the individual-specific growth rate and sampling interval (distance between each sampling point (cm)) then assigned a date to each point based on the cumulative days since the time of last known growth (stranding date) (see **Supplementary Table 1** for functions). We assumed isotopic assimilation was constant in all animals despite potential differences in individual physiology, e.g., reproductive state, breeding condition, and fasting (Hobson et al., 1993; Lee et al., 2012; Clark et al., 2016). However, this study is the first step in investigating links between isotope values in baleen and climate cycles and how individual physiology impacts these relationships is the next step in this work.

Climate Data

El Niño-Southern Oscillation

ENSO is an important driver of climate in the Pacific Ocean, but its influence is broader across the Southern Hemisphere. We used the Southern Oscillation Index (SOI, as a measure for ENSO) which measures the pressure differences between Tahiti and Darwin, Australia and indicates the development and intensity of El Niño and La Niña events between 1876 and present. We extracted data from the Australian Bureau of Meteorology (BOM).[1] The BOM calculates the SOI using the Troup SOI method which is the standardised anomaly of the Mean Sea Level Pressure difference between Tahiti and Darwin (Troup, 1965) with multiplication by 10 used as a convention to quote a whole number that ranges between –35 and ∼ +35. The BOM specifies sustained negative SOI values below –7 typically indicate periods of El Niño, while sustained positive SOI values greater than +7 typically indicate La Niña events. Monthly SOI values were extracted for use in models with isotope data. Yearly averages were also calculated by taking the average of all monthly indices for each year of interest (SOI dataset available upon request).

Indian Ocean Dipole

The IOD is an important driver of climate in the Indian Ocean. We used the Dipole Mode Index (DMI) to identify the influence of the IOD. DMI is an indicator of the east-west temperature gradient, represented by anomalous sea surface temperatures (SST) along the western equatorial Indian Ocean and the southeastern equatorial Indian Ocean (Saji et al., 1999). We extracted DMI data from the National Oceanic and Atmospheric Administration (NOAA).[2] Monthly DMI values were extracted in the DMI: Standard PSL Format. Positive IOD events are represented by positive DMI values while negative IOD events are shown through negative DMI values (DMI dataset available upon request).

Southern Annular Mode

The SAM, also known as the Antarctic oscillation index (AAO), is a circumpolar climate driver in the Southern Ocean. It describes the north-south movement of the westerly wild belt that

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[1] http://www.bom.gov.au/climate/enso/soi_monthly.txt

[2] https://psl.noaa.gov/gcos_wgsp/Timeseries/Data/dmi.had.long.data

circulates Antarctica, thus dominating the mid-to-high-latitude regions of the Southern Hemisphere (Gong and Wang, 1999). We used AAO data extracted from the NOAA[3] to identify the influence of SAM. Monthly mean AAO values were extracted from 1979 to 2021. The NOAA calculates monthly indices of SAM by projecting the monthly mean (700-hPa) height anomalies onto the leading Empirical Orthogonal Function mode. This is then normalised by the standard deviation of the monthly index over a base period from 1979 to 2000. Yearly averages were also calculated by taking the average of all monthly indices for each year. Isotope data for one of the southern right whales (individual “63/6”) was outside this time frame and therefore this individual was excluded from the SAM analysis (AAO dataset available upon request).

Statistical Analysis

There is large intraspecific variation in $\delta^{15}N$ and $\delta^{13}C$ values for both humpback and southern right whales, as shown by the high R^2 conditional values relative to R^2 marginal values. This, among other things may be due to individual whales feeding in different regions of the Southern Ocean or feeding on prey of different sizes or species. Alternatively, it may be due to shifts in the isotopic baseline in the ocean (McMahon et al., 2015) or multiple biochemical factors associated with or influenced by isotopic fractionation (Newsome et al., 2010). As a result of this intraspecific variation, we developed indices for $\delta^{15}N$ and $\delta^{13}C$ stable isotope values. These indices allowed us to determine the relative importance of data points and compare values among individuals. To do this we used individual-specific weighted averages for the stable isotope values of each whale, equalising the frequency of the values in the data set so that the final index values reflect the relative importance of each observation, placing individuals on the same scale. Firstly, individual-specific means of $\delta^{15}N$ and $\delta^{13}C$ values were calculated. Then, per individual, each isotope value along the baleen plate was subtracted from the individual-specific mean, resulting in a positive or negative variance from that mean. These values formed the nitrogen index (for $\delta^{15}N$ values) and carbon index (for $\delta^{13}C$ values):

$$\text{Nitrogen index} = \mathrm{a} - ((\Sigma\ \mathrm{a})/\mathrm{N})$$

Where within an individual whale’s baleen plate, a is the $\delta^{15}N$ value at any position; Σa is the sum of all $\delta^{15}N$ values; and N is the total number of $\delta^{15}N$ observations.

$$\text{Carbon index} = \mathrm{c} - ((\Sigma\ \mathrm{c})/\mathrm{N})$$

Where within an individual whale’s baleen plate, c is the $\delta^{13}C$ value at any position; Σc is the sum of all $\delta^{13}C$ values; and N is the total number of $\delta^{13}C$ observations.

Isotopic results are expressed as a ratio. To calculate weighted averages for ratios each value needs to be multiplied by their respective weight (i.e., by the denominator of the ratio). Here the assumption is that the values of the denominators across the samples were equal, which may not be true. The transformation of the original stable isotope values to our nitrogen and carbon index values means they are no longer stable isotope ratios as we traditionally know them, but values that reflect the relative importance of any data point within each whale’s series.

We did not adjust raw $\delta^{13}C$ values in baleen to account for the Suess effect (Young et al., 2013). This was because we did not directly compare absolute $\delta^{13}C$ values between years. Instead we compared the intra-individual variability using our aforementioned carbon index.

Linear mixed-effects models (LMM) were fitted using the lmer function (Bates et al., 2014) to determine the model of best fit. This approach assumes the relationship is strictly linear. Individual whale was included as a random effect across all models as there were multiple sequential samples taken from the baleen of each individual. Species were analysed separately to avoid comparisons between animals with different feeding and spatial patterns and humpbacks were analysed within their feeding group (E1 classical feeders: $n = 5$, data points = 208; E1 supplementary feeders: $n = 5$, data points = 122; E1 temperate feeders: $n = 2$, data points = 58; D classical feeders: $n = 6$, data points = 184). For both humpback and southern right whales monthly and yearly anomalies of ENSO, IOD and SAM were included as predictor variables alongside lags of 6 months and 1–4 years for IOD and SAM and 6 month and 1–7 years for ENSO. Lastly, nitrogen and carbon indices were included as the response variable in models with all environmental combinations, resulting in a total of 390 models. The Akaike Information Criterion (AIC) was used to select the most parsimonious models owing to model simplicity. Due to the theoretical problems associated with R^2 as outlined by Nakagawa and Schielzeth (2013), marginal and conditional R^2 values were initially reported, displaying the influence of fixed effects alone and combined with the random effects, respectively. However, after removing individual variation by establishing both indices, only R^2 marginal values were reported. R^2 marginal values were used to compare the models of best fit across these data sets of different sizes and to provide the absolute value for goodness-of-fit which cannot be provided by the aforementioned information criteria. This was done using the MuMIn package (Burnham and Anderson, 2002). All analyses were conducted in R (R Core Team, 2021).

Multicollinearity between stable isotope values and the climate predictors ENSO, SAM, and IOD was assessed using variance inflation factor (VIF) scores. The results indicated an absence in multicollinearity for humpbacks (1.1, 1.6, 1.4) and southern right whales (2.7, 1.1, 2.9) based on established criterion (Gareth et al., 2013). While the VIF of 2.6 and 2.9 are close to 3, when each climate driver was removed for testing it did not signify a correlation. Thus, all three climate predictors were kept within 390 models.

RESULTS

Due to large individual variation in $\delta^{15}N$ and $\delta^{13}C$ values for humpback and southern right whales, all statistical analysis was

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[3] https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/aao/monthly.aao.index.b79.current.ascii

done through indices to put individuals on the same scale, known as their nitrogen index and carbon index. We observed changes in stable isotope values within the baleen of both humpback and southern right whales alongside changes in climate cycles. Particularly, we found that humpback whales from the Southwest Pacific that primarily feed in the Southern Ocean show a positive (+) relationship between stable isotope values and ENSO/SAM with a 4-year lag. We observed enriched δ^{15}N and δ^{13}C values during + SAM and La Niña phases and depleted δ^{15}N and δ^{13}C values during negative (–) SAM and El Niño phases when lagged 4 years. On the other hand, Southern Ocean feeding humpback and southern rights in the Indian Ocean, show the opposite negative relationship with SAM at a lag period of 2–4-years, observing enriched δ^{15}N and δ^{13}C values during – SAM and depleted δ^{15}N and δ^{13}C during + SAM.

Southwest Pacific Ocean

Classical Southern Ocean Feeders of the E1 Breeding Stock

Humpback whales of the E1 breeding stock (Southwest Pacific) that predominately feed in the Southern Ocean (classical feeders), showed a positive relationship between both their nitrogen and carbon indices and changes in ENSO and SAM at 4-year lags. For their nitrogen index, we found higher δ^{15}N values with less variation during La Niña periods with a monthly 4-year lag ($p < 0.01$; R^2m = 0.04) (**Figure 1**), while there appears to be lower δ^{15}N values with greater variation observed during El Niño periods. There was also a positive relationship between the carbon index and SAM anomalies at a yearly 4-year lag, whereby, higher δ^{13}C values correlated with + SAM anomalies and lower δ^{13}C values with—SAM anomalies ($p < 0.01$; R^2m = 0.15)

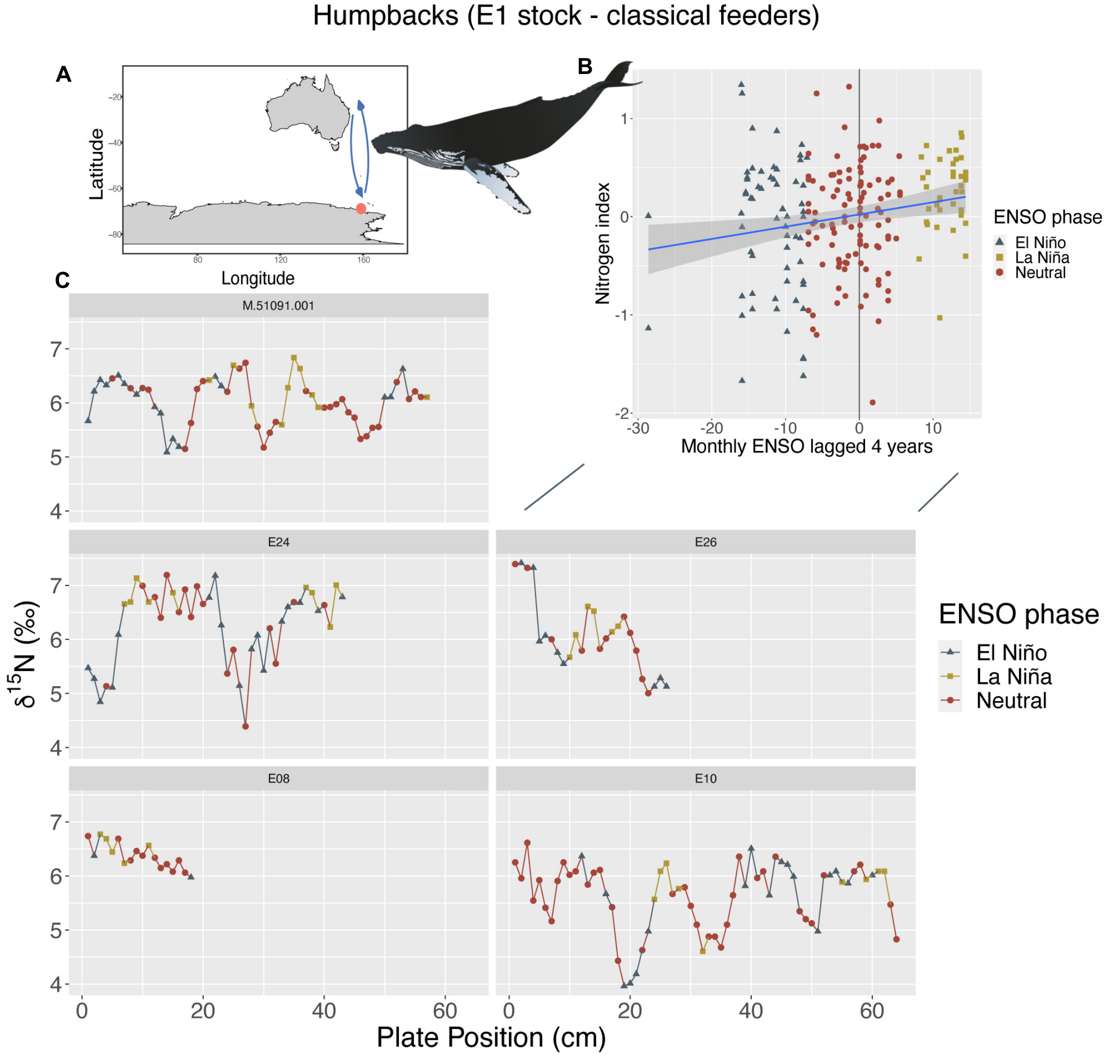

FIGURE 1 | (A) Humpbacks from the E1 breeding stock (*n* = 5, sample points = 208) that primarily feed within the Southwest Pacific Ocean (known as classical feeders, orange circle = feeding location, arrows = migration route), show a positive linear relationship between their nitrogen index and ENSO **(B)** with a 4-year lag period ($p < 0.01$; R^2m = 0.04). **(C)** Shows where these changes in ENSO phases occur along baleen and resulting stable isotope patterns of δ^{15}N for each individual. Whale image attribution: Tracey Saxby, Integration and Application Network (ian.umces.edu/media-library).

(**Supplementary Figure 1**). While there were other models of statistical significance, these models explained the most variance having the highest R^2m and lowest AIC.

Supplementary and Temperate Zone Feeders of the E1 Breeding Stock

Humpbacks from the E1 breeding stock that supplement their feeding outside of the Southern Ocean showed a positive relationship between their nitrogen index and yearly SAM anomalies with a zero-lag period ($p < 0.01$; R^2m = 0.16). We found that higher δ^{15}N values occur during + SAM and lower δ^{15}N values toward—SAM phases (**Figure 2**). Their carbon index showed a negative relationship with yearly IOD anomalies at a 1-year lag ($p < 0.01$; R^2m = 0.11), with higher δ^{13}C values toward—IOD and lower δ^{13}C values toward + IOD phases (**Supplementary Figure 2**). However, all humpbacks that supplemented their feeding mainly assimilated isotopic signals during times of positive IOD events, therefore visual trends across phases cannot accurately be seen.

Humpback whales from the E1 breeding stock who remained in temperate regions year-round displayed variability in isotopic values alongside changes in SAM at 2- and 3-year lags. We found a positive relationship between their nitrogen index and monthly SAM anomalies at a 2-year lag ($p < 0.01$; R^2m = 0.25), where enriched δ^{15}N values occurred during + SAM and depleted δ^{15}N values during –SAM (**Figure 2**). Their carbon index showed a negative relationship between δ^{13}C values and yearly SAM anomalies at a 3-year lag ($p < 0.01$; R^2m = 0.75), where enriched

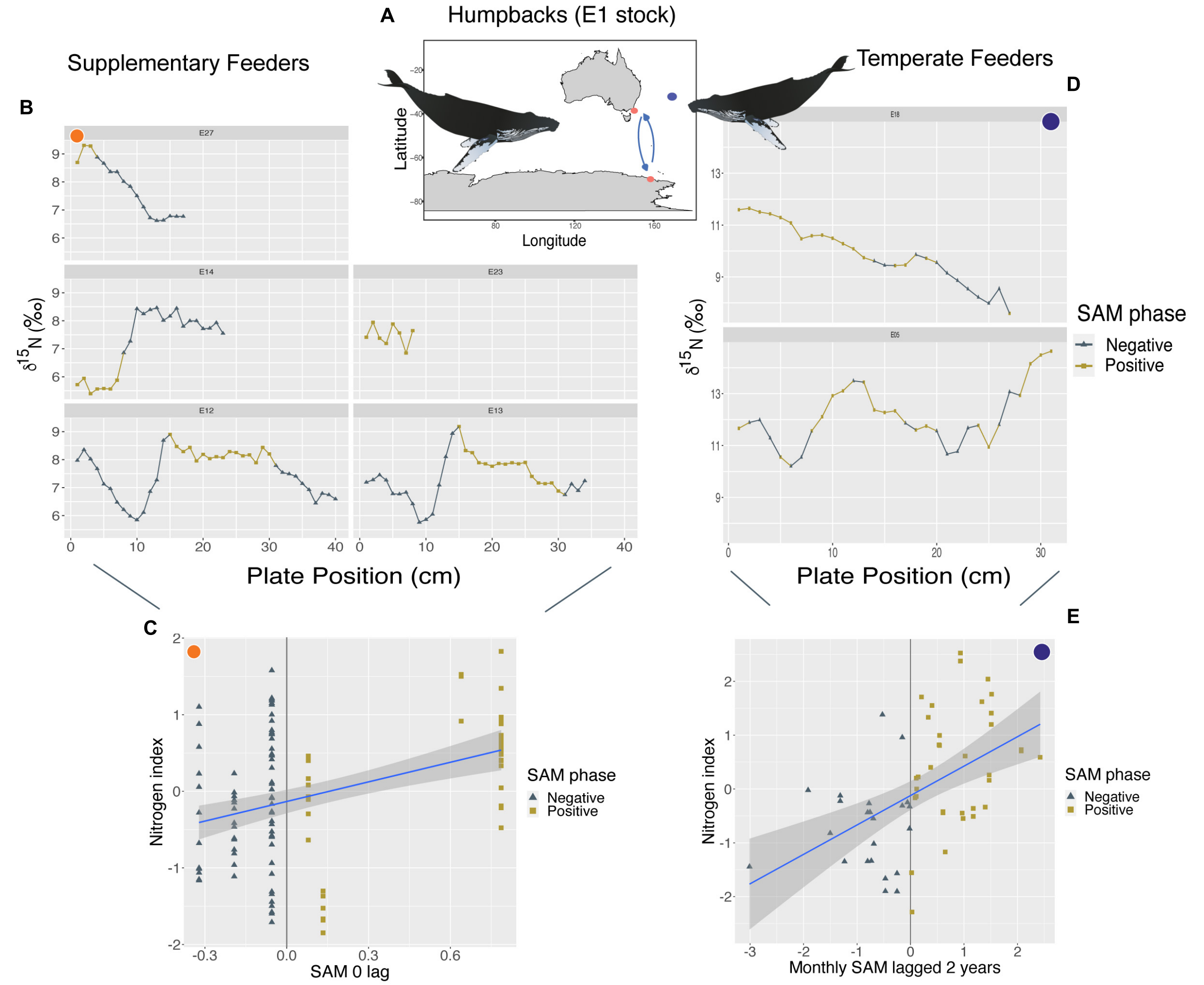

FIGURE 2 | (A) Orange circles represent the approximate feeding locations of humpbacks from the E1 breeding stock (Southwest Pacific Ocean) that supplement their feeding in Australian waters (n = 5, sample points = 122). Purple circle represents an approximate location of humpbacks from the same breeding stock that remain in Australian waters year-round (known as temperate feeders, n = 2, sample points = 58). **(C,E)** Show a positive linear relationship between their nitrogen index and SAM, however, supplementary feeders **(C)** at a 0-year lag ($p < 0.01$; R^2m = 0.16), and temperate feeders **(E)** at a monthly 2-year lag ($p < 0.01$; R^2m = 0.25). **(B,D)** Show where these changes in SAM phases occur along baleen and resulting stable isotope patterns of δ^{15}N of each individual. Whale image attribution: Tracey Saxby, Integration and Application Network (ian.umces.edu/media-library).

δ^{13}C values were observed during -SAM and depleted δ^{13}C values during + SAM phases (**Supplementary Figure 3**). However, this relationship is only driven by 2 individuals (58 samples) and so we caution that it represents possible trends.

South Indian Ocean

Humpback Whales (D Breeding Stock) and Southern Right Whales (South African Stock) in the Indian Ocean

Both the humpback whales of the D breeding stock (Southeast Indian Ocean), and the southern right whales of the South African stock (Southwest Indian Ocean) feed predominantly within the Indian Ocean sector of the Southern Ocean and show the same negative relationship between nitrogen indices within baleen and changes in SAM. While the nitrogen index for D stock humpback whales was primarily influenced by monthly SAM anomalies at a 2-year lag (p < 0.01; R^2m = 0.04), the nitrogen index of southern right whales was linked to yearly SAM anomalies at a 4-year lag (p < 0.05; R^2m = 0.04). Despite the different time lags, both show higher δ^{15}N values during—SAM phases and lower δ^{15}N values during times of + SAM when lagged their respective years (**Figure 3**). δ^{15}N values for D stock humpbacks also show a positive relationship with monthly IOD anomalies at a 2-year lag (p < 0.01; R^2m = 0.04), with enriched δ^{15}N values during + IOD and lower δ^{15}N values during—IOD when lagged 2 years.

We also found links between SAM and the carbon index of humpback and southern right whales within the South Indian Ocean. Specifically, both had a negative relationship between their carbon index and SAM, with humpback values driven by monthly SAM anomalies at a 3-year lag (p < 0.01; R^2m = 0.07) and southern right whale values driven by monthly SAM anomalies at a 4-year lag (p < 0.01; R^2m = 0.11). For both species within the Indian Ocean, we observed higher δ^{13}C values during-SAM and lower δ^{13}C values during + SAM for both lag periods (**Supplementary Figure 4**). However, only ~2 southern right whales were available for

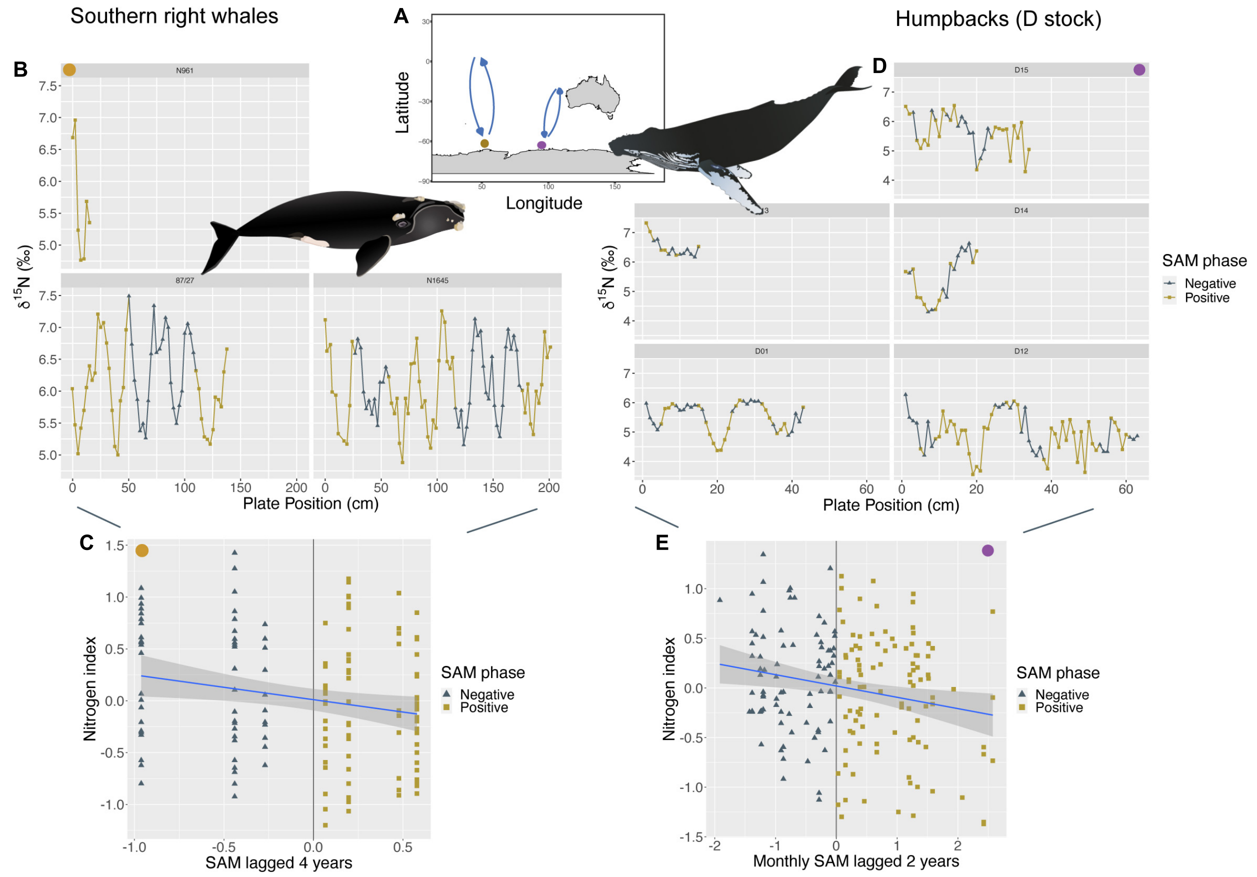

FIGURE 3 | (A) The brown circle represents an approximate feeding location of southern right whales (SRW) from the South African population (Southwest Indian Ocean, n = 3, sample points = 144). While the light purple circle represents an approximate feeding location for humpbacks from the D breeding stock (Southeast Indian Ocean, n = 6, sample points = 184). **(C,E)** Show a negative linear relationship between their nitrogen index and SAM, however, SRW **(C)** at a 4-year lag (p < 0.05; R^2m = 0.04) and D humpbacks **(E)** at a monthly 2-year lag (p < 0.01; R^2m = 0.04). **(B,D)** Show where these changes in SAM phases occur along baleen and resulting stable isotope patterns of δ^{15}N for each individual. Individual "D11" was removed from the image based on having a short baleen length. Humpback whale image attribution: Tracey Saxby, Integration and Application Network (ian.umces.edu/media-library). SRW image attribution: Jamie Testa, Integration and Application Network (ian.umces.edu/media-library).

analysis with SAM; therefore, more data is needed to confirm these relationships.

DISCUSSION

We show that for Southern Ocean feeding humpback and southern right whales, variation in baleen stable isotope values correlates with changes in large-scale climate cycles and that these relationships differ depending on the region in which individuals feed (**Figure 4**). For whales that feed predominantly in the Southwest Pacific, there is a positive relationship between both nitrogen and carbon stable isotope values with ENSO and SAM cycles when lagged 4 years. On the other hand, whales that feed predominantly in the Southeast and Southwest Indian Ocean show a negative relationship between nitrogen and carbon stable isotope values with SAM lagged 2–4years. The variation we observed in the isotopic values of whale baleen may reflect a shift in the resources available to individuals (as they feed on different prey types) and/or a change in isotopic baseline values as a response to variation during different environmental conditions.

We suggest that the spatial and temporal variation in ENSO and SAM (e.g., a positive SAM/La Niña phase may be beneficial in one region while not in another) as well as different lag periods (e.g., potentially the offset in SAM cycle timings within the Southern Ocean) could be reflected in the stable isotope values in baleen. However, there is little direct data on resource availability in regions where these whales are known to feed. Finally, our results demonstrate that climate cycles could be a source of isotopic variation, contributing to our understanding in interpreting isotopic patterns in baleen.

Southwest Pacific Ocean

Humpback Whales—Classical Southern Ocean Feeders of the E1 Breeding Stock

For humpbacks from the Southwest Pacific that primarily feed within the Southern Ocean, the climate cycles ENSO and SAM were positively associated with variation in nitrogen and carbon stable isotope values in baleen when lagged 4 years. We also found the same positive relationship between the stable isotope values and shorter lags in ENSO (6-month) and SAM (zero-lag) to be statistically significant. Stable isotope values were

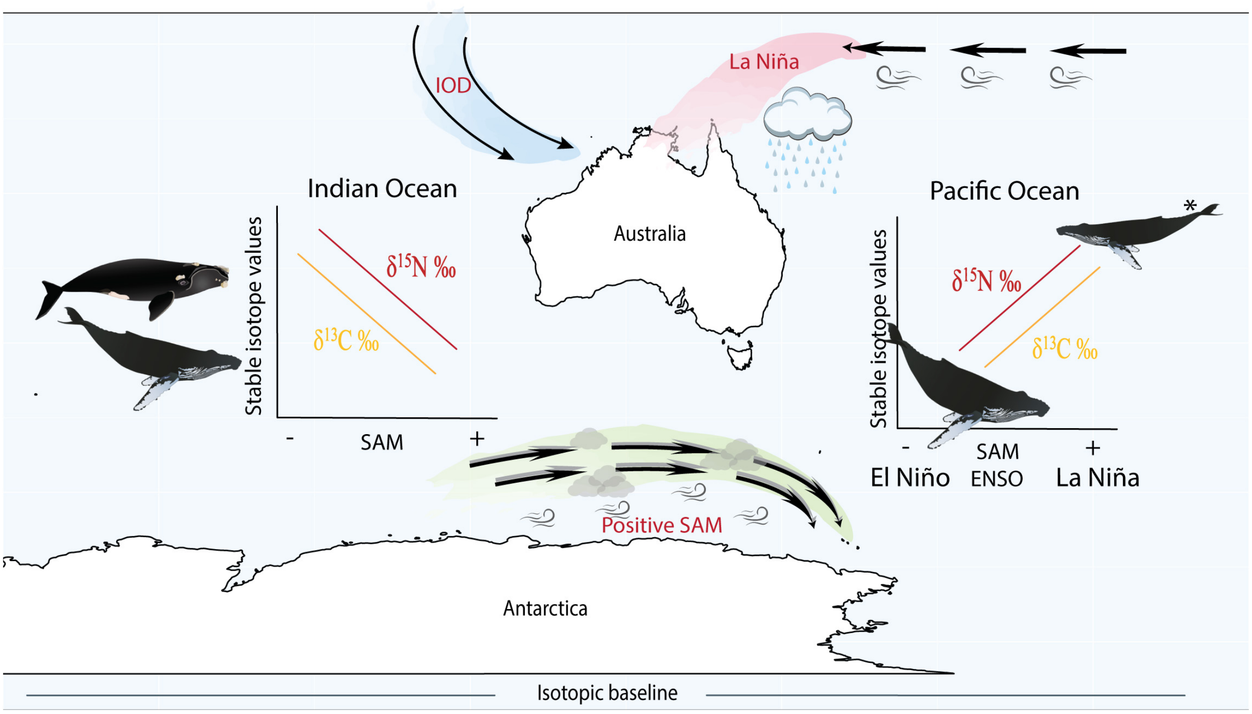

FIGURE 4 | Schematic figure illustrating the main findings from the study and the positioning of climate cycles. La Niña (a phase of ENSO) corresponds to warmer and increased wet conditions in the west Pacific Ocean, while positive SAM (known to correspond to La Niña phases of ENSO) also drives an increase in storm conditions, however, has a stronger influence over the Southern Ocean. IOD is more prominent in the Indian Ocean and positive and negative phases are more complicated and not strictly in phase with either ENSO or SAM, making it difficult to compare with these climate cycles. Within the Pacific Ocean, we found that humpback whales displayed enriched nitrogen and carbon stable isotope values during positive SAM and La Niña periods (potentially reflecting poor feeding conditions) and depleted stable isotope values during negative SAM and El Niño phases. In the Indian Ocean we found the opposite trend, where humpback and southern right whales exhibited depleted nitrogen and carbon stable isotope values during positive SAM (potentially reflecting improved feeding conditions) and enriched isotope values during negative SAM. *In the Pacific Ocean during La Niña/positive SAM, whales from the same population were found to be in a lean body condition due to reduced sea ice concentration and resource availability (Bengtson Nash et al., 2018). However, such information is unavailable for whales in the Indian Ocean. Our interpretations assume variation in isotope values reflect changes in resource availability rather than variation in baseline isotope values.

enriched and less varied during and 4 years following La Niña and positive SAM events but depleted and more varied during and 4 years following El Niño and negative SAM events. It is possible that the short and long-term lags reflect reoccurring cycles (4 years apart) of either ENSO (La Niña/El Niño) or SAM (positive/negative). Specifically, if similar anomalies in both ENSO and SAM occurred 4 years apart during the time baleen grew, isotopic values at short and long-term lags may reflect similar responses to resource availability and/or isotopic baseline changes associated with the reoccurring phase of either ENSO or SAM. These links between climatic conditions and isotopic variability may reflect different relationships. Firstly, changes in isotopic variability may imply that there has been a direct impact upon the whale's feeding opportunities due to certain climatic conditions. Alternatively, there may have been a shift in the isotopic values at the base of the food chain (shifting baselines) rather than a true change in prey availability.

If these climate cycles do directly impact on resource availability, it may be possible that enriched and less variable stable isotope values in baleen during and 4 years following La Niña and positive SAM phases indicate that the whales experience less favourable feeding opportunities and/or longer fasting periods during these times. On the other hand, lower and more varied stable isotope values during and 4 years following El Niño and negative SAM events could suggest better feeding opportunities. Eisenmann et al. (2016) suggest that times of enriched nitrogen stable isotope values along baleen oscillations represent periods of fasting for this population, while slightly elevated carbon values coincide with times the whales were in Australian waters. Furthermore, they show that lower nitrogen stable isotope values predict times when the whales were feeding in the Southern Ocean, matched to lower carbon values within the Antarctic range (Eisenmann et al., 2016).

Within the Western Antarctic Peninsula, there is a reduction in sea ice duration following periods of positive SAM and La Niña phases (Stammerjohn et al., 2008). Furthermore, in the same region there is a reduction in krill recruitment following positive SAM events (Atkinson et al., 2019), which is said to be a result of reduced sea ice conditions that favour the survival of krill larvae (Siegel and Loeb, 1995; Quetin et al., 2007; Saba et al., 2014; Atkinson et al., 2019). Within the Pacific Ocean sector of the Southern Ocean, Bengtson Nash et al. (2018) showed that during La Niña and positive SAM events there was a similar trend between sea ice concentration and krill availability. Using the same breeding population, they also showed (*via* adiposity markers) that during these times of La Niña and positive SAM events, the southwestern Pacific humpbacks were in a lean body condition which they proposed was due to the reduced krill availability because of less sea ice. Similarly, in this study we infer that during positive SAM and La Niña periods, whales experience enhanced fasting seen through consistently enriched isotopic values in their baleen. Furthermore, the opposite occurs during negative SAM and El Niño phases, where there are signs of enhanced krill recruitment along the Western Antarctic Peninsula due to enhanced sea ice conditions favouring the survival of krill larvae (Siegel and Loeb, 1995; Quetin et al., 2007; Saba et al., 2014; Atkinson et al., 2019). The 4-year lag may alternatively represent a biological lag and/or cycle in krill development. It takes Antarctic krill approximately 3 years to develop into mature adults (Siegel, 1987), therefore the link seen between ENSO, SAM, and isotopic values in baleen may reflect changes in krill abundance according to their developmental stage. However, more research is required to confirm this link as there is no available krill data from the area in which these whales feed.

For the southwestern Pacific humpbacks, variability in isotope values is linked to two different climate cycles, where nitrogen stable isotope values are linked to ENSO and carbon values are linked to SAM. However, given the correlated nature of ENSO and SAM (particularly La Niña/positive SAM and El Niño/negative SAM; Fogt and Bromwich, 2006; Stammerjohn et al., 2008), it appears the relationship between nitrogen and ENSO and carbon and SAM may represent a similar 4-year signal. Within the Pacific Ocean, ENSO and SAM may modulate one another (Simmonds and King, 2004; Kohyama and Hartmann, 2016), potentially explaining why we see the positive influence of both ENSO and SAM on baleen isotope values for the southwestern Pacific feeding humpback whales.

La Niña events occurred more frequently among the dataset for the classical feeders, especially in the year prior to stranding. Based on the link we found between enriched and less varied nitrogen stable isotopes and La Niña events, we suggest that reoccurring La Niña phases could contribute to the likelihood of individual whales stranding (i.e., the source of baleen data used in this study). While we were limited by sample size and unable to statistically test this, Meynecke and Meager (2016) show a positive relationship between La Niña events also lagged 4 years and increased stranding occurrences in Queensland, Australia. This is supported further by Bengtson Nash et al. (2018) showing that humpbacks tend to be leaner and in poorer body condition during La Niña times. Therefore, there is growing evidence to suggest that, during La Niña years, humpback whales that feed in the Southwest Pacific suffer reduced feeding success, resulting in whales having a leaner body condition (Bengtson Nash et al., 2018) and thus a higher chance of stranding (Meynecke and Meager, 2016). Under scenarios predicting an increase in La Niña intensity (Cai et al., 2015), more research is needed to understand this potential link between resource availability, body condition and stranding potential for humpback whales of the E1 breeding stock.

Alternatively, the link we found between baleen isotopic variability and climatic cycles may be due to changes in the isotopic values at the base of the food web during different phases of ENSO and SAM. Baseline isotopic values of both nitrogen and carbon fluctuate seasonally, as well as spatially across the Southern Ocean (St John Glew et al., 2021). Therefore, this could mean that the observed enriched and depleted baleen stable isotope values of nitrogen and carbon (relative to other years) simply represents a baseline isotopic shift rather than the whales feeding on different prey or the same prey, but of different sizes. However, as we analysed the variability in isotope values within an individual *via* nitrogen and carbon indices rather than comparing the absolute nitrogen or carbon stable isotope values across whales, the variation shown here is less likely to be purely an artifact of a shifting baseline, although this cannot be discounted.

Southwestern Pacific Humpback Whales—Supplementary and Temperate Feeders of the E1 Breeding Stock

Humpback whales from the same southwestern Pacific population (E1) can use alternate strategies and deviate from classical Southern Ocean feeding, i.e., supplement their feeding or stay in Oceania year-round (Eisenmann et al., 2016). Much less is known about humpback whales that supplement their feeding during their annual migration, as well as individuals that refrain from migration and remain at lower latitudes year-round. Therefore, the feeding behaviour of these groups is more difficult to interpret as they can feed across multiple regions with different isotopic baselines and as a result are influenced by Southern Ocean and temperate systems.

Whales that feed both in the Southern Ocean and temperate waters (known as supplementary feeders) show the same positive relationship between their nitrogen stable isotope values and SAM to the classical feeders with elevated nitrogen values during positive SAM and lower values during negative SAM, however, without any lagged effect. We suggest like the classical feeders, this may signify either changes in feeding patterns or isotopic baseline shifts during these different environmental conditions. For supplementary feeders, prolonged elevated nitrogen stable isotopes during positive SAM correspond to sustained low carbon values within the Antarctic range. If the isotopic variation reflects changes in feeding patterns, the sustained and elevated nitrogen values (seen alongside Antarctic carbon values) may either show prolonged times of fasting or feeding at higher trophic levels within the Southern Ocean. In the first instance, like the classical feeders of the same E1 breeding stock, it is possible that elevated nitrogen values may reflect a reduction in resource availability (e.g., krill) associated with a reduction in sea ice during positive SAM/La Niña phases (Bengtson Nash et al., 2018) and thus increased fasting. Secondly, the signal may reflect feeding at higher trophic levels within the Southern Ocean (Eisenmann et al., 2016). If the latter were true, it is possible these whales may switch to other food items within the Southern Ocean in the absence of abundant krill. Alternatively, like the classical feeders, isotopic variability may simply be reflecting baseline changes during these times. These prolonged isotopic signals are ended by the whales supplementing their feeding in Australian waters (as seen by higher nitrogen and carbon stable isotope values within the Australian range). Evidently, we showed that two individuals (E12 and E13) tended to supplement their feeding after a prolonged positive SAM event. We suggest it is possible that whales within this study either supplement their feeding due to a reduction in available resources within the Southwest Pacific Ocean during these times or as a result of increased productivity in temperate waters. Nevertheless, more data from whales that supplement their feeding as well as the influence of climate cycles in temperate waters is needed to explore this theory.

While supplementary feeders may show similarities in their relationship between stable isotope values and SAM to classical feeders, their nitrogen values are not impacted by a lag period as seen in the classical feeders (4-year lag). This may suggest individuals choose to supplement their feeding based on environmental conditions at that time. Alternatively, Australian krill (*Nyctiphanes australia)* have shorter life cycles and are unlikely to live longer than 1 year (Ritz and Hosie, 1982) and therefore supplementary feeders may not be influenced by the biological lags in growth in the larger, longer-lived Antarctic krill. We also note that this data may be restricted in showing longer interannual trends as supplementary and temperate feeders within this study have shorter baleen lengths (and thus less assimilated long-term data).

There are many possible reasons behind why whales may supplement their feeding, one being due to environmental conditions that favour higher productivity in feeding hotspots (e.g., Eden) in the Tasman Sea off eastern Australia (Stamation et al., 2007). Humpback “super-groups” from the same E1 breeding stock have been documented feeding off Southeast Australia (Pirotta et al., 2021). Super-group formation has been linked to phytoplankton blooms 1 month prior as well as reduced outward transport favouring an increase in humpback whale prey in coastal waters, as found in Southern Benguela (Dey et al., 2021). E1 humpbacks are known to supplement their feeding anywhere between Eden, NSW, all the way down through the Bass Strait, Tasmania, and New Zealand, as shown through satellite tracking of the same population (Andrews-Goff et al., 2018). This could explain the relationship of IOD on their carbon stable isotope values as the influence of IOD is mostly seen across the Indian Ocean and southern Australia (Saji et al., 1999) where they may supplement their feeding. However, little is known about the influence of IOD within the regions where these whales feed. Secondly, all assimilated isotopic data collected from supplementary feeders occurred mostly during positive IOD phases; therefore, we suggest while a negative relationship with IOD may be occurring, more data from negative IOD alongside research focusing on supplementary feeders and environmental conditions are needed to understand this link and alternate strategy.

For whales who remain in Oceania year-round (known as temperate feeders), their continued presence and feeding in temperate waters may be driven by either poor Southern Ocean conditions or sustained localised productivity within temperate Tasman Sea waters. However, for temperate feeders, only two individuals were available and therefore we are not able to make assumptions on potential relationships. Interestingly, most whales that supplement their feeding in temperate waters appear to be males, however, more individuals of known sex are needed to explore the influence of sex differences among alternative feeding strategies.

South Indian Ocean

Humpbacks of the D Breeding Stock and the Southern Right Whales of the South African Stock

The Indian Ocean humpback *(Southeast Indian)* and southern right whales *(Southwest Indian)* that predominantly feed within the Southern Ocean show similar relationships between the variability of stable isotope values in their baleen and SAM, despite their different locations within the Indian Ocean. During positive SAM, both populations show an increase in low nitrogen and carbon stable isotope values, though with different lagged periods (humpbacks at monthly lags of 2 and 3 years, respectively, and southern rights at both yearly and monthly 4-year lags, respectively). According to both studies where the data was extracted from, low nitrogen and carbon stable isotope values reflect feeding signals in Antarctic regions (Best and Schell, 1996; Eisenmann et al., 2016). Therefore, unlike southwestern Pacific humpbacks (E1 classical feeders) who show signs of enriched nitrogen and carbon stable isotope values during positive SAM/La Niña periods (and potentially experience poor feeding conditions during summer), whales that feed within the South Indian Ocean show depleted isotope values during positive SAM phases (and potentially experience greater feeding opportunities).

Within the South Indian Ocean the opposite trend in sea ice extent occurs during positive SAM, where, unlike the Southwest Pacific Ocean sector showing sea ice decreases during positive SAM and La Niña events (Bengtson Nash et al., 2018), there is greater sea ice extent during positive SAM (as well as La Niña periods) (Kohyama and Hartmann, 2016). This was also shown through intense negative SST anomalies associated with positive SAM in the Indian Ocean, while negative SAM events were associated with positive SST anomalies (Sabu et al., 2020). Therefore, if the isotopic variability reflects changes in feeding success, it may be possible whales within the South Indian Ocean experience better feeding opportunities (i.e., better krill recruitment) during these times as seen through an increase in low nitrogen and carbon stable isotope values. Similarly, like the southwestern Pacific humpbacks, while we analysed isotopic variability *via* indices rather than absolute values of stable isotopes, the impact of shifting isotopic baselines may still impact these conclusions.

Humpbacks from the D breeding stock also show a positive relationship between nitrogen stable isotope values in baleen and changes in monthly IOD when lagged 2 years, displaying lower nitrogen stable isotope values during negative IOD phases, with higher values during positive IOD phases. Within the South Indian Ocean, the impact of IOD on this population is unclear. Unlike the southwestern Pacific humpbacks (E1 stock), where feeding grounds are known from satellite tracked individuals (Andrews-Goff et al., 2018), there is less information available for humpbacks as well as the influence of IOD on resource availability within the Southeast Indian Ocean. Therefore, it is difficult to interpret this relationship, especially when isotopic data is from predominantly positive IOD phases and lacks isotope values during negative IOD periods.

The 4-year lag for southern right whales may reflect the biological timing in longer-lived Antarctic krill development and/or growth (as discussed for the southwestern Pacific classical feeders) or the frequency in reoccurring phases of SAM captured in these individuals. The 2- and 3-year lags for the humpback whales could also reflect biological lags and/or phase reoccurrences, however, the slightly shorter lag periods may be due to their different feeding location within the Southern Ocean. Thus, lags between stable isotope values and climate anomalies may differ depending on the feeding location within the Southern Ocean due to the temporal and spatial variability in climate cycles.

Indian Ocean humpbacks (D stock) show less variation in feeding strategies than the southwestern Pacific humpbacks (E1 stock) (Eisenmann et al., 2016). Unlike the humpbacks from the Indian Ocean, humpbacks from the Southwest Pacific, may be able to supplement their feeding on reliable spring blooms each year in the Tasman Sea. For example, the southeastern NSW coast is subject to high productivity in spring due to warmer East Australian Current water overlaying uplifted sub-Antarctic waters high in nutrients (Hallegraeff and Jeffrey, 1993; Bax et al., 2001). However, in the Southeast Indian Ocean, there has been comparably little documentation of supplementary behaviour. Therefore, during times of increased productivity within their Southern Ocean feeding grounds, humpbacks from the Indian Ocean may decide to prioritise feeding and spend more time at higher latitudes as a result. This is potentially what we see in this population through greater variability in their nitrogen and carbon stable isotope values during positive SAM events.

If variability among isotope values reflect changes in feeding success in southern right whales (and humpback individual D12), they did not appear to be as adversely impacted by fasting during positive SAM events, as seen through lower peaks in nitrogen isotope values. This further suggests they may experience better feeding opportunities during these times. While limited by sample size and the availability of isotopic baseline data within the Indian Ocean, an increase in feeding success may allow the whales to withstand the impacts of fasting better (meaning less enrichment of nitrogen stable isotopes). However, more research tracking these populations as well as on the effect of climate cycles within the area is necessary to understand what these relationships mean.

Baleen Oscillation Patterns

In this study, we show that some of the isotopic variability in baleen oscillations is related to changes in climate cycles and thus may assist in the interpretation of complex stable isotope patterns in baleen. We recommend analysing the influence of climate on stable isotope patterns across multiple individuals and species through an index. This technique allowed us to compare changes and variability in stable isotopes (e.g., feeding patterns) across individuals that may be feeding on different food items in different regions. Also, this allowed us to compare variability on the same scale and avoid direct comparisons of absolute values that may be influenced by the known Suess effect (Young et al., 2013). Furthermore, the time stamp attribution allowed us to assign each section of baleen to a date for comparison with climate anomalies. However, this assumed that baleen growth rate is linear and that all baleen plates were collected in a similar manner (e.g., including the unerupted section within the gum) for accurate time attribution. We acknowledge the R^2 values within this study are low, however, we suggest that the nature of our data, being patchy between years (from different stranding dates), as well as our limited sample size may result in weakening potential relationships. Data from more adult individuals to fill these sampling gaps may assist in establishing stronger trends.

This is the first step in defining what links exist between isotopic signatures in baleen and climate, however, more research is needed to understand how these links are impacted by baseline changes as well as the whale's reproductive state, condition and fasting behaviour. There is large intraspecific and intra-individual variation in oscillation cycles lengths (which are assumed to be annual), however, the data was not at hand to examine this here. Therefore, our next step will be addressing this variation seen in cycle lengths in terms of environmental and/or physiological drivers. Future work on how isotopic baselines shift with large-scale climate cycles on an interannual scale would be beneficial to understand what long-term isotopic values are responding to in marine predators.

CONCLUSION

We show that a relationship exists between the nitrogen and carbon stable isotope values in whale baleen and changes in climate cycles. In addition, we show that these relationships differ depending on the whale's feeding location within the Southern Ocean. We propose this variability in isotope values may reflect changes in resource availability driven by these climate cycles (regardless of which ocean sector they reside in), however, further research is needed to understand how a whale's physiology, reproductive state, and changes in the isotopic baseline may contribute to these relationships. This research contributes to our understanding and interpretation of complicated stable isotope oscillation patterns along baleen plates of whales. Understanding long-term patterns will become extremely important within a changing climate, considering how the frequency and intensity of climate cycles are predicted to change. However, given the complexity of interpreting bulk stable isotopes across multiple isoscapes, particularly within rapidly changing environments, challenges remain in defining links between isotope signatures in whale baleen and climate/environmental cycles. Considering the temporal and spatial variability across the Southern Ocean in terms of climate cycles and resulting resource availability, we recommend future research focus on multiple species across different ocean sectors to understand broad scale responses to environmental change.

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 and approval was not required for the animal study because ethics for this study was not required, as data was sourced from available online literature or specimens for analysis provided on loan to us from the Australian Museum.

AUTHOR CONTRIBUTIONS

AD and TR conceived the ideas, designed the project, and interpreted the results and their significance. AD extracted data, conducted lab work and isotopic analysis, and statistical analysis. Both authors contributed critically to the drafts and gave final approval for publication.

FUNDING

This work was funded to TR from Scott Foundation under grant RG161708.

ACKNOWLEDGMENTS

We would like to thank Gary Truong for his assistance with coding for this project, particularly for the time stamp attribution. We would also like the thank Junlin Lyra Huang for her advice and assistance with aspects of coding. We thank the mammal lab at UNSW, in particular Anna Lewis for providing comments on draft manuscripts. We would like to thank Leanne and Lewis at the Bioanalytical Mass Spectrometry Facility at UNSW for their assistance in running a small number of samples for this study. We also thank the Australian Museum, in particular Sandy Ingleby (Collection Manager, Mammalogy) for the loan and access of opportunistic baleen for this research. We thank NSW National Parks and Wildlife Service staff in assisting with baleen collection on site at Newcastle. We also thank Tracey Saxby and Jamie Testa (Integration and Application Network) for the use of whale images on figures as referenced within figure captions.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.832075/full#supplementary-material

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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 | Frontiers in Marine Science

ORIGINAL RESEARCH
published: 19 April 2022
doi: 10.3389/fmars.2022.867258

Range-Wide Comparison of Gray Whale Body Condition Reveals Contrasting Sub-Population Health Characteristics and Vulnerability to Environmental Change

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

Received: *31 January 2022*
Accepted: *21 March 2022*
Published: *19 April 2022*

Citation:
Torres LG, Bird CN, Rodríguez-González F, Christiansen F, Bejder L, Lemos L, Urban R J, Swartz S, Willoughby A, Hewitt J and Bierlich KC (2022) Range-Wide Comparison of Gray Whale Body Condition Reveals Contrasting Sub-Population Health Characteristics and Vulnerability to Environmental Change. Front. Mar. Sci. 9:867258. doi: 10.3389/fmars.2022.867258

Climate change is a global phenomenon, yet impacts on resource availability to predators may be spatially and temporally diverse and asynchronous. As capital breeders, whales are dependent on dense, predictable prey resources during foraging seasons. An Unusual Mortality Event (UME) of Eastern North Pacific (ENP) gray whales (*Eschrichtius robustus*) was declared in 2019 due to a dramatic rise in stranded animals, many emaciated. Climate change impacts may have affected prey availability on the primary foraging grounds of ENP gray whales (~20,000 individuals) in the Arctic and sub-Arctic region and in coastal habitats between northern California, USA and British Columbia, Canada where a small sub-group of ENP whales called the Pacific Coast Feeding Group (PCFG; ~230 individuals) forages. To investigate variability of gray whale body condition relative to changing ocean conditions, we compare two datasets of gray whale aerial photogrammetry images collected *via* Unoccupied Aircraft Systems (UAS) on the ENP wintering grounds in San Ignacio Lagoon, Mexico (SIL; n=111) and on the PCFG feeding grounds in Oregon, USA (n=72) over the same three-year period (2017–2019). We document concurrent body condition improvement of PCFG whales in Oregon while body condition of whales in SIL declined. This result indicates that the UME may have affected ENP whales due to reduced energetic gain on some Arctic/sub-Arctic foraging grounds, while PCFG whales are recovering from poor prey conditions during the NE Pacific marine heatwave event of 2014–2016. Surprisingly, we found that PCFG whales in Oregon had significantly worse body condition than whales in SIL, even when accounting for year and phenology. We derive support for this unexpected finding *via* photogrammetry analysis of opportunistic aerial images of gray whales on Arctic foraging grounds (n=18) compared to PCFG whales in Oregon (n=30): the body condition of PCFG whales was significantly lower (t=2.96, p=0.005), which may cause PCFG whales to have reduced reproductive capacity or resilience to environmental perturbations compared to ENP whales. Overall, our study elucidates divergent gray whale body condition across sub-groups and time, and we demonstrate the value of UAS to effectively monitor and identify the physiological response of whales to climate change.

Keywords: body condition, drones/UAS, ecosystem variability, photogrammetry, population health, prey availability, uncertainty, whales

INTRODUCTION

A major avenue of climate change impacts on biodiversity is disruptions to availability and predictability of prey resources (Hamilton et al., 2017; Bastille-Rousseau et al., 2018), making the monitoring and metrics of body condition (relative energy reserves) a valuable tool to assess population response and resiliency to climate variability (Jirinec et al., 2021). As capital breeders, whales are particularly vulnerable to changes in prey resource patterns as their phenology requires efficient foraging periods to rapidly gain energetic stores to support reproduction and basal metabolic demands (Jönsson, 1997; Stephens et al., 2014). Declines in availability of crucial prey can lead to reduced body condition within a year (Braithwaite et al., 2015), and potentially reduced reproductive output and eventual death following some threshold of multiple years of low prey (Williams et al., 2013).

Yet, the impacts of climate warming on ecosystem variability are not uniform across space and time, particularly in the marine environment where multiple dynamic forces can delay, compound, disperse, or amplify (Lenoir et al., 2020). If a hypothetical whale population relies on a single foraging ground, individuals in the population should generally display similar body condition responses (excluding the potential influence of demographic unit and individual foraging specializations). However, if the population disperses to multiple foraging grounds and display flexible prey selection, then individuals will likely show variable body condition responses to climate driven ecosystem changes. Therefore, monitoring body condition of whales can inform how different segments of a population respond to climate variation over space and time, revealing non-uniform impacts of climate change.

Over the past decade, the advent and proliferation of Unoccupied Aircraft Systems (UAS) has enabled the safe, rapid, and non-invasive collection of high-resolution photogrammetry datasets to quantify and describe the body condition for multiple species of free-living whales (Johnston, 2019). These data have illustrated seasonal changes across individuals in a population (Christiansen et al., 2016; Durban et al., 2016; Lemos et al., 2020), maternal costs (Christiansen et al., 2018), interannual variability (Lemos et al., 2020; Christiansen et al., 2021), and differences between populations (Christiansen et al., 2020). However, cross population (and cross research lab) comparisons using UAS-based photogrammetry data are rare due to non-standardization of methods and UAS equipment across labs that leads to a lack of interoperability. Yet, methods recently developed by Bierlich et al. (2021b) account for these differences by quantifying uncertainty in photogrammetric measurements, which allows unification and cross-comparison of datasets. Furthermore, we apply the Body Area Index (BAI; Burnett et al., 2018), which has high precision with low uncertainty (Bierlich et al., 2021a), to compare whale body condition.

Application of UAS technology in cetacean studies is flourishing, making cross dataset comparisons a highly feasible and valuable method to identify differences between populations, sub-groups, and life-history stages, and to describe potential drivers of whale body condition variability. During overlapping years (2017 to 2019) separate research programs used UAS to monitor the body condition of gray whales (*Eschrichtius robustus*) feeding in coastal waters of Oregon, USA during summer and fall months, and on their wintering grounds in San Ignacio Lagoon (SIL) on the west coast of the Baja California Peninsula, Mexico. During this period, an Unusual Mortality Event (UME) of gray whales was declared in January 2019 due to elevated numbers of stranded gray whales along the Pacific coast from northern Mexico through the Arctic region of Alaska, USA. Dead whales were frequently in emaciated body condition, indicating that reduced energetic gain could be a causal factor of death, either due to reduced foraging success, increased energy expenditure, or disease (Christiansen et al., 2021). We utilize these two photogrammetry datasets in a comparative analysis to (1) assess temporal patterns of gray whale body condition between feeding and wintering grounds within the context of variable ocean conditions that controlled prey availability leading up to the UME period, and (2) investigate potential sub-population differences in body condition.

The population size of the gray whales in the North Pacific has undergone significant variation over the past two centuries. Pre-whaling estimates of population size exceed 60,000 individuals (Alter et al., 2007), with a dramatic decline to less than 4,000 individuals by 1900 (Butterworth et al., 2002; Swartz et al., 2006). Through international protection, the Eastern North Pacific (ENP) population has recovered, to a peak of 26,916

(CV = 0.058) in 1987 (Laake et al., 2012). The abundance of the ENP population has continued to fluctuate, including undergoing two UMEs that reduced the population size significantly: After the 1999–2000 UME, the population reduced from 21,135 (CV = 0.068) in 1997 to 16,033 in 2001 (CV = 0.069) (Laake et al., 2012), and during the current 2019-Present UME the population has dropped from 26,960 (95% CI = 24,420–29,830) in 2016 to 20,580 (95% CI = 18,700–22,870) in 2020 (Stewart and Weller, 2021). This variation in abundance implies that gray whales are susceptible to variation in ocean conditions, resource availability, and other impacts, yet are capable of population rebound when conditions are favorable.

The majority of ENP whales migrate annually to foraging grounds in Alaska, targeting benthic amphipods as prey (Moore et al., 2003; Brower et al., 2017). However, a sub-group of 232 (SE = 25.2) ENP gray whales called the Pacific Coast Feeding Group (PCFG) truncates their migration about halfway up the Pacific west coast and forages in coastal habitats between northern California, USA and British Columbia, Canada, including Oregon (Calambokidis et al., 2019). The PCFG has been studied through photo-identification methods since 1980, indicating high residency, site-fidelity, and calf recruitment (Darling et al., 1998; Calambokidis and Pérez, 2017b; Calambokidis et al., 2019). The drivers for the existence of this PCFG sub-group remain unclear, yet caloric analysis of prey items indicates that prey in the PCFG range is of equal or higher value than the main amphipod prey (*Ampelisca macrocephala*) in the Arctic and sub-Arctic, leading to the hypothesis that greater prey density and/or lower energetic costs of foraging in the Arctic and sub-Arctic may explain the greater number of whales foraging in that region (Hildebrand et al., 2021). Furthermore, although gray whales from both the ENP and PCFG migrate to wintering grounds in the Baja California Peninsula (Rice and Wolman, 1971), the population connectivity between the two groups remains unclear, with mitochondrial DNA comparison showing low genetic exchange between sub-groups and microsatellite markers showing no evidence of reproductive isolation (Frasier et al., 2011; Lang et al., 2014). Gray whales on the wintering grounds in SIL are predominantly from the relatively abundant ENP, yet individuals from the PCFG and the Western North Pacific (WNP) gray whale population also occur in SIL during the winter months (Weller et al., 2012; Mate et al., 2015; Calambokidis and Pérez, 2017a; Urbán et al., 2019). The WNP is an endangered population (2019 abundance estimate = 231 non-calves; Cooke et al., 2019) that forage in far east Russia during summer months with some portion of the population migrating to the Baja California Peninsula lagoons (~20%–55%; Cooke et al., 2019).

Previous analysis of the UAS photogrammetry dataset of PCFG gray whales in Oregon waters demonstrated increasing body condition through the foraging season, variation in body condition by demographic unit, and interannual variation in body condition that was hypothesized to be linked with carryover effects of local oceanographic conditions one year prior (Lemos et al., 2020). A marine heat wave known as "The Blob" affected the oceanography, productivity, and biodiversity in the Pacific northwest from 2014 through 2016 (Peterson et al., 2017; Fewings and Brown, 2019), and may have also impacted PCFG gray whale foraging efficiency (Lemos et al., 2020). Furthermore, the body condition of PCFG gray whales determined by lateral photographs captured between 1996 and 2013 showed an increase across the foraging season, and interannual variation had a significant negative correlation with the Pacific Decadal Oscillation (running average of the two prior years; Akmajian et al., 2021).

The UAS photogrammetry dataset of gray whales on their wintering grounds in SIL has also been analyzed previously, indicating decreasing body condition from 2017 to 2020, which aligns with the onset and duration of the UME (Christiansen et al., 2021). While gray whales from the ENP, PCFG, and WNP all occur on SIL wintering grounds, ENP whales likely dominate the UAS photogrammetry dataset collected in SIL based on their considerably higher population abundance. Therefore, we assume that the SIL dataset reflects the body condition of ENP gray whales that feed in Arctic and sub-Arctic foraging grounds, including Kodiak Island in the Gulf of Alaska, along the Aleutian Chain, in the Chirikov Basin, and the northern Bering and Chukchi seas (Braham et al., 1984; Moore et al., 2003; Coyle et al., 2007; Moore et al., 2007; Brower et al., 2017). Climate change in the Arctic and sub-Arctic regions has impacted the biological oceanography and productivity across the region (Overland et al., 2019; Huntington et al., 2020; Lewis et al., 2020), and while the density of amphipod prey of gray whales has declined in the Chirikov Basin and Northern Bering Sea since the late 1980s (Highsmith and Coyle, 1992; Moore et al., 2003), changes in prey availability on other foraging grounds have not been documented (Grebmeier et al., 2015).

Since climate variability and subsequent impacts on gray whale prey availability may manifest at different rates and spatio-temporal scales across Arctic, sub-Arctic, and Pacific northwest foraging grounds, we compare the body condition of gray whales on their PCFG feeding grounds in Oregon and ENP wintering grounds in SIL using UAS-based photogrammetry to elucidate sub-population physiological response to variable environmental forces on different foraging grounds. We test the following hypotheses: (H_1) The body condition of gray whales on Oregon feeding and SIL wintering grounds is the same when compared at similar phenological time points: End of summer feeding seasons (departure Oregon vs. arrival SIL); End of wintering season (arrival Oregon vs. departure SIL). (H_2) If similar environmental conditions regulate prey availability in Arctic, sub-Arctic, and Oregon feeding grounds - allowing gray whales equivalent access to energetic gain - we expect the same trajectory of body condition change across years in Oregon and SIL. Gray whale oxygen consumption rates (Sumich, 1983) and derived metabolic rates (Villegas-Amtmann et al., 2017) are much lower during migration than on foraging grounds; thus we assume that gray whales incur low energetic cost during migration. We also analyze an opportunistic dataset of aerial images of gray whales foraging in the Northeastern Chukchi Sea (NCS) of the Arctic region collected from a survey plane to compare body condition across foraging grounds (NCS vs.

Oregon). Overall, our study compiles aerial image data collected by three different research programs using five different platforms (four UAS, one plane). Through robust assessment of uncertainty, we utilize this collaborative dataset to cross compare gray whale body condition at multiple phenological time steps on foraging and wintering grounds to inform population response to environmental change.

MATERIALS AND METHODS

To reduce body condition variation due to demographic unit, our analysis is limited to adult whales only, not including lactating and pregnant females determined by the presence of a calf at the sighting or in the next year respectively, although undetected pregnancies (e.g., lost calf) were possible. Additionally, the photogrammetry datasets from Oregon and SIL are limited to the beginning and end of season periods to enhance detection of body condition change between periods. For each UAS image of a gray whale, we incorporate photogrammetric uncertainty to account for error in altitude recorded using an on-board barometer or laser altimeter (Bierlich et al., 2021b). An opportunistic dataset of 18 aerial images of gray whales foraging in the Arctic collected from a survey plane is also analyzed in this study to support conclusions and direct future research efforts. We calculate the Body Area Index (BAI) for each imaged whale as the comparative metric of overall body condition. BAI is a unitless and scale-invariant metric that accounts for whale length, allowing direct comparison of body condition across all individuals (Burnett et al., 2018), and demonstrated to have high precision with low uncertainty (Bierlich et al., 2021a).

Primary Analysis

Data Collection

Oregon:

We recorded videos of gray whales off the coast of Newport (44° 38′13″ N, 124°03′08″ W) and Port Orford (42°44′59″ N, 124°29′ 53″ W), Oregon, USA during the 2017–2019 foraging seasons (June–October) using three UAS quadcopters: DJI Phantom 3 Pro (P3Pro), DJI Phantom 4 (P4), and DJI Phantom 4 Pro (P4Pro) (**Figure 1**). The cameras on both the P3Pro and P4 had a 6.16 x 4.6 mm sensor, 3840 x 2160 pixel-resolution, and a 3.61 mm focal length lens. The camera on the P4Pro had a 13.2 x 8.8 mm sensor, 3840 x 2160-pixel resolution, and 8.8 mm focal length lens. The P3Pro and P4 were both flown in 2017 and the P4Pro was flown in 2017, 2018, and 2019. Each aircraft had an onboard barometer for recording altitude and the launch height of the drone (measured as the surface of the water to the camera lens) was later added to the recorded barometer to account for bias introduced from the barometer zeroed at the launch point (Bierlich et al., 2021b). We conducted boat-based UAS flights as described in Burnett et al. (2018). Videos were collected at altitudes between 20 and 36 m of whales as they surfaced to breathe.

Although PCFG whales have high site fidelity to this foraging range, individuals also show variability of where they feed within and between years (Calambokidis et al., 2019; Lagerquist et al., 2019). We assume the body condition of whales imaged off Oregon reflect the prey availability across the whole PCFG range, not just conditions in Oregon. To confirm the representativeness of our sampled whales to reflect conditions in this range, rather than vagrant whales migrating through, we calculate the sighting histories of the imaged whales to describe their foraging site fidelity to our study system.

SIL:

We recorded videos of gray whales inside San Ignacio Lagoon, Baja California Sur, Mexico during the 2017–2019 breeding seasons (January–April) using a DJI Inspire 1 Pro (I1Pro) quadcopter (**Figure 1**). The I1Pro was fitted with a Zenmuse X5 camera with a Micro Four Thirds (17.3 x 13 mm) sensor, 3840 x 2160-pixel resolution, a 25 mm focal length lens, and a Lightware SF11/C laser altimeter for recording altitude. We conducted shore- and boat-based UAS flights following Christiansen et al. (2021). Videos were collected of whales at altitudes between 22 and 49 m as they surfaced to breathe.

Data Processing

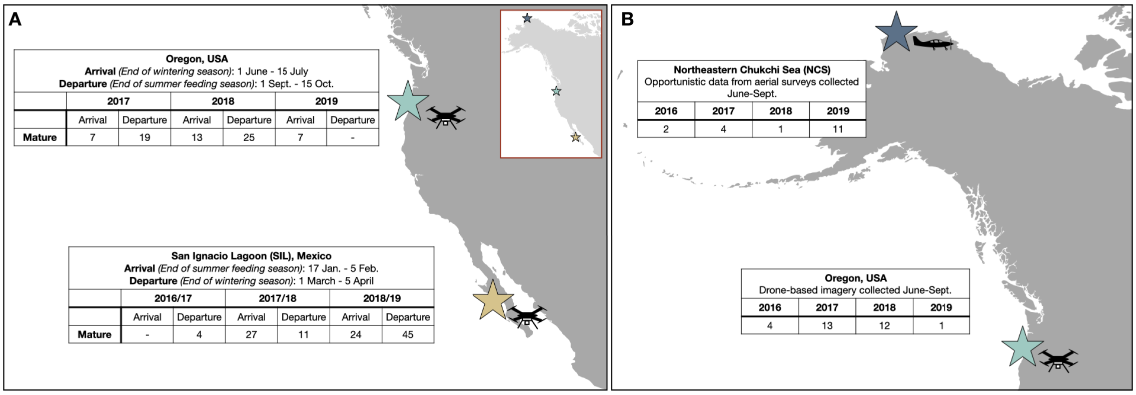
Image Filtering:

To avoid individual replicates within phenology group and site, individual whales were identified by assessing unique skin pigmentation and markings visible from the UAS and photo-identification images of the left-hand side, right-hand side, and fluke. Snapshots of each individual were taken from the UAS videos using VLC Media player software (version 3.0.16; VideoLAN, Paris, France). Each snapshot was ranked and filtered for quality in measurability based on body posture and image clarity and contrast following Christiansen et al. (2018).

Morphometric calculations and uncertainty:

We measured the total body length (TL) from rostrum to fluke notch and perpendicular widths at 5% increments of the TL in pixels using MorphoMetriX open-source photogrammetry software (Torres and Bierlich, 2020) for whales from Oregon (**Figure 2A**) and using a custom R script (Christiansen et al., 2016) for whales from SIL. To confirm measurements from the two software were comparable, we calculated the coefficient of variation for a subsample of 15 whales measured by a single analyst in both software. Results showed a mean CV% = 1.31% (sd = 1.09, min = 0.15, max = 3.67), indicating that the two software produce comparable measurements.

Bierlich et al. (2021b) demonstrate that photogrammetric uncertainty varies depending on the camera, focal length lens, altimeter, and altitude of the UAS, highlighting the necessity of evaluating uncertainty in assessments of whale body condition *via* UAS imagery. Bierlich et al. (2021b) developed a Bayesian statistical model to quantify and incorporate uncertainty by using measurements of known-sized objects at various altitudes as training data to predict the length measurements of unknown sized whales. These Bayesian statistical model outputs of measurement uncertainty for whale TL and width



Oregon, USA
Arrival *(End of wintering season)*: 1 June - 15 July
Departure *(End of summer feeding season)*: 1 Sept. - 15 Oct.

	2017		**2018**		**2019**	
	Arrival	Departure	Arrival	Departure	Arrival	Departure
Mature	7	19	13	25	7	-

San Ignacio Lagoon (SIL), Mexico
Arrival *(End of summer feeding season)*: 17 Jan. - 5 Feb.
Departure *(End of wintering season)*: 1 March - 5 April

	2016/17		**2017/18**		**2018/19**	
	Arrival	Departure	Arrival	Departure	Arrival	Departure
Mature	-	4	27	11	24	45

Northeastern Chukchi Sea (NCS)
Opportunistic data from aerial surveys collected June-Sept.

2016	**2017**	**2018**	**2019**
2	4	1	11

Oregon, USA
Drone-based imagery collected June-Sept.

2016	**2017**	**2018**	**2019**
4	13	12	1

FIGURE 1 | Maps illustrating the sample sites, sample sizes, and time periods of the datasets. **(A)** Dataset used for the primary analysis based on drone-based data collected off of Oregon, USA and San Ignacio Lagoon, Baja California Sur, Mexico (SIL). The tables provide sample size of images analyzed per period and sub-group. **(B)** Opportunistic dataset of images collected during aerial surveys in the Arctic (Northeastern Chukchi Sea; NCS) and a subset of drone-based images collected during the same years and months off the Oregon coast, USA. The inset in **(A)** illustrates the locations of all three sites.

measurements can then be incorporated into estimations of whale body condition, including BAI (Bierlich et al., 2021a; **Figure 2**). Therefore, we account for measurement uncertainty associated with each UAS used in this study by applying the Bayesian statistical model described in Bierlich et al. (2021b). For the P3Pro, P4, and P4Pro, images of a known-sized board (1.0 m) floating at the surface collected at altitudes between 20–36 m were used as training data. For the IP1Pro, we used

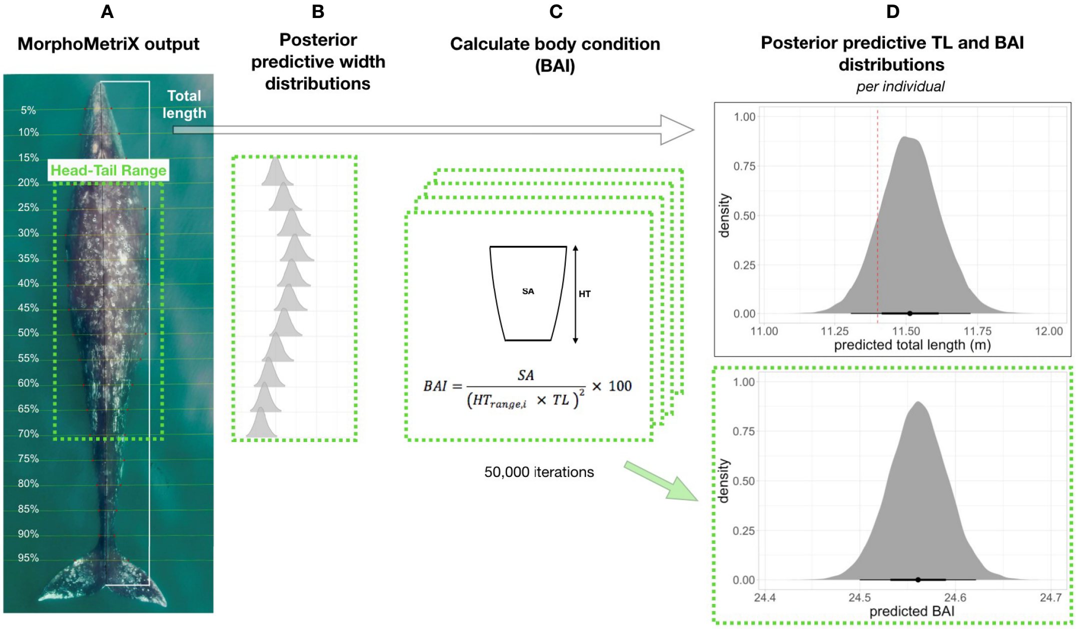


FIGURE 2 | Overview of Bayesian framework for calculating the body condition of gray whales. **(A)** An example of a MorphoMetriX output (Torres and Bierlich, 2020) from a UAS image of a gray whale. Total length (TL) measured from rostrum to fluke notch with perpendicular widths segmented in 5% increments of TL. Head-Tail Range (20–70%) represents the region of the body used to calculate body condition, which excludes the fins, head, and tail. **(B)** Posterior predictive distributions for each 5% width included in the Head-Tail Range that is used to calculate body condition. **(C)** Body condition is calculated as Body Area Index (BAI) for each iteration in the Markov Chain Monte Carlo output of each posterior predictive width distribution using CollatriX (Bird and Bierlich, 2020). **(D)** Posterior predictive distributions for TL and BAI for a single individual. On the x-axis, the longer thin black bars represent the 95% highest posterior density (HPD) interval, the thicker shorter black bars represent the 65% HPD interval, and the black dot represents the mean value. The red dashed line represents the maturity cutoff length (11.4 m).

measurements of a known sized mat (1.45 m) on land flown between 4–120 m altitude (from Christiansen et al., 2018). We measured widths between a Head-Tail Range of 20–70% of each whale's TL following Bierlich et al. (2021a) to then calculate body condition using BAI (Burnett et al., 2018; **Figure 2**). Rather than a single point estimate, the model quantifies uncertainty in TL, width measurements, and BAI for each individual whale through the model's posterior distribution. We summarize uncertainty using 95% highest posterior density (HPD) intervals (**Figure 2**). Model development was conducted in R (Version 4.0.2; R Development Core Team, 2020) as described in Bierlich et al. (2021a; 2021b). To compare measurement uncertainty amongst each UAS, we calculated the coefficient of variation (CV%) for each individual's posterior predictive distribution for TL and BAI. The CV% compares the relative width of an individual's posterior predictive distribution, with a lower CV % translating to a more precise predicted measure (Bierlich et al., 2021a).

Maturity and Reproductive Status:
Maturity was assigned using either minimum age estimated from the individual's date of first sighting or a TL cutoff when sighting history data was insufficient or unavailable. Age estimates derived from sighting history data were available for a subset of the Oregon dataset and unavailable for the SIL dataset. Individuals were assumed to be mature if they had a minimum age of at least eight years (Rice and Wolman, 1971). Whales were assumed to be immature if they were originally sighted as a calf, meaning that they were of known age, and were younger than eight years old. Individuals not seen as calves with minimum ages under eight years were considered to be of an unknown age; maturity was subsequently assigned to these individuals using a TL cutoff. It was assumed that (1) calves were small whales (<8 m) closely associated with large whales (>11 m) who were assumed to be the mother and mature, lactating females, (2) lactating females become post-weaning females once they are no longer associated with their calves in that year, and (3) lactating females were pregnant the previous year. When maturity was assigned using TL, individuals were considered mature if at least 50% of their posterior predictive distribution for TL was above a cutoff of 11.4 m (Rice and Wolman, 1971; Bierlich et al., 2021b; **Figure 2**).

Statistical Analysis

The temporal phases of gray whale phenology were grouped as follows (**Figure 1A**): "Departure Oregon" whales were imaged between 1 September and 15 October, and "Arrival SIL" whales were imaged between 17 January and 5 February, forming the *End of summer feeding season* group. "Departure SIL" whales were imaged between 1 March and 5 April, and "Arrival Oregon" whales were imaged between 1 June and 15 July, forming the *End of wintering season* group. Longer sampling windows were used in Oregon (6 weeks) than in SIL (3–4 weeks) to increase sample size.

This analysis included only mature adults, excluding pregnant, lactating, and post weaning females, that were imaged on foraging or wintering grounds. A Monte Carlo analysis of ANOVA tests was used to account for uncertainty associated with BAI measurements. We apply a unified model to test both hypotheses since BAI is potentially impacted by site, phenological time point, and year. We assume each BAI measurement without uncertainty has a mean specified with a full interactions model via

$$\mathrm{BAI}_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk} + \epsilon_{ijkl},$$

with μ quantifying a baseline BAI value, α_i quantifying the mean-shift attributable to site (i = 1 for Oregon, and 2 for SIL); β_j quantifying the mean-shift attributable to phenological timepoint (j = 1 for End of Winter, and 2 for End of Summer); γ_k quantifying the mean-shift attributable to year (k = 1 for 2017, 2 for 2018, and 3 for 2019); $\alpha\beta_{ij}$, $\alpha\gamma_{ik}$, and $\beta\gamma_{jk}$ quantifying the mean-shifts attributable to the pairwise interactions between site and phenology, site and year, and phenology and year, respectively; $\alpha\beta\gamma_{ijk}$ quantifying the three-way interaction between all terms; and ϵ_{ijkl} quantifying individual variation. The term ϵ_{ijkl} is modeled as a mean zero normal random variable, with a common variance parameter across all groups (to be estimated). The model treats the observation year as a categorical predictor because the study is not long enough to identify consistent, long-term relationships across time; this modeling decision also allows us to model the data without assuming BAI follows a linear trend across years.

Monte Carlo methods allow us to account for the uncertainty in BAI observations by averaging the results of 10,000 replications of our ANOVA analyses. Each replicate uses a dataset in which the BAI measurement for each whale is sampled from the photogrammetric model's posterior distributions, which are approximately normally distributed. For each ANOVA replicate, we sample each whale's BAI measurement from a normal distribution parameterized with the photogrammetric model's posterior mean and variance for that whale's BAI value.

To test H_1 for each replicate dataset, a generalized linear hypothesis test is employed. The test's null hypothesis is that mean BAI between OR and SIL is the same within phenological time steps between years—i.e., that $E(\mathrm{BAI}_{11kl}) = E(\mathrm{BAI}_{21kl})$ for k=1,2,3, and $E(\mathrm{BAI}_{12kl}) = E(\mathrm{BAI}_{22kl})$ for k=1,2. The null hypothesis does not assess $E(\mathrm{BAI}_{12kl}) = E(\mathrm{BAI}_{22kl})$ for k=3 because SIL data are not available for the End of Summer phenology time point in 2019. To test H_2 for each replicate dataset, a nested ANOVA F-test is employed. The test's null hypothesis is that the mean BAI between OR and SIL experience the same changes across time—i.e., that all interaction effects between site and observation year are zero, $\alpha\gamma_{ik} = 0$ and $\alpha\beta\gamma_{ijk} = 0$ for i,j=1,2, and k=1,2,3. The average p-values from the replicated tests serve as the overall, Monte Carlo p-values used to evaluate H_1 and H_2. Analyses were conducted in R (R Development Core Team, 2020).

Opportunistic Analysis

Data Collection

The Aerial Surveys of Arctic Marine Mammals (ASAMM) project obtained aerial images of gray whales encountered during line-transect surveys in the Northeastern Chukchi Sea (NCS; 67°–72°N, 157°–169°W) in June–October, from 2016 to 2019 (Clarke et al., 2020; **Figure 1B**). Images were obtained using a Canon 1DX or 7D DSLR camera with a 100–400 mm zoom lens. While circling whales in the plane at ~40° bank, an observer used an open window located on the port side of the aircraft to obtain images at a nearly nadir angle (~90° below; see **Supplementary Material** for details). A stratified-random sample of gray whale UAS images in Oregon waters (n = 30) during the same years and months as the collected NCS images were selected for body condition comparison.

Post Processing

Image Filtering

NCS images were rated based on the body regions visible, the angle of the whale's body relative to the aircraft, and the overall image quality (Full description of methods in **Supplemental Material**). Only high-quality images taken near nadir where the full body of the whale was visible and flat at the surface were selected. Images from Oregon were filtered following the protocol described in the *Primary analysis* above in the *Data processing* subsection *Image filtering*.

Morphometric Calculations

Images from both the NCS and Oregon were measured by a single analyst following the protocol described in the *Morphometric calculations and uncertainty* subsection in *Primary analysis*. There was no altitude information for images collected in the Arctic, therefore we were unable to incorporate uncertainty and BAI was calculated from raw pixel count measurements using the CollatriX body condition function (Bird and Bierlich, 2020). BAI measurements are usable and comparable because BAI is a standardized length invariant metric that can be equally calculated and interpreted using raw pixel counts as metric units (Burnett et al., 2018; Lemos et al., 2020; Bierlich et al., 2021a).

Statistical Analysis

Images collected between June and September of 2016–2019 in the NCS and Oregon waters were used for this analysis (**Figure 1B**). A Welch's t-test was used to compare BAI between sites. Analyses were conducted in R (R Development Core Team, 2020).

RESULTS

Across the three years of this study, images of 183 mature gray whales captured in Oregon and SIL were included in the analysis (**Figure 1**). Of the 71 whales imaged in Oregon water during the Arrival and Departure periods, 64 whales (90%) were observed on other days and years (between 2016 and 2021) in our study region, indicating residency by these whales to the PCFG foraging grounds.

Measurement uncertainty, measured as the coefficient of variation (CV%), varied among each UAS aircraft for TL and BAI. The I1Pro had the least amount of uncertainty associated with TL measurements (CV%: mean = 2.42, sd = 0.27, min = 1.56%, max = 3.23%) followed by the P4Pro (CV%: mean = 10.10, sd = 1.83% min = 6.96, max = 14.22%) and the P3Pro and P4 (CV%: mean = 11.93%, sd = 1.08%, min = 10.09%, max = 13.55%). The same trend followed for uncertainty associated with BAI, with I1Pro having the least uncertainty (CV%: mean = 0.12%, sd = 0.01%, min = 0.08%, max = 0.18%), followed by the P4Pro (CV%: mean = 0.91%, sd = 0.46%, min = 0.39%, max = 1.88%), and the P4 and P3Pro (CV%: mean = 2.97%, sd = 0.40%, min = 2.66%, max = 3.86%).

Assessment of predicted gray whale BAI values by site and phenological time point illustrates the expected trend that whales are in better body condition at the end of the summer foraging season compared to the end of the wintering season (**Figure 3**). The generalized linear hypothesis test compared the BAI of gray whales in Oregon and SIL within phenological time points across observation years and found significant evidence to reject an assumption that H_1 is true, which expected similar body condition of gray whales imaged in Oregon and SIL when compared at the same phenological time points ($p = 1e^{-6}$). Simultaneous Monte Carlo confidence intervals associated with H_1 reveal that mean BAI for SIL whales tends to be higher than mean BAI for Oregon whales (**Figure 4**). Furthermore, the BAI of PCFG gray whales in Oregon (n = 30) was significantly lower (Welch's t-test, t(39) = 2.96, p = 0.005; **Figure 5**) than gray whales imaged while feeding in the NCS region of the Arctic (n = 18), providing more evidence of an intrinsic difference in body condition between PCFG gray whales foraging in Oregon and ENP whales foraging in the Arctic and sub-Arctic. This result also supports our assumption that the majority of gray whales imaged in SIL are from the ENP, and does not reflect the body condition of PCFG whales.

The nested ANOVA test for H_2 assessed differences in the BAI trajectories between sites across years, finding significant evidence to reject an assumption that H_2 is true ($p = 1e^{-3}$). Monte Carlo confidence intervals associated with H_2 suggest the BAI of gray whales at departure from SIL decreased over time, while the BAI of whales departing from Oregon increased over time (**Figure 6**). Rejecting H_2 indicates that environmental conditions that influence prey availability on Oregon and Arctic or sub-Arctic foraging grounds are different, causing different trajectories of body condition change across the study years.

DISCUSSION

Through a comparative analysis of gray whale body condition at multiple temporal periods during different phenology stages we document contrasting trends and ranges of body condition. Gray whale body condition on the wintering grounds in SIL deteriorated across the study years (2017–2019), while the body condition of PCFG gray whales on the foraging grounds off Oregon concurrently increased. These juxtaposing trajectories of body condition between the ENP and PCFG suggests use of distinct foraging grounds with different prey availability, likely

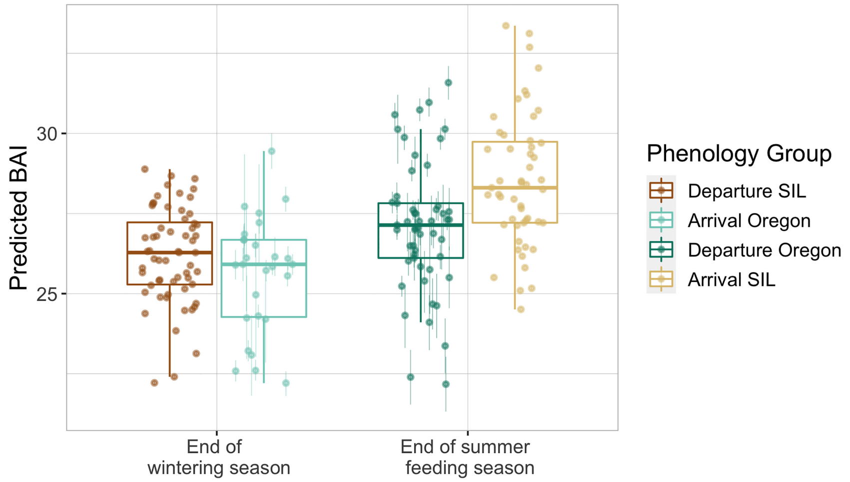


FIGURE 3 | Boxplots illustrating the distribution of predicted Body Area Index (BAI) values of gray whales imaged by UAS in San Ignacio Lagoon (SIL), Mexico and Oregon, USA as produced by the Bayesian statistical model accounting for measurement uncertainty. Data are grouped by phenology group: End of summer feeding season (departure Oregon vs. arrival SIL) and End of wintering season (arrival Oregon vs. departure SIL). The group median (horizontal line), interquartile range (IQR, box), maximum and minimum 1.5*IQR (vertical lines), and outliers (dots) are depicted in the boxplots. The overlaid points represent the mean of the posterior predictive distribution for BAI of an individual and the bars represent the upper and lower bounds of the 95% HPD interval.

driven by variable oceanographic patterns in the Arctic/sub-Arctic region and PCFG range. Additionally, we document significantly lower overall body condition of PCFG whales feeding in Oregon coastal waters compared to whales imaged in SIL or the NCS region of the Arctic. This lower body condition of PCFG whales may cause reduced resilience to perturbations in prey quality or availability relative to ENP whales, and could have implications for the reproductive capacity of the PCFG sub-group.

The decreasing body condition of gray whales imaged in SIL reflects declining nutritive gain by the ENP population, which may be associated with environmental change in the Arctic and sub-Arctic regions that impacted the predictability and availability of gray whale prey. In contrast, the increasing body condition of PCFG gray whales imaged in Oregon may reflect recovery of these whales from a period of low prey resource availability in the PCFG foraging range as the ecosystem rebounded from the marine heatwave event of 2014–2016 known as “The Blob” (Peterson et al., 2017; Fewings and Brown, 2019). While global climate change drives environmental change in both regions, our results demonstrate that dynamic oceanographic processes cause temporal variability of resource availability to gray whales in geographically distinct regions. Although the deteriorating body condition of whales in

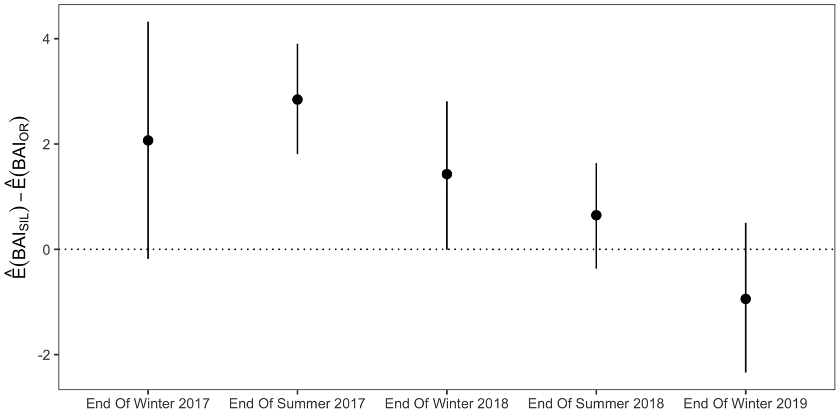


FIGURE 4 | Simultaneous Monte Carlo confidence intervals produced by the generalized linear hypothesis test of H_1 illustrating estimated differences between mean Body Area Index (BAI) by site (SIL – OR) within phenology groups. Points represent the mean estimated difference and vertical lines represent simultaneous Monte Carlo confidence intervals.

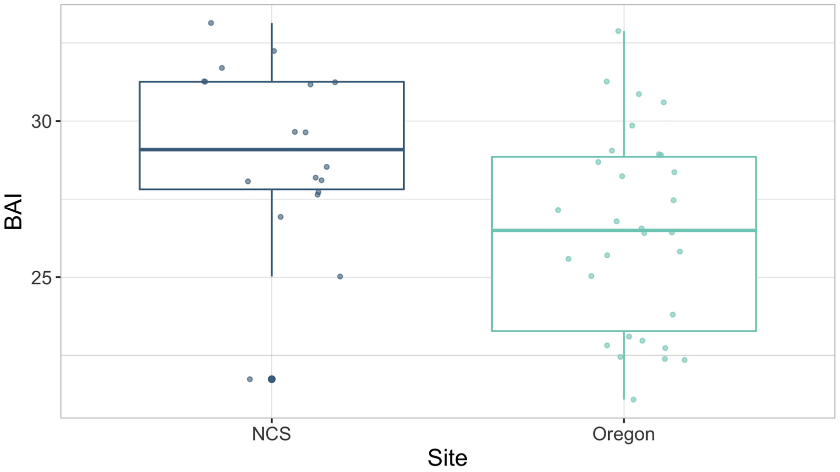


FIGURE 5 | Boxplots illustrating the distribution of Body Area Index (BAI) values of gray whales imaged by survey plane in the Northeastern Chukchi Sea (NCS) of the Arctic and by UAS in Oregon. Data are grouped by site. The group median (horizontal line), interquartile range (IQR, box), maximum and minimum 1.5*IQR (vertical lines), and outliers (dots) are depicted in the boxplots. The overlaid points represent the BAI values from each image.

SIL indicates malnourishment of ENP whales on foraging grounds in the Arctic and sub-Arctic, it is interesting to note that the body condition of PCFG whales in Oregon is regularly and significantly lower than the body condition of whales in SIL (and the NCS). In fact, only when whales were at their lowest BAI as they departed SIL in 2019 was the mean body condition of whales arriving in Oregon higher (**Figure 6**).

Gray whales make fine-scale foraging decisions, within diverse foraging habitats, using different strategies to target varied prey across their whole North Pacific range

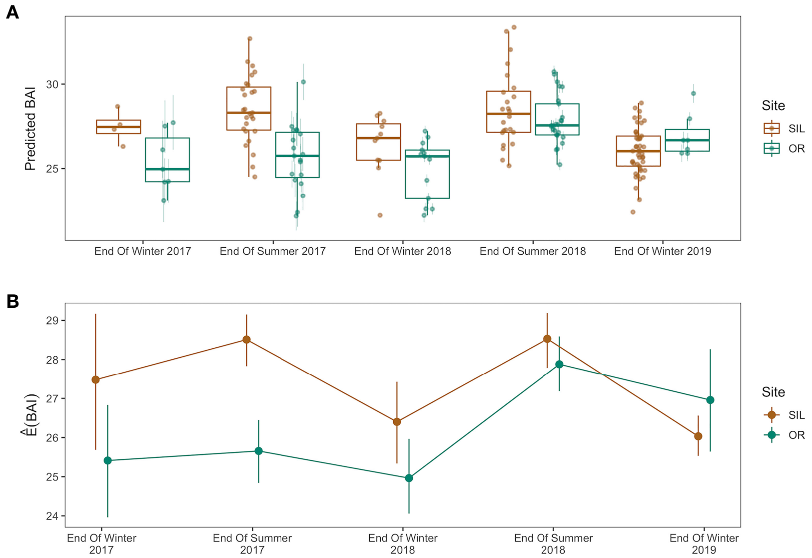


FIGURE 6 | Change in gray whale body condition in San Ignacio Lagoon (SIL), Mexico and Oregon, USA by phenology group and year: End of wintering season (arrival Oregon vs. departure SIL) and End of summer feeding season (departure Oregon vs. arrival SIL). **(A)** Boxplots illustrating the distribution of gray whale estimated Body Area Index (BAI) values across years and phenology group as produced by the Bayesian statistical model accounting for measurement uncertainty. The group median (horizontal line), 75% distribution (box), 95% range (vertical lines), and outliers (dots) are depicted. The overlaid points represent the mean of the posterior predictive distribution for BAI for an individual and the bars represent the upper and lower bounds of the 95% HPD interval. **(B)** Estimated mean BAI values for SIL and Oregon across phenology groups and years derived from the nested ANOVA test of H_2. Points represent the mean BAI estimate and vertical lines represent simultaneous Monte Carlo confidence intervals.

(Nerini, 1984; Mallonée, 1991; Darling et al., 1998; Dunham and Duffus, 2001; Stelle et al., 2008; Torres et al., 2018). Gray whales may make similar, flexible foraging decisions at multiple scales to optimize energy intake. This non-stereotyped approach to energy acquisition has potentially led to the adaptability of gray whales to target novel prey resources (e.g. herring roe, crab larvae, ghost shrimp; Darling et al., 1998; Haifley, 2021; Hildebrand et al., 2021) and responsiveness to environmental change through behavioral adaptations over short evolutionary time scales. This behavioral plasticity can buffer animals from resource shortages and shifts (e.g., Riddell et al., 2018) if the energetic tradeoffs between prey quality and capture costs of novel prey enable adequate energetic gain to support population viability. Yet, if environmental change happens too quickly or too broadly, gray whales may not be able to adapt fast enough or find adequate prey alternatives, leading to increased competition for limited prey and eventual malnutrition.

Our finding that PCFG gray whales in Oregon have lower body condition than gray whales foraging in the NCS of the Arctic (small sample size) and whales on the wintering grounds in SIL (larger sample size) is surprising and raises many prudent questions. Do whales with lower body condition recruit into the PCFG because this strategy is adapted to a smaller morphology, perhaps due to the use of specialized foraging strategies (Torres et al., 2018)? Or is the PCFG range a culturally inherited foraging destination (e.g., Baker et al., 2013) where lower body condition is a genetically inherited trait and whales are adapted to survive with reduced energy stores? Energetic costs of gray whale migration appear to be low (Sumich, 1983), indicating that the lower body condition of PCFG whales may not be entirely related to the truncated migration distance. However, given the lower body condition of PCFG whales, even the additional energetic cost of migration to continue to the Arctic or sub-Arctic may be unsupportable. Alternatively, PCFG whales may be unable to accumulate as much fat reserves relying on prey in the PCFG range as compared to Arctic/sub-Arctic foraging whales. This possibility may explain why gray whales departing summer foraging grounds in Oregon were regularly in worse body condition than whales arriving in SIL after the migration south (**Figures 3**, **6A**). Yet, PCFG whales do recruit calves to this sub-group regularly (Calambokidis and Pérez, 2017b), indicating that females can obtain adequate energy stores to support the demands of reproduction and lactation. However, the calving interval of PCFG female whales is unknown and could be less than ENP females (2 years; Jones, 1990), as it may take PCFG females longer to recover from previous pregnancies and amass enough energetic storage to support another reproductive cycle. Additionally, the age at first reproduction of PCFG whales may be higher if whales are slower to mature and gain adequate mass. Future research efforts should focus on determining the calving rate and age at first reproduction of PCFG whales relative to ENP whales and applying photogrammetry methods to quantify the threshold of body condition necessary to support pregnancy in gray whales. These factors are critical pieces of information needed to inform realistic population models.

The timing of the 2019–2021 gray whale UME aligns with the decline in body condition of whales imaged in SIL between 2017 and 2019 (this study and Christiansen et al., 2021), indicating that the ENP population was primarily impacted in this die-off, not PCFG whales that showed an increase in body condition during this same time period. This coincident timing between the UME and deteriorating body condition of SIL whales suggests that a threshold of malnutrition was met by many ENP whales, as suggested by Christiansen et al. (2021), potentially due to sustained low prey availability on Arctic or sub-Arctic foraging grounds over several years. While the PCFG appears to be less affected by this 2019-2021 UME, this distinct sub-group of gray whales shows significant interannual variation in body condition (Lemos et al., 2020; Akmajian et al., 2021) that is likely related to prey limitations in response to local oceanographic disruptions (e.g., marine heat waves in the NE Pacific Ocean) and broad-scale climate change. Given their apparent lower body condition, PCFG gray whales may have a lower energetic buffer to prolonged periods of low resource availability than ENP whales. If the PCFG did succumb to a die-off event, this small sub-group (~230 individuals) risks losing the cultural knowledge of this foraging range. Prey availability in the PCFG range may only be sufficient to support this small population segment of whales, but this resource and strategy may be less stochastic than foraging in the Arctic or sub-Arctic where the ENP has undergone two UMEs in that last two decades, with dramatic population fluctuations including potentially reaching carrying capacity limits (Moore et al., 2001; Coyle et al., 2007). Therefore, continued and expanded monitoring of gray whale body condition across their entire range, including wintering grounds in Baja California, the PCFG range, the Arctic and sub-Arctic foraging grounds, and on the foraging grounds of the WNP whales in eastern Russian, would provide critical information on the health and response of each population to ecosystem change, particularly in a collaborative and comparative fashion as demonstrated in this study.

UAS collection of whale photogrammetry data is cost-effective, non-invasive, and data rich. Cross-population studies of baleen whale body condition can provide valuable insight, and as demonstrated in this study is feasible even if data are collected by multiple UAS platforms, with different image and data quality. We united and robustly compared these diverse datasets through the comprehensive assessment of uncertainty and calculation of the scale-invariant BAI metric of whale body condition. In addition to behavioral and distributional shifts in response to changes in prey availability (e.g., Torres et al., 2013; Ramp et al., 2015; Brower et al., 2017), baleen whales will respond physiologically through variation in body condition, making UAS assessment of body condition a powerful tool to document how whale populations respond to climate change.

DATA AVAILABILITY STATEMENT

The body area index (BAI) dataset used in this analysis can be accessed via FigShare: https://doi.org/10.6084/m9.figshare.19469966.v1. Further inquiries can bedirected to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by Oregon State University, Animal Program Office and Murdoch University. Research conducted in Oregon was done under the NOAA/NMFS permits #16011 and #21678 issued to John Calambokidis. UAS operations were conducted by a Federal Aviation Authority (FAA) certified private pilot with a Part107 license. All field Research in San Ignacio Lagoon, Baja California Sur was carried out under scientific research permits from the Secretaría del Medio Ambiente y Recursos Naturales, Subsecretaría de Gestión Para La Protectión Ambiental, Dirección General De Vida Silvestre, de México (SGPA/DGVS/ 013210/18, SGPA/DGVS/ 000531/18, SGPA/DGVS/ 01822/ 17) and an animal ethics permit from Murdoch University (R3012/ 18), Australia.

AUTHOR CONTRIBUTIONS

LT, CB, KB, and FC contributed to conception and design of study. LT, CB, FR-G, FC, LB, LL, JR, SS, and AW contributed to data collection. LT, CB, KB, FC, AW, and LL contributed to data processing. LT, CB, KB, and JH contributed to data analysis and visualization. LT, FC, LB, JR, SS and AW contributed to funding acquisition. LT, CB and KB led manuscript writing with all authors contributing to revision and in agreement to the published version of the submitted version.

FUNDING

Data collected in Oregon was supported by the NOAA National Marine Fisheries Service Office of Science and Technology Ocean Acoustics Program [2016 and 2017; 50-27], the Oregon Sea Grant Program Development funds [2018; RECO-40-PD], and the Oregon State University Marine Mammal Institute [2019]. Data collected in San Ignacio Lagoon, Baja California Sur, was funded by Murdoch University, the Universidad Autónoma de Baja California Sur and The Laguna San Ignacio Ecosystem Science Program, a Project of The Ocean Foundation. Data collected in the Arctic was funded by the Bureau of Ocean Energy Management (BOEM), Alaska Region, under Interagency Agreements M16PG00013 and M17PG00031 with the Alaska Fisheries Science Center (AFSC). The Aerial Surveys of Arctic Marine Mammals project was co-managed by BOEM and the Marine Mammal Laboratory, AFSC, National Oceanic and Atmospheric Administration. Data collected in the Arctic was funded by the Bureau of Ocean Energy Management (BOEM), Alaska Region, under Interagency Agreements M16PG00013 and M17PG00031 with the Alaska Fisheries Science Center (AFSC). The Aerial Surveys of Arctic Marine Mammals project was co-managed by BOEM and the Marine Mammal Laboratory, AFSC, National Oceanic and Atmospheric Administration.

ACKNOWLEDGMENTS

We thank Todd Chandler for dedicated UAS operations in Oregon. We thank Cascadia Research Collective for assistance with the photo-identification analysis of whales observed in Oregon. We thank Sergio Martínez-Aguilar, Fabien Vivier and Hunter Warick for contributing to the data collection in Baja California Sur. We also thank Amanda Mayfield for photogrammetry analysis of images collected in the Arctic, and two anonymous reviewers for insightful feedback.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.867258/full#supplementary-material

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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.

The reviewer SM declared a shared affiliation with the author AW to the handling editor at the time of review.

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ORIGINAL RESEARCH
published: 10 May 2022
doi: 10.3389/fmars.2022.837772

High-Resolution Projections of Global Sea Surface Temperatures Reveal Critical Warming in Humpback Whale Breeding Grounds

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

Received: *17 December 2021*
Accepted: *11 April 2022*
Published: *10 May 2022*

Citation:
von Hammerstein H, Setter RO, van Aswegen M, Currie JJ and Stack SH (2022) High-Resolution Projections of Global Sea Surface Temperatures Reveal Critical Warming in Humpback Whale Breeding Grounds.
Front. Mar. Sci. 9:837772.
doi: 10.3389/fmars.2022.837772

Anthropogenic greenhouse gas emissions are triggering changes in global climate and warming the ocean. This will affect many marine organisms, particularly those with high site fidelity and habitat temperature preferences, such as humpback whales on their breeding grounds. To study the impacts of a warming ocean on marine organisms, large-scale projections of climatic variables are crucial. Global models are of 0.25 - 1° (~25-100 km) resolution, and not ideal to predict localized changes. Here, we provide 0.05° resolution (~5 km) sea surface temperature (SST) projections, statistically downscaled using the delta method. We illustrate the shifting isotherms of the critical 21 and 28°C boundaries, which border the climatic envelope that humpback whales prefer for their breeding grounds, over the course of the 21st century on a decadal temporal resolution. Results show by the end of the 21st century, 35% of humpback whale breeding areas will experience SSTs above or within 1°C of current thresholds if present-day social, economic, and technological trends continue ('middle of the road' CMIP6 greenhouse gas trajectory SSP2-RCP4.5). This number rises to 67% under the scenario describing rapid economic growth in carbon-intensive industries ('fossil-fueled development' CMIP6 greenhouse gas trajectory SSP5-RCP8.5). These projections highlight the importance of reducing global greenhouse gas emissions and minimizing further SST increases to preserve ecological integrity of humpback whale breeding areas. In this context, our results emphasize the need to focus on protection of critical ocean habitat and to provide high-resolution climate data for this purpose.

Keywords: humpback whale (*Megaptera novaeangliae*), breeding grounds, sea surface temperature (SST), climate change, climate modeling, statistical downscaling, delta method, general circulation models

INTRODUCTION

Anthropogenic greenhouse gas emissions are impacting the global climate and are projected to cause irreversible ocean temperature increases on centennial to millennial time scales (IPCC, 2021). Throughout the 21st century, climatic changes in the oceans are projected to have consequences across all ecological levels, from individual organisms to ecosystems (Sunday et al., 2012; Vergés et al., 2019; Pinsky et al., 2020). In response to changing conditions in the oceans, free-swimming marine organisms will adapt physiologically as far as their tolerance limits allow or will avoid unsuitable conditions by following the geographic shifts of their environmental niche (Donelson et al., 2019; Pinsky et al., 2020). While small, short-lived organisms may adapt fast enough to climatic changes to remain in their current geographic ranges, large long-lived mammals will likely not be able to adapt in time, instead responding with poleward shifting geographic ranges or face increased risk of extinction (Learmonth et al., 2006; Hastings et al., 2020). Climate-driven species distribution shifts have progressed four times faster in marine taxa compared to terrestrial taxa, leading to the development of novel interspecific dynamics, changes in ecosystem functions and large-scale redistributions of marine resources (Stein et al., 2014; Pecl et al., 2017; Vergés et al., 2019). To develop effective conservation management strategies, it is important to anticipate potential habitat range shifts, especially regarding long-lived, slow adapting species of high ecological and economical importance.

Fitting in this category are humpback whales (*Megaptera novaeangliae*), whose presence is of great ecological, economic, and cultural importance within their seasonal habitats (O'Connor et al., 2009; National Oceanic and Atmospheric Administration, 2020; Savoca et al., 2021). Humpback whale populations are typically migrating between cold, polar foraging areas and warmer tropical breeding grounds, utilized for calving and mating. Reasons for such migrations are debated, but are likely related to reduced predation risk and/or energetics, specifically in relation to calves (Rasmussen et al., 2007; Avgar et al., 2014). Lactating humpback whales accumulate 26 – 37% higher lipid stores than non-lactating whales to offset elevated energetic demands associated with reproduction (Irvine et al., 2017). Such energetic stressors experienced by lactating females typically occur while fasting on distinct breeding grounds to which they show high site fidelity (Calambokidis et al., 2008; Christiansen et al., 2016). Tracking environmental variables connected to habitat suitability of these distinct sites is therefore crucial for effective management and protection of the species (Dransfield et al., 2014). While on a localized scale within breeding grounds, humpback whale distribution is likely associated with bathymetry and does not respond to minor sea surface temperature (SST) variations (Cartwright et al., 2019), humpback whale breeding and calving grounds generally seem to be associated with an envelope of suitable temperatures ranging between 21 and 28°C (Rasmussen et al., 2007; Derville et al., 2019). This temperature envelope could be an important indicator for upcoming population shifts, and humpback whale encounter rates were shown to respond to variation in SSTs on the Oceanian and East Australian breeding grounds, with greater encounter rates corresponding to cooler temperatures within the 21–28°C range (Smith et al., 2012a; Derville et al., 2019). Over the next century, SST increases are expected for most ocean regions, even under implementation of moderate global greenhouse gas mitigation efforts (Zhang et al., 2016). Should the mean SST in respective humpback whale breeding months rise above the optimal temperature range, distribution shifts are the most likely response (Sydeman et al., 2015; Silber et al., 2017). Such shifts could trigger substantial changes in marine systems of the breeding areas with consequences on ecological and economic levels (O'Connor et al., 2009; Savoca et al., 2021).

To understand the trends of projected climate-driven SST increases in humpback whale habitats, climatologic data needs to be available on a spatial resolution suitable to detect changes in these distinct areas that are often of small extent or along complex coastlines. Global SST projections derived from the latest Coupled Model Intercomparison Project (CMIP6; World Climate Research Programme) are of 0.25-1° (~25-100 km at the equator) resolution, encompassing crucial humpback whale breeding grounds, such as the Hawaiian Islands, in just a few grid cells. This is too coarse to draw conclusions on localized ecological issues and depict the habitat affinities of these animals in such coastal areas. Downscaling the data to a high resolution suitable to represent climate on a regional scale is crucial in creating a solid basis for understanding such studies. Statistical downscaling *via* the delta method approach can be a robust yet relatively low computational cost tool to produce high-resolution projections by adding monthly low-resolution SST change increments derived from general circulation models (GCMs) on present-day high resolution SST fields (Pourmokhtarian et al., 2016). For example, the delta method has been used to downscale global temperature and precipitation models for Alaskan stakeholders (Walsh et al., 2018), to downscale various global CMIP5 projections for climate change impact assessment purposes (Navarro Racines et al., 2019), and to downscale European climate data for studying regional and local climatic effects (Moreno and Hasenauer, 2016).

Here, we downscale decadal 1-degree (~100 km at the equator) SST projections to a 0.05-degree resolution (~5 km at the equator) in order to track changes in the 21–28°C isotherm envelope in relation to humpback whale habitats globally. This work compares SST projections between two greenhouse gas concentration trajectories ('middle of the road' and 'fossil-fueled development') and visualizes the shifting isotherm lines of the thermal envelopes bordering humpback whale breeding areas for each scenario. This information could be used to anticipate possible distribution shifts and consequent changes in the ecosystems on a finer scale than previously possible, likely leading to more substantiated conclusions. Furthermore, it can be fed into multivariate models to allow for more accurate modelling of current drivers and future trends in the distribution of various taxa. We focus on the example of shifting thermal boundaries of humpback whale breeding grounds, analyze our results from a conservation perspective, discuss options for climate-flexible management strategies and opportunities to use these results to inspire climate mitigation measurements.

MATERIALS AND METHODS

The future SST conditions were computed with a delta method statistical downscaling approach (Ramírez Villegas and Jarvis, 2010). In this methodology, monthly SST warming increments derived from CMIP6 projections ('deltas') are added to recent high-resolution observational SST data to produce a high-resolution map of SST changes over the upcoming century. This downscaling method has the advantage of allowing inclusion of the wide array of relevant climate variables and modelling power of global CMIP models while effectively bias correcting the projections through the usage of observationally-based high-resolution reference data (Navarro-Racines et al., 2020). The simplicity of the approach comes with a number of limitations that will be discussed in detail in the limitations section. The two scenarios that were chosen for this analysis are Shared Socio-economic Pathway 2-4.5 ('middle of the road' SSP2-RCP4.5), describing a future of medium challenges for mitigation and adaptation, and Shared Socio-economic Pathway 5-8.5 ('fossil-fueled development' SSP5-RCP8.5), describing a future of high human development paired with high, fossil-fueled economic growth (O'Neill et al., 2016; O'Neill et al., 2017). R code to replicate the methodology is provided in an online repository, allowing for further application of this method to other climate variables, climate change trajectories, or time scales. A workflow diagram can be accessed in the supplementary materials (**Supplementary Figure 1**).

Deriving 'Delta' Values From CMIP6 Projections

Global SST CMIP6 projections for the scenarios were extracted from the CMIP6 data portal (https://esgf-node.llnl.gov/search/cmip6/, World Climate Research Programme, 2019; see **Supplementary Table 1**). This was done for the months with the highest humpback whale abundance in breeding areas of the Northern Hemisphere (February) (Jorge Urbán and Anelio Aguayo, 1987; Kobayashi et al., 2016; Martin et al., 2021) and the Southern Hemisphere (August) (Jenner et al., 2001; Trudelle et al., 2018; Derville et al., 2019) for each year until 2100. Historical CMIP6 data for the months of August and February from the same model ensemble were extracted for years 1985 to 2001 (see **Supplementary Table 1**). SST values were regridded with bilinear interpolation to a rectilinear grid of 1° resolution on a WGS 1984 projection using Climate Data Operator v. 1.9.7.1 (Schulzweida, 2019). This interpolation was done to match the projection of the CMIP data to the target high-resolution SST data. SST data was then imported into R v.4.0.3 (R Core Team, 2020) using the 'raster' R package v.3.4-5 (Hijmans, 2020). From the annual data, mean SSTs were calculated for each of the two months for the historical time period (1985–2001) as well as each future decade until 2100 for both climate trajectories. SST change ('delta') was computed as the difference between the projected mean monthly SST per future decade in February and August and the 1985-2001 historical CMIP6 data for February and August, for each of the 18 'fossil-fueled development' scenario and 19 'middle-of-the-road' scenario CMIP6 ensemble models, respectively. Multi-model medians of 'delta' values for each decade were then calculated. Mean and median are both established summary statistics for multi-model ensembles (Sillmann et al., 2013; Martre et al., 2015). A Taylor diagram was used to visually compare the multi-model mean and median to empirical SST data and, in this case, the multi-model median proved to be a better fit. A list of these models as well as a Taylor diagram showing the mean, median, correlation and standard deviation among the ensemble models can be found in the supplementary material section (**Supplementary Table 1** and **Supplementary Figure 2**). Using a multi-GCM ensemble in downscaling approaches reduces uncertainty induced by individual GCM simulations, allowing for a more robust projection of future climate (Xu et al., 2019).

Adding Delta to High-Resolution Climatologies

The 'delta' SST change increments were added to observational high-resolution mean SST for February and August. For this purpose, 1985-2001 monthly mean SST climatology for February and August at 0.05-degree resolution was derived from the ESA (European Space Agency) Sea Surface Temperature Climate Change Initiative (Good et al., 2019). This data source was chosen due to the high product resolution, suitable for a variety of different uses and filling a gap that is unlikely to be addressed by dynamical downscaling approaches in the near future, the availability of a historical data timeframe matching our needs, and the availability of monthly data needed for our purpose. The 1985-2001 time period was chosen for best possible overlap with the period in which the data for the thermal envelope of 21-28°C was generated (Rasmussen et al., 2007), in order to minimize possible error due to deviations of SST and thus deviations from the basic assumption of the correlation between SST and whale presence in breeding areas. By adding the calculated CMIP6 SST 'delta' values to this current SST data, we produced a 0.05° (~5 km) resolution raster of future SST projections. This step adds a bias correction to the CMIP6 modelled data since the ESA high-resolution observationally based SST data contains empirical information on small-scale SST variations which are factored into the final product. Processing times were optimized using the 'doParallel' v.1.0.16 and 'foreach' v.1.5.1 R packages (Microsoft Corporation and Weston, 2020a; Microsoft Corporation and Weston, 2020b).

Visualizing the Data

The resulting 0.05° WGS 1984 projections were imported into QGIS v.3.16.1 (QGIS Development Team, 2021) and mapped with isotherm contours corresponding to lower (21°C) and upper (28°C) isotherms associated with humpback whale breeding grounds. Outer humpback whale breeding area coordinates were derived from the compilation published in Rasmussen et al., 2007 and classified as 14 Distinct Population Segments (DPS) identified by NOAA (NMFS and NOAA, 2016). Numerical population codes were assigned to these segments to simplify their representation and comparability in figures and tables.

RESULTS

Comparison of Coarse CMIP6 SST Data and Downscaled SST Data

The downscaled data show clear improvements in resolution when compared with raw mean values of the CMIP6 SST models used in this study (**Figure 1**). Details of SSTs along the coastlines are visible on a km-scale in the downscaled data, allowing for better estimation of local changes in future SST patterns. SST in DPS 6 (Central America) is displayed with only 31 grid cells in the raw data (**Figure 1A**) and with 12,230 cells in the downscaled data (**Figure 1B**). The bias correction step of the downscaling approach is resulting in small-scale SST differences when comparing coarse CMIP6 data and downscaled data (compare **Figures 1A, B**). On a global level, the mean difference in SST between coarse CMIP6 SST data and downscaled SST data is -0.36°C (SD = 0.97) but varies by region. While the bias correction leads to net decreases in SST in the low and high latitudes, it leads to net SST increases in the tropics and subtropics where most humpback whale breeding areas are located. The differences in SST values between coarse CMIP6 data and downscaled data were mapped globally and can be accessed in **Supplementary Figure 3**. These differences in SST values have an impact on the number of humpback whale breeding areas approaching the critical 28°C isotherm, with this number being 8% higher according to the downscaled SST data when compared to the coarse CMIP6 SST data. Tables with detailed comparisons of SST increases in humpback whale breeding grounds between coarse CMIP6 multi-model median and downscaled data are available in the supplementary materials (**Supplementary Tables 2, 3**).

Fossil-Fueled Development Scenario SSP5-RCP8.5

Mean SST in 64% of humpback whale breeding habitats in the Northern Hemisphere and 69% of humpback whale breeding habitats in the Southern Hemisphere could rise beyond or near (within less than 1°C of) the 28°C isotherm by the end of the 21st century if global greenhouse gas emissions develop according to the 'fossil-fueled development' scenario (**Figures 2B, C**; **Tables 1**, **2**). The current 28°C warm-limit isotherm will shift poleward by ~10-degree latitudes in the Northern and ~5-degree latitudes in the Southern Hemisphere under this high emission scenario (**Figures 2B, C**). The warmest humpback whale breeding area in the Northern Hemisphere is located in the Eastern Tropical Pacific and utilized by the endangered Central American Population Segment. This area could reach unprecedented mean SST in February, reaching up to 32°C by 2100, if no greenhouse gas mitigation measures are implemented (**Table 1**). In the Southern Hemisphere, the Southeast Pacific population segment is exposed to the highest mean August SST, reaching ~30°C at the end of the 21st century (**Table 2**). Animated decadal projections (2020-2100) can be found in the **supplementary materials**.

Middle of the Road Scenario SSP2-RCP4.5

Following the 'middle of the road' emission trajectory, by the end of the 21st century ~ 36% of humpback whale breeding areas in the Northern Hemisphere and ~38% on the Southern Hemisphere would experience SSTs above (or within a 1°C range of) 28°C in the months most frequented by humpback whales (**Figures 2A, B**; **Tables 1**, **2**). End-of-century mean monthly SST projections for February and August under the 'middle of the road' emission scenario show a substantially weaker latitudinal shift of the suitable temperature envelope compared to the 'fossil-fueled development' scenario. The 28°C isotherm would shift poleward by ~5 degrees latitude in the Northern and ~2 degrees latitude in the Southern Hemisphere under such mitigation measures (**Figures 2A, B**). Global implementation of moderate greenhouse gas mitigation measures as outlined in the middle-of-the-road scenario could prevent ~ 50% of the humpback whale areas pushed above the 28°C isotherm under 'fossil-fueled development' scenario from reaching that threshold. The maximum temperatures under this scenario are also far less pronounced. Central America, the hottest humpback whale breeding area worldwide, could experience SSTs up to 30°C by the end of the century. In the Southern Hemisphere, the maximum mean SST in August 2100 are expected to be achieved in the Southeastern Pacific. With ~28°C, they are just touching on the maximum temperatures currently recorded in humpback whale breeding areas. Animated decadal projections (2020-2100) can be found in the **Supplementary Materials**.

DISCUSSION

SSTs Throughout the 21st Century and Beyond

Past analyses have shown that humpback whale breeding areas are found worldwide in warm coastal waters restricted to a temperature envelope of 21–28°C, irrespective of latitude (Rasmussen et al., 2007). Notably, in the decade since these data were published, the warmest breeding area (Central America) has already risen above 28°C mean February SST. Population trend estimates for this DPS are currently lacking (Sato and Wiles, 2021) therefore it is not known what population-level impacts may be occurring as a result of this temperature change. Our results indicate clear latitudinal shifts of the 28°C surface isotherm throughout the 21st century, causing mean 2100 SSTs in up to ~ 67% ('fossil-fueled development' trajectory) of humpback whale breeding areas globally to rise above any historically utilized thermal envelope. It also must be considered that SST increases do not necessarily stop by the year 2100. While in the 'middle of the road' trajectory, temperature increases may plateau at the end of the 21st century, this is not the case if the global community continues to follow a high-emission 'fossil-fueled development' trajectory. Continuing on the 'fossil-fueled development' trajectory would mean that all areas marked as within one degree of 28°C by the year 2100 (as indicated in light grey in **Tables 1**, **2**) may well surpass this threshold in the first decade of the 22nd century. Moreover, mean SSTs close to the tolerance limit of organisms may reduce their capacity to cope with marine heatwaves, which are projected to increase in frequency, duration and intensity over the 21st century (Oliver et al., 2019).

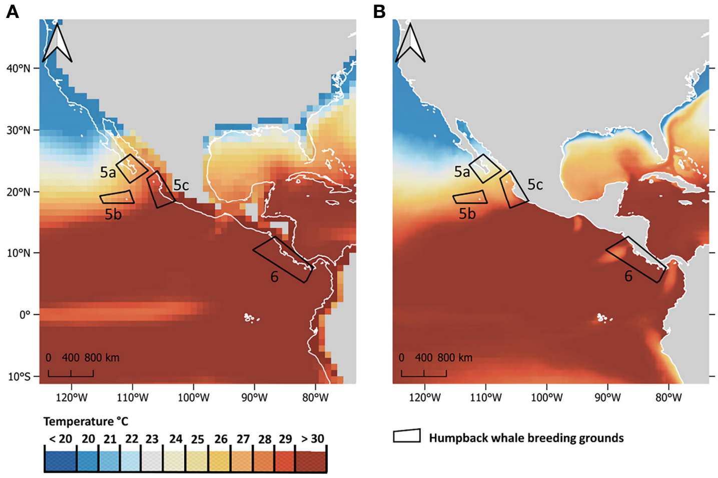

FIGURE 1 | Comparison of **(A)** non-downscaled mean CMIP6 SST data at a 1° (~100 km at the equator) resolution and **(B)** statistically downscaled CMIP6 SST data at a 0.05° (~5 km at the equator) resolution. SSTs projections shown are for the month of February, scenario SSP5-RCP8.5 by the year 2100. Boxes outline humpback whale DPS 5a (Mexico: Baja California), 5b (Mexico: Revillagigedos), 5c (Mexico: Mainland) and 6 (Central America).

Humpback Whale Ecology Implications

In order to follow these latitudinal SST shifts and continue wintering, breeding and calving in a 21–28°C temperature range, humpback whales would need to relocate their breeding habitats. Habitat range shifts are considered the most likely response of large cetaceans to climate change (Sydeman et al., 2015). These shifts could occur at differing rates depending on the location. Along coastlines or far spread island groups, gradual latitudinal population shifts matching the temporal rate of isotherm shifts are possible, with areas along the higher SST isotherms being affected more immediately. In contrast, in isolated areas such as the Hawaiian Islands these shifts could prove a difficult task as there are no suitable areas available in proximity. Humpback whale distribution shifts require availability of suitable habitats in proximity to the previously occupied range, due to their reliance on social aggregations and male song (Derville et al., 2019). Isolation is a restricting factor for this process, as it prevents these continuous shifts guided by social behavior. Remaining in suboptimal habitat conditions however could induce chronic stress and impair fitness, which can ultimately lead to population declines (Wright et al., 2011; Tulloch et al., 2019). Shrinking population sizes due to suboptimal habitat conditions could severely impact ecosystem integrity and livelihoods in such remote breeding areas, as well as in the associated summer foraging habitats in higher latitudes.

If suboptimal habitat conditions were to cause a decline of humpback whale population sizes, there would be further compounding effects on the global carbon budget and nutrient cycle. Humpback whales are important ecosystem engineers; they are known to accumulate carbon throughout their life and sequester that carbon at the seafloor when whale carcasses sink to the bottom of the ocean (Roman et al., 2014). Whales also cycle nutrients throughout the ocean by feeding and defecating while diving and migrating which, in turn, stimulates primary production in the ocean (Roman et al., 2014). Therefore, to mitigate anthropogenic climate change and sustain primary productivity levels, it is important to maintain or increase whale stocks around the world.

It is unclear whether there could be any possible positive consequences associated with latitudinal distribution shifts in those areas where shifts are an option. Shortened migration routes could benefit energetic budgets of lactating humpback whale cows (Braithwaite et al., 2015). However, this is dependent on a variety of other environmental factors determining the suitability of these alternative habitats, such as bathymetry or anthropogenic activities. Another possible consequence of SST increases are temporal shifts in migration patterns. However, the timing of migration may be dictated by environmental conditions in the summer feeding habitats rather than in the winter breeding areas (Ramp et al., 2015). Apart from latitudinal or temporal shifts in their migration, humpback whales could be pushed into deeper waters further from the shores of their breeding grounds to stay within habitable temperatures.

Interpreting Results From a Conservation Perspective

In the Northern Hemisphere, four of the humpback whale breeding areas of DPS that have a 'threatened' or 'endangered' conservation status under the Endangered Species Act (ESA) would reach SSTs surpassing past thermal maxima in their breeding areas by the end of the century under the 'fossilfueled development' trajectory. This represents 50% of the humpback whale breeding areas of DPS currently listed as 'threatened' or 'endangered' under the ESA globally. Under the 'middle of the road' trajectory, only two breeding areas of the currently threatened or endangered DPS would surpass that SST threshold. Notably, one of the most vulnerable DPS, the Central American DPS listed as 'endangered', utilizes the

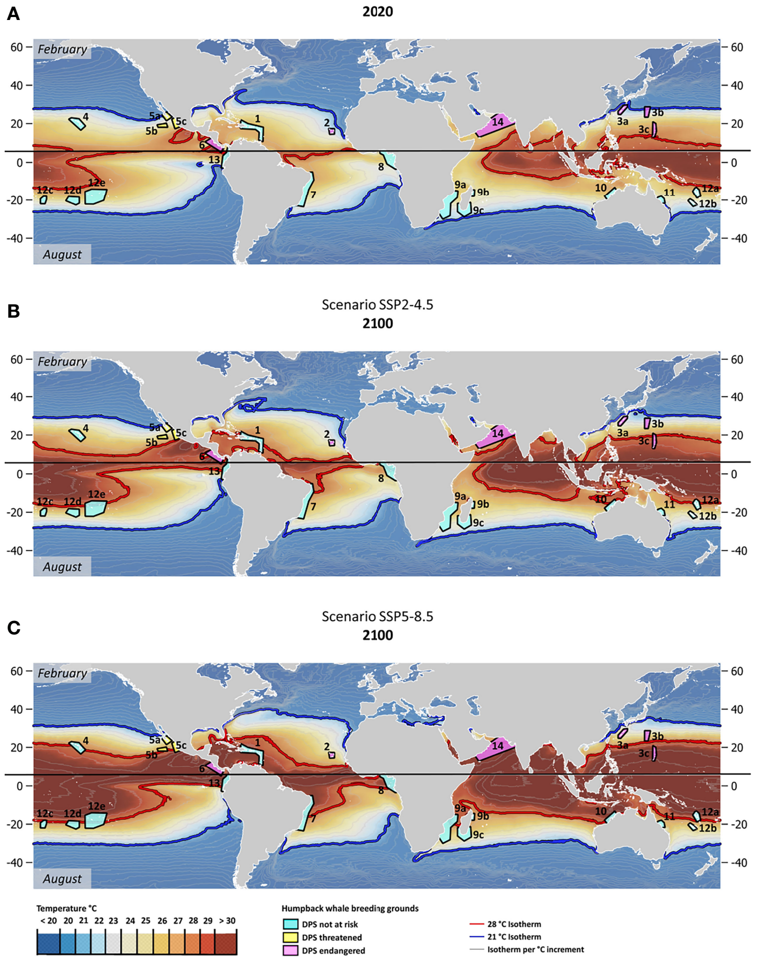

FIGURE 2 | **(A)** Year 2020 mean monthly SST (in °C) for February (Northern Hemisphere) and August (Southern Hemisphere); **(B)** Year 2100 mean monthly SST projections for February (Northern Hemisphere) and August (Southern Hemisphere) under the SSP2-RCP4.5 greenhouse gas concentration scenario and **(C)** Year 2100 mean monthly SST projections for February (Northern Hemisphere) and August (Southern Hemisphere) under the SSP5-RCP8.5 greenhouse gas concentration scenario. Polygons correspond to humpback whale breeding areas colored according to the Distinct Population Segments' (DPS) conservation status. Grey lines are corresponding to 1°C isotherms. The 21°C isotherm is highlighted in blue and the 28°C isotherm in red. Northern and Southern Hemispheres (February and August means) separated by a black bar. Numerical population codes correspond to DPS as listed in **Tables 1** and **2**.

breeding area with the most extreme SSTs and has already surpassed the 28°C isotherm within the last decade. In the 2016 NOAA Revision of Species-Wide Listing, this DPS population size was estimated at ~411 individuals; vessel collisions and entanglement in fishing gear were listed as the greatest threats, and the Extinction Risk Analysis concluded a moderate to high risk of extinction (NMFS and NOAA, 2016). End-of-century breeding months temperatures as high as 30-32°C, as shown for this area by our results, could add an additional stressor to this vulnerable population segment and warrant a reassessment of the Extinction Risk Analysis.

In order to protect vulnerable migratory species such as humpback whales, spatially flexible conservation strategies should be developed for areas along coasts that could facilitate gradual distribution shifts, such as the Central American DPS (Bonebrake et al., 2018). Some frameworks have been proposed in the form of dynamic protected areas, aiming to meet shifting conservation targets (Pressey et al., 2007; Reside et al., 2018; D'Aloia et al., 2019). Detailed data on organisms' physiological and ecological responses to all relevant climate variables are needed to develop accurate range shift projections that would provide ideal baselines for such reserves. However, such data are currently still lacking for many species, including humpback whales. In order to prepare for these upcoming changes, conservationists and management agencies have to plan complex adaptive measures such as dynamic protected areas based on information that is currently available (D'Aloia et al., 2019). Simple metrics aimed at estimating shifts in species' distributions without the need for detailed ecological models, such as climate velocity (Brito-Morales et al., 2018) or shifting isotherm boundaries as presented in this paper, can therefore be important and readily available tools for decision-makers. These

TABLE 1 | Northern Hemisphere humpback whale DPS names, numerical population codes (corresponding to **Figure 2**) and conservation status.

DPS	*Numerical population code (Figure 2)*	*Status (as DPS)*	*Current mean February SST*	*SSP2-RCP4.5: mean February end-of-century SST*	*SSP2-RCP4.5: decade SST surpasses 28°C isotherm*	*SSP5-RCP8.5: mean February end-of-century SST*	*SSP5-RCP8.5: decade SST surpasses 28°C isotherm*
West Indies	1	Not at risk	26.67	**28.02**	**2100**	**29.32**	**2060**
NW Africa	2	Endangered	22.48	24.03	ND	25.52	ND
Japan: Ryukyu Islands	3a	Endangered	22.17	23.33	ND	24.54	ND
Japan: Bonin Islands	3b	Endangered	22.21	23.58	ND	25.34	ND
Mariana Islands	3c	Endangered	**27.41**	**28.70**	**2050**	**30.33**	**2040**
Hawai'i	4	Not at risk	24.81	26.25	ND	**28.00**	**2100**
Mexico: Baja California	5a	Threatened	21.45	22.60	ND	24.17	ND
Mexico: Revillagigedos	5b	Threatened	24.60	25.72	ND	**27.38**	2100+~2
Mexico: Mainland	5c	Threatened	24.96	26.12	ND	**27.71**	2100+~1
Central America	6	Endangered	**28.94**	**30.40**	**2010**	**31.91**	**2010**
Arabian Sea	14	Endangered	25.16	**26.47**	ND	**28.57**	**2090**

Current SSTs and projected SSTs under greenhouse gas emission scenarios SSP2-RCP4.5 and SSP5-RCP8.5 are displayed together with the decade in which each DPS area could surpass the 28°C isotherm (otherwise ND, 'not detected'). Light grey cells indicate SSTs within 1°C of the 28°C threshold, dark grey cells indicate those SSTs where the threshold is surpassed. For areas reaching SSTs within 1°C of the 28°C isotherm by the end of the century, estimates for the decade they may surpass this threshold are given as '2100+~ number of decades' (only for the SSP5-RCP8.5 trajectory, since SSTs are projected to further increase past the year 2100 under this scenario).

TABLE 2 | Southern Hemisphere humpback whale DPS names, numerical population codes (corresponding to **Figure 2**) and conservation status.

DPS	*Numerical population code (Figure 2)*	*Status (as DPS)*	*Current mean August SST*	*SSP2-RCP4.5: mean August end-of-century SST*	*SSP2-RCP4.5: decade SST surpasses 28°C isotherm*	*SSP5-RCP8.5: mean August end-of-century SST*	*SSP5-RCP8.5: decade SST surpasses 28°C isotherm*
Brazil	7	Not at risk	25.17	26.42	ND	**27.59**	2100+~1
SW Africa	8	Not at risk	25.30	**27.37**	ND	**28.68**	**2070**
East Africa	9a	Not at risk	23.87	25.25	ND	26.71	ND
NE Madagascar	9b	Not at risk	24.57	25.90	ND	**27.30**	2100+~2
S Madagascar	9c	Not at risk	23.32	24.42	ND	25.98	ND
West Australia	10	Not at risk	25.83	**27.31**	ND	**29.02**	**2080**
East Australia	11	Not at risk	23.49	24.27	ND	26.10	ND
Vanuatu	12a	Not at risk	26.43	**27.87**	ND	**29.12**	**2070**
New Caledonia	12b	Not at risk	23.48	24.61	ND	26.16	ND
Tonga	12c	Not at risk	24.71	25.49	ND	**27.01**	2100+~2
Cook Islands	12d	Not at risk	25.17	26.02	ND	**27.26**	2100+~2
French Polynesia	12e	Not at risk	26.45	**27.06**	ND	**28.56**	**2100**
SE Pacific	13	Not at risk	**27.10**	**28.18**	**2100**	**30.24**	**2050**

Current SSTs and projected SSTs under greenhouse gas emission scenarios SSP2-4.5 and SSP5-8.5 are displayed together with the decade in which each DPS area could surpass the 28°C isotherm (otherwise ND, 'not detected'). Light grey cells indicate SSTs within 1°C of the 28°C threshold, dark grey cells indicate those SSTs where the threshold is surpassed. For areas reaching SSTs within 1°C of the 28°C isotherm by the end of the century, estimates for the decade they may surpass this threshold are given as '2100+~ number of decades' (only for the SSP5-8.5 trajectory, since SSTs are projected to further increase past the year 2100 under this scenario).

metrics can be used to point out general recommendations for the development of reserve networks, considering suitable corridors for movement as well as the need for protected area establishment in areas of new or future suitability (Bonebrake et al., 2018). In spatially isolated breeding areas, where gradual distribution shifts are not possible, other measures of preparation and protection have to be taken. Whales will likely be exposed to suboptimal thermal conditions, which can act as a stressor on the organism (Chambault et al., 2018; Sanderson and Alexander, 2020). Given their preference for coastal habitats, humpback whales are often exposed to additional stressors such as anthropogenic noise and approaches by vessels (Currie et al., 2021). Being subjected to multiple stressors can have compounding negative effects on organism's health (IPCC, 2019) and consequently weaken the fitness of a population segment (Pirotta et al., 2019). This emphasizes the importance to rigorously target and reduce other possible stressors through implementation of sector-specific management strategies on a local level in current and projected humpback whale habitats, for example through regulation of vessel numbers and speed. Such actions would be even more crucial if humanity cannot manage to reach sufficient emission mitigation globally to keep temperatures within known thermal tolerance ranges for humpback whales, especially in geographically isolated breeding areas.

Lastly, the development of simple metrics such as shifting isotherms as presented in this paper to track climatic changes in the habitat of charismatic flagship species opens opportunities to inspire climate mitigation measurements in policy and public (Thomas-Walters and Raihani, 2017). Large charismatic marine mammals can invoke emotional responses in supporters, stakeholders and donors which can benefit climate mitigation advocacy, a prominent example being the plight of polar bears on shrinking ice shields (Smith et al., 2012b). Humpback whales, especially mother calf pairs in their breeding areas, a favorite among whale watching tourists, could convey a similar message. Humpback whales are an especially interesting flagship species to advocate climate action, as their successful protection would boost emission mitigation through the species' ecological function as a carbon sequesterer (Roman et al., 2014). Developing easily understandable visual aids, such as the red isotherm lines shifting across humpback whale breeding habitats provided in this study (**Supplementary Materials**) can be beneficial in disseminating the key message to a broad, non-scientific audience. Furthermore, these visualizations of different greenhouse gas emission scenarios provide a clear and traceable trajectory, highlighting possible consequences of current global policy efforts and provoking demands for more rigorous action.

Limitations of the Delta Method Downscaling Approach

There are several limitations associated with statistical downscaling of climatological data following the delta method. The disaggregation of coarse grid values is based on the assumption that the same temperature trends are prevalent in the entire grid cell, which may not be the case. This makes the delta approach less accurate than regional climate models, since the approach assumes climate drivers act at coarse scales while local-scale dynamics remain unchanged. This means, while possible small-scale climate interactions are incorporated in the model through the observational high-resolution baseline, possible future changes in their dynamics are not captured. Gradual SST downscaling starting at intermediate resolutions to track these small-scale changes as they develop is not possible with the delta approach, as the target resolution is determined by the observationally based data layer. Other downscaling methods, for example dynamical regional downscaling, would be needed for such comparisons. However, a recent study testing the delta method approach robustness and analyzing model error found that this method produces reliable projections of climate variables for use in impact assessment (Navarro-Racines et al., 2020). Another possible limitation is that the modelling process requires some transformations from curvilinear to rectilinear coordinate systems in order to match the CMIP6 data to the observational ESA SST data. Transforming projections, in this case with bilinear interpolation, could always lead to information losses or minor inaccuracies (Dobesch et al., 2013). However, the achieved high resolution and the usage of a multi-model median give the data a higher degree of certainty compared to individual CMIP6 models at a low computational cost (Xu et al., 2019). The results are easier to interpret than coarse projections and therefore applicable tools for various end-users.

Limitations to the Humpback Whale Case Study

It must be emphasized that this case study only aims to visualize potentially critical SST increases in humpback whale breeding grounds and does not claim to make projections on possible future humpback whale population trends. In order to make such projections and gain a more comprehensive perspective, it is crucial to develop multivariate models and address other climatic and ecological key variables within not only the winter breeding but also the summer foraging areas (Meynecke et al., 2020). This would include factors such as changes in climate affecting primary productivity, with potential consequences across the entire food web. Shifting ranges of a multitude of species could affect predator-prey dynamics and intra- as well as interspecific competition.

There are also other possibilities apart from geographic range shifts in which humpback whales could respond to these climatic and ecological drivers, for example shifts in the timing of migrations or in their depth distribution during the breeding season. In order to address these possibilities, it would be necessary to assess SSTs throughout the year and not just limited to the two months of current highest abundance in breeding grounds. Furthermore, it would require including temperatures in different ocean depth layers. Insights into these possible dynamics could be gained by analyzing how varying temperatures in the ocean and humpback whale breeding grounds have corresponded in the past.

Focusing on mean SSTs within the 21-28°C range could represent another limitation to this approach, as it disregards potential hot or cold spikes. However, during recent heatwaves

SSTs in some of the humpback whale breeding grounds temporarily surpassed 28°C in the relevant months (Central American DPS, Good et al., 2019), yet humpback whales have returned to these areas in subsequent years. This could indicate that temperatures need to consistently surpass the 21-28°C bands to cause habitat shifts in a long-lived slow responding species such as humpback whales. We would therefore argue that the usage of mean SSTs is a suitable concept for the purpose of this study.

CONCLUSIONS

This study showcases the application of the delta method to statistically downscale global SST data on the example of shifting isotherm boundaries of relevance for humpback whale breeding habitats, highlighting the importance of reducing greenhouse gas emissions, implementing mitigation measures and minimizing SST increases. The methodology produces high-resolution visualizations of robust SST projections at relatively low computational cost while adding a layer of bias correction which refines further modelling or study outcomes. The results can be used to create a sense of urgency in climate policy and conservation and act as a guide to data-informed and timely action. Climate strategies should be developed aiming to avoid ocean warming above currently known temperature tolerance levels of humpback whales, especially in light of remaining uncertainties of their ecological responses to SST increases. The results show that even with moderate mitigation measures it is possible to keep temperature ranges in most humpback whale breeding areas within the envelope of known tolerable temperatures. To achieve this level of mitigation, United Nations member states would have to meet all of the national determined mitigation efforts outlined in the agreement of their 26th Conference of Parties (COP26) in order to meet the nearterm emission targets for 2030 (Meinshausen et al., 2021). Unfortunately, recent reports on the state of these commitments show that the member states with the largest economies (G20 states) are projected to fall short of achieving their emission mitigation goals (United Nations Environment Programme, 2021). The possible compounding effects of humpback whale relocations or population declines on ecosystem integrity and ecosystem services are yet another striking example highlighting the need to hold governments and emission-heavy industries accountable to act and to implement effective greenhouse gas mitigation measures with urgency.

DATA AVAILABILITY STATEMENT

The datasets and R code presented in this study can be found in online repositories. The names of the repository/repositories accession number(s) and R code can be found below: https://github.com/rsetter/whalescc.

AUTHOR CONTRIBUTIONS

Conceptualization was led by HH and supported by RS, MA, JC, and SS. Data curation was led by RS and supported by HH. Computational analysis was performed by RS. HH wrote the original draft and visualized the data. JC and SS supervised the work. All authors reviewed and discussed the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

Funding was provided by the University of Hawai'i Department of Geography and Environment and the Pacific Whale Foundation.

ACKNOWLEDGMENTS

We thank Dr. Abby G. Frazier for her advice and support in applying the methodology and her feedback on the early manuscript. We acknowledge the World Climate Research Programme, which, through its Working Group on Coupled Modeling, coordinated and promoted CMIP6. We thank the climate modeling groups for producing and making available their model output, the Earth System Grid Federation (ESGF) for archiving the data and providing access, and the multiple funding agencies who support CMIP6 and ESGF.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.837772/full#supplementary-material

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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.

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BRIEF RESEARCH REPORT
published: 17 May 2022
doi: 10.3389/fmars.2022.847032

Blue Whale Body Condition Assessed Over a 14-Year Period in the NE Pacific: Annual Variation and Connection to Measures of Ocean Productivity

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Large marine mammals can serve as an indicator of the overall state of the environment due to their apex position in marine food webs and their functions as sentinels of change. Reductions in prey, driven by changes in environmental conditions can manifest in reduced fat stores that are visible on whales. We developed a non-invasive technique using photographs of blue whales taken on the US west coast from 2005-2018 (n=3,660) and scored body condition based on visible undulations from the vertebral processes and body shape. We analyzed patterns in the body condition of whales across years and their relation to oceanographic conditions. Females with calves had significantly poorer body conditions and calves had significantly better body conditions compared to other adult whales (Chi-Square, $x^2 = 170.36$, df=6, p<2.2e-16). Year was a significant factor in body condition (Chi-Square, $x^2 = 417.73$, df=39, p<0.001). The highest proportion of whales in poor body condition was observed for 2015 (one of the only two years along with 2017 where >50% had poor body condition) coincides with the marine heat wave that affected the NE Pacific 2014-2016. A cumulative mixed model examining the relationship between body condition and environmental variables revealed that negative Pacific Decadal Oscillation and longer upwelling seasons correlated with better blue whale body condition, likely to be due to higher primary productivity and prey availability. This study indicates that with an adequate scoring method, photographs collected during boat based surveys can be used to effectively evaluate whale health in response to a changing ocean.

Keywords: blue whale, body condition, environmental variability, photo-identification, marine heat wave

OPEN ACCESS

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

Received: *31 December 2021*
Accepted: *12 April 2022*
Published: *17 May 2022*

Citation:
Wachtendonk R, Calambokidis J and Flynn K (2022) Blue Whale Body Condition Assessed Over a 14-Year Period in the NE Pacific: Annual Variation and Connection to Measures of Ocean Productivity. Front. Mar. Sci. 9:847032. doi: 10.3389/fmars.2022.847032

INTRODUCTION

Large marine mammals can serve as an indicator of the overall state of the environment due to their apex position in marine food webs and their functions as sentinels of change (Moore, 2008; Williams et al., 2013). Changes in environmental conditions can result in decreased prey availability at the base of the food web, which impacts predators further up the trophic chain (Acevedo-Whitehouse and Duffus, 2009; Benoit-Bird and McManus, 2012; Soledade Lemos et al., 2020; Rasmussen et al., 2021). In the case of whales, reduced food availability results in visible reductions in fat stores (Lockyer, 1986; Konishi, 2006; Christiansen et al., 2013; Braithwaite et al., 2015). Whales with a compromised body condition may be unable to take on the challenges of their extreme life history, such as their long migrations and periods of fasting, which can lead to reduced survivorship and reproductive fitness (Greene et al., 2003; Lockyer, 2007; Bradford et al., 2012; Soledade Lemos et al., 2020). This can have adverse impacts on the population or species as a whole, which is compounded in recovering populations (Acevedo-Whitehouse and Duffus, 2009).

These impacts are magnified in pregnant and lactating females who rely on bountiful foraging seasons in order to sustain themselves and their calf during the different phases of pregnancy (Lockyer, 1984; Miller et al., 2012; Christiansen et al., 2013; Christiansen et al., 2014). Body condition affects the fertility of many mammalian species, including whales, where a minimum threshold of body fat is needed for ovulation, and therefore, pregnancy (Young, 1976; Frisch, 1984; Lockyer, 1987; Miller et al., 2011). Poor foraging can also influence future pregnancies through a process known as the carry-over effect- where a reduced body condition of a reproductive female can decrease her ability to carry a pregnancy to term in future years, ultimately impacting population growth rates (Soledade Lemos et al., 2020).

Blue whales (*Balaenoptera musculus*) are the largest animal on Earth and thus have the highest prey demands (Savoca et al., 2021). These large animals feed almost exclusively on euphausiids (krill) and consume up to 22 tons of prey per day, often employing energetically costly maneuvers to obtain their prey (Acevedo-Gutiérrez et al., 2002; Croll et al., 2005; Calambokidis et al., 2008; Goldbogen et al., 2011; Goldbogen et al., 2015; Barlow et al., 2020; Savoca et al., 2021). Blue whales were hunted extensively during the whaling era, facing reductions in populations of 90% or more (Jefferson et al., 2015; Thomas et al., 2015). After they became a protected species by the International Whaling Commission in 1966 blue whale populations started to increase, but they are still considered endangered. The eastern North Pacific population of blue whales is currently estimated to be at 1,898 (lower and upper 20th percentile values of 1,767 to 2,038) individuals (Calambokidis and Barlow, 2020) and is considered to be at or near pre-whaling estimates (Monnahan et al., 2015).

Due to their narrowly focused prey regime, blue whale health is closely linked with environmental factors that determine prey abundance and concentration (Croll et al., 2005; Calambokidis et al., 2007; Silber et al., 2017). The eastern North Pacific blue whales forage partially in the highly productive California Current System which spans from British Columbia, Canada (~50°N) to Baja California, Mexico (~15-25°N) (Huyer, 1983; Di Lorenzo et al., 2008; McClatchie et al., 2008; Checkley and Barth, 2009; Palacios et al., 2019). Productivity in the California Current System is driven by patterns of variability on various spatial and temporal scales from local and seasonal upwelling to ocean basin level interannual/decadal Pacific Decadal Oscillation. From 2014 to 2016 the California Current System also experienced a large marine heat wave with sea surface temperature anomalies exceeding 3°C, which was the warmest three- year stretch on record (Schwing et al., 2006; McClatchie et al., 2008; Checkley and Barth, 2009; Di Lorenzo and Mantua, 2016; Gentemann et al., 2017; Thompson et al., 2018).

Body condition is commonly used to assess the health of individuals in both terrestrial and aquatic ecosystems (Lockyer et al., 1985; Lockyer, 1986; Batzli and Esseks, 1992; Pettis et al., 2004; Konishi, 2006; Acevedo-Whitehouse and Duffus, 2009; Bradford et al., 2012; Williams et al., 2013; Braithwaite et al., 2015; Soledade Lemos et al., 2020; Akmajian et al., 2021; Rasmussen et al., 2021). Body condition studies are important to gauge the health of recovering populations of animals and the environment as a whole (Williams et al., 2013). However, measuring large whale body condition at sea is logistically challenging due to their size, sighting frequency, and remoteness (Pettis et al., 2004; Konishi, 2006). Previous studies have used blubber thickness and whaling measurements of girth in carcasses to estimate health (Lockyer et al., 1985; Lockyer, 1986; Konishi, 2006; Williams et al., 2013; Braithwaite et al., 2015). But these studies have limitations as few countries have allowed the lethal removal of whales since the 1980s when international whaling was outlawed. Other studies have used ultrasound to measure the blubber thickness on live right whales (Miller et al., 2011), but such methodology would be challenging for faster, more streamlined whales.

Alternatively, the use of photographic data has been developed as a low cost, easy to implement, and non-invasive way to monitor whale health. Qualitative visual body condition assessments of target areas make this methodology valuable for long-term studies (Pettis et al., 2004; Bradford et al., 2012; Akmajian et al., 2021). Photographic studies show temporal trends in the body condition of baleen whales over years for species such as North Atlantic right whales (*Eubalaena glacialis*) (Pettis et al., 2004), and gray whales (*Eschrichtius robustus*) (Bradford et al., 2012; Soledade Lemos et al., 2020; Akmajian et al., 2021).

The aims of this study were (1) to determine if photographs, especially those used for individual identification (ID) of blue whales can be used to assess body condition, (2) to determine if body condition varied by year or reproductive class, and (3) to investigate the relationships between blue whale body condition and environmental indices representative of upwelling strength and productivity in the California Current System. This research provided a non-invasive model for monitoring blue whale body condition in the future and determining how blue whales may respond to a quickly changing ocean.

METHODS

Sighting Data

This project analyzed photos collected yearly by Cascadia Research Collective and contributors from 2005 to 2018 from the US West Coast which represented 3,660 sightings of 1,112 unique blue whales that were deemed fit for assessment. Each image was scored on a scale of 1 to 3 for photo quality and proportion visible (see **Supplementary Material** for details). Sightings took place in all months and between 25-47°N. Most sightings were in the summer feeding season between June and October (97%), and between Ensenada, Mexico and the Gulf of the Farallones, US (30-39°N, 93%). (Calambokidis et al., 2007; Calambokidis, 2009; Calambokidis and Barlow, 2020).

Body Condition Scoring

Methods in this study were modified from the protocol developed for determining the body condition of North Atlantic right whales (Pettis et al., 2004) and western gray whales (Bradford et al., 2012) and were originally developed by Cascadia Research Collective to study the impact of tags on whales. One analyst (RKW) scored all images, an approach known to improve the consistency of qualitative scoring (Pettis et al., 2004). The lateral flanks forward of the dorsal fin were visually assessed for several features that were potentially indicative of the overall body conditions of the whale: 1) visible undulations along the ridge of the back reflecting the vertebral processes and 2) degree of depression (dorsal ridge) or rotundness along the lateral flanks. Body condition was scored on a scale from 0 to 3 where a score of 0 indicated that the whale had rounded sides, no undulations from vertebrae visible, and presumed to be in the best body condition (**Figure 1A**). A score of 1 indicated that the whale had a well-defined dorsal ridge but whose vertebrae were hardly visible (**Figure 1B**). A score of 2 indicated that the whale had well defined dorsal ridge and multiple vertebrae were slightly visible (**Figure 1C**). Finally, a score of 3 indicated that the whale had well defined dorsal ridge, multiple vertebrae are visible, and presumed to reflect the poorest body condition (**Figure 1D**).

Environmental Data

Several environmental indices are known to reflect prey availability in the California Current System on different spatial and temporal scales (Brinton and Townsend, 2003; Bograd et al., 2009; Checkley and Barth, 2009). In this study, we included the Pacific Decadal Oscillation (PDO) and the length of the upwelling season (LUSI) in the creation of our model to see if they can be linked to blue whale body condition. The PDO is the primary driver of sea surface temperature in the ocean basin and influences regime shifts (1-20 years) of many marine organisms from primary producers to marine mammals (Mantua and Hare, 2002). We looked at both the average annual PDO value for each year and PDO as a binomial factor (positive or negative). On a smaller temporal and spatial scale, seasonal upwelling occurs in the spring/summer and varies in duration (LUSI) at different latitudes along the current, which leads to high levels of primary and secondary production (Huyer, 1983; Fiedler et al., 1998; Croll et al., 2005; Bograd et al., 2009; Checkley and Barth, 2009). The California Current System also experienced a heat wave from 2014-2016 and we considered all months of those years to be under the influence of the heat wave.

Statistical Analysis

We tested the effect of year and reproductive class on blue whale body condition determined through photographic scoring. First the number of whales in each body condition score ranging from 0 to 3 (healthy, moderately healthy, moderately unhealthy, and unhealthy) were summed for each reproductive class (lactating female, calf, or other) and each year (2005-2018). Lactating females and calves were determined to be in those classes for the entire year after they had been observed as a mother-calf pair. We did not otherwise consider the sex and age class of other whales since this information was only known for a small proportion of individuals. Then Chi-squared goodness of fit tests were run in the program R (R Core Team, 2019) to examine the difference in proportion of body condition scores among reproductive classes and year to determine if body condition scores differed. In addition, Kruskal-Wallis tests were run to determine if there were significant annual variations in the PDO and LUSI during the study period.

Then, we used ordinal regression models to explore what environmental variables had an effect on blue whale body condition (see **Supplementary Material** for details). Using the Cumulative Mixed Model test from the Ordinal package (Christensen, 2019) within the program R, we determined the effect that two categorical variables (reproductive class and proportion of image seen) and two environmental indices (PDO, LUSI) had on body condition score (0 to 3). In this analysis reproductive class is lactating female, calf, or other (IDs that did not have a known sex or age class assigned); and proportion of image seen is the score on the three-point scale (see **Supplementary Material** for details) for the primary image being scored. Since blue whales are highly mobile (Calambokidis et al., 1990; Mate et al., 1999; Calambokidis et al., 2009; Busquets-Vass et al., 2021) and body condition would be determined by feeding success over an extended period and range, we used a single annual average value for both the PDO and the LUSI. In each model the year was included as random effects to account for pseudoreplication.

To determine the most parsimonious model, first a full model was created with the two categorical variables (reproductive class and proportion of image seen) and then complexity (interactions between variables) and each covariate were singularly removed. Additional covariates were removed from selective models until we were able to determine the model with the lowest Akaike information criterion (AIC) score using the performance package (Lüdecke et al., 2021). A Pearson's cross-correlation analysis was performed for all environmental variables and highly correlated variables were not included in the same models. Then environmental indices were added to the model until the model with the lowest AIC score was found. This was repeated with a one-and two-year lag for environmental

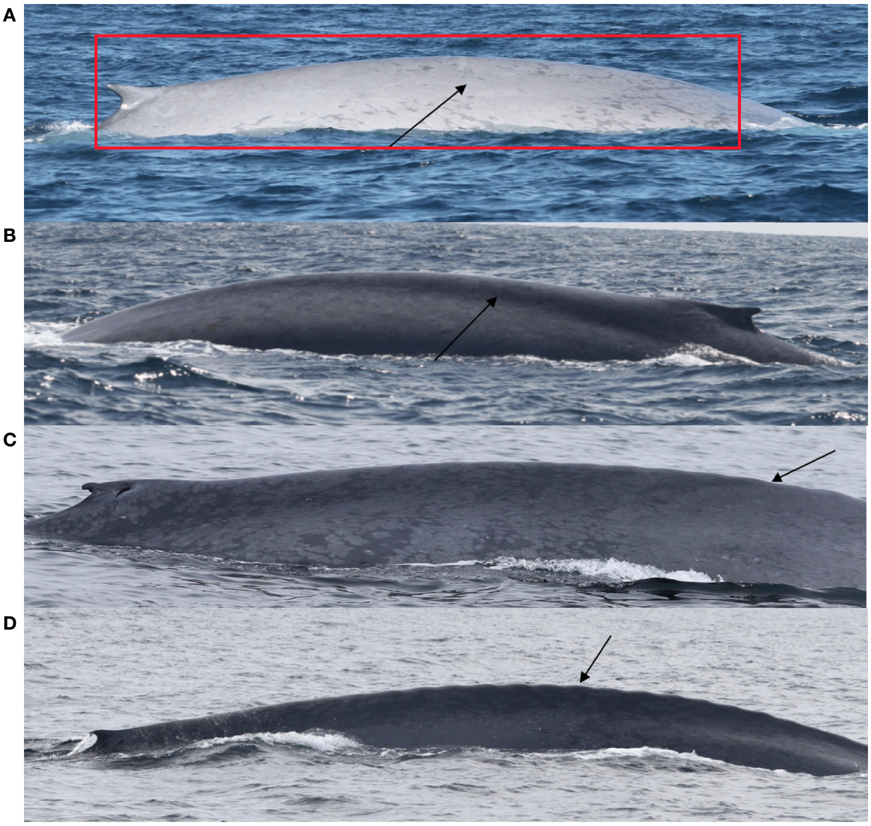

FIGURE 1 | Examples of whales in each category of body condition. **(A)** Score 0, good body condition, rounded sides and no vertebrae are seen. **(B)** Score 1, moderately good body condition, a definite dorsal ridge and possible detectable vertebrae. **(C)** Score 2, a moderately poor body condition, a definite dorsal ridge and slight but multiple detectable vertebrae. D) Score 3, poor body condition, a definite dorsal ridge and obvious multiple vertebrae seen. Arrows indicate rounded sides **(A)**, dorsal ridge **(B)**, and detectable vertebrae **(C, D)**. The red box indicates the area assessed for body condition and proportion of image seen. All images have scores of 1 for both image quality and proportion of image seen. All images were taken by Cascadia Research Collective.

variables to determine if environmental changes had a delayed effect on body condition. The final models were then compared and the best fitting model was chosen (all models tested can be found in **Supplementary Material**).

RESULTS

Body Condition Scoring

The lateral flanks forward of the dorsal fin showed variations through differences in visible undulations reflecting the vertebral processes and the degree of depression or rotundness along the lateral flanks, confirming photographic assessments of body condition can be used for blue whales (**Figure 1**). The distribution of scores for the study period showed that 34.5% of photographed whales were in good body condition (score 0), 32% of photographed whales were in moderately good body condition (score 1), 18.6% of photographed whales were in moderately poor body condition (score 2), and 14.9% of photographed whales were in poor body condition (score 3). The reproductive class had a significant impact on overall body condition (**Figure 2**; Chi-Square, $x^2 = 170.36$, df=6, p<2.2e-16). Lactating females had a higher probability of being in poor body condition (60.5% score 3) and calves had a higher probability of being in good body condition (76% score 0) compared to the general population that displayed fairly evenly spread body condition scores, with more whales being in good body condition (34.4% score 0, 32.6% score 1, 19% score 2, 14% score 3).

The year was also a highly significant factor in the overall body condition for all scores (**Figure 3A**; Chi-Square, $x^2 = 417.73$, df=39, p<0.001). For any given year the proportion of whales in moderately poor to poor body condition (scores 2 & 3) was 33%. But this varied widely across years with a low of 18% in 2008 to a high of 55% of whales in poor body condition in 2015. The percentage of whales in moderately poor to poor body condition did not exceed 50% except for 2015 and 2017.

Environmental Data

Two environmental indicators varied significantly by year, PDO (Kruskal-Wallis, $\chi^2 = 105.37$, df=13, p < 2.2e-16) and LUSI (Kruskal-Wallis, $\chi^2 = 358.14$, df=14, p < 2.2e-16). Only three of

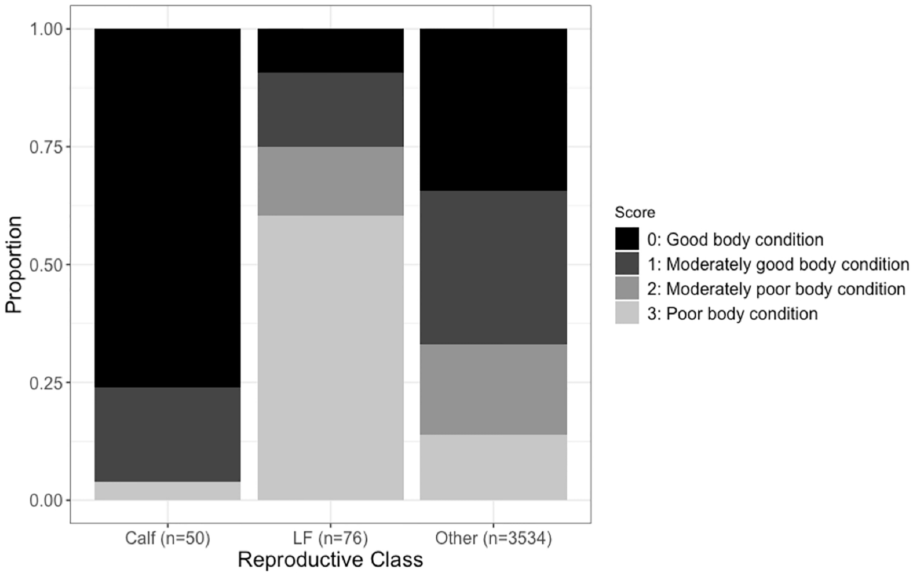

FIGURE 2 | The proportion of each body condition score by reproductive class as a stacked bar graph (LF, lactating female).

the fifteen years (2014-2016) had positive annual mean PDO values, and on average, the PDO was negative during the study period (-0.57 ∓ 1.09). PDO was lowest in 2011 with a value of -1.81 and highest in 2015 with a value of 0.92. On average the length of the upwelling season was 326∓21 days. LUSI was the shortest in 2014 at 304 days and longest in 2008 and 2012 at 335 days.

Model Results

Of the five final models, the model incorporating the proportion of image seen, PDO value, and interaction between reproductive class and LUSI was most parsimonious (**Table 1**). The interaction between reproductive class and LUSI means that the length of the upwelling season impacted the groups differently. Lactating females were only observed during times that had the same LUSI value, which may explain this interaction. The significant parameters in the model were the reproductive class being a lactating female (p=0.019), the proportion of image seen (linear, p< 2e-16), the proportion of image seen (quadratic, p=2.64e-08), PDO value (p=5.10e-05), and the interaction between lactating females and the LUSI value (p=0.010, see **Supplementary Material** for details).

In general, peaks in PDO value coincided with dips in LUSI (except for 2015) and the two variables were moderately correlated (Pearson's cross-correlation -0.3653, t=-23.734, df=3657, p<2.2e-16)). Years that had positive PDO values (2014-2016) had an increase in the number of whales in poor body condition (scores 2 and 3; **Figure 3B**). The opposite was true for LUSI, with an increase in the length of the upwelling season leading to an increase in whales with good body condition (**Figure 3C**).

DISCUSSION

This study shows that visual health assessments based on foundational studies (Pettis et al., 2004; Bradford et al., 2012) can be applied to blue whales to track body condition over time. The lateral flanks varied in the amount of subcutaneous fat in that area which made differentiation between condition scores possible. This region had the added benefit of being the target for photo identification images, making it possible to use historical data in our analysis. Our study could be used as a basis to investigate other streamlined whales such as the minke (*Balaenoptera acutorostrata*), sei (*Balaenoptera borealis*), and fin (*Balaenoptera physalus*) whales.

The reproductive class of blue whales had a highly significant impact on body condition. Calves had the best body condition scores in the population and females who were seen with dependent calves had the worst scores, though this study did not account for variation among other demographic groups. Other body condition studies have found that cows who are nursing their calves are in the worst condition of observed whales (Pettis et al., 2004; Bradford et al., 2012; Soledade Lemos et al., 2020). The high reproductive costs of nursing a mysticete whale calf has been well documented, as cows must consume enough during their feeding season to sustain themselves and their quickly growing calf while in calving grounds, although all North Pacific blue whales forage year-round (Busquets-Vass et al., 2021). Blue whale calves are nursed over a period of 7-8 months during which their size more than doubles (Mackintosh and Wheeler, 1929; Jefferson et al., 2015) and this period of lactation is the costliest part of reproduction, requiring 3-5 times more energy than gestation (Miller et al., 2012).

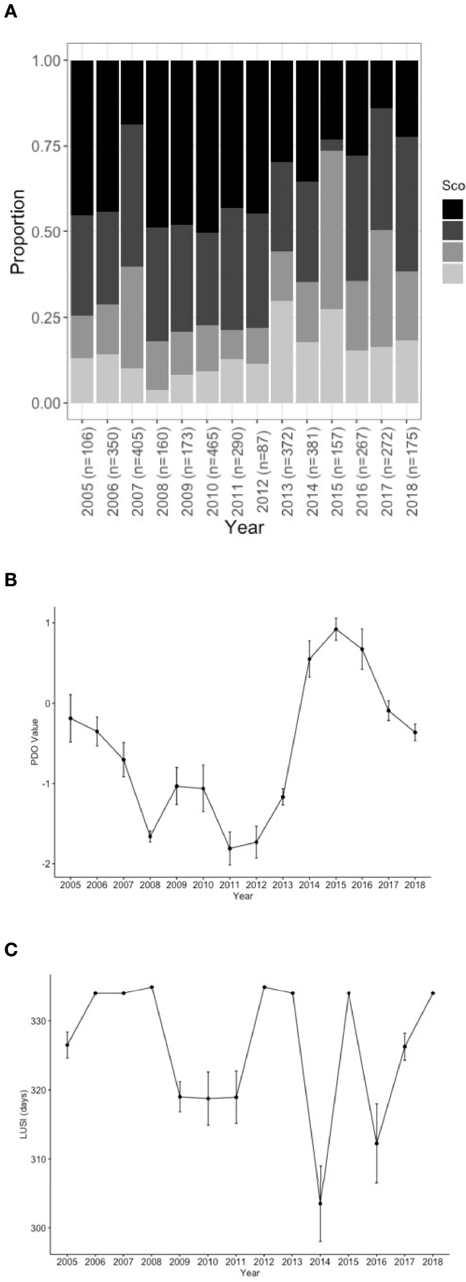

FIGURE 3 | **(A)** the proportion of each body condition by year as a stacked bar graph compared to **(B)** average Pacific Decadal Oscillation (PDO) value **(C)** and the length of the upwelling season (LUSI). The marine heat wave occurred from 2014-2016. Error bars show standard error.

Like Bradford et al., 2012, we saw small variations in the body condition of calves across years with 76% being scored as having good body condition scores (score 0) despite a variation of conditions being observed in the other groups. This could be due to the link between health and reproductive success seen in many species (Lockyer, 1984; Lockyer, 1986; Greene et al., 2003; Christiansen et al., 2013; Williams et al., 2013; Soledade Lemos et al., 2020). Females in poor body condition may be unable to become pregnant (Young, 1976; Frisch, 1984; Lockyer, 1987; Miller et al., 2011), and those that do then must minimize the energy expended on their fetus to maximize their own chance of survival (Christiansen et al., 2014). This means poor foraging conditions can lead to drops in calving rates- something that is especially concerning for an endangered species (Greene et al., 2003). A year of bad foraging can also influence more than just the pregnancies for that year, as a reduced body condition of a

TABLE 1 | Results comparing the three final qumulative mixed models of blue whale body condition.

Model	K	AIC	RMSE
Score~ RepClass * LUSI + BestProp + PDO.Value + (1|Year) + (1|ID)	14	8442.150	1.316
Score~ RepClass * LUSI + BestProp + PDO.Value + Lag2HeatWave + (1|Year) + (1|ID)	15	8439.070	1.316
Score~ RepClass + BestProp + Lag2HeatWave + (1|Year) + (1|ID)	11	8454.832	1.316
Score~ RepClass + BestProp + Lag1PDO + (1|Year) + (1|ID)	11	8453.292	1.316
Score~ RepClass + BestProp + Lag1HeatWave + (1|Year) + (1|ID)	11	8453.292	1.316

Body condition score (Score) relative to predictor variables reproductive class (RepClass), the proportion of image seen (BestProp), PDO value, LUSI, presence of a heat wave (HeatWave), and PDO being positive or negative (PDO). Lag models have a one-or two-year lag of environmental predictor variables. Since the best two models with a 1-year lag had the same AIC score they were both included in the final model analysis. The most parsimonious model is shown in bold. K, number of parameters; AIC (Akaike Information Criterion), relative model fit; RMSE (Root Mean Square Error), standard deviation of the residuals.

reproductive female can decrease their ability to carry a pregnancy to term in future years (carry-over effect; Christiansen et al., 2014; Soledade Lemos et al., 2020). If foraging conditions are poor for consecutive years, the long term recovery of endangered populations, especially if they are dealing with the effects of human activities, can be in jeopardy.

Blue whale body condition varied by year, but overall the proportion of whales in poor body condition remained generally low, except for two years (2015 and 2017) when more than half of the whales were in poor health. While this study focused on the blue whales feeding on the US west coast, the eastern North Pacific population feed year-round and has a much broader feeding range that extends from the Eastern Tropical Pacific to Alaska (Mate et al., 1999; Stafford et al., 1999; Calambokidis et al., 2009; Monnahan et al., 2014). After their numbers were greatly reduced from whaling, blue whales were rarely seen in Alaska; but starting in the late 1990s an increase of whales in more northern waters coincided with a decrease of blue whales off California (Calambokidis et al., 2009). It has been hypothesized that when foraging around California is poor due to decreased krill availability or increased competition, some blue whales may continue elsewhere to look for better foraging opportunities. It is likely that the pattern in blue whale body condition we observed results from a combination of some whales shifting foraging grounds and others being influenced by the feeding conditions off of California (Calambokidis et al., 2009; Busquets-Vass et al., 2021).

Variation in energy reserves (body fat) has been linked to prey availability, where oftentimes environmental conditions are used as a proxy (Braithwaite et al., 2015; Soledade Lemos et al., 2020). We looked at several environmental indices that we believed would drive prey availability and therefore body condition. PDO and LUSI were the environmental drivers selected in our final model. While our final model included data from environmental indices taken in the same year as the sightings, other models that performed well had one- or two-year lags for the environmental indices, which may reflect that blue whale body condition is a function of both conditions in the current year, as well as previous years.

PDO varied significantly by year over our study period with high values in 2014-2016. Only four years of our study period had positive PDO values (2014-2017), which followed the same pattern of poor body condition. PDO reflects sea surface temperature in the Pacific Ocean basin with positive PDO values signifying warmer ocean temperatures (Mantua and Hare, 2002; Brinton and Townsend, 2003; Di Lorenzo and Mantua, 2016). We also looked at LUSI since upwelling occurs on a smaller temporal scale than PDO, seasonally leading to high levels of primary and secondary production (Huyer, 1983; Fiedler et al., 1998; Croll et al., 2005; Checkley and Barth, 2009). The seasonal upwelling coincides with the summer feeding period for blue whales (Croll et al., 2005; Barlow et al., 2020) and therefore its length could drive overall foraging success. The worst body conditions occurred in years with the shortest upwelling seasons. Our results suggest that warm sea surface temperatures driven by positive PDO values and short upwelling seasons are detrimental to blue whale health by reducing food resources for the whales feeding off the US west coast. PDO was linked to changes in blue whale distribution and their use of areas off the US west coast versus further north into the Gulf of Alaska for present day as well as for historical whaling data showing that PDO may predict broad shifts of blue whale distribution in the eastern North Pacific (Calambokidis et al., 2009).

While not all environmental indices are highly correlated, they do play off one another and have a cumulative impact on the California Current System and the organisms that live there. Future studies may be required to quantitatively link specific indices and environmental events to whale body condition. It would be interesting to perform a similar study on other whales that forage in the same region, like humpback whales (*Megaptera novaeangliae*). Unlike blue whales, humpbacks forage only seasonally so the environmental factors may have a larger impact on their body condition.

We provided a basis for evaluating large whale health using historic records that can provide context for present and future conditions. This methodology can also be used to monitor populations over the long term which will only become more important in the context of a changing climate. Marine heat waves are expected to become more frequent and more intense in the future (Oliver et al., 2018) due to anthropogenically driven climate change (Frölicher et al., 2018; Oliver et al., 2018). This study indicates that with an adequate scoring method, photographs collected during boat based surveys can be used to effectively evaluate whale health in response to a changing ocean.

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 Cascadia Research IACUC.

AUTHOR CONTRIBUTIONS

The authors confirm contribution to the paper as follows: RW, JC, and KF conceived the study. JC and KF collected original data. RW scored the data and created the model. RW was the lead author on the draft and revisions. JC and KF gave assistance in analysis and editing the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

Support for long term photo ID effort was provided through various contracts and grants over the years from the National Oceanic and Atmospheric Administration (NOAA) as well as support for this project through a NOAA Section 6 grant through the Washington Department of Fish and Wildlife. Support for initial assessment of blue whale body condition provided through a grant from the Office of Naval Research with funding from the Bureau of Ocean Energy Management through the National Oceanographic Partnership Program.

ACKNOWLEDGMENTS

We thank the following people and institutions: NOAA for providing the principle support for the long term photo ID project over the years; Ben Miner for guidance in developing the models; Jarrod Santora, Karin Forney, and Elizabeth Becker on advice on environmental variables to use; the other staff, interns, and collaborators of Cascadia Research Collective who aided in obtaining, processing and matching photographs of blue whales especially Annie Douglas, Elana Dobson, and Azucena Ugalde; and José Pedro Andrade for his helpful advice during this project.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.847032/full#supplementary-material

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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 | Frontiers in Marine Science

ORIGINAL RESEARCH
published: 09 June 2022
doi: 10.3389/fmars.2022.880910

Maternal Lineage and Habitat Use Patterns Explain Variation in the Fecundity of a Critically Endangered Baleen Whale

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OPEN ACCESS

Edited by:
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Reviewed by:
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University of Utah, United States
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Specialty section:
This article was submitted to
Marine Megafauna,
a section of the journal
Frontiers in Marine Science

Received: 22 February 2022
Accepted: 02 May 2022
Published: 09 June 2022

Citation:
Bishop AL, Crowe LM, Hamilton PK and Meyer-Gutbrod EL (2022) Maternal Lineage and Habitat Use Patterns Explain Variation in the Fecundity of a Critically Endangered Baleen Whale. Front. Mar. Sci. 9:880910. doi: 10.3389/fmars.2022.880910

The critically endangered North Atlantic right whale population (*Eubalaena glacialis*) has experienced multiple periods of decreased reproduction within its observable history, which have played a role in the overall decline of the species. In addition to this synchronized variation in reproduction across the population, there exists considerable individual variation in fecundity. To determine the impacts of family history and habitat use behavior on these individual variations in fecundity, photo identification data collected during four decades of visual monitoring were used to create a calving index for sexually mature females that could be used to evaluate matrilineal influence on fecundity. Reproductive life histories were analyzed to assess fecundity variation within matrilines over time. Individual variations in fecundity were also assessed with respect to a recent climate-driven habitat distribution shift by a loyal cohort of right whales that use the Gulf of St. Lawrence during the summer and autumn seasons. Lifetime fecundity in the oldest known living reproductive female, or matriarch, in a matriline was positively associated with the fecundity of her female progeny. Sexually mature females that have used the Gulf of St. Lawrence since 2015 were significantly more likely to give birth over this time period compared to individuals who did not use that habitat. Individuals of both sexes were significantly more likely to use the Gulf of St. Lawrence if their mothers did as well; however, this association declined as offspring aged. These results provide insight on the environmental, behavioral, and genetic factors that contribute to individual variation in fecundity. Low calving rates and increased dangers posed by habitat use shifts in the past decade have played a major role in the species' decline, and these new insights into the mechanistic drivers of right whale reproduction and habitat use show that lineage guides progeny behavior and reproductive success. As anthropogenic climate change continues to disrupt right whale seasonal distributions through changing ocean circulation patterns, understanding the demographic consequences of novel habitat use patterns will be essential to updating protective policies.

Keywords: fecundity, matriline, reproduction, habitat, climate, right whale, mother-calf

INTRODUCTION

The North Atlantic right whale (*Eubalaena glacialis*) is one of the most critically endangered baleen whale species in the world, with an estimated population size of less than 350 individuals in 2020 (Kraus et al., 2001; Pettis et al., 2022). The species has struggled with dangerously low population numbers since the 20th century, if not longer (McLeod et al., 2008; Reeves, 2001), and the population is currently in a state of decline (Pettis et al., 2022). High rates of anthropogenic mortality from ship strikes and entanglements in fishing gear have played a dominant role in this decline (Knowlton and Kraus, 2001; Kraus et al., 2005; Knowlton et al., 2012; van der Hoop et al., 2015; Sharp et al., 2019), with mortalities rapidly increasing since 2013 (Meyer-Gutbrod et al., 2018; Pace et al., 2021).

In addition to the high mortality rates, decadal-scale fluctuations in reproduction, linked to climate induced changes in prey availability (Greene et al., 2003; Greene and Pershing, 2004; Meyer-Gutbrod and Greene, 2014; Meyer-Gutbrod and Greene, 2018), have contributed to depressed population growth. In the 1990s, a population-wide decline in reproduction was documented and later shown to be the result of limited prey availability (Caswell et al., 1999; Fujiwara and Caswell, 2001; Meyer-Gutbrod et al., 2015). Despite a rebound in reproduction in 2000, the population has once again entered a period of low reproduction as of 2010 (Meyer-Gutbrod et al., 2021; Pettis et al., 2022). Low reproductive rates and high calving intervals (the number of years that occur between subsequent births) have been observed in this species (Knowlton et al., 1994; Caswell et al., 1999; Meyer-Gutbrod et al., 2015). The average calving interval increased from 4.0 to 9.2 years between 2009–2021 (Pettis et al., 2022), and the frequency of high calving intervals (defined here as 6+ years, which is double the calving interval that females are biologically capable of) increased as well (Knowlton et al., 1994; Kraus et al., 2001). Individual and population-level variation in right whale reproduction occurs in part due to the high energetic requirements of pregnancy and lactation (Fortune et al., 2013). To satisfy these requirements, adult females require an adequate amount of body fat to successfully reproduce (Miller et al., 2011). In years when prey availability is low, many females are unable to build a blubber layer that is thick enough to sustain successful reproduction; therefore, reproduction is delayed until enough food can be consumed (Miller et al., 2011). Fluctuations in prey availability are exacerbated by chronic non-fatal entanglements which limit an individual's ability to forage (Stewart et al., 2021).

Previous studies have shown that matrilineal family structure also has a significant impact on survival and reproduction rates in cetacean species, and this is best documented in odontocetes. For example, the presence of both reproductive and post-reproductive females has been shown to increase the survival of young offspring in resident killer whales (Foster et al., 2012). In addition, post-reproductive females are known to be important sources of ecological knowledge, including feeding and breeding information, in various cetacean species (Brent et al., 2015; Wright et al., 2016; Nattrass et al., 2019). Their knowledge and leadership are particularly important in periods of low prey years (Brent et al., 2015). The social structure of mysticetes is poorly understood and, while post-reproductive females are not known to exist in the right whale population, similar dynamics of maternally-influenced habitat use and matrilineal transmission of ecological and behavioral knowledge may exist within this species, which potentially impact the survivability and fecundity of specific kin groups.

Individual matrilines with characteristically distinct fecundities have already been observed in the Northwest Atlantic humpback whale population (Rosenbaum et al., 2002) which may have arisen, in part, because learned behavior and site fidelity are passed down by family members. Baleen whale species including southern right whales, humpbacks, and North Atlantic right whales have been documented exhibiting fidelity for specific sites (Schaeff et al., 1993; Palsbøll et al., 1995; Larsen et al., 1996; Malik et al., 1999; Stevick et al., 2006; Patenaude et al., 2007; Crowe et al., 2021), with direct evidence of maternally inherited feeding site fidelity being observed in southern right whales (Carroll et al., 2015). Southern right whale ecological knowledge of nursery and feeding grounds has been shown to be communicated to a calf by its mother during its first migration (Valenzuela et al., 2009). Similar carbon and nitrogen isotopic values found between specific southern right whale matrilines indicated that individual families follow the same migratory patterns, further supporting the idea of matrilineal site fidelity (Valenzuela et al., 2009).

North Atlantic right whales live largely within the northwest Atlantic Ocean (Winn et al., 1986). The spring and summer months are spent primarily foraging in the Great South Channel, Cape Cod and Massachusetts Bays, the Bay of Fundy, and the southern Scotian Shelf (Winn et al., 1986; Baumgartner & Mate, 2003; Mayo et al., 2018; Ganley et al., 2019). Most of these areas have been designated as critically important habitats (Department of Fisheries and Oceans Canada, 2007; Brown et al., 2009; National Marine Fisheries Service, 2016). Reproductive females in calving years spend the winter at their only known calving grounds in the Southeast United States, along the Georgia and Florida coasts (Winn et al., 1986), where they can be found through late spring (Kraus et al., 1986). The winter movement patterns of all other demographics are not well known, though a southward migration has been hypothesized, with some individuals spotted in the Gulf of Maine and off of Cape Cod (Winn et al., 1986; Brown et al., 2009). Despite these observations, movement and habitat occupancy patterns for large portions of the population and significant seasonal periods remain unknown.

Calves typically remain with their mothers for one year, and follow their mother's migration patterns during that time (Hamilton et al., 1995). There is evidence that individuals display site fidelity for the habitats they were taken to during their weaning period as calves. One study reported that individuals who visited the Bay of Fundy as a nursery site were documented using it as a feeding ground in later life, while individuals who were not taken to the Bay of Fundy as calves did not subsequently migrate there to feed (Schaeff et al., 1993). Strong, but nonsignificant evidence was later found that the transmission of this site information is linked between mothers and daughters (Malik et al., 1999). Finally, recent genetic evidence from ancient whale bones revealed that maternally inherited site fidelity likely played a significant role in defining the habitat use patterns of historic right whale populations (Frasier et al., 2022).

In recent years, an occupancy and distribution shift has been observed for North Atlantic right whales throughout their range (Davis et al., 2017; Simard et al., 2019; Meyer-Gutbrod et al., 2021). This shift began in the early 2000s, when the proportion of the population observed using Cape Cod Bay increased significantly (Mayo et al., 2018; Ganley et al., 2019). Over the past decade, the Gulf of St. Lawrence has been used as a foraging habitat (Meyer-Gutbrod et al., 2021), and survey effort in recent years has indicated that a loyal subset of the population uses this habitat during the summer and autumn months (Crowe et al., 2021). While there is a long record of sporadic right whale sightings in the Gulf of St. Lawrence (McLeod et al., 2008; Brown et al., 2009; Reeves et al., 1999), the current group of users, comprising approximately 40% of the population, predominantly returns to this habitat annually (Crowe et al., 2021). This novel habitat use pattern is most likely caused by climate-driven declines in prey availability in traditional summertime right whale foraging habitats (Record et al., 2019; Meyer-Gutbrod et al., 2021).

With the population being regularly affected by low prey availability and resultantly low reproduction rates, it is critical to understand the more nuanced, underlying mechanisms driving female reproductive success as well as factors driving habitat use. While previous studies have confirmed that prey availability drives interannual variation in right whale reproduction (Greene et al., 2003; Meyer-Gutbrod et al., 2015; Gavrilchuk et al., 2021), some sexually mature females still fail to reproduce in high prey years, as evidenced by the continuously declining birth rate within the population despite concurrent spikes in the abundance of their primary prey, *Calanus finmarchicus* (Kraus et al., 2001; Meyer-Gutbrod and Greene, 2014). In years when prey is anomalously low and population-wide reproduction is stunted (ex: 1998–2000), some females still manage to birth healthy calves. What drives variations in fecundity outside of broad-scale environmental conditions? This study aims to determine whether lifetime fecundity patterns are consistent among kin groups (matrilines) and how these fecundity patterns are related to recent climate-induced habitat use behaviors. Determining drivers of fecundity variation between individuals could be used to advance our understanding of population dynamics and inform initiatives to support species recovery.

MATERIALS AND METHODS

Data Collection and Life History

Right whale demographic and sightings data were obtained from the North Atlantic Right Whale Consortium Identification database and Sightings database (North Atlantic Right Whale Consortium, 2021a; 2021b). These databases contain right whale sightings data occurring from 1935 to 2021, and were collected through aerial surveys, boat surveys, and opportunistic sources, with dedicated survey effort beginning in the late 1970s (Kenney, 2018). Survey effort occurs along the eastern seaboard of the United States and Canada to monitor the population, though the effort is not comprehensive or consistent in all regions annually. In the past decade of published data (2009–2019), the total survey effort fell between 141,000 km and 271,000 km surveyed annually, with 57–93% of the presumed alive population observed each year (Pettis et al., 2022). Individuals are presumed alive if they have been seen within five years of their last sighting (Knowlton et al., 1994).

Individual right whales are primarily identified by unique callosity patterns, rough patches of skin on their heads that are colonized by whale lice (Payne et al., 1983; Kraus et al., 1986), though scars, natural variations in pigmentation, and DNA can also be used for identification (Hamilton et al., 2007). Age, matriline, calving history, and sightings location data were used to observe patterns in individual fecundity variations. This study utilized complete demographic data through 2019; however, calving data for 2020 and 2021 were obtained from the National Oceanic and Atmospheric Administration and the North Atlantic Right Whale Consortium to ensure up-to-date calving analysis (National Oceanic and Atmospheric Administration, 2021; Right Whale News, 2021; Pettis et al., 2022). R Statistical Software Version 1.4.1103 was used for all data visualization and statistical analysis (R Core Team, 2020).

Calf birth data were analyzed to assess individual variations in fecundity. Females were classified as sexually mature if they were 1) at least 9 years old, 2) had an observation history of 8 or more years, or 3) had been previously sighted with a calf (Hamilton et al., 1998). Since not all sexually mature females have given birth, we separately examined the age distribution of females that have not yet produced a calf. Only females with known ages from the sighting record and that were at least 10 years old in 2021 were used in this analysis.

Two case studies of matrilines that had highly fecund matriarchs but produced substantially different numbers of progeny were presented. These case studies highlight the differences in matrilineal reproductive success that can occur. One showcased a highly productive matriline, while the other represented a matriline that was far less productive. Birth years, death years, last sighting years, reproduction events, and family patterns were documented and analyzed for both case studies to qualitatively assess factors that contribute to matrilineal fecundity. Individuals classified as “presumed dead” within these case studies have not been sighted for at least five years (Knowlton et al., 1994), while individuals classified as “confirmed dead” are those whose carcasses have been observed and identified.

Matrilineal Influence on Fecundity

Matrilineal influence on fecundity was analyzed by developing a calving index based on sighting histories to compare adult female reproductive history regardless of age. Individual calving indices were calculated by dividing a female’s total number of known calves by her total number of years spent as a sexually mature adult. For example, a calving index of 0.25 corresponds to a female that has given birth, on average, once every four years since becoming sexually mature. Notably, births are determined on an observational basis; therefore, unseen calves, including those that died during birth or soon after, could not be included in this analysis.

Fecundity patterns were examined within matrilines to assess potential genetic or learned behavioral influences on fecundity. For each matriline considered in this study, the matriarch was determined from the life history data available through the North Atlantic Right Whale Consortium database, and the matriarch is defined here as the oldest known reproductive female in a line of direct descendants. The calving indices of individual sexually mature females were compared to the calving indices of their oldest living matriarch to determine whether fecundity is linked within matrilines. Kendall's tau rank order correlation was used to determine whether there was a significant relationship between matriarch fecundity and the fecundity of their descendants.

Influence of Habitat Use on Fecundity

To assess whether recent shifts in habitat use impact fecundity, individual demographics and recent calving success were compared between individuals grouped into one of two habitat use patterns: those sighted in the Gulf of St. Lawrence between 2015 and 2019 (see Crowe et al., 2021 supplementary for the list of these whales), and those that were not sighted in the Gulf of St. Lawrence during that time period. Calving success in sexually mature females was compared between whales who did and did not go to the Gulf of St. Lawrence to determine the influence of this habitat use pattern on reproduction. The right whale calving year begins one month before the calendar year to accurately account for the calving season (Pace et al., 2017), and we analyzed calf births from 1 December 2015 through 30 November 2021 to encompass all calving years that were potentially impacted by the distribution shift described in Crowe et al. (2021). Reproduction was coded as a binary variable, where sexually mature females were classified as "Reproductive" if they had one or more calves or "Non-Reproductive" if they had zero calves during that period. A chi-square test was used to assess the relationship between reproductive status and habitat use pattern.

Matrilineal Influence on Habitat Use

We examined matrilineally directed habitat use between the group of whales that use the Gulf of St. Lawrence and the remainder of the population. For all analyses, the type of habitat use exhibited by each whale was defined by whether an individual was seen in the Gulf of St. Lawrence at least once between 2015–2019. The high site fidelity noted in whales who use this habitat (Crowe et al., 2021) supports the assumption that an individual sighted there once will likely return to forage there again. Only whales sighted since 2015 were used so that our analyses exclusively accounted for habitat use patterns that occurred during the current distribution shift. Two chi-square tests were performed to assess whether an individual was more likely to use the Gulf of St. Lawrence if its mother or matriarch did as well. Two additional chi-square tests were conducted to assess whether the habitat use patterns of individual sexes were individually more likely to match their mothers'. Finally, we examined whether an individual's age impacted their tendency to match the habitat use behavior of their mother. All individuals with known birth years were sorted into two classes based on their age in 2019: "Age <5" include individuals born in or after the year 2015, and thus had the chance to use the Gulf of St. Lawrence as calves with their mothers during the 2015–2019 survey period; "Age 5+" is defined as individuals born before the year 2015, who did not have the chance to use the Gulf of St. Lawrence as calves with their mothers while the distribution shift was taking place. The number of individuals who match their mothers' habitat use patterns was analyzed between each age class, parsed by the habitat usage pattern of their mothers, using Fisher exact tests (Fisher, 1934).

RESULTS

The life histories of 766 individually identified right whales were examined and 260 sexually mature females were identified since 1980. There were 586 calf births documented over the same time period (**Figure 1**). The calving index of sexually mature females ranged from 0 to 0.286 calf births over their full lifetime reproductive period observed to date. As of 2021, there were 49 females in the database who were presumed alive and reached sexual maturity, but were never observed with a calf. Of those with known ages (n = 43), these non-reproductive females ranged in age from 10 years old to 34 years old, but tended to be relatively young (**Figure 2**), with the majority falling at or below the age of 13 (67.4%). Only four of the females, or 9.30% of the demographic, were above the age of 20.

Matrilineal Influence on Fecundity

There were 580 individual calves visually observed in a mother/calf pair, thereby confirming their maternal lineage and allowing them

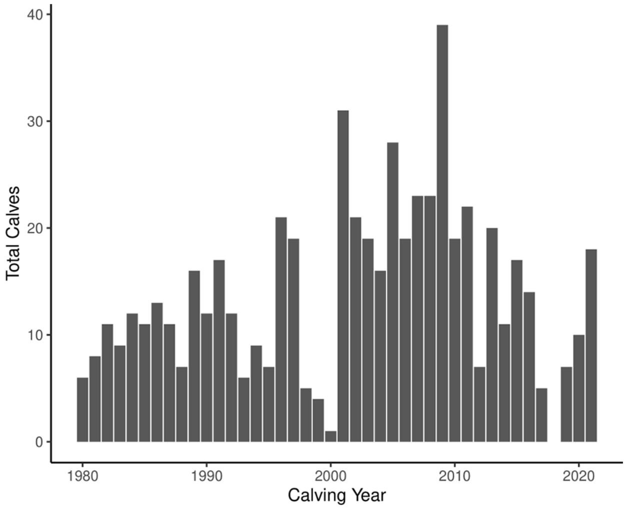

FIGURE 1 | Total number of observed right whale calves born each year since 1980.

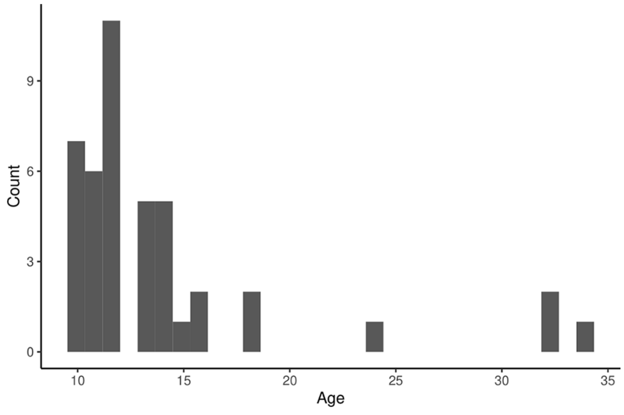

FIGURE 2 | Histogram showing the age frequencies of known-age, sexually mature females that have never been observed with a calf and were presumed alive as of 2021.

to be assigned to distinct matrilines. There were 97 matrilines determined, consisting of two to four observed generations (2 generations: 58.8%; 3 generations: 28.9%; 4 generations: 12.4%). The longevity of the matrilines ranged from 3–53 years (calculated by finding the difference between the earliest year and latest year a member from each matriline was sighted), with some matriline observation periods spanning over 30 years in all generational categories (two, three, and four generation matrilines). Periods of low reproduction were most apparent in 1998–2000 and 2017–2019 (**Figure 1**). There was a significant positive association between the calving index of individual females and the calving index of their matriarchs ($p = 0.01$, $\tau = 0.22$), therefore supporting that fecundity is matrilineally linked.

The case studies shown in **Figure 3** provide specific examples of matrilines who differed in their reproductive success over the same time period. The matriline of matriarch #1140, also known as "Wart", produced four observed generations in 40 years, and included 29 individuals total (**Figure 3A**). This matriline maintained high fecundity throughout its generations; matriarch #1140 had a calving index of 0.175 that fell within the highest 50% of the overall calving index range of the population (0–0.286), and five of her progeny's calving indices fell within this range as well. In contrast, matriarch #1281, also known as "Punctuation", had a higher calving index of 0.229, but fewer total progeny; three generations were observed in 38 years, which only included ten individuals total (**Figure 3B**). Factors beyond the individual fecundity of each sexually mature female contributed to the differences in matriline size in these two case studies, including premature death and offspring sex ratio. Matriarch #1140 had a higher ratio of female calves compared to matriarch #1281, which created higher potential for growth within the matriline. Both matrilines included female descendants that died prematurely, including four of the 11 known female descendants of #1140 as well as the only two known female descendants of #1281. These case studies illustrate how high anthropogenic mortality rates and associated premature mortality reduce population fecundity.

Influence of Habitat Use on Fecundity

Reproductive success between GSL and non-GSL females was significantly different ($x^2 = 4.45$, $p = 0.035$; **Figure 4**). Of the sexually mature females who used the Gulf of St. Lawrence ($n = 44$), 47.7% gave birth at least once between 2016 and 2021, while out of the sexually mature females who did not use the Gulf of St. Lawrence ($n = 100$) only 28.0% gave birth within the same period. Notably, four females gave birth twice within this time span, and all four mothers used the Gulf of St. Lawrence. From the 2021 calving year alone, there were 18 new calves (National Oceanic and Atmospheric Administration, 2021; Right Whale News, 2021; Pettis et al., 2022), and half of their mothers were recorded in the Gulf of St. Lawrence between 2015–2019. The pattern of high Gulf of St. Lawrence usage amongst fecund females was also seen in our case studies: of the individuals in #1140's matriline with known habitat use patterns ($n = 17$), 64.7% visited the habitat (**Figure 3A**), while 75.0% of #1281's matriline who had known habitat use patterns ($n = 4$) did the same (**Figure 3B**).

Matrilineal Influence on Habitat Use

Use of the Gulf of St. Lawrence was significantly associated between an individual and its mother ($x^2 = 14.46$, $p = 1.43\text{x}10^{-4}$; **Figure 5**), but not between matriarchs and their progeny, which encompasses multiple generations within a matriline. Of the 187 individuals that used the Gulf of St. Lawrence in the years 2015–2019 (Crowe et al., 2021), 78 had a mother that was observed at some point during that time. Of the 54 mothers who used the Gulf of St. Lawrence, the majority of their offspring used the habitat as well (64.8%). Similarly, of the 109 mothers who did not use the Gulf of St. Lawrence, the majority of their offspring also did not use it (67.9%). It was found that both female and male offspring were significantly likely to follow their mother's habitat use patterns (females: $x^2 = 7.05$, $p = 7.94\text{x}10^{-3}$; males: $x^2 = 6.07$, $p = 0.01$), with 68.0% of female and 65.1% of male habitat use matching that of their mothers.

Finally, our analysis showed that offspring of mothers who used the Gulf of St. Lawrence between 2015–2019 were less likely to match their mother's habitat use patterns as they aged. In contrast, no such tendency existed within offspring of mothers who did not use the Gulf of St. Lawrence (GSL: $p = 0.02$; Non-GSL: $p = 0.1$, **Figure 6**). It was found that 92.3% of offspring born in or after 2015 matched the habitat use patterns of their mothers who used the Gulf of St. Lawrence, while 56.1% of offspring born before 2015 did the same. In contrast, 68.8% of offspring born in or after 2015 matched the habitat use patterns of their mothers who did not use the Gulf of St. Lawrence, while 67.7% born before 2015 did the same.

DISCUSSION

Matriarchs with higher lifetime fecundity were more likely to produce more fecund female offspring. A matrilineal predisposition for high fecundity could be an underlying driver of reproductive resilience, even during periods of low fecundity at the scale of the population. Fecundity within a matriline is also heavily impacted by premature deaths (primarily caused by

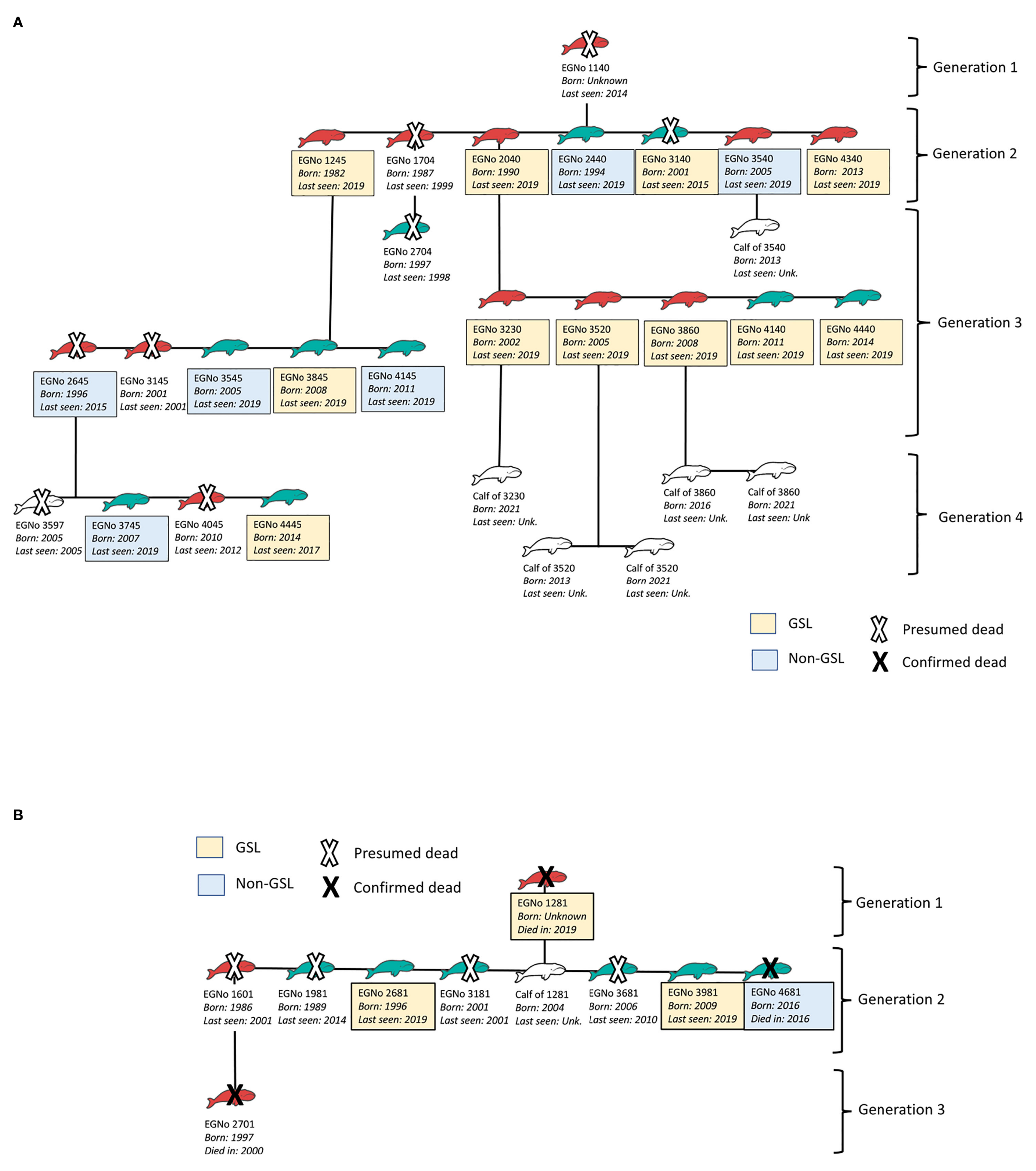

FIGURE 3 | Schematics showing the direct descendants of two right whale matriarchs and their progeny. **(A)** shows the matriline produced by matriarch #1140, and **(B)** shows the matriline produced by matriarch #1281. Blue icons indicate males, red icons indicate females, and white icons are individuals of unknown sex. Text below each icon lists the individual identification number, birth year, and year last sighted or year of death. Complete sightings data in this study were only assessed through 2019, so individuals last seen in 2019 may have been seen more recently, but complete calving data is shown through the 2021 birthing season. Text boxes with a yellow background indicate individuals that have been seen in the Gulf of St. Lawrence since 2015, and text boxes with a blue background indicate individuals that have been sighted since 2015, but not in the Gulf of St. Lawrence. Text boxes without a colored background indicate individuals that have not been sighted in 2015 or after. Whale icons with a white X are presumed to have died, and those with a black X have had their death visually confirmed.

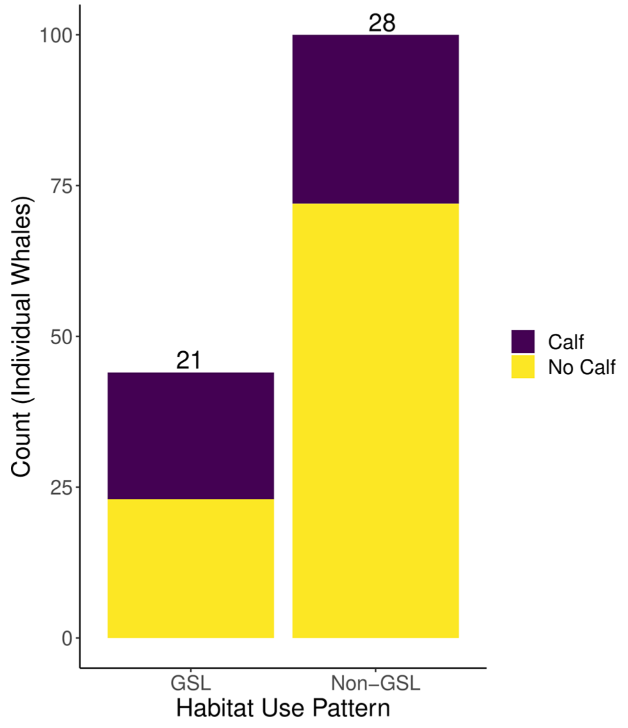

FIGURE 4 | A comparison of the number of females who were sexually mature by 2016 that did and did not have a calf between the years 2016–2021, parsed by habitat use. "GSL" indicates individuals that used the Gulf of St. Lawrence at least once during the years 2015–2019. "Non-GSL" indicates individuals that were not seen in the Gulf of St. Lawrence during the same period. The numbers at the top of the bars show the total number of mothers who gave birth in each habitat category.

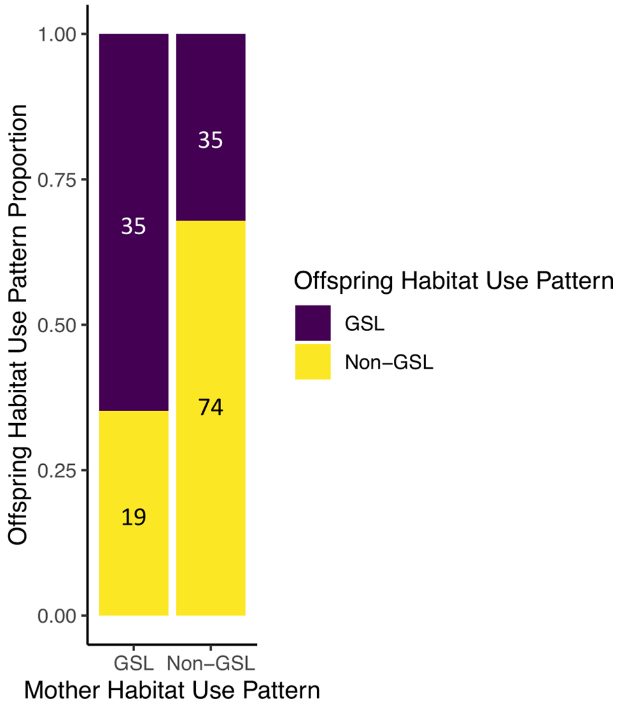

FIGURE 5 | The proportions of individuals' observed habitat use patterns relative to the habitat use patterns of their mothers. "GSL" indicates individuals that used the Gulf of St. Lawrence at least once during the years 2015–2019. "Non-GSL" indicates individuals that were not seen in the Gulf of St. Lawrence during the same period. The numbers within the bars are the total number of offspring represented by the respective bar/color coding.

vessel strikes and fishing gear entanglements) and offspring sex ratio. Females who used the Gulf of St. Lawrence during or after 2015 have been more reproductively successful than their counterparts who did not use the habitat during that time. Finally, a significant number of offspring emulate their mother's habitat use patterns. However, the likelihood of offspring matching their mother's habitat use behavior decreases with age. These habitat use patterns provide evidence that learned behavior is maternally transmitted, which could contribute to differences in reproductive success that have been observed between matrilines.

Matrilines and Their Fecundity

We chose the case studies of matriarchs #1140 and #1281 to highlight the factors that can contribute to a matriline's reproductive success, as well as how these factors converge to determine the matriline's growth and longevity. The matriarchs in both case studies were highly fecund, having given birth to at least seven offspring each. Despite this, key differences contributed to the fate of their respective matrilines, and revealed the impact that sex ratio and survivability of offspring can have on reproductive success. When considering the results of this analysis, it is important to note that our matrilineal design did not account for the reproductive success of male progeny. Out of #1140's seven offspring, five were female which allowed for more opportunities for reproduction than in #1281's matriline. The descendants of #1140 followed in their matriarch's highly fecund footsteps: all of #1140's female descendants that lived long enough to reach sexual maturity gave birth at least once, and five of these females have given birth multiple times at a substantial rate. The matriline of #1140 shows that having many female offspring, combined with high survivability, can lead to a more successful matriline that exponentially contributes to the overall species' growth. However, reproductive potential was lost in this matriline with the early deaths of two females, #1704 and #2645.

In contrast, #1281 was also highly fecund with eight offspring, but only one of these individuals was female. As a result, there was less opportunity for the matriline to expand. The sole female offspring, #1601, demonstrated the potential to be highly fecund since she gave birth to her first calf at 11 years old. Both #1601 and her female calf, #2701 have presumably died since they have not been sighted in several years. Moreover, the matriarch, #1281, died of a vessel strike in the Gulf of St. Lawrence in 2019 (Pettis et al., 2020), so it appears this matriline has ended. These case studies show that growth of a matriline depends on individual fecundity, sex ratio and timing of male vs. female calf births, and the occurrence of premature mortality.

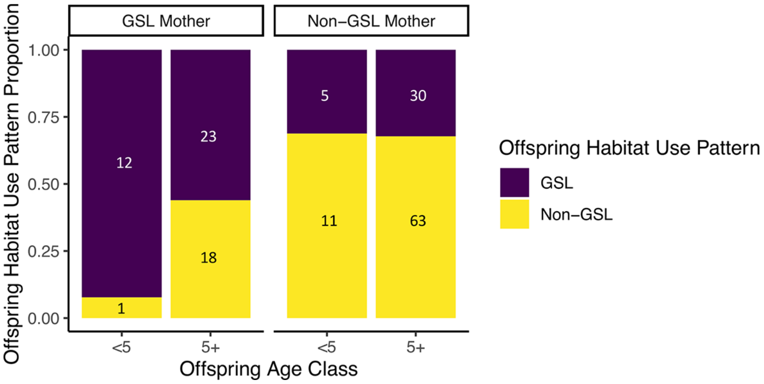

FIGURE 6 | Comparison of habitat use patterns between mothers and their offspring, with offspring categorized by age and parsed by the habitat usage pattern of their mother. The x-axis labels correspond to the individual whale's age in 2019, where "Age < 5" represents offspring younger than five, and "Age 5+" represents offspring that were at least five years old.

Comparing the births that occurred within matrilines highlights missed opportunities for reproduction, and provides detailed insight into the generally low birth rates of North Atlantic right whales (Kraus et al., 2001). The considerably higher birth rates of southern right whale populations (Best, 1990; Payne et al., 1990; Kraus et al., 2001; Corkeron et al., 2018) indicate that North Atlantic right whales should be biologically capable of higher reproduction. These low birth rates are particularly troubling when considered with the fact that there are currently less than 100 breeding females in the population (Pettis et al., 2022). This study finds that the fecundity of an individual female is positively linked to the fecundity of her matriarch, and the premature losses of females in successful matrilines from vessel strike or entanglement therefore disproportionately reduce population growth potential. For this reason, the high level of documented mortality in Gulf of St. Lawrence in 2017 and 2019 (Daoust et al., 2018; Bourque et al., 2020) and the fact that mothers that use Gulf of St. Lawrence are more productive than other cohorts of the population is particularly concerning. Our case studies show that a large number of females with high survivability are critical for a productive population, yet female survival rates are currently declining species-wide, and there are fewer females than males in the population as a result (Pace et al., 2017). Anthropogenic pressures, including vessel strikes and fishing gear entanglements, are causes of these early deaths (Knowlton & Kraus, 2001; van der Hoop et al., 2013; Sharp et al., 2019), but they can also contribute to non-lethal health impacts that hinder reproductive potential (van der Hoop et al., 2016). The recovery of the population largely depends on the ability of these females to survive and successfully reproduce.

Gulf of St. Lawrence Usage and Fecundity

Gulf of St. Lawrence users were significantly more likely to give birth during the 2016–2021 period than their counterparts, and this may have occurred because prey conditions are more favorable in that habitat. Sightings data show that most of the population does not use the Gulf of St. Lawrence (Crowe et al., 2021), and the prey quality and location of the summertime foraging grounds for 60% of the population is largely unknown. Because of this gap in knowledge, a comparison between prey fields is not currently possible, but the reproductive rates of females who did and did not use the Gulf of St. Lawrence in recent years give us a proxy for how supportive the habitat is compared to these unknown locations. Gaining better insight into the drivers of habitat usage will be useful for predicting the capacity that the Gulf of St. Lawrence, and other habitats, will be used in the future. This is especially important since climate-driven shifts in prey distributions are projected to continue (Reygondeau & Beaugrand, 2011; Ross et al., 2021), causing right whales to seek out new foraging areas.

Although the Gulf of St. Lawrence seemingly played a significant role in supplying enough energy to support these pregnant females, the energetic costs associated with traveling there must be noted when considering the habitat's ability to support the population. Usage of the Gulf of St. Lawrence occurs during peak foraging season (Baumgartner & Mate, 2003; Crowe et al., 2021), and while it is unknown whether foraging occurs during travel to the area, this consistent and extended transit could impact their seasonal energy budget. Within the Gulf of St. Lawrence, individuals aggregate on the western side (Crowe et al., 2021) which is about 1000 km swimming distance farther north than the traditional summertime foraging areas in the Gulf of Maine (Winn et al., 1986; Greene and Pershing, 2004). Using 3.5 km/hr as an estimated migratory speed (Mate et al., 1997; Zerbini et al., 2016; Mackay et al., 2020), it would take about 11–12 days of swimming 24 hr/day for a whale to travel the distance from the Gulf of Maine to Shediac Valley in the Gulf of St. Lawrence. Further study is warranted to determine the energetic budget and foraging opportunities associated with this transit. It is possible that the remaining 60% of the population that have not been recently sighted in the Gulf of St. Lawrence incurs similar energetic costs during their transits, but the increased reproductive success of the Gulf of

St. Lawrence-users indicates there may be energetic differences existing between the two groups that should be explored. Furthermore, while the GSL may become a regular foraging habitat, there's evidence that the effort to find and establish this new habitat costs them energy and foraging success (Pershing and Pendleton, 2021). Higher reproductive success in Gulf of St. Lawrence users may reflect a behavioral dichotomy between whales with good health and fitness that are able to manage the challenge of consistently traveling farther north compared to whales in poorer health. However, if the Gulf of St. Lawrence can provide adequate nutrition for all demographics that compensates for the potential energy expended, the habitat may benefit the population as a whole.

While a large, consistent number of individuals going to the Gulf of St. Lawrence is an extension of the whales' typical habitat, historical documents indicate that right whales visited this area regularly in past centuries (Reeves et al., 1999; McLeod et al., 2008; Brown et al., 2009). Studies have also shown that the species has a precedent for travelling outside of its typical habitat, likely motivated by a need to forage (Knowlton et al., 1992; Jacobsen et al., 2004; Smith et al., 2006; Mellinger et al., 2011; Fortune et al., 2013). Given that the whales' energetic needs were likely not being met at their typical feeding grounds due to climate-driven declines in prey abundance (Record et al., 2019; Meyer-Gutbrod et al., 2021), it is likely that they are traveling to the Gulf of St. Lawrence for the same reason.

Low birth rates in 2017–2020 (Meyer-Gutbrod et al., 2021; Pettis et al., 2022) and an analysis of *Calanus* spp. densities in the southern Gulf of St. Lawrence (Gavrilchuk et al., 2021) indicated that the habitat may not be supporting successful reproduction. However, the significant reproductive success of mothers that used the Gulf of St. Lawrence that we found in our study contradicts this idea, and indicates that the prey supply has been suitable. Though it is unknown whether individuals who forage in the Gulf of St. Lawrence remain there exclusively, the success of the 2016–2021 mothers who used it shows that the habitat likely played an important role in supporting their nutritional needs. The high rate of inter-annual return exhibited by the whales who use the Gulf of St. Lawrence (Crowe et al., 2021) underscores the likelihood that these individuals are being reinforced to return due to favorable conditions. However, reproductive success is only an indirect assessment of potential habitat quality. Coupled with the fact that the distribution shift is a relatively new phenomenon, further research is essential to determine long-term suitability of this habitat.

Maternally Influenced Habitat Use

Analysis of habitat use behaviors of kin shows that individuals are more likely to use the Gulf of St. Lawrence if their mother does as well, mirroring maternally influenced migratory and foraging site fidelity documented in southern right whales (Valenzuela et al., 2009; Carroll et al., 2015), and providing further support for matrilineally directed site fidelity in North Atlantic right whales that has been previously observed in both current and historical populations (Malik et al., 1999; Frasier et al., 2022). This result, as well as the size of the proportion of the population that uses the Gulf of St. Lawrence, suggests that learned behavior exists within family groups, including older juveniles and sexually mature whales. This behavior could indicate that some matrilines pass down knowledge of more productive foraging grounds than others, leading to superior reproductive success and higher fecundity. However, the strength of this pattern decreases with age. Could older whales, who were likely brought to other foraging grounds as calves that are now far less productive (Meyer-Gutbrod et al., 2021), be diverging from their learned habitat use patterns in favor of more productive areas? Given the increase in Gulf of St. Lawrence users over the 2015–2019 period (Crowe et al., 2021), this seems likely, but further research regarding the age and generational distribution of Gulf of St. Lawrence users relative to their family lines would be valuable.

While the patterns in fecundity and habitat use among kin shown in this analysis suggest that learned behavior likely impacts reproduction, it is unclear if genetics are also a component. Investigating the genetics of matriline members would provide valuable understanding of family dynamics that may not be accessible by reviewing traditional photographic data (Hamilton et al., 2022). There may also be patterns in individual size and health history that are consistent between the Gulf of St. Lawrence and non-Gulf of St. Lawrence sub-populations that contribute to the difference in fecundity between these two groups. Further analysis is required to understand the mechanistic drivers between these complex demographic and behavioral phenomena.

Limitations and Future Work

Dedicated monitoring of the right whale population and individual life histories largely began in the early 1980s, which limits our designations of matrilines and their founding matriarchs. As a result, some matrilines which were classified as distinct may share a common ancestor who was not documented, and the number of distinct matrilines may be overestimated. Furthermore, although the survey effort dedicated to this population is unparalleled relative to other baleen whale species in the North Atlantic, visual surveys are an imperfect method of detecting births. It is possible that some calves have been missed within the survey range, particularly those who died at birth. Therefore, our calving index may be underestimated for some individuals.

The scope of our study is also limited by the lack of sighting data corresponding to the foraging grounds of individuals who do not use the Gulf of St. Lawrence as well as the limited sightings data from the Gulf of St. Lawrence prior to 2015. Without knowing the recent summertime foraging habitats of this large subset of the population, it is difficult to determine the specific benefits of Gulf of St. Lawrence usage and its relative impact on reproduction. For instance, it is possible that the more reproductively successful mothers who used the Gulf of St. Lawrence are not exclusively feeding there, and are traveling to other foraging grounds as well. Identifying where the rest of the population is feeding would provide valuable insight into the exclusive benefits and/or limitations that the Gulf of St. Lawrence provides, specifically regarding the extent of the role it plays in fecundity and successful reproduction.

When considering these results, it should be noted that the threat posed to reproductive females by anthropogenic pressures is significant (Corkeron et al., 2018). Recent studies have found that the stress of entanglement and vessel-strike injuries causes poor body condition within the population (Stewart et al., 2021), which negatively impacts the body condition and survival of offspring and decreases the female's capacity to reproduce (Kraus et al., 2001; van der Hoop et al., 2016; Christiansen et al., 2018). We did not factor the impact of anthropogenic pressures or maternal condition into our assessment of female fecundity, and future work should consider the impact of these factors. This study assumed that whales had equal fecundity potential throughout their entire adult life, which was supported by a lack of correlation between age and calving index within females who had given birth at least once. However, further analysis to examine fluctuations in fecundity with age would be valuable. This relationship is difficult to explore because the high rate of anthropogenic mortalities within the population results in widespread premature death, and thus older reproductive females are relatively rare.

Implications

The results of this study illustrate a complex ecological dichotomy that has been emerging over the past few years regarding whether the distribution shift to the Gulf of St. Lawrence is beneficial. Usage of this habitat may be driven by anomalously low prey densities in the traditional foraging grounds consistent with anthropogenic climate change (Meyer-Gutbrod et al., 2021). Analysis of the densities of calanoid copepods in the southern Gulf of St. Lawrence have identified the region as a substantial foraging area, with its shallow bottom contributing to accumulations of copepods that provide notable foraging potential (Plourde et al., 2019; Sorochan et al., 2021). Our study revealed evidence that the foraging opportunity provided by the area supported increased reproduction, and these factors could possibly reinforce individuals to return to the Gulf of St. Lawrence each year as a result.

While communication between individuals and shared habitat use behaviors can benefit whales by improving foraging success, they can also harm the population when the habitat presents ecological risks. The Gulf of St. Lawrence is hazardous, causing the whales to pass through a heavily trafficked area that includes various fixed gear fishing grounds and shipping lanes that serve as the economic highway to the U.S. and Canada (Daoust et al., 2018; Crowe et al., 2021). The dangers of using this area were realized in 2017, when an unprecedented 17 mortalities were recorded, including 12 mortalities in the Gulf of St. Lawrence (Daoust et al., 2018; Meyer-Gutbrod et al., 2018). An unusual mortality event was declared as a result, and another mass mortality was recorded in 2019 that included ten mortalities, seven of which occurred in the Gulf of St. Lawrence (Pettis et al., 2020). The high mortality and injury rates associated with use of this habitat poses a significant threat to the species. These risks are compounded by our findings that female fecundity is positively associated with her matriarch's fecundity, and learned habitat use behavior is communicated between mother and calf. With more fecund females utilizing the Gulf of St. Lawrence, and passing this habitat use pattern onto highly fecund offspring, future population growth may hinge on adequate protection of this habitat.

DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: The datasets used for our study are curated and managed by the North Atlantic Right Whale Consortium. A written proposal must be submitted and approved in order to access any of the Consortium's datasets. Instructions for accessing these datasets can be found at https://www.narwc.org/.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because no physical experiments were done during this project. This project exclusively utilized pre-existing aerial, boat, and opportunistic survey data.

AUTHOR CONTRIBUTIONS

EM-G conceptualized this research. AB and EM-G performed the data analyses. AB wrote the manuscript, with significant contribution from EM-G. LC and PH curated the data, and provided additional reviews and edits for this manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

Support for this work was provided by the University of South Carolina's SURF and Magellan Scholar grants.

ACKNOWLEDGMENTS

Many thanks to the North Atlantic Right Whale Consortium for granting the data used for this project and particular thanks to the New England Aquarium Catalog team for their impeccable curation, the field teams for collecting these data over a long time series, and the geneticists whose work have helped reveal maternal lineages. We thank Heather Pettis for assistance with these data.

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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.

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ORIGINAL RESEARCH
published: 23 June 2022
doi: 10.3389/fmars.2022.843875

Changes of Oceanic Conditions Drive Chagos Whale Migration Patterns in the Central Indian Ocean

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Marine ecosystems are experiencing rapid shifts under climate change scenarios and baleen whales are vulnerable to environmental change, although not all impacts are yet clear. We identify how the migration behaviour of the Chagos whale, likely a pygmy blue whale (*Balaenoptera musculus brevicauda*), has changed in association with shifts in environmental factors. We used up to 18 years of continuous underwater acoustic recordings to analyse the relationships between whale acoustic presence and sea surface temperature (SST), chlorophyll-a concentration, El-Niño Southern Oscillation (ENSO) and the Indian Ocean Dipole (IOD). We compared these relationships between two independent sites Diego Garcia southeast (DGS) and Diego Garcia northwest (DGN) where Chagos whales are detected and are suspected to move interannually across the Chagos-Laccadive ridge. We showed that the number of whale songs detected increased on average by 7.7% and 12.6% annually at DGS and DGN respectively. At the DGS site, Chagos whales shifted their arrival time earlier by 4.2 ± 2.0 days/year ± SE and were detected for a longer period by 7.3 ± 1.2 days/year ± SE across 18 years. A larger number of songs were detected during periods of higher chlorophyll-a concentration, and with positive IOD phases. At the DGN site, we did not see an earlier shift in arrival and songs were not detected for a longer period across the 13 years. Whale presence at DGN had a weaker but opposite relationship with chlorophyll-a and IOD. The oceanic conditions in the Indian Ocean are predicted to change under future climate scenarios and this will likely influence Chagos whale migratory behaviour. Understanding how environmental factors influence whale movement patterns can help predict how whales may respond to future environmental change. We demonstrate the value of long-term acoustic monitoring of marine fauna to determine how they may be affected by changing environmental conditions.

Keywords: baleen whale, long-term change, climate change, interannual variability, environmental drivers, Indian Ocean Dipole (IOD), El Nino Southern Oscillation (ENSO), sea surface temperatures

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

Received: *27 December 2021*
Accepted: *26 May 2022*
Published: *23 June 2022*

Citation:
Huang JL, Leroy EC, Truong G and Rogers TL (2022) Changes of Oceanic Conditions Drive Chagos Whale Migration Patterns in the Central Indian Ocean. Front. Mar. Sci. 9:843875. doi: 10.3389/fmars.2022.843875

1 INTRODUCTION

Marine ecosystems are experiencing rapid shifts in structure and function globally (Belkin, 2009; Bryndum-Buchholz et al., 2019), which challenges the ability of marine wildlife to adapt (Poloczanska et al., 2013; Miller et al., 2018). Ocean warming and acidification, resulting from anthropogenic climate change, pose a threat to the marine environment and biodiversity (Miller et al., 2018). For example, increasing sea temperature has been associated with changes in biodiversity of the deep-sea fish community (Yasuhara and Danovaro, 2016). Global environmental changes such as heat shocks and ocean acidification also have negative impacts on the temperate seagrass ecosystem (Perry et al., 2019). Current predictions indicate that global warming will continue, with or without mitigation (IPCC, 2021). Furthermore, greater variability such as more frequent and more extreme events (i.e., such as heatwaves, tropical cyclones, and flooding) as well as changes to the phases of natural climate phenomena (i.e., ENSO, the El Niño Southern Oscillation and IOD, the Indian Ocean Dipole) are predicted with increased global warming (Cai et al., 2014; Cai et al., 2015). The large-scale climate phenomena ENSO and IOD affect weather globally, and the frequency of extreme ENSO and IOD conditions is likely to increase under increased greenhouse warming (Cai et al., 2014; Cai et al., 2015). Marine ecosystems are experiencing fluctuations due to this large-scale environmental variability, such as an increase in sea surface temperature (SST), changes to currents and upwelling systems, and changes to primary productivity. The potential effects of these changes may require marine species to adapt their behaviour (Gibson et al., 2007). Therefore, we need to better understand how marine wildlife responds to large-scale environmental changes.

Measuring the changes in the timing of migration is an excellent way to study the response of fauna to environmental variability particularly where important life history events are tied to specific timing (i.e., breeding or foraging is tied to times of high-resource availability). The responses of marine animals to environmental change vary across individuals, populations, and communities (Miller et al., 2018). For example, phenological changes, such as the variation in the timing of migration, will affect essential components of a species' life history (Forrest and Miller-Rushing, 2010). Understanding potential drivers of mammal migration will help us predict how they will respond to future warming scenarios (Gnanadesikan et al., 2017). The drivers of migration vary across species and ecosystems. Round-trip migration patterns are driven by the need for refuge (to avoid unfavourable conditions), to breed (to reproduce) and to forage (to increase access to food) (Shaw, 2016). Many marine species migrate to breed (Shaw, 2016). For example, the cuttlefish *Sepia officinalis*, the squid *Loligo gahi*, and the bivalve *Macoma balthica* are proposed to have latitudinal or longitudinal migration for spawning seasons in different ocean basins (Hiddink, 2003; Arkhipkin et al., 2004; Keller et al., 2014; Shaw, 2016). On the other hand, mammals display diverse migration types (Gnanadesikan et al., 2017). Large baleen whales tend to be long-distance migrants, moving poleward in summer to the feeding areas and migrating towards lower latitudes in winter to breed and calve (Horton et al., 2011). Migration timing between feeding and breeding grounds may be influenced by species-specific environmental shifts and complex internal and external mechanisms (Dingle and Drake, 2007). Global climate change is considered greater driver of change in the distribution and phenology of marine compared to terrestrial animals (Poloczanska et al., 2013). Studying the shifts of migration timing could be an ideal approach to gain insight into how marine wildlife responds to environmental variability.

Large baleen whales are potentially vulnerable to environmental changes. Many baleen whale species and populations are endangered, following the 20th century industrial whaling. For instance, as the largest animals in the world, blue whales (*Balaenoptera musculus*) were targeted by whalers, with only 0.15% of the Southern Hemisphere population surviving commercial whaling (Branch et al., 2007; Thomas et al., 2016). Large baleen whales such as blue whales have few natural predators and feed on prey at low trophic levels, occupying a rare niche with few other species. Thus, if global change that leads to their loss occurs, it is unlikely that they could be easily replaced within the food web. Furthermore, their long-distance migration behaviour requires considerable energy (Branch et al., 2007). Thus, large baleen whales require predictable and high-energy food sources for the few months they feed. This makes them vulnerable and less able to adapt when climate change and other anthropogenic-related conditions reduce food availability and predictability. Using a decade of acoustic data, a previous study showed that the distributions and movement patterns of six baleen whale species were shifting in the western Atlantic (Davis et al., 2020). Moreover, previous studies have shown the relationships between baleen whales phenology and environmental factors. For example, Derville et al. (2019) assessed humpback whales' habitat shifting under the impact of ocean warming in Oceania breeding grounds using 19 years of survey data. Charif et al. (2020) used a 6-year dataset to analyse the phenological changes of North Atlantic right whales as environmental conditions change. An eight-year humpback whale acoustic dataset was used to study the whale presence and climate oscillations (Schall et al., 2021).

The Indian Ocean is an ideal location to identify how environmental changes affect whale behaviour because of its high biodiversity. It is a complex marine system with nutrient-poor water, but diverse marine fauna species (Anderson et al., 2012). It is the warmest of the ocean basins, with the southern parts of the Indian Ocean experiencing higher rates of warming compared to the northern areas (Han et al., 2014). Variant blue whale species are recorded acoustically within this region including Antarctic blue whale (*B.m. intermedia*); and four acoustic populations of the pygmy blue whale: Sri Lankan; Madagascan; Australian and Oman whales (Stafford et al., 2004; Stafford et al., 2011; Samaran et al., 2013; Double et al., 2014; Leroy et al., 2016; Leroy et al., 2018; Cerchio et al., 2020). Blue whales produce stereotypical calls, repeated over days, months, and years. Each blue whale population has a distinct vocal characteristic, which is used to identify their 'acoustic populations' (McDonald et al., 2006). The Chagos whales are possibly a new acoustic population of blue whales (*B.m. brevicauda spp.*) (Leroy et al., 2021). Chagos songs were initially considered as a variant of the Madagascan pygmy blue whale song (McDonald et al., 2006). Preliminary reports have shown that Chagos whales have acoustically presented all year at the southern end of the Seychelle-Chagos thermocline ridge (Sousa and Harris, 2015; Leroy et al., 2021). The area of the Seychelle-Chagos thermocline ridge is a region of low sea surface temperature and high nutrients (Jayakumar et al., 2011). Yet we know little about the ecology and migration patterns of the Chagos whales, especially how their movement are linked with the environmental shifting in the nutrient-rich tropical region.

This study aims to give an insight into how marine species respond to environmental shifts. The detections of the Chagos whale songs in almost two decades of continuous acoustic data recorded in either side of the Chagos-Laccadive ridge are used first to quantify inter- and intra-annual variations in the acoustic presence and then, to identify if acoustic presence changes with shifts in environmental conditions such as sea surface temperature (SST), primary production (chlorophyll-a concentration), Southern Oscillation Index (SOI) and Indian Ocean Dipole (IOD). The hypothesis for the environmental factors impacting Chagos whale presence is as follows: if the sea surface temperature (SST) is low and if primary production is high then more Chagos whales will be present. We aim to give an insight on how climate change may affect the migration phenology of the Chagos whale in the tropical central Indian Ocean.

2 MATERIALS AND METHODS

2.1 Study Area

Underwater acoustic data was obtained from the international data system of the Comprehensive Nuclear Test-Ban Treaty Organisation (CTBTO). Two hydrophone arrays were located 220 km apart on either side of Diego Garcia Island: one on the northwest side (Diego Garcia North - DGN), and the other on the southeast side (Diego Garcia South – DGS) (**Figure 1**). Within each array, a set of three hydrophones was moored in the sound fixing and ranging (SOFAR) channel, where sound achieves the maximum speed (Hanson, 2001).

The CTBTO hydroacoustic stations continuously monitor underwater sound waves with a sampling frequency of 250 Hz. For the DGN site, the data recorded between January 2002 and February 2014 by the hydrophone number H08N1 (6.34°S, 71.01°E) were used, and for DGS the data recorded between January 2001 and December 2019 by the instrument number H08S1 (7.65°S, 72.47°E) were used. The instrument depths were respectively 1248 and 1413 m (see Leroy et al., 2021 for more details). The recording sites are separated by the Chagos bank (Pulli and Upton, 2001). Thus, we used the DGN and DGS sites to represent the soundscapes northwest and southeast of Diego Garcia respectively.

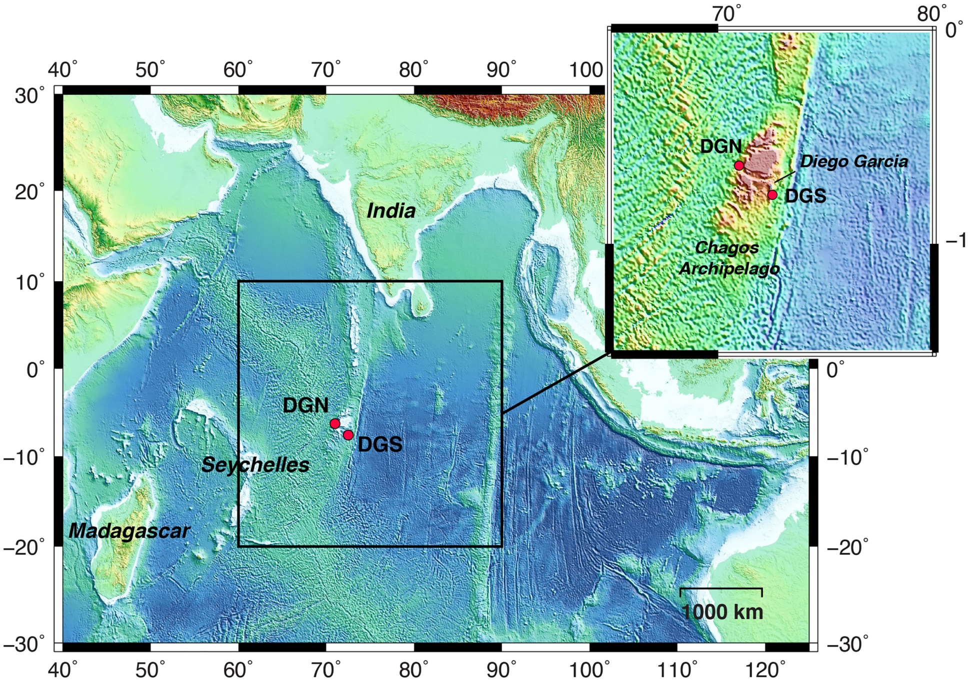


FIGURE 1 | Map of the study area in the central Indian Ocean. Red dots indicate the locations of the hydrophone stations: north-western site off Diego Garcia (referred to as DGN), and south-eastern site off Diego Garcia (referred to as DGS). The dotted rectangle shows the location of the Chagos-Laccadive Ridge. B This figure is modified from Leroy et al., 2021.

2.2 Whale Acoustic Presence Data

Hourly presence or absence of Chagos whale songs was inferred from automated detections of the signal as described in Leroy et al. (2021). All data from the DGN site and data prior to February 2018 from the DGS site were from Leroy et al., 2021, however, data after February 2018 to the end of 2019 from the DGS site were obtained and tested for this study using the same approach as described in Leroy et al. (2021).

The individual detections were logged into Matlab matrices along with the information related to each individual song, such as the exact date-time of the detected event. The data from each site were divided into eight-day blocks (192 hours), consistent with the local environmental data (see *2.3 Environmental Data*, below). Whale acoustic presence is defined as the proportion of hours in the eight-day block in which whale songs were detected. In cases where acoustic recording had been interrupted, and if the recorded hours were less than 50% of the time block, these blocks were considered to have insufficient data and were excluded from the analysis. In 13 years of acoustic data, 82.3% (498 eight-day blocks) of DGN recordings and in 18 years 91.7% (760 eight-day blocks) of DGS data had sufficiently complete data to be included in the analysis. Acoustic presence at both sites was pooled to analyse seasonal variability (Similar method to aggregate presence data for right whale see (Similar method to aggregate presence data for right whale see Charif et al., 2020). Pooled data was divided into months for comparison to oceanic data (see *Environmental Data*, below).

We used the eight-day grouped whale acoustic presence data to analyse the peak and extended peak seasons. To identify the peak and the extended peak seasons, the following algorithms were applied: firstly, we found the eight-day time blocks when whale acoustic presence was greater than 90% in the 192-hour block throughout the entire time series, then we chose the peak to be eight-day period with the highest whale acoustic presence among consecutive periods containing data. When there was more than one period satisfying the criteria, for example, multiple consecutive 100% whale acoustic presence periods, all 100% eight-day periods were defined as peaks. Next, the growth rate of the whale acoustic presence was calculated as the difference between the two adjacent periods divided by the whale acoustic presence of the preceding period. The maximum rate (defined as the start date of the extended peak) and minimum rate (defined as the end date of extended the peak) are the ones with the most rapid change at the local range. Lastly, the time between the start date and the end date containing the peak whale acoustic presence was defined as the extended peak season. Similar methods to define extended peak seasons were applied in Charif et al. (2020), where they used the smoothed eight-period differences.

2.3 Environmental Data

Two local drivers and two oceanic drivers were considered in this study. Data for the two local drivers, sea surface temperature (SST) and chlorophyll-a (as an indicator of phytoplankton abundance), were downloaded from the NOAA ocean watch website (https://oceanwatch.pifsc.noaa.gov/doc.html#currents). The seasonal oceanic data including Dipole Mode Index (DMI) representing the event of Indian Ocean Dipole (IOD) and Southern Oscillation Index (SOI) representing El-Nino Southern Oscillation (ENSO) were extracted from the Australian Bureau of Meteorology (BOM) (http://www.bom.gov.au/climate/enso/soi/) and the NOAA Physical Science Laboratory of Global Climate Observing System (https://psl.noaa.gov/gcos_wgsp/Timeseries/DMI/).

SST was downloaded through the CoralTemp dataset of the NOAA website. The analysed data were continuously recorded (24 hours per day) throughout the study period. The mean SST was computed (In total four data spots with two units at each side, spatial resolution for one unit is approximately 5 km) in the approximately 100 km2 encompassing the hydrophone stations. Then the mean SST was calculated for the corresponding eight-day period. Mean SST and minimum SST were calculated for each year and for two seasons: December to May and June to November.

Chlorophyll-a was used as a proxy of phytoplankton biomass. Blue whales almost feed exclusively on krill (*Euphausiid* spp.). Krill information in the Indian Ocean is limited. We will therefore use the concentration of chlorophyll-a (as an indication of phytoplankton biomass) as blue whale food approximation (Allen, 1971). Chlorophyll-a data were acquired from the MODIS-Aqua 8-daily dataset. Like SST, we computed the mean chlorophyll-a (In total six data spots with two units at one side, three units at the other side, spatial resolution is approximately 4 km per unit) containing the hydrophone stations of 96 km^2. Mean chlorophyll-a was calculated for each year and both seasons (December to May; June to November). One potential caveat is that the measurement of the chlorophyll-a was from the water surface, hence the data may not reflect krill density in deep water (Branch et al., 2007).

SOI was downloaded from the BOM website where it was calculated using the pressure difference between Tahiti and Darwin. DMI was extracted from the NOAA Physical Sciences website, which was based on the HadISST1.1 SST dataset. Both oceanic variables were recorded on a monthly scale.

2.4 Statistical Analysis

2.4.1 Overall Trends and Interannual Difference in the Number of Chagos Whale Songs

To identify if there were trends in the number of Chagos whale songs detected we computed the correlation of annual average whale songs per day (continuous variable) versus year (ordinal variable) for both sites. Spearman rank coefficients were used to represent the correlation and the corresponding p-values were calculated.

Linear models were used to analyse the trend of average songs per day of the Chagos whales versus year for both sites. To compute the percentage of increasing rate, we used the linear model of the logarithm of the average songs per day versus year. To quantify the shift of the start date of the extended peak seasons, linear models were used.

To test whether whale acoustic presence at the DGS and DGN was significantly different, we used the Wilcoxon rank sum test.

2.4.2 Correlation Between Whale Acoustic Presence and Environmental Factors

To assess the correlation of whale acoustic presence and environmental factors at each site we used SST and chlorophyll-a (continuous variables) versus year (ordinal variable) using spearman rank coefficients and calculated the corresponding p-values.

Generalised linear models were used to interpret the relationship between whale acoustic presence (proportion of hours where whale songs were detected) and environmental factors. Whale acoustic presence was paired with SST, chlorophyll-a, DMI and SOI at each site with a binomial family (weight = number of recording hours in the corresponding eight-day period). The effect of year was considered by using 'glm.er' function (Bates et al., 2021) in RStudio.

Generalised linear models (binomial) were chosen because 1) They fit the analysis we made with the acoustic whale song data. Since we aggregated the binary whale songs into 8 days (192 hours), and generalized linear models probabilities, the model can indicate the correlations between the independent and dependent variables. 2) They provide a multiple-period view. Both whale acoustic data and the environmental data for DGN and DGS were continuous and spanning for years, thus binomial models were suitable.

2.4.3 Extended Peak Seasons of the Chagos Whale Songs

For all extended peak seasons detected at both sites, the correlations between the start date (Julian day) with environmental variables (yearly mean SST, mean chlorophyll-a concentration, the corresponding mean and minimum SST and chlorophyll-a concentration) were calculated using Spearman rank coefficients. The correlations between the length of extended peak seasons with environmental variables were calculated using Pearson coefficients.

We identified the first extended peak seasons of each year across 18-year at the DGS site and 13-ear at the DGN site. The spearman rank correlations between the start date (Julian day) with year and the environmental variables were calculated. The years with unclear start dates due to missing data were considered insufficient for analysis. For those years with clear start dates of extended seasons, we calculated the total length of extended peak seasons and calculated the Pearson correlations with the environmental variables. We also calculated the spearman rank coefficient between the total length and year.

3 RESULTS

3.1 Overall Trends and Interannual Difference in the Number of Chagos Whale Songs

We assessed the number of Chagos whale songs detected within a total of 92,180.8 hours of underwater hydroacoustic data from the DGN site and 143,406.7 hours from the DGS site, over 598 and 828 eight-day periods, spanning across 13 and 18 years, respectively. In total, 486,320 Chagos songs were detected at the DGN site over 13 years and 837,640 Chagos songs were detected at the DGS site during the 18-year period. The average number of songs per hour was higher at the DGS site (5.84 per hour) than at the DGN site (5.27 per hour). Chagos song occurrence increased over time for both the DGN and DGS sites (**Figure 2**), although the rate was higher at the DGN compared to the DGS site. The lowest number of Chagos songs recorded was in 2008 at both sites, whereas the greatest number of songs was recorded in 2012 at the DGN site. The greatest number of songs recorded at the

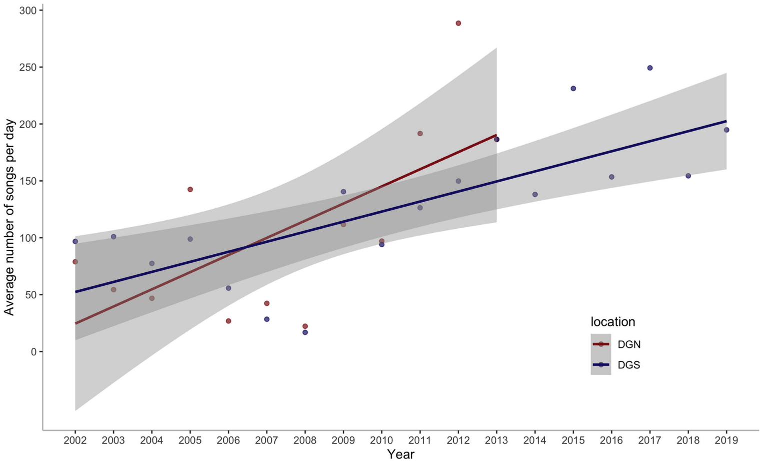


FIGURE 2 | Annual change in the average number of Chagos whale songs detected per day off Diego Garcia/Chagos Archipelago at the north-western (DGN) site where the linear trend has a slope of 15.1 songs/day/year (12.6%/year) with corresponding ρ = 0.56 and p-value of 0.06, and the south-eastern (DGS) site where the linear trend has a slope of 8.8 songs/day/year (7.7%/year) with corresponding ρ of 0.79 and p-value < 0.001. ρ is the Spearman rank coefficient of the average number of songs per day with year.

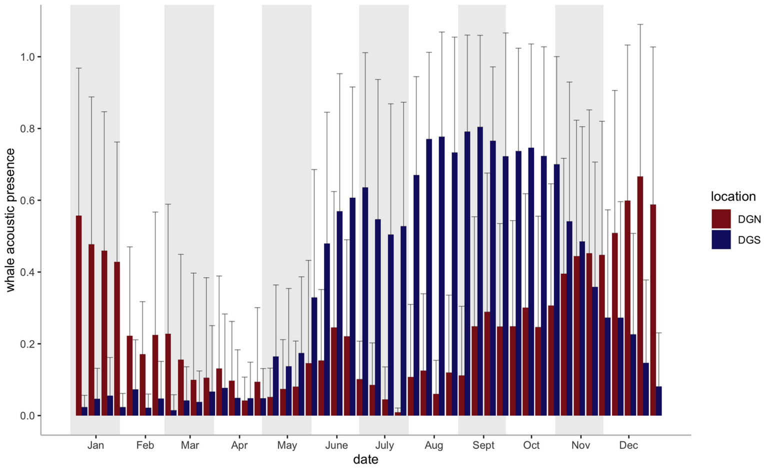


FIGURE 3 | Mean Chagos whale acoustic presence (%) + Standard error (defined as the percentage of hours when whale songs were detected, see *Material and Methods*) on the DGS and DGN site for each eight-day period (46 bins for each site) during the study period (2002- 2014 on the DGN site: N = 9 years for 2 of the 46 bins, N = 10 for 17 bins, N = 11 for 20 bins, N = 12 for 7 bins; 2002- 2019 on the DGS site: N = 16 for 22 bins, N = 17 for 24 bins). Vertical bars (blue bars for SE site, red bars for DGN site) represent the average whale acoustic presence (%).

DGS site was in 2017, although hydroacoustic data was not available for the DGN site this year.

Seasonal variabilities were found at both sites in the 46 eight-day periods across the study (18 years at the DGS and 13 years at the DGN) (**Figure 3**). The whale acoustic presence was different on the DGS and DGN sites throughout the mutual study period that whale songs were recorded at both sites between 2002 and 2014 (Wilcoxon rank sum test, test statistics = 122688, p-value = 0.033). There was a seasonal influence in the number of whale song detections, as more whales were found at the DGN site in the warmer months (May to October), whereas in the cooler months, November to April, there were more whales at the DGS site.

3.2 Correlation Between the Whale Acoustic Presence and Environmental Factors

The mean concentration of chlorophyll-a was relatively stable with only a slightly decreasing trend at both Diego Garcia sites over 13 and 18 years respectively (**Table 1**). However, the average SST and minimum SST increased overall at both sites (**Table 1**). The increasing rates of both mean SST and minimum SST at the DGS site were higher than those at the DGN site.

TABLE 1 | Linear model coefficients of mean sea surface temperature (SST); minimum SST; mean chlorophyll-a concentration versus year at the two oceanic sites off Diego Garcia, DGN refers to the north-western site (n = 13 years) and DGS to south-eastern site (n = 18 years).

	DGN		DGS	
	coefficients	**p-value**	**coefficients**	**p-value**
Mean SST	0.0154	0.1934	**0.0270**	**0.0224**
Minimum SST	0.0183	0.5669	0.0491	0.0693
Mean chlorophyll-*a*	-0.0025	0.0747	-0.0013	0.0812

Bold fonts are relationships that corresponding p-values are less than 0.05.

There was a seasonal effect observed on the number of whale songs detected at both sites (**Figure 4**; **Table 2**). At the DGS site, SST was negatively correlated with the whale acoustic presence, whereas at the DGN site, SST and whale acoustic presence had a positive relationship.

The relationship between chlorophyll-a concentration and whale acoustic presence was negatively correlated at the DGN site and positively correlated at the DGS site. When the chlorophyll-a concentration is higher, we observed more whale songs at the DGN site and less whale songs at the DGS site. At the DGN, the negative correlation between chlorophyll-a and whale acoustic presence was weaker, whereas at the DGS site the positive correlation between chlorophyll-a and whale acoustic presence was stronger (**Table 2**).

El Niño Southern Oscillation (measured by Southern Oscillation Index, SOI) and Indian Ocean Dipole (measured by Dipole Mode Index, DMI) both had critical relationships with the whale acoustic presence (**Table 2**). DMI had a stronger correlation with whale acoustic presence compared to SOI. In the DGS, DMI and whale acoustic presence were positively correlated, while SOI and whale acoustic presence were negatively correlated. When DMI is higher or ENSO index is lower, we observed more whale presence. In the DGN, DMI was negatively correlated with whale acoustic presence and SOI was positively correlated with whale acoustic presence. We observed less whale songs when DMI is lower or when ENSO index is higher. The correlation between both SOI and DMI and whale presence was stronger in the DGS compared to in the DGN.

3.3 Extended Peak Seasons of the Chagos Whale Songs

At the DGS site, 30 extended peak seasons were identified over 18 years (**Figures 5A**, **6**). The mean duration of the extended peak

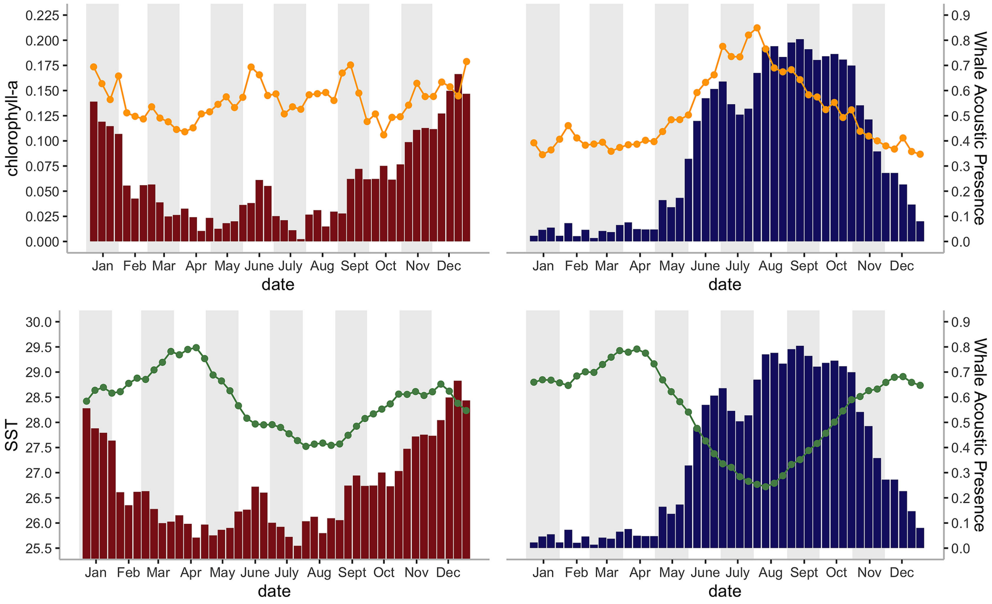


FIGURE 4 | Histograms of the mean Chagos whale acoustic presence (%) (defined as the percentage of hours when whale calls were detected, see *Material and Methods*) during each eight-day period and their corresponding a) mean SST (°C), indicated by orange line chart; and 2) chlorophyll-a concentration (mg/m^3) indicated by green line chart; for 2002 – 2014 on the DGN site (red bars; N = 16 for 22 bins, N = 17 for 24 bins) and for 2002 -1 2019 on the DGS site (blue bars; N = 9 years for 2 bins, N = 10 for 17 bins, N = 11 for 20 bins, N = 12 for 7 bins).

seasons was 54 days. Unlike the DGN site, most extended peak seasons in the DGS were in cooler periods between May and December. Most extended peaks started between May and August. The starting time of the extended peak seasons shifted earlier throughout the study period (Spearman rank correlation = -0.53; p-value = 0.05; **Supplementary Table 1**). The average shift of arrival time is 4.2 ± 2.0 days/year ± SE. The probability of having two peaks instead of one was higher after 2011. Also, consecutive peaks (more than 90% of whale acoustic presence) were more frequent in later years. The total length of extended period increased by 7.3 ± 1.2 days/year ± SE across 18 years. At the DGN site (**Figures 5B**, **6**), we detected 15 extended peak seasons over 13 years and the average period length was 50 days. Most extended peaks started between October and December and finished in January or February. Extra extended peaks were found in 2005, 2006, 2009, and 2013. Extended peak seasons were similar in pattern between 2002 and 2004. There were more and longer extended peak seasons in 2005. However, information was limited in 2006 and 2007 due to missing data. There was no peak found in 2008. In 2009 and 2010, extended peaks were similar to the previous pattern between 2002 and 2004. Longer and stronger extended peak seasons were observed from 2011 and 2013. The extended peak season analysis was not complete in 2014 due to missing data and therefore the end date of the last extended peak could not be determined. There was no strong correlation between the start time of the extended peak season and the year (Spearman rank correlation = -0.45; p-value = 0.31; **Supplementary Table 1**).

While the mean annual chlorophyll-a concentration was similar between DGN (0.14 mg/m^3) and DGS (0.13 mg/m^3), there was a difference between sites in the interannual change in chlorophyll-a concentration (**Figure 7**). At the DGS site, there were higher average chlorophyll-a concentrations in peak seasons than non-peak seasons however there was little seasonal difference at the DGN site.

TABLE 2 | GLM model coefficients for the south-eastern (DGS) site and north-western (DGN) site.

	DGS		DGN	
Variable	coefficient	p-value	coefficient	p-value
8-day				
SST	-1.173	<0.001	0.279	<0.001
chlorophyll-a	16.954	<0.001	-1.782	<0.001
Monthly				
SOI	-0.016	<0.001	0.005	<0.001
DMI	1.299	<0.001	-0.190	<0.001

For each coefficient, it is the coefficient for the GLM (family = binomial, weights = number of hours recorded) between the whale acoustic presence (%) and the corresponding sea surface temperature (SST) and chlorophyll-a concentration (N = 498 for DGN; N = 760 for DGS); Southern Oscillation Index (SOI) and Dipole Mode Index (DMI) (N = 134 for DGN; N = 205 for DGS).

4 DISCUSSION

This study provides insights into the association between environmental variation and long-term patterns of Chagos whale phenology. Whale presence data are almost continuous

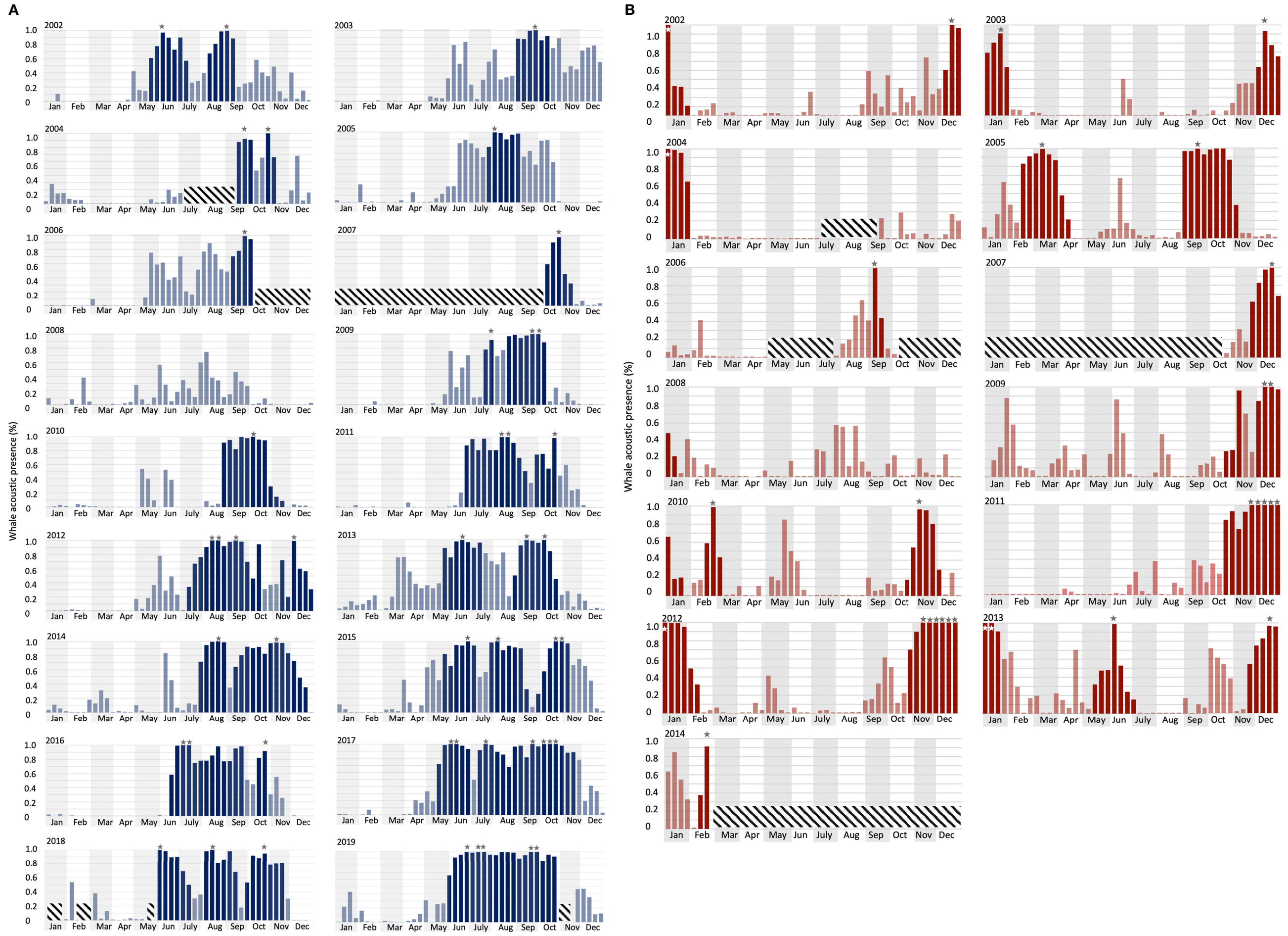


FIGURE 5 | Long-term whale acoustic presence (defined as the percentage of hours when whale songs were detected, see *Material and Methods*) at **(A)** DGS (from 2002 to 2019) and **(B)** DGN (from 2002 to 2014). Vertical bars indicate the proportion of hours that one or more Chagos whale songs were detected in each eight-day period. Grey/white stars indicate peak time when there were more than 90% of the hours with Chagos song detections. Darker bars are the extended peak seasons that contain (as defined in the *Methods* section). Diagonal crosshatch-filled shades were unavailable data (See *Material and Methods* for the definition of the extended peak season).

at the two acoustically independent sites over 18 years (January 2002 – December 2019) and 13 years (January 2002 – February 2014), which covers episodes of rapid ocean warming throughout the Southern Hemisphere oceans. We found that the number of songs per day had increasing trends at both sites throughout the years. This study also suggests that Chagos whales may be feeding at the DGS site, in association with nutrients provided by the upwelling effect in the positive IOD phase. In addition, we found that the Chagos whales were arriving at their potential feeding ground earlier in the year in recent times (**Figure 8**).

4.1 Overall Trends and Interannual Difference in the Number of Chagos Whale Songs

The Chagos whales are present near Diego Garcia each year across the entire study period, with over five songs per hour detected at both sites, as also shown in Leroy et al. (2021). Peaks in different seasons were identified at both sites for almost every year (except for 2008, where the least number of Chagos songs were detected at each station). This suggests that the tropical Indian Ocean is a crucial habitat for this population of whales. The central Indian Ocean is a complex marine system with rich cetacean fauna (Anderson et al., 2012). Distinct blue whale acoustic groups are observed and produce more song types than in any other oceanic region (McDonald et al., 2006; Samaran et al., 2013). At Diego Garcia, besides the best-described Antarctic blue whale (McDonald et al., 2006), there have been at least four other pygmy blue whale populations (*B. m. brevicauda or B. m. indica*) detected from acoustic recordings, including the Sri Lankan/Northern Indian Ocean, the Madagascan/Central Indian Ocean, the Australian/Southeastern Indian Ocean and the Arabian sea/Northwestern Indian Ocean (NWIO) (Stafford et al., 2004; Stafford et al., 2011;

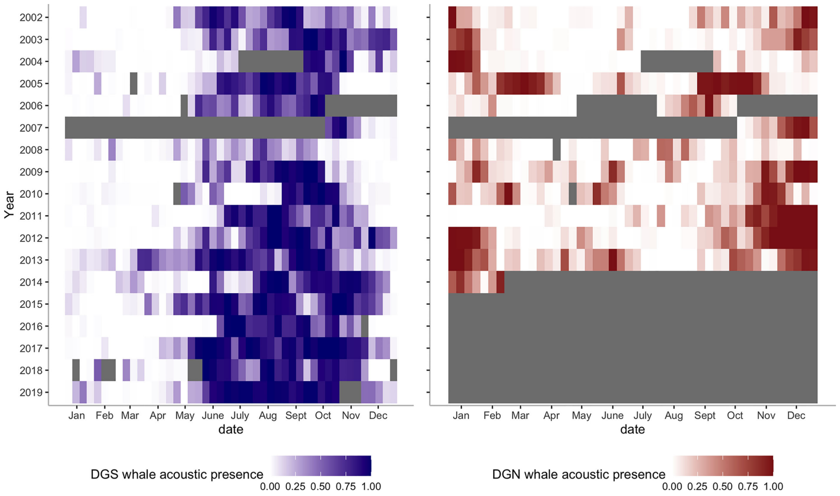


FIGURE 6 | Heatmaps of Chagos whale acoustic presence at DGS (left, blue colour, from 2002 to 2019) and at DGN (right, red colour, from 2002 to 2014). Grey bars are missing data.

Samaran et al., 2013; Double et al., 2014; Leroy et al., 2016; Leroy et al., 2018; Cerchio et al., 2020). Cerchio et al. (2020) recorded NWIO songs at the DGS and DGN sites over the 2010 – 2013 period. They observed considerably fewer songs and peak seasons than Chagos songs identified in this study; for instance, in 2010 NWIO songs were only recorded in May at the DGS site while we recorded Chagos song all year with two extended peak seasons at the same site. This provides further evidence that the central Indian Ocean is a crucial habitat of the Chagos whale population and Chagos whales are likely one of the most abundant populations in this area.

This study shows that the number of Chagos whales' songs has increased over time. A 7.8% increase in song numbers was observed on the southeastern side of the Chagos-Laccadive Ridge, while songs increased by 12.6% on the northwestern side. Changes in acoustic presence could, to some extent, reflect changes in the number of whales in a given area (Charif et al., 2020). The values are within the range of population trends in other blue whale species (i.e., Antarctic blue whales 7%, Branch et al., 2004) and other baleen whales (i.e., 12% humpback whales, Wedekin et al., 2017; 4-5% eastern North Pacific fin whales, Zerbini et al., 2006), and are much higher than North Atlantic right whale (i.e., 2.8% from 1980 to 2010, decline post-2010, Pace et al., 2017). Acoustic data is not a reliable source to estimate the abundance of whale population because of the unknown distance that whale songs travel, but relative densities from the number of songs recorded can be inferred (Branch et al., 2007).

4.2 Correlation Between the Number of Whale Songs Detected and Environmental Factors

Although the DGN and DGS sites are close, they are acoustically independent due to the existence of Chagos-Laccadive Ridge. The Chagos Bank acts as a natural acoustic barrier and sounds produced on either side of the Chagos Bank are unlikely to be detected on the other side (Pulli and Upton, 2001). Clear seasonal patterns in Chagos whale presence were identified throughout the entire study period (Leroy et al., 2021). The relationship we predicted matches with the condition presented by the 18-year data from the DGS site as there were more whale songs detected when there were more food and lower temperature; while at the DGN site, more whales were present when there were less food and higher temperature. Chagos whales were more frequently detected at the DGN site between December and May (average SST: DGN site: 28.85°C; DGS site: 28.92°C), while most extended peak seasons of whale presence at the SE site were between June and November, in the cooler season (average SST: DGN site: 28.01°C; DGS site: 27.53°C). The mean and minimum SST tended to increase at both sites, although it increased at higher rates in the DGS site compared to in the DGN site.

Chlorophyll-a (a proxy for krill, the whales' main prey) has an influence on whale presence. As we found that Chagos whales were present at the DGS site at times with higher chlorophyll-a concentrations, it is possible that Chagos whales use this region seasonally to feed. The correlation between chlorophyll-a and whale acoustic presence is stronger at the DGS site than at the DGN site.

It is therefore likely that whales are feeding in the vicinity of the DGS site at the Chagos-Laccadive ridge because chlorophyll-a and whale acoustic presence correlated positively. Chagos whale presence is negatively correlated with chlorophyll-a in the DGN, suggesting they are not feeding substantially at or near the DGN site.

Indian Ocean Dipole (IOD) was correlated with Chagos whale presence. At the DGS site, IOD and Chagos whale acoustic presence were correlated positively, whereas at the DGN site, IOD and Chagos whale acoustic presence were

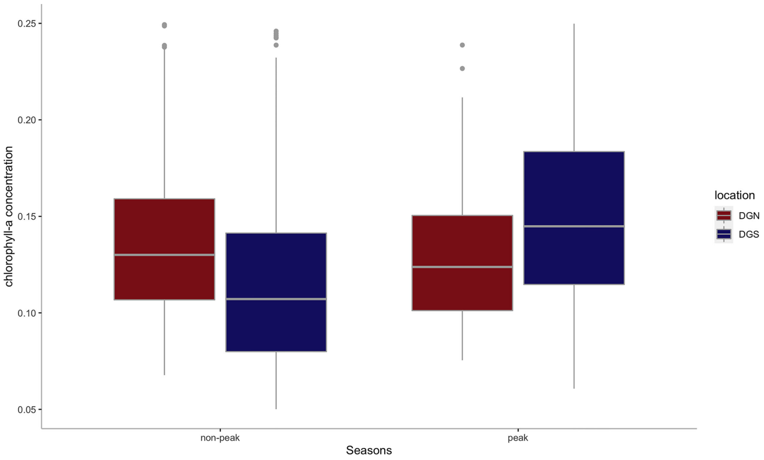


FIGURE 7 | Boxplot of the mean chlorophyll-a concentration(mg/m^3) for DGS (n = 13 from 2002 to 2014) and DGN (n = 18 from 2002 to 2019) during the corresponding peak seasons and non-peak seasons. Boxes represent interquartile ranges (IQR); solid white lines represent medians; black lines encompass data range 1.5*IQR below and above IQR; dots represent potential outliers.

correlated negatively. The existence of Chagos-Laccadive ridge makes the two sites acoustically independent, and the effect of IOD may be different between sites. Chagos whales were more likely to be detected at the DGS site during positive IOD phases. During positive IOD phases, cooler SST is recorded at the DGS site and upwelling events may occur (Saji et al., 1999). It is likely that the cold upwelling water brings nutrients that may influence the presence of Chagos whales. The negative correlation between IOD and Chagos whale presence at the DGN site suggests a higher whale abundance during the negative IOD phase, in association with cooler water and upwelling (**Figure 9**). Similar patterns were found in Sri Lankan pygmy blue whales where they fed in the Arabia Sea off the coast of Somalia during the period of intense upwelling of the monsoon season (Anderson et al., 2012).

In addition, ENSO was correlated to whale songs detected, but the influence was not as strong as the IOD. It may be because

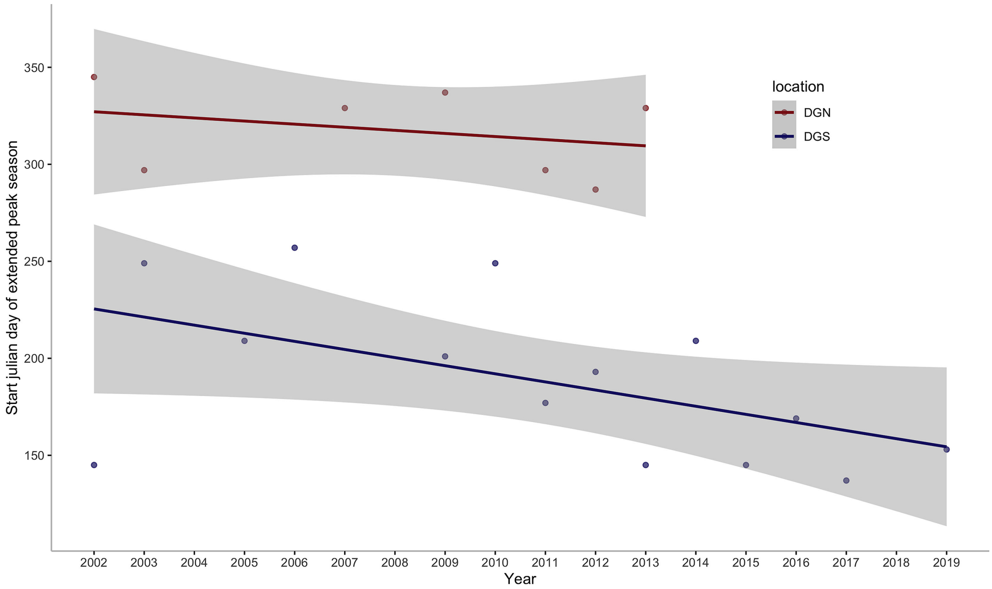
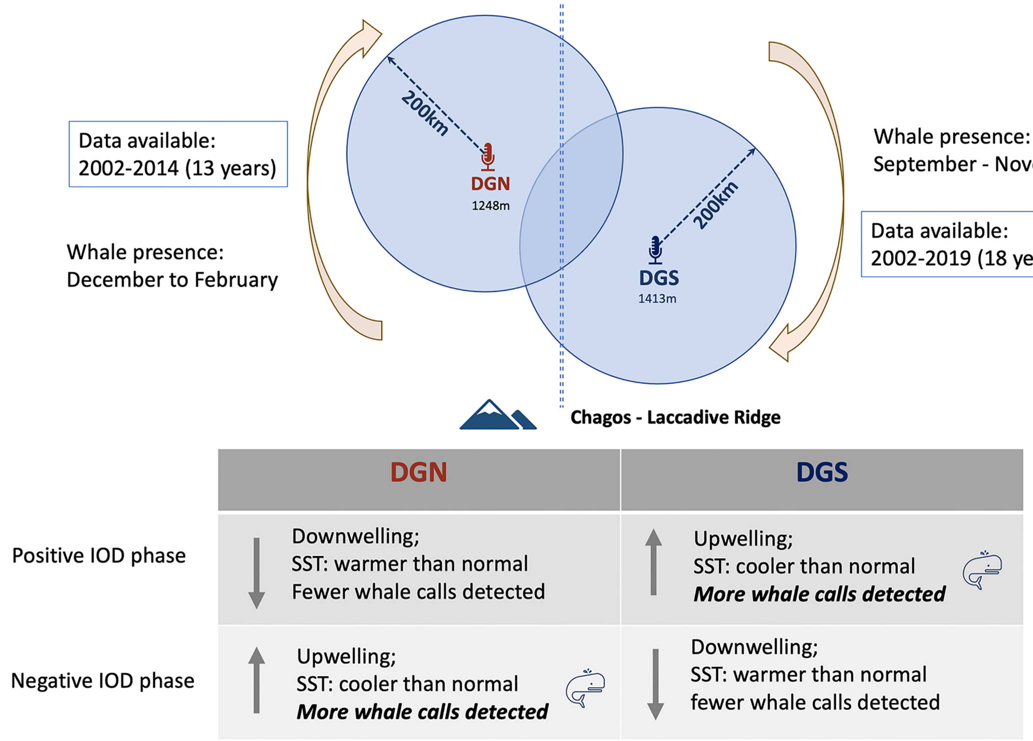


FIGURE 8 | Annual change in the start julian day of the first extended peak season per year off Diego Garcia at the DGN site where the linear trend has a slope of -1.6 days/year (sample size is too small to calculate a p-value) and DGS site where the linear trend has a slope of -4.2 days/year with corresponding ρ of -0.53 and p -value of 0.05. ρ is the spearman coefficient of the start julian day of the first peak season with year.



	DGN	DGS
Positive IOD phase	↓ Downwelling; SST: warmer than normal Fewer whale calls detected	↑ Upwelling; SST: cooler than normal ***More whale calls detected***
Negative IOD phase	↑ Upwelling; SST: cooler than normal ***More whale calls detected***	↓ Downwelling; SST: warmer than normal fewer whale calls detected

FIGURE 9 | Conceptual figure of the relationship between Indian Ocean Dipole (IOD) and whale song detected at DGN and DGS. Positive and negative IOD phases influence in the Indian Ocean were described by Saji et al., 1999.

Diego Garcia is in the central Indian Ocean while ENSO has a stronger influence in the Pacific Ocean.

4.3 Extended Peak Seasons of the Chagos Whale Songs

This study shows that Chagos whales stay near the southeastern side of Diego Garcia, potentially to feed in the vicinity of the highly productive zones, during the cooler seasons (June to November). Pygmy blue whale song detection has interannual differences, peaking in activity between August and October at DGS and between November and February at DGN, suggesting the area may represent a natural migratory corridor between the north and south of Diego Garcia. After March, they may disperse as far north as the Laccadive Sea off Sri Lanka or as far south as Kimberley region of Australia (Leroy et al., 2021). The migration of Chagos whales was proposed to be in a clockwise pattern across the equatorial Indian Ocean (Leroy et al., 2021). Unlike the Chagos blue whales, other blue whales migrate north-south so that their distribution spans across latitudes (Branch et al., 2007). For example, Antarctic blue whales are frequently found south of 70°S in the austral summer where they feed, while in the winter they migrate to low latitudes further north to calve and mate (Double et al., 2014; Balcazar et al., 2015). This study showed that Chagos whales are most frequently present from September to November at the DGS site, and they move to DGN site and stay there from December to February. In line with preliminary reports of occurrence of the Chagos whale songs (Sousa and Harris, 2015; Leroy et al., 2021), this study suggest Chagos whales may have a different migration pattern, rather than moving north-south, as the other blue whales do, that instead they migrate from east-to-west.

This study shows that Chagos whales are recorded in the tropical central Indian Ocean year-round. Not all whales migrate, as Širović et al. (2004) recorded Antarctic blue whales songs year-round in the Southern Ocean, near the Antarctic Peninsula. Tripovich et al. (2015) also found blue whale songs all year round in southern Australian waters off Portland, South Australia. The proportion of the blue whale population that migrates remains unclear. We found that Chagos whales were present year-round however their occurrence was highly seasonal. Further study of the acoustic presence of Chagos whales in further north or south (e.g., Sri Lanka and Kimberley) could reveal if Chagos whales have long-term habitats other than central Indian Ocean.

Chagos whales tended to arrive earlier at the DGS site each year in the study. The extended peak season at the DGS site starting time shifted from around September to May (Except for the year 2002, the starting time of the extended peak season was May on the DGS). Former studies suggest that blue whales are arriving earlier at their feeding area, and the starting time of the peak season is correlated with colder SST anomalies of the previous seasons in Southern California (Szesciorka et al., 2020). Ramp et al. (2015) show that the humpback whales and fin whales were arriving at their feeding ground earlier from 1984 to 2010. Our analysis reveals that the Chagos whales are likely to arrive at their feeding ground earlier.

It is important we understand how the long-term warming of the tropical Indian Ocean (Levitus et al., 2009; Xue et al., 2012) is influencing its marine life; given this region has warmed faster than the equivalent tropical Pacific and Atlantic and that the warming is accelerating (Rayner, 2003). Although it is difficult to sustain long-term monitoring studies in remote regions, like the central tropical Indian Ocean, this study demonstrated how continuous multiyear acoustic surveillance reveals that Chagos whales change the timing of their migration from year to year, and that local and oceanic environmental conditions may be implicated. The migration pattern of the pygmy blue whales is poorly known in the Indian Ocean (Branch et al., 2007). Understanding the migration pattern helps model the distribution of these whales and assists the prediction of whale presences into the future. It can also benefit conservation managers to develop conservation strategies for wildlife protection (i.e., establishment of marine protected area). Further study of the Chagos whales' movement will provide insights on how environmental changes influence marine life.

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 and approval was not required for the animal study because the acoustic data was used.

AUTHOR CONTRIBUTIONS

JH and TR conceived the project and designed methodology. EL provided acoustic detection data. JH and TR analysed the data; JH and TR led the writing and GT and EL contributed to editing and gave final approval for publication.

FUNDING

Funding was provided by the Winnifred Scott Foundation.

ACKNOWLEDGMENTS

Hydroacoustic data was made available *via* a Virtual Data Exploitation Centre contract with the Comprehensive Test Ban Treaty Organization (CTBTO). We thank Anant Mathur for his suggestion on statistics. We would also like to thank mammal lab, especially Anna Lewis for providing comments on the draft manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.843875/full#supplementary-material

Supplementary Figure 1 | Scatter plots of the Chagos whale acoustic presence (%) (defined as the percentage of hours when whale songs were detected, see *Material and Methods* section) during each eight-day period and their corresponding environmental factors: chlorophyll-a concentration (mg/m^3); SST (°C); SOI; and DMI for the south-eastern (DGS) site (red) and north-western (DGN) site (blue). The red and blue lines indicate their binomial relationships.

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frontiers | Frontiers in Marine Science

ORIGINAL RESEARCH
published: 02 August 2022
doi: 10.3389/fmars.2022.877580

Detection of Habitat Shifts of Cetacean Species: A Comparison Between 2010 and 2017 Habitat Suitability Conditions in the Northwest Atlantic Ocean

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

Received: 16 February 2022
Accepted: 17 June 2022
Published: 02 August 2022

Citation:
Chavez-Rosales S, Josephson E, Palka D and Garrison L (2022) Detection of Habitat Shifts of Cetacean Species: A Comparison Between 2010 and 2017 Habitat Suitability Conditions in the Northwest Atlantic Ocean. Front. Mar. Sci. 9:877580. doi: 10.3389/fmars.2022.877580

The simultaneous effects of human activities in the ocean and climate change have already produced a series of responses from the marine ecosystems. With the potential increment of future human activities, such as offshore renewable energy developments, proactive management is required. To facilitate effective management and conservation actions, it is imperative to identify species potentially at risk and their critical habitats. Here we examine 16 cetacean species habitat suitability in the western North Atlantic Ocean using generalized additive models developed from data collected by NOAA- Northeast and Southeast Fisheries Science Centers from 2010 to 2017. The models were based on observed species distribution as a function of 21 environmental covariates and compare species-specific core habitats between 2010 and 2017. We identified seasonal differences in patterns of habitat change across guilds and an average northward shift of 178 km across the study area. The effects of these shifts are still unknown, but for already stressed species, the contraction or displacement of their historical habitat could worsen their population status. Therefore, the imminent development of offshore regions, in addition to the effects of climate change emphasize the need of adaptively managing ecosystems on the face of multiple challenges.

Keywords: habitat, shift, cetaceans, suitability, models, climate change

INTRODUCTION

Marine species are being affected by global climate changes, where and in most cases the documented responses include distribution shifts from their historical habitat (Chang, 2020). In addition, human-caused drivers such as the noise and physical disturbances from oil and gas exploration, fishing, boat traffic and infrastructure such as offshore renewable energy developments, as well as other maritime activities could also result in shifts (Chang, 2020). A more complete understanding of the potential impacts of climate change on cetaceans is necessary to ensure their conservation (van Weelen et al., 2021) However, identifying species-specific habitats and whether change is occurring is limited by our ability to identify the extent of the change. This uncertainty is due to the lack of sufficient information to accurately identify the historic distribution range, seasonal and interannual variability, and individual species' tolerance to environmental change (Chang, 2020).

Our goal in this paper is to use Northwest Atlantic cetacean location data collected in its changing environment to investigate if their habitats are changing, and if so, to what extent.

The premise of the redistribution of marine organisms and directional shifts based on their preferred temperatures has been well established for fish, seabird, sea turtle and invertebrate species (Pinsky et al., 2013; Kleisner et al., 2016). In addition, projections of sea surface temperature (SST) has been used as a proxy to predict potential distribution shifts in multiple species. For example, Hazen et al. (2012) using climate change scenarios predicted significant changes in core habitats for fish, seabirds and sea turtle species and a northward displacement across the North Pacific. Morley et al. (2018) used the SST pattern changes to identify changes in distribution among 686 species of fish and invertebrates in regions of United States and Canada. Lavender et al. (2021) predicted contractions in thermal habitat suitability of fish species at the tropics and habitat expansion at higher latitudes. Patel et al. (2021) used thermal habitat patterns to predict loggerhead sea turtle shifts in response to scenarios of warming temperatures. Van Weelen et al. (2021) concluded that changes in SST and the reduction of sea ice extend affects the distribution of cetaceans in subarctic and subantarctic regions, with some species displaying a poleward shift to higher latitudes following their preferred SST.

However, a shift in distribution of marine animals, in particular for mobile predators such as cetaceans' in temperate and warm regions is not necessarily directly related to changes in SST. Instead, as Pinsky et al. (2020) described, the distribution patterns are a consequence of interactions between the individuals and their entire thermal, oxic and biotic environment Current climate changes are indicated by increasing sea surface temperature. But the climate changes also involve increasing levels of carbon dioxide, increasing thermal heat, and decreasing oxygen levels throughout the entire water column. Consequently, these changes result in changes in water column stratification, primary productivity, and ocean circulation patterns (such as the location and strength of the Gulf Stream in the Northwest Atlantic). For highly mobile, large animals, such as cetaceans, their distribution and response to a changing environment is influenced by its feeding behaviors, preferences, and flexibilities, along with its physiological needs and tolerances, particularly those of the newborns. For example, Meynecke et al. (2021) reviewed over 148 studies to identify humpback whale habitat preferences during their annual cycle. They found in feeding grounds the explanatory covariates included upwelling strength, high chlorophyll-a concentrations, depth and currents. In calving grounds, the explanatory covariates included shallow areas, and warm temperatures with slow water movement. During migration, humpback whales prefer shallow waters close to shorelines with high chlorophyll-a concentrations.

Focusing on the Northwest Atlantic Ocean, regional ocean current pattern indicators remain at unprecedented levels. In 2019, the Gulf Stream was at its most northern position since 1993 (US NMFS NFSC, 2021). A higher proportion of warm salty Slope Water in the Northeast Channel increased sea surface height along the U.S. east coast (Goddard et al., 2015). Also, the second lowest proportion of cool and fresh water from the Labrador Slope Water was observed entering the Gulf of Maine since 1978. These changed the proportions of source water affecting temperature, salinity, and nutrient patterns to the Gulf of Maine ecosystem (US NMFS NFSC, 2021). Ocean temperatures continue to warm at both the surface and bottom, although warming is not seasonally uniform. The 2020 winter and spring surface temperatures were just slightly warmer than average, while the summer and fall temperatures were 2-4°C above the climatological mean (US NMFS NFSC, 2021). Increased temperatures, as reported above, can increase the rate of photosynthesis by phytoplankton. As a result, annual primary production has increased over time, primarily driven by increased productivity in the summer months and larger than average phytoplankton blooms were observed from late fall into winter in 2020 (US NMFS NFSC, 2021).

Given the complexity of all the changing attributes of the Northwest Atlantic Ocean, a comprehensive data collection program and its associated analyses are required to understand the relationship between environmental factors and the distribution of cetacean species. The Atlantic Marine Assessment Program for Protected Species (AMAPPS) program has provided such cetacean data on over 250,000 km of systematic line transects. Chavez-Rosales et al. (2019), used the AMAPPS aerial and shipboard survey data from 2010-2013 to develop a habitat suitability baseline for 17 cetacean species in the western North Atlantic using 17 candidate covariates to model their habitat usage. To improve the habitat models of the previous study, new models were developed using the same methodology with a longer time series of data collected from 2010 to 2017 and additional candidate covariate characteristics of the marine environment (Palka et al., 2021). The seasonal distribution maps and underlying data are available through https://apps-nefsc.fisheries.noaa.gov/AMAPPSviewer/ and are downloadable from https://github.com/NEFSC/READ-PSB-AMAPPS-public in addition monthly average distribution maps are also available in the github site. Hereby, the objective of this paper is to use the habitat density models developed from these survey data to compare the species-specific core of the habitat suitability between 2010 and 2017 to identify seasonal differences in patterns of habitat suitability in the Northwest Atlantic.

METHODS

Study Area

The study area ranged from Halifax, Nova Scotia, Canada to the southern tip of Florida; from the coastline to slightly beyond the US exclusive economic zone and covers approximately 1,193,320 km^2 (**Figure 1**). Locations of the line transect track lines were developed to systematically cover the survey area with a random starting point within a stratum, in accordance to standard line transect procedures to produce approximate equal survey coverage within a stratum (Laake and Borchers, 2004). The cetacean distribution and abundance data were collected by the AMAPPS surveys. In coastal regions NOAA Twin Otter aircrafts were used, and for the offshore regions NOAA ship *Henry B.*

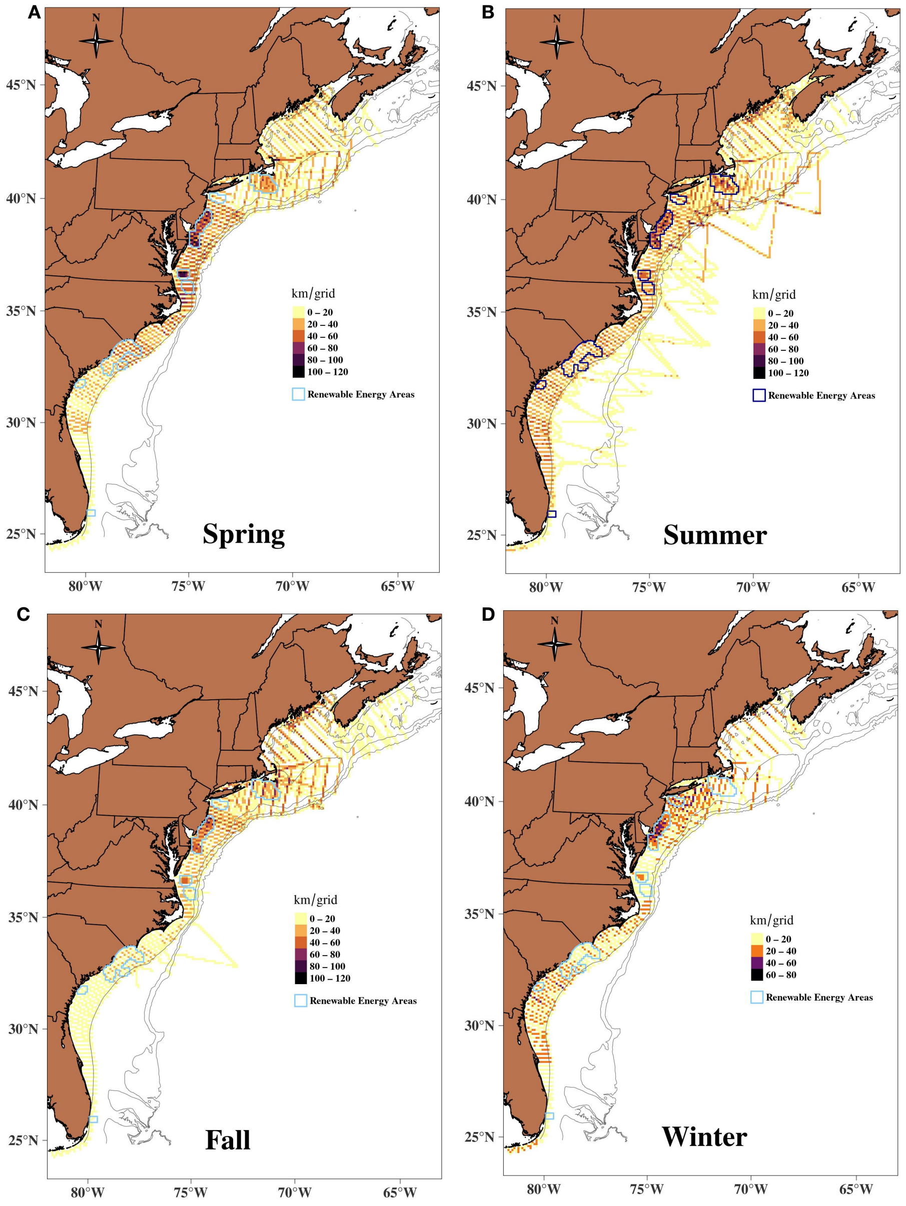

FIGURE 1 | Seasonal coverage of the survey effort in the study area during 2010–2017 by the AMAPPS surveys. **A**) Spring, **B**) Summer, **C**) Fall and **D**) Winter. Most spatiotemporal grid were repeatedly surveyed.

Bigelow was used by the Northeast Fisheries Science Center (NEFSC), and the NOAA ship *Gordon Gunter* was used by the Southeast Fisheries Science Center (SEFSC). The track lines were repeatedly surveyed in all seasons and in all years.

Static and dynamic covariate characteristics of the environment within the study area were compiled from a variety of sources (**Table 1**). All line transect and environmental covariate data were subdivided into 10x10 km cells and 8-day time periods. In addition, average sea state and glare collected during the line transect surveys within each spatiotemporal cell was included as a continuous predictor variable, to account for sighting conditions encountered on the surveyed track lines.

Analysis Methods

Two-step density surface modeling techniques were used to develop seasonal spatial models and maps of the density of the cetacean species (Miller et al., 2013) using the line transect sighting data collected during 2010 to 2017. The first step fits the detection functions to model the probability of observing animals away from the track line. The second step models the observed density estimated in the first step as a function of environmental covariate data and then uses the model to predict density over the entire survey area. The advantage of model-based techniques is the use of the additional environmental covariate data generally lead to more precise abundance estimates and the ability to

TABLE 1 | Contemporaneous habitat covariates and interactions included in the habitat models; MDE is the mean deviance explained by a covariate when included in a model; Frequency is the number of models in which the covariate was included.

Covariate	Description	Original Resolution	MDE	Frequency
SSTMUR	SST multi-scale ultra-high resolution	1 km mapped to 2 km	7.43	5
SSTF	Strength of SST fronts	1 km mapped to 2 km	5.19	7
CHLA	Chlorophyll-a concentration	1 km mapped to 2 km	4.27	4
CHLF	Strength of chlorophyll fronts	1 km mapped to 2 km	5.32	4
PIC	Particulate inorganic carbon	1 km mapped to 2 km	3.00	4
POC	Particulate organic carbon	1 km mapped to 2 km	1.15	2
PP	Primary productivity	1 km mapped to 2 km	5.00	4
SLA	Sea Surface Height Anomaly	1/4°	1.94	1
MLD	Mixed layer depth,	1/12°	3.96	4
MLP	Mixed layer thickness	1/12°	3.77	5
SALINITY	Surface salinity	1/12°	7.30	3
BTEMP	Bottom temperature	1/12°	8.61	12
DGSNW	Distance to the Gulf Stream north wall	meters	6.11	6
DGSSW	Distance to the Gulf Stream south wall	meters	4.40	2
Depth	Depth	3 arc-sec	10.02	5
Dist2shore	Distance to coastline	0.04°	5.40	4
Slope	Seafloor slope	3 arc-sec	3.15	2
Dist200	Distance to the 200 m isobath/contour	meters	7.60	5
Dist125	Distance to the 125 m isobath/contour	meters	6.57	3
Dist1000	Distance to the 1000 m isobath/contour	meters	9.50	7
Lat	Latitude		14.25	13
Interaction	Interaction time-DGSSW		28.18	1
Interaction	Interaction time-Latitude		16.1	2
Interaction	Interaction time-DGSNW		14.38	1
Interaction	Interaction time-SSTMUR		8.66	1
Interaction	Interaction time- CHLF		8.13	1

predict abundance in regions in between the surveyed track lines. A key advantage of this technique is unbiased abundance estimates can be produced even when the data do not come from surveys designed to achieve equal coverage probability of the survey area (Hammond et al., 2021).

Mark-Recapture and Distance Analysis

The first step of the density surface modeling technique developed species-specific estimates of the line-transect detection probability parameters based on survey effort conducted in Beaufort Sea states from 0 through 4 (Palka, 1996; Barlow et al., 2001; Palka, 2012).

The density estimates were based on the independent observer approach assuming point independence (Laake and Borchers, 2004), calculated using mark-recapture distance sampling (MRDS) (Thomas et al., 2010), for each sampled spatiotemporal cell using a Horvitz-Thompson-like estimator (Borchers et al., 2006). With this approach, there was no need to independently model group size. To capture sightability differences between observation platforms and regions, data collected by each aircraft and ship from the SEFSC and NEFSC surveys were analyzed independently due to the differences in observers, data collection methods and habitats surveyed. Traditional MRDS distance analyses were used for the data collected by the shipboard surveys (Palka, 2020; Palka, 2012; Garrison, 2020). Data collected by the aerial surveys were analyzed using a two-step process as described by Palka et al. (2017) and Garrison (2020) to account for the slightly unbalanced area surveyed by the two teams in the planes.

Significant covariates were chosen following the method suggested by Marques & Buckland (2003) and Laake & Borchers (2004). For all of the analyses, the detection probabilities were estimated using right truncated perpendicular distances as suggested in Buckland et al. (2001) and model selection was based on the goodness-of-fit using the AIC score, Chi- squared test, Cramer-von Mises goodness-of-fit test and a visual inspection of the fit. The results of these test are available in Palka et al. (2021). The estimated sighting probability included an estimation of g(0) which is the probability of detecting an animal on the survey track line.

To ensure sufficient sample sizes to accurately estimate model parameters, when needed, several similar species were pooled. The criteria used to define species guilds included shape of the species' detection functions, general animal behavior, perceived sightability of the species, and sample size. The estimated global parameters from the guild models were applied to the values of the covariates associated with each individual species in the guild to account for species-specific detection functions. An overall species-specific abundance estimate was then calculated for each spatiotemporal cell and corrected for species-specific availability bias by platform, as described in Palka et al. (2021); Palka et al. (2017).

Modeling Analysis

The second step in the density surface modeling technique developed a density habitat model. Generalized Additive Models (GAM) were developed in R (v. 4.1.1) using the package "mgcv" (v.1.8-36). Density estimates from the mark -recapture/ distance analysis in sampled spatiotemporal cells were defined as the response variable in the generalized additive models. A habitat model was produced for each species to identify the extent of their habitat suitability over space and time. Potential habitat predictors included in the models consisted of a suite of 7 static physiographic characteristics in the study area and 14 contemporaneous dynamic environmental covariates (**Table 1**). The data sources are described in Palka et al. (2021).

The parameter estimates were optimized using restricted maximum likelihood criterion and the data were assumed to follow an overdispersed Tweedie distribution (Miller et al., 2013) with null space penalization and thin plate splines with shrinkage (Wood and Augustin, 2002). Further, to avoid overfitting that could render parameter estimates difficult to interpret biologically, the maximum number of degrees of freedom was limited to 5 and all models were checked to ensure this limit was appropriate. Correlations among environmental covariates ranged from 0.01–0.80 in absolute values. Although "mgcv" is considered to be robust to such correlations (Wood, 2011), both variables in a highly correlated pair were not used together in the same model.

Variable selection was performed with automatic term selection (Marra and Wood, 2011) and a suite of diagnostic tests as proposed by Kinlan et al. (2012) and Barlow et al. (2009). Models with the lowest prediction error and the highest percentage of deviance explained were selected for further testing which included k-fold cross-validation with 25 random data subsets.

Habitat Suitability Analysis

It was assumed that habitat suitability (HS), is directly correlated with the species' abundance in relation to the unique combination of environmental predictors, as defined in Chavez-Rosales et al. (2019):

$$HS = \sum_{i}^{n} \widehat{N}_i$$

where $\breve{N}_i$ is the estimated abundance from species-specific model for each spatiotemporal cell *i*. For this study the seasonal core habitat was defined as the area within a seasonal density map comprising of spatiotemporal cells with the upper 20% of predicted abundance values, based on the criteria defined in Hazen et al. (2012). Spring was defined from March to May, summer from June to August, fall from September to November and winter from December to February. Under this definition, the seasonal core habitat is meant to capture seasonal variability of the primary habitat used by each species. To determine if there were habitat shifts, we compared the core habitats for 2010 and 2017 in two ways. First, we compared the locations of the weighted centroids defined as the average coordinate of all points within the core habitat polygon weighted by the density estimates of the core habitat. Second, we compared the latitudinal distributions of the estimated abundance within the core habitat, which was calculated by summing the proportion of the estimated abundance within the core habitat by every 0.5-degree latitude.

RESULTS

The 2010 – 2017 data were collected from over 250,000 km of on-effort line transect track lines from AMAPPS surveys (**Table 2**) resulting in the detection of 8,332 groups of cetaceans of over 110,068 individuals from 16 species (**Supplementary Tables S1**, **S2**). Approximately 68% of these groups were detected by the northern surveys. After the data processing, the final input data for the habitat models included 25,856 surveyed spatiotemporal cells for the 2010-2017 timeframe.

A total of 17 habitat models were developed that included data from all four seasons for most of the species. The exception was for species that inhabit only deeper shelf-edge waters that were only surveyed by the shipboard surveys during summer, such as Cuvier's beaked whales and Sowerby's beaked whales. In the case of harbor porpoise, two habitat models were developed to explain their distinct annual distribution patterns. One model included only data collected from months where the harbor porpoises were spatially clustered (June to October). The second model included data from months where the species was spatially spread out (November to May) (**Supplementary Table S3**; **Supplementary Figures S1–S15**).

The most frequent covariates included in the habitat models were latitude (13 models), bottom temperature (12 models), strength of the SST fronts (7 models), and distance to the 1000 m depth isobaths (7 models). Overall, the deviance explained by the habitat models ranged from 28% for bottlenose dolphin to 71% for striped dolphin. The models included between 3 to 9 habitat covariates, the mean contribution to the model by individual covariates ranged from 1.15% for particulate organic carbon to 28.18% for the interactions between time (8-day period for each year) and distance to the Gulf Stream south wall (**Supplementary Table S3**; **Table 1**). For all species, the average abundance estimates within the core habitat comprised 0.77 of the total abundance for 2010 and 2017. In 2010, the proportion of estimated abundance in the core habitat ranged from 0.55 for minke whale for fall to 0.98 for long-finned pilot whale during winter. In 2017, the proportion of estimated abundance in the core habitat ranged from 0.54 for minke whale for summer to 0.99 for long-finned pilot whale during fall (**Supplementary Table S4**). Comparisons of the weighted centroid for species-specific core habitat identified seasonal differences in patterns of habitat change for most species north of 34° latitude. The greatest shifts and magnitudes varied by season and species, but the shift tendency was towards the northeast (NE) (**Figure 2**). On average, fall showed the greatest shifts of the weighted centroid, with 168 km, followed by winter (134 km), spring (115 km) and

TABLE 2 | Seasonal effort in kilometers by platform from the AMAPPS surveys included in the analysis.

Platform	Spring	Summer	Fall	Winter	TOTAL
NE Shipboard	–	37,529	1,065	–	38,594
NE Aerial	13,314	25,867	37,850	12,179	89,210
SE Shipboard	8,853	12,968	3,012	–	24,833
SE Aerial	41,293	28,236	18,974	8,950	97,453
TOTAL	63,460	104,600	60,901	21,129	250,090

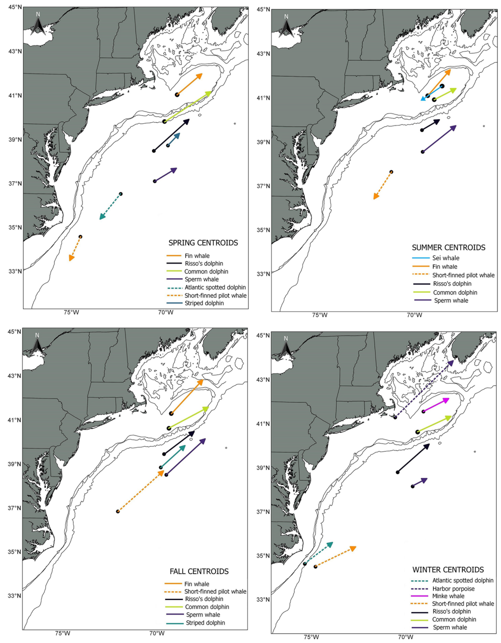

FIGURE 2 | Direction and magnitude of core habitat shifts, represented by the length of the line of the seasonal weighted centroid for species with more than 70 km difference between 2010 (black dot) and 2017 (tip of arrow).

summer (96 km). The largest shifts in the core habitat was for bottlenose dolphin, fin whale, short-finned pilot whale, Risso's dolphin, sei whale, common dolphin, sperm whale and striped dolphin (**Table 3**).

Overall, for species that showed a clear NE displacement of the weighted centroid, the average magnitude of the shift was 178 km. Bottlenose dolphin habitat showed the most drastic shift for all seasons except during winter: spring= 294 km,

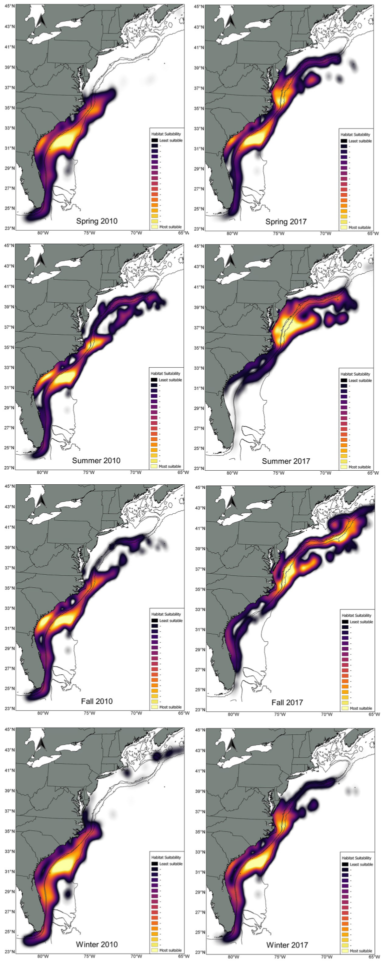

FIGURE 3 | Difference in kilometers on the location of the core habitat weighted centroid and direction of the habitat shift between 2010 and 2017.

TABLE 3 | Difference on the location of the core habitat weighted centroid (in km) and direction of the habitat shift between 2010 and 2017.

Species	Spring	Direction	Summer	Direction	Fall	Direction	Winter	Direction
Atlantic spotted dolphin	151	SW	25	SE	15	SE	165	NE
Beaked whale, Cuvier's	NA	NA	69	NE	NA	NA	NA	NA
Beaked whale, Sowerby's	NA	NA	5	SE	NA	NA	NA	NA
Common bottlenose dolphin	294	NE	505	NE	753	NE	211	NE
Fin whale	154	NE	162	NE	223	NE	33	NE
Harbor porpoise	17	SW	3	NE	10	SW	397	NE
Humpback whale	17	S	17	S	14	NW	3.9	SW
Minke whale	40	NE	14	NW	10	W	133	NE
Short-finned pilot whale	120	SW	149	SW	296	NE	218	NE
Long-finned pilot whale	39	NE	38	NE	69	E	2	NE
Risso's dolphin	232	NE	89	NE	182	NE	202	NE
Sei whale	70	SW	97	SW	134	SW	179	SW
Common dolphin	267	NE	111	NE	216	NE	205	NE
Sperm whale	114	NE	202	NE	255	NE	71	NE
Striped dolphin	71	NE	41	NE	155	NE	30	NE
White-sided dolphin	29	NE	13	W	23	NW	26	NE
Mean	115		96		168		134	

The difference in kilometers.

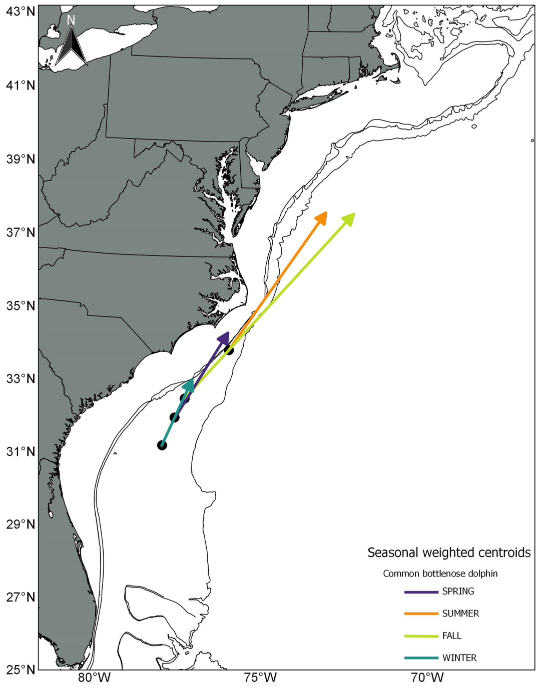

FIGURE 4 | Direction and magnitude of core habitat shifts represented by the length of the line of the seasonal weighted centroid, for bottlenose dolphin between 2010 (black dot) and 2017 (tip of arrow).

summer=505 km, fall= 753 km and winter = 211 (**Table 3**; **Figures 3**, **4**). There was a clear tendency where the proportion of the estimated population in southern latitudes decreased, while north of 35° the proportion of the estimated population increased, especially during summer 2017 (**Figure 5**). Other species that on average, showed a moderate-to-no spatial shift included humpback whale, minke whale, white-sided dolphin, Sowerby's beaked whale, and long-finned pilot whale (**Table 3**; **Supplementary Figures S1 —S14**).

DISCUSSION

Climate change, most notably ocean warming is affecting the ecosystem in various ways leading to large and sometimes abrupt changes in the ecosystem's structure. Those changes affect the interaction of multiple system covariates and can result in ecosystem reorganization (US NMFS NFSC, 2021). Previous studies used the premise of redistribution of marine organisms linked to their preferred thermal habitat, and several projections with future scenarios of species shifts were produced using coarse resolution global and earth climate models (Hobday et al., 2016; Tommasi et al., 2017). However, the difference in regional projections of climate change limit the confidence on the utility of those projections (Hawkins and Sutton, 2009; Frölicher et al., 2016). Our study explored a wider more expansive list of possible habitat predictors. We found bottom temperature and latitude more often correlated with the animal density, in comparison to SST or strength of SST fronts.

Latitude was the most common covariate included in the habitat density models. This covariate could be interpreted as denoting the general spatial patterns of a species distribution. Positive near-linear relationships between latitude and density were in the density-habitat models of the northern species usually found in waters north of North Carolina, about 37°N. In contrast, negative relationships were in the models for the southern species, such as the Atlantic spotted dolphins found mostly in waters south of New Jersey (about 40°N).

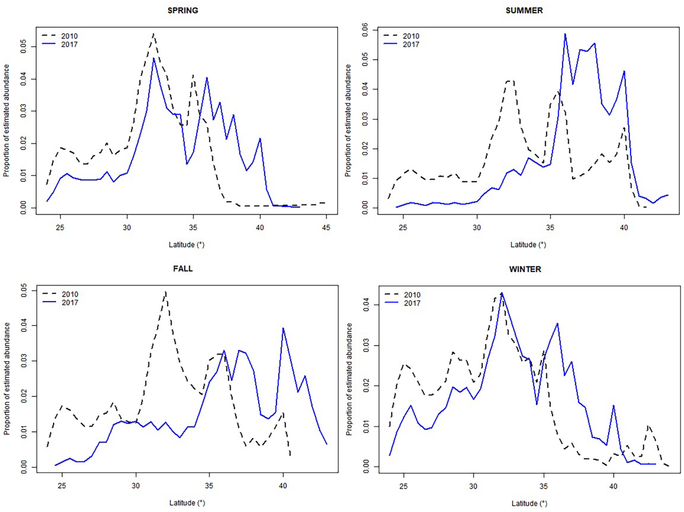

FIGURE 5 | Seasonal comparison of the proportion of the estimated abundance within the core habitat for bottlenose dolphin by 0.5° latitudinal bins. 2010 dotted-black line, 2017 solid blue line.

The humpback whale's model had a bimodal relationship with latitude that reflected its seasonal migration patterns up and down the coast. To model the large interannual variability in sei whale densities off the US coast, the most significant covariate was an interaction between latitude and time.

The second most common covariate included in the habitat density models was bottom temperature. Although SST and bottom temperature are somewhat related, the physical forcing factors for the two locations are different. It appears that bottom temperature was a good predictor of density for deep diving species, where this covariate could be interpreted to represent their prey preferences. The deepest divers that commonly feed at depths greater than 1500 m deep are the various beaked whales and *Kogia* sp. Their models indicated that high densities are in waters where the bottom temperature was below about 8°C. Other deep divers that commonly feed higher in the water column, at about 200 – 1000 m depth on species such as squid, appeared to be found in only a limited range of warmer bottom waters, such as about 7-17°C for sperm whales, pilot whales, Risso's dolphins, common dolphins, bottlenose dolphins, and striped dolphins. The bottom temperature values with the higher than average densities of Atlantic spotted dolphins was bimodal, <6°C and >20°C, which appears to reflect the bimodal distribution of these animals off Florida and off Massachusetts.

Abiotic factors that are usually considered indicative of environmental (climate) changes include latitude, bottom temperature, SST, distance to the Gulf Stream. Biotic factors that could be indicative of organisms reacting to changing abiotic factors include primary productivity and chlorophyll a. These are the types of factors that were in the common bottlenose dolphin density-habitat model, which demonstrated dramatic seasonal shifts. The model covariates, in order of the contribution to the deviance explained, were interaction between SST and time, distance to the northern wall of the Gulf Stream, primary productivity, bottom temperature, bottom slope, chlorophyll a, and surface salinity.

Previous studies showed several limitations associated with statistical correlative models when used to extrapolate in time and areas where sampling effort was absent (Elith and Leathwick, 2009; Webber et al., 2011). For instance, the relationships implied from field data may not adequately describe factors determining species distributions, especially if the data are not collected consistently with a standardized protocol. Another limitation is large-scale environmental relationships developed from available data on past conditions, are generally considered less reliable to predict responses to extreme events or novel conditions under future climate changes (Hothorn et al.2011; Williams et al., 2007).

This study uses data collected with standardized protocols from only the area of interest for the 2010-2017 time period. We also used high resolution contemporaneous values of the habitat covariates in the models to increase the confidence in the estimation of the habitat suitability. In addition, this study presumed a robust environmental multivariate nonlinear relationship with the distribution of cetacean species in the region (see Palka et al., 2021).

The tendencies on the cetacean habitat shifts identified in this paper are consistent with the shifts observed in fishing stocks within the same regions, which showed movement towards the northeastward and into deeper waters (US NMFS NFSC, 2021).

These species are primarily distributed in the Georges Bank and Gulf of Maine during summer and fall seasons. This study does not attempt to answer why they did not shift. However, perhaps it could be because all of these species typically inhabit the same areas, are considered prey generalists (as they can feed on a variety of prey ranging from krill to small schooling fish), and Northern sand lance (*Ammodytes dubius*) is known to be a key prey to all of these species (Weinrich et al. 2001; Craddock et al., 2009; Smith et al., 2015; Staudinger et al., 2020). As generalists they could be more adaptable to newly-available or changing prey species, if new prey species are arriving. Also, in this time and area since 2010 sand lance have probably been increasing because Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) have been decreasing. Although scientists do not conduct assessments of Northern sand lance, this supposition is because the sand lance populations have been observed to oscillate out of phase with Atlantic herring and Atlantic mackerel (Staudinger et al., 2020; Suca et al., 2021), who have been decreasing since 2010 (Stock SMART 2021).

The results presented in this paper indicated the utility of using habitat models to estimate the core of habitat suitability. By including static and dynamic environmental covariates in the habitat models, these models provided an indicator of the seasonal and interannual variability and a good metric to detect habitat shifts and their magnitude. One important assumption of these models is the consistent statistical relationship within the spatiotemporal environment and the animal density (Chavez-Rosales et al., 2019). Based on this assumption, it is possible to interpolate the habitat preference of species in areas or periods of time within the study area and timeframe where surveys did not actually occur (Guisan et al., 2002). However, while these models are robust for the study area and timeframe, as indicated by the cross-validation analysis, the models are unable to directly detect changes in fundamental ecological processes such as predator-prey relationships through time and space. For this reason, in the future there is the need to incorporate more biological data related to possible prey availability into the habitat models formulation. Doing so would improve our understanding of the abundance and distribution of cetaceans in the region.

Habitat suitability estimated by specific habitat-based models such as those presented in this paper provide information to document past changes in the distribution and abundance of cetaceans as related to changes in their abiotic and biotic habitat. These past changes could then be used to predict potential future changes. Therefore, these habitat-based models have the potential to support management decisions related to the development of offshore regions for renewable energy and other activities and to promote conservation measures in a marine spatial planning context.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://github.com/NEFSC/READ-PSB-AMAPPS-public.

AUTHOR CONTRIBUTIONS

DP and LG conceived the study, collected the cetacean survey data and assisted with the analyses. EJ processed survey and environmental data. S-CR conducted the analysis, prepared the figures and wrote the manuscript in collaboration with DP. All authors reviewed and edited the manuscript.

FUNDING

This study was funded by the US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Services, by Interagency Agreements M14PG00005, M10G00075, and M19PG00007 between the US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Services and the US Department of the Interior, Bureau of Ocean Energy Management, and by Interagency Agreements NEC-11-009, NEC-15-004, and NEC-16-011 between the US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Services and the Department of the Navy, Office of the Chief of Naval Operations.

ACKNOWLEDGMENTS

We would like to thank the crews of the NOAA ships *Henry B. Bigelow* and *Gordon Gunter* and the NOAA Twin Otter aircrafts, all of the shipboard and aerial observers, and all the people involved in the data collection and analyses.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.877580/full#supplementary-material

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Conflict of Interest: SC-R and EJ are employed by Integrated Statistics in support of NOAA-Northeast Fisheries Science Center.

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 | Frontiers in Marine Science

TYPE Brief Research Report
PUBLISHED 05 September 2022
DOI 10.3389/fmars.2022.927276

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

RECEIVED 24 April 2022
ACCEPTED 16 August 2022
PUBLISHED 05 September 2022

CITATION
Pelayo-González L, Herra-Miranda D, Pacheco-Polanco JD, Guzmán HM, Goodman S and Oviedo L (2022) Decreases in encounter rate of endangered Northeast Pacific humpback whales in Southern Costa Rica: Possible changes in migration pattern due to warming events. *Front. Mar. Sci.* 9:927276.
doi: 10.3389/fmars.2022.927276

Decreases in encounter rate of endangered Northeast Pacific humpback whales in Southern Costa Rica: Possible changes in migration pattern due to warming events

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Warming events in the Pacific Ocean are becoming more frequent, intense, and on a larger temporal and spatial scale. This has caused critical habitats of marine species to lose their quality and marine organisms respond by modifying their critical feeding and reproduction behaviors, as well as their distribution. The Northeast Pacific humpback whale of the Central America distinct population segment (DPS) remains Endangered due to its small population size and because its response to climate change and human interventions is unknown. In this work, we showed the encounter rates of humpback whales in their breeding grounds in Costa Rica for breeding seasons comprised in the period 2000-2020. We analyze the influence of climatic indices that influence the Pacific and environmental variables related to temperature and productivity in the feeding grounds of this population (United States). We hypothesize that the more intense the warming events, the fewer humpback whales complete their migration to Costa Rica. We conclude that the humpback whales of this population could be finding thermally favorable areas in intermediate latitudes (p. e.g., Mexican-Guatemala coasts), which could be related to the decreases in the presence of humpback whale adults and calves in Costa Rica. These observed changes could inform how humpback whales might respond to climate change.

KEYWORDS

Central America DPS, climate change, El Niño, encounter rate, *Megaptera novaeangliae*, migration, Northeast Pacific, wintering grounds

Introduction

Marine warming events are becoming more frequent, lasting, and intense which has affected the quality of marine habitats and the population status of species (Wernberg et al., 2013; Scannell et al., 2016; Frölicher et al., 2018). The evaluation of the quality of critical habitats (feeding, reproduction, and migration areas) can be done through indicator species (Gregr and Trites, 2001; Bailleul et al., 2012; Trudelle et al., 2016). In this sense, the humpback whale (*Megaptera novaeangliae*) is considered an indicator species because its abundance, reproductive success, distribution, and diet are affected by abnormal environmental conditions (Fleming et al., 2016; Schall et al., 2021; Gabriele et al., 2022).

The humpback whale has been in recovery since 1985, after its near extinction by whaling; however, some of its populations remain listed as "Endangered" under the Endangered Species Act (81 FR 62259; September 2016; NMFS and NOAA, 2016). Among the main anthropogenic threats that have limited their recovery are fishing gear entanglement, vessel strikes, and the degradation of their critical habitats (Bettridge et al., 2015; NMFS and NOAA, 2016).

The Northeast Pacific humpback whales of the Central America DPS are classified as "Endangered" due to their small population size (approximately 1400 individuals) (Wade, 2021; Curtis et al., 2022). This population makes extensive migrations (≈ 5100 km) from their breeding grounds in Central America (southern Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama) to their feeding grounds off California-Oregon-Washington in the United States (Calambokidis et al., 2000; Rasmussen et al., 2011; NMFS and NOAA, 2016; Curtis et al., 2022). This region is under the influence of wind upwellings of the California Current System and different patterns of Pacific climate variability such as the El Niño-Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and the North Pacific Gyre Oscillation (NPGO) (Jacox et al., 2014; Jacox et al., 2016).

During El Niño conditions the upwelling weakens, the thermocline deepens, and warm subtropical water enters the California Current, which causes low productivity and changes in prey availability for humpback whales (Fleming et al., 2016; Cartwright et al., 2019; Gabriele et al., 2022). Low prey availability can mean that humpback whales do not have sufficient energy reserves to complete the migration, gestation or to ensure the survival of their calves, which can have long-term negative effects on the population (Cartwright et al., 2019; Kershaw et al., 2021; Gabriele et al., 2022).

Humpback whale populations that have been monitored for decades showed that the abundance of mothers with calves at breeding grounds decreases considerably when abnormal warm conditions occur at their feeding grounds, as well as temporary changes in the arrival of whales to their feeding grounds related to the early melting of ice (Ramp et al., 2015; Cartwright et al., 2019; Frankel et al., 2021). Humpback whales are modifying the timing of their migration and their distribution, as well as their stay in their breeding and feeding grounds (Avila et al., 2020; Meynecke et al., 2021).

The Northeast Pacific humpback whale Central America DPS is one of them with the highest category of threat and it is unknown how this population has responded to warming events (Endangered Species Act, 81 FR 62259, September 2016; NMFS and NOAA, 2016). Therefore, in this work, we use the best available historical data on humpback whale encounter rates in their wintering grounds in Costa Rica, to describe the pattern of occurrence since the early 2000s. In addition, we address the possible effects of warming events on the migration and presence of humpback whales with calves in Costa Rica.

Method

Study area

Humpback whale wintering grounds are located on the coast of the Osa Peninsula, Costa Rica (Figure 1). This area is limited to the east by the coasts of the Térraba-Sierpe River System, Drake Bay, and Corcovado National Park up to Punta Salsipuedes, including the surroundings of Caño Island. The study area has an approximate size of 3800 km^2 and is within the 200 m isobath. In this area, there is a stable sea surface temperature (around 28°C) throughout the year (Rasmussen et al., 2007; Oviedo and Solís, 2008; Rasmussen et al., 2011).

Encounter rate of humpback whales

Opportunistic records of humpback whales were made during the breeding seasons 2000-2006, 2014-2015, 2015-2016, and 2019-2020 (Figure 1). The surveys have been carried out since 1998 by Fundación Vida Marina aboard their whale-watching vessels. The records were obtained from December to May on citizen science-oriented surveys focusing on cetaceans' fauna in the study area. The port of departure and landfall was at Drake Bay, Osa Peninsula. The boat trips were directed to areas of known predictable occurrence and the observations were performed from 08:00 to 15:00 hours. Information was recorded on group size, group composition, and geographic position. The encounter rate was assessed as group sightings per unit search effort; dividing the number of all groups of whales sighted and sub-groups containing mother-calf pairs by the effort made every 1000 km as in Palacios et al. (2012). The study used data from 2272 total hours of field efforts between breeding seasons 2000-2006, 2014-2015, 2015-2016, and 2019-2020 at an average speed of

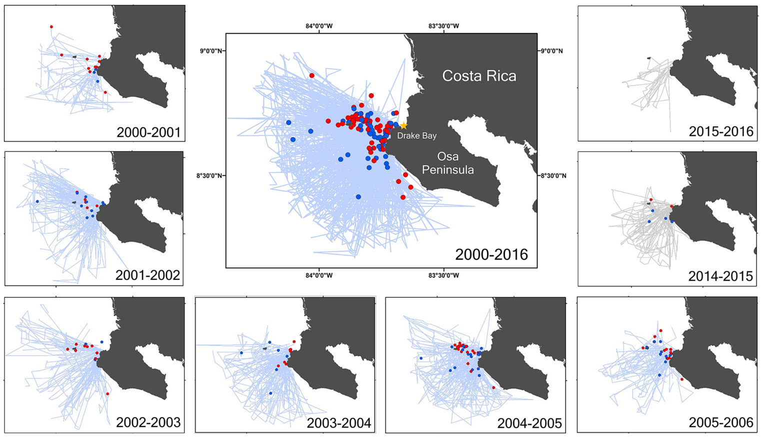

FIGURE 1
Breeding grounds of the Northeast Pacific humpback whales in Osa Peninsula, Costa Rica. Effort (blue lines); Adult humpback whale sightings (blue dots); Mother-calf pairs sightings (red dots). The port of departure and landfall was at Drake Bay, Osa Peninsula.

14.09(± 1.11) km/hr and an average search distance of 3526.55 (± 1442.27) km.

Climatic indices and environmental variables

Monthly values of the El Niño Multivariate Index (MEI), the Pacific Decadal Oscillation (PDO), and the North Pacific Gyre Oscillation (NPGO) for the 2000-2020 period were obtained through the ***rsoi*** package (Albers, 2020) in R version 4.2.0 (R Core Team, 2022). These indices consider large-scale ocean-atmosphere processes that influence the upwelling of the California Current System and cause changes in sea surface temperature, the concentration of nutrients, and abundance of marine species of different trophic levels whose effects can last from months to decades (Chenillat et al., 2012; Peterson et al., 2014; Fleming et al., 2016).

Sea surface temperature (SST), Chlorophyll a concentration (CHL-a), and coastal upwelling index (UPW) were analyzed for the period 2000-2020 given that they are good indicators of abundance and availability of zooplankton and small pelagic fish which are the main prey for humpback whales (Mackas et al., 2006; Munger et al., 2009). The area considered to extract the environmental information corresponds to the feeding grounds of humpback whales of the Central America DPS (34-48°N and 120-128°W, https://www.fisheries.noaa.gov/resource/map/humpback-whale-critical-habitat-maps-and-gis-data). Daily SST values were obtained through satellite images, level 4 and with a 0.25° resolution of Optimum Interpolation Sea Surface Temperature (https://www.ncei.noaa.gov/products/optimum-interpolation-sst). CHL-a data were monthly and from the NASA combined-satellite time series that are constructed from the SeaWiFS and MODIS-Aqua sensors (https://oceancolor.gsfc.nasa.gov/). Also, monthly values of the Biologically Effective Upwelling Transport Index (UPW) constructed with satellite and *in situ* data were obtained for the west coast of the United States (https://oceanview.pfeg.noaa.gov/products/upwelling/cutibeuti). A monthly series by environmental variable was obtained from 2000 to 2020. For each month, the average monthly value of the series was subtracted to calculate the time series of monthly anomalies. Positive values of anomalies indicate that environmental conditions were above the average historical conditions and vice versa, if anomalies present negative values, the conditions were below the historical average. Finally, annual and semi-annual averages of the climatic indices and anomalies of environmental variables were calculated to analyze their relationship with the annual encounter rates of humpback whales in Costa Rica.

To assess the influence of climatic indices and environmental variables on the encounter rate of humpback whales Spearman correlations were performed (Robinson et al., 2009; García-Morales et al., 2017).

Results

Encounter rate of humpback whales

The humpback whale records were consecutive between 2000 and 2006, then there was a seven-year gap and were resumed on 2014-15, 2015-16, paused again, and restarted on the breeding season 2019-20. The highest encounter rates were recorded in the breeding seasons 2000-01, 2004-05, and 2005-06 while the lowest encounter rate was during the 2015-16 breeding season (Figure 2). Although the effort was not the same in all

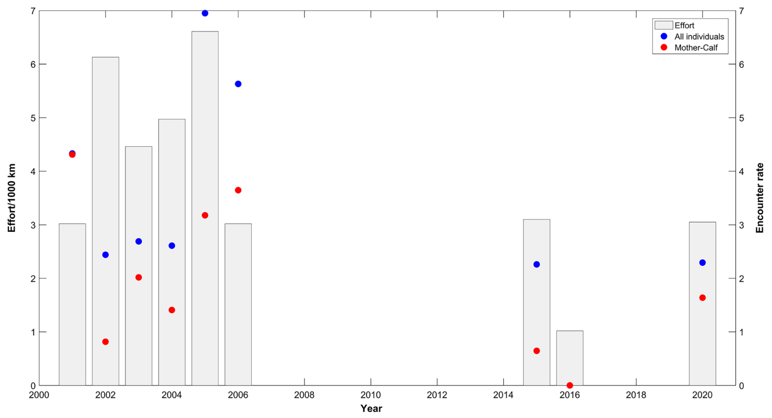

FIGURE 2
Encounter rates of humpback whales in the Osa Peninsula, Costa Rica. Effort made in each breeding season (gray bars); Encounter rate including adults and mother-calf pairs (blue dots); and Encounter rate of mother-calf pairs (red dots).

years and opportunistic data was retrieved, the entire wintering ground in southern Costa Rica was covered, so these data represent the best available estimates of the occurrence of this population in the area.

Climatic indices and environmental variables

During the study period, there were two warm phases of the PDO during 2002-2005 and 2014 to 2020. During these periods there were negative phases of the NPGO that represent low productivity in the feeding grounds of the humpback whale. Also, during the study period, moderate and strong El Niño events occurred in 2002-03, 2009-10, and 2015-16. Positive anomalies of SST were observed in the feeding grounds of humpback whales from 2014 to 2020. During this period there was great variability in CHL-a anomalies and mostly negative anomalies in UPW between 2014-2016 (Figure 3).

Influence of environmental conditions on encounter rates

Negative trends were detected between the annual averages of the MEI (Spearman's rank coefficient: r = –0.65, $p = 0.05$), SST (Spearman's rank coefficient: r = – 0.64, $p = 0.06$), and CHL-a (Spearman's rank coefficient: r = – 0.68, $p = 0.04$) with the encounter rates of humpback whales' mother-calf pairs. As MEI and SST anomalies intensity increases fewer whales were observed on the wintering grounds. Positive CHL-a anomalies were related to lower encounter rates in the wintering grounds (Figure 4). No relationships were found with the PDO, NPGO, and UPW values nor with semi-annual averages calculated for all the variables.

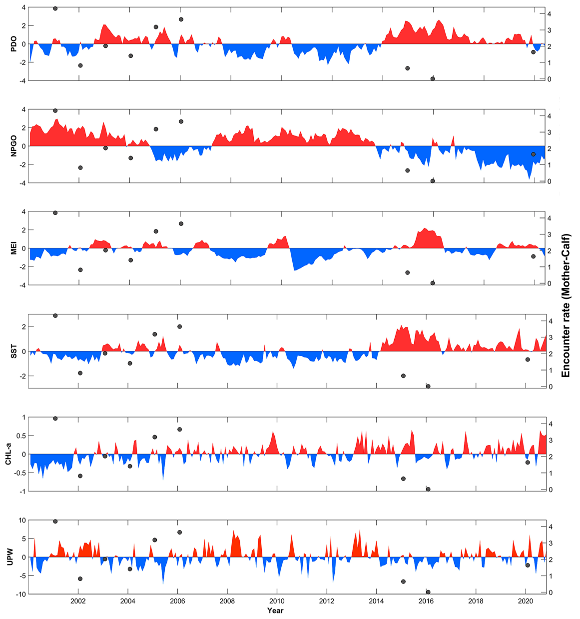

FIGURE 3
Monthly values of the Pacific Decadal Oscillation index (PDO), the North Pacific Gyre Oscillation index (NPGO), and the Multivariate ENSO Index (MEI) and anomalies of Sea surface temperature (SST), Chlorophyll a concentration (CHL-a), and the coastal Upwelling Index (UPW) obtained from the feeding grounds of humpback whales off California-Oregon-Washington in the United States (area graphs). Encounter rate of humpback whale mother-calf pairs recorded during the breeding season in the Osa Peninsula, Costa Rica (gray spots).

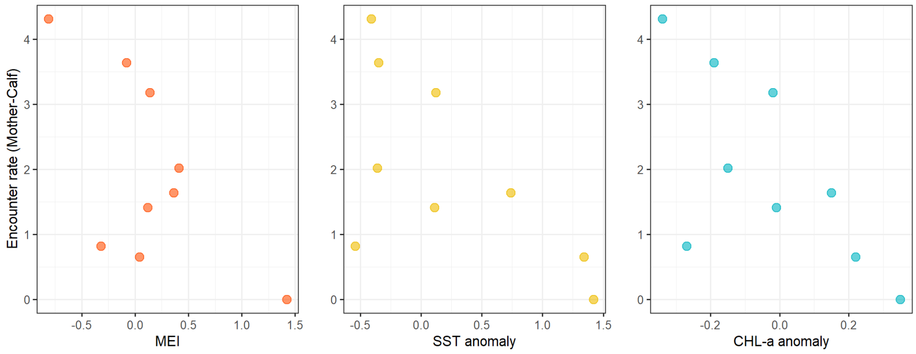

FIGURE 4
Relationships between encounter rates of humpback whales' mother-calf pairs and the averages of the Multivariate ENSO Index (MEI), anomalies of sea surface temperature (SST) and Chlorophyll a concentration (CHL-a).

Discussion

Opportunistic data in the study of cetaceans has been widely used due to the difficulties associated with the costs to carry out systematic surveys to obtain accurate estimates (Embling et al., 2015). The main limitations of the use of this type of data are the error associated with the analysis due to the lack of data standardization, non-consecutive information, and gaps in spatial coverage (Richardson et al., 2012). However, thanks to the use of opportunistic data, it has been possible to make inferences about general population trends, abundances, and distribution of some species or populations whose aspects of their population ecology are unknown, and which have been used in species conservation plans (Williams et al., 2006).

The Northeast Pacific humpback whales of the Central America DPS is one of the four DPSs that remain endangered, mainly due to its reduced population size (NMFS and NOAA, 2016; Curtis et al., 2022). The estimates of the population size of the Central America DPS have been assessed considering the sightings of humpback whales in their breeding grounds from southern Mexico to Central America, and whose most recent data date from 2021 (Calambokidis et al., 2008; Barlow et al., 2011; Curtis et al., 2022).

In this work, we incorporated data from humpback whale sightings in Costa Rica during the breeding seasons of 2000-2006, 2014-15, 2015-16, and 2019-20. This information is relevant because, in addition to having recent occurrence estimates for this area, it allows us to make inferences about the responses of humpback whales to current climate change and about their critical behaviors of migration and reproduction.

The feeding grounds of the humpback whale, Central America DPS are off California-Oregon-Washington in the United States (Steiger et al., 1991; Calambokidis et al, 2000). Environmental conditions in these areas are often affected by interannual warming events such as El Niño and the presence of marine heatwaves (Bond et al., 2015; Tseng et al., 2017; Newman et al., 2018). In addition to these phenomena, the warm phase of the PDO generates positive SST anomalies in the area and the negative phase of the NPGO is related to a decrease in productivity in this region (Di Lorenzo et al., 2008). These conditions cause changes in prey distribution and availability for humpback whales, which has induced the species to modify their local distribution and feed at higher latitudes or in more coastal areas, increasing their exposure to bycatch or vessel strikes (Fleming et al., 2016; Santora et al., 2020).

According to the analysis, the more intense the El Niño events and the greater the SST anomalies, the fewer whales and calves are observed in their southern breeding grounds in Costa Rica. The most drastic decrease in the encounters rate of adult and mother-calf pairs occurred during intense and long-lasting warming events such as the 2015-16 El Niño and the 2014-2016 marine heatwave (Gentemann et al., 2017). An independent study recorded two sightings that included mother-calf pairs of humpback whales during the 2010 breeding season in Golfo Dulce, Costa Rica, and during the 2020 breeding season there were three encounters, but all the sightings were single adults with no calves (Brooke Bessesen, *pers comm*). These dramatic declines were also recorded in the Hawaiian DPS during the same period (Cartwright et al., 2019; Frankel et al., 2021). In addition, a recent study showed that the breeding areas of the Central America DPS are the ones with the warmest conditions in the North Pacific (temperatures greater than 28°C) and that it is possible that if these high temperatures are maintained through the years can cause habitat shifts (von Hammerstein et al., 2022).

Humpback whales migrate to their breeding grounds looking for warmer and shallower waters without turbulence to optimize the use of their energy for gestation and lactation and not for thermoregulation, thereby ensuring the survival of the calf (Braithwaite et al., 2015; Meynecke et al., 2021). The energy needs of whales vary according to their sex and reproductive status, being reflected in the temporal variability at the time of arrival to their breeding grounds and in the length of stay (Craig et al., 2003; Avila et al., 2020). In other humpback whale populations, it has been observed that individuals that do not have sufficient energy reserves do not migrate to their breeding grounds so that the abundance of adults and calves decreases in these areas (Frankel et al., 2021; Meynecke et al., 2021; Schall et al., 2021).

The monthly values of the PDO, as well as the monthly anomalies of SST show a warming period from 2013, which continued until 2017. This warming period, in addition to having a large temporal scale, also had a great spatial scope (Menne et al., 2018; Yu et al., 2019). It is possible that presence of warmer conditions recorded in intermediate latitudes (Mexican coasts) could have favored humpback whales in finding thermally favorable areas for calving and could be one of the causes of decreases in the encounter rates in Costa Rica (Cavole et al., 2016; Robinson, 2016). In previous years, humpback whales from Central America DPS have been observed off Mexican coasts, which leads us to hypothesize that the whales are responding to these warming events by modifying their migratory behavior (Calambokidis et al., 2008; Taylor et al., 2021).

Climate change is modifying the conditions of the critical habitats of the humpback whales (Askin et al., 2008; De Weerdt and Ramos, 2019; Dey et al., 2021). The increase in SST has triggered several responses in humpback whales, such as changes in the timing of their migration, and variations in the length of stay in their feeding and breeding areas, humpback whales have also been observed feeding in more coastal areas and forming aggregations from tens to hundreds of individuals to feed (Ramp et al., 2015; Findlay et al., 2017; Avila et al., 2020; Santora et al., 2020).

Humpback whales are organisms considered resilient due to their ability to modify their feeding and migration behaviors mainly in response to thermally abnormal conditions (Moore and Huntington, 2008; Meynecke et al., 2021; Cabrera et al., 2022). It is possible that the Northeast Pacific humpback whale population might be modifying its critical migration behaviors (shortening the migratory route) in response to warming events in the Pacific Ocean. Therefore, it is necessary to increase efforts in carrying out systematic surveys and studies that address migration and the quality of their critical habitats in terms of environmental conditions and human interventions such as vessel disturbance, fishing gear, and ocean pollution to have a solid scientific basis that allows for improving conservation strategies for humpback whales of the Central America DPS.

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 and approval were not required for the animal study because we were based on observational data in situ, following current guidelines in place in Costa Rica for marine mammals sightings, the majority of it from 2000-2006.

Author contributions

LP-G, LO, and HG contributed substantially to the conceptualization, data analysis, document writing, and figure editing. DH-M, JP-P, and SG contributed to the logistics and data collection. DH-M, JP-P, and SG contributed to the writing and revision of the manuscript. All authors agree that this work be submitted for publication.

Funding

This study has been supported by funding from Vida Marina Foundation, The Divine Dolphin, Centro de Investigacion de Cetaceos de Costa Rica CEIC, and by fields grants (2013-2021) from Earthwatch Institute. Model processing and reporting were supported by a kind donation of Christ Redstone and Whale and Dolphin Conservation. LP-G was supported by the National Council on Science and Technology (CONACyT: No. 790305) scholarship.

Acknowledgments

We thank the Posgrado en Ciencias del Mar y Limnología, UNAM and the National Council on Science and Technology (CONACyT: No. 790305) for a scholarship. This research initiative has been supported by Centro de Investigación de Cetáceos Costa Rica CEIC, Fundación Vida Marina, Earthwatch Institute, and the many national and international volunteers we have had during our surveys.

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.

Publisher's note

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TYPE Original Research
PUBLISHED 19 December 2022
DOI 10.3389/fmars.2022.1086763

OPEN ACCESS

EDITED BY
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SPECIALTY SECTION
This article was submitted to
Marine Megafauna,
a section of the journal
Frontiers in Marine Science

RECEIVED 01 November 2022
ACCEPTED 30 November 2022
PUBLISHED 19 December 2022

CITATION
Gosby C, Erbe C, Harvey SE,
Figueroa Landero MM and
McCauley RD (2022) Vocalizing
humpback whales (*Megaptera
novaeangliae*) migrating from Antarctic
feeding grounds arrive earlier and
earlier in the Perth Canyon,
Western Australia.
Front. Mar. Sci. 9:1086763.
doi: 10.3389/fmars.2022.1086763

Vocalizing humpback whales (*Megaptera novaeangliae*) migrating from Antarctic feeding grounds arrive earlier and earlier in the Perth Canyon, Western Australia

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Migratory species undertake seasonal, long-distance travel between feeding and breeding grounds, and time their arrivals with high-quality resources. The Breeding Stock D population of humpback whales (*Megaptera novaeangliae*) migrates from Antarctic to Western Australian waters every austral winter. Based on 16 years (2002-2017) of passive acoustic recordings in the Perth Canyon, Western Australia, the hourly presence/absence of humpback whale vocalizations was used as an indicator of inter-annual changes in migration timing. A trend of earlier arrivals in the Perth Canyon by 1.4 days/year during the northward migration and possibly earlier departures from the Perth Canyon during the southward migration was observed. A distance-based linear model and a generalized linear model (GLM) both identified sea surface temperature (SST) as the most significant predictor for acoustic presence in the Perth Canyon. A 1 °C increase in SST corresponded to a decrease in humpback whale acoustic presence by 4.4 hours/day. Mean SST at the peak of the humpback whale season in the Perth Canyon was 19 °C. Exploratory analysis of the metocean environment of the Antarctic feeding grounds suggested that whales were leaving the Antarctic at the end of the austral summer, as sea ice concentration (SIC) increased and SST decreased. Further research should investigate whether changes in the metocean conditions on Australian breeding grounds correspond to changing departures from the Perth Canyon during the southward migration. If environmental conditions on breeding and feeding grounds change out-of-sync, migrating whales might be unable to arrive at either ground during optimal conditions.

KEYWORDS

humpback whale, migration, arrival, acoustics, Australia, Antarctica

1 Introduction

Migration is an evolved survival mechanism prevalent across a multitude of taxa around the world (Dingle and Drake, 2007). It is defined as a long-range, mass movement of a population towards high-quality habitat or resources (Dingle, 2014). Long-distance travel such as this is energy costly, and the decision to disperse is a trade-off between prey availability, suitability of habitat, and opportunities to breed (Alerstam et al., 2003; Bauer et al., 2011). To ensure synchronicity between seasonal resources, migration timing is triggered by both extrinsic and intrinsic factors (Dingle and Drake, 2007). Some examples of migration drivers include environmental factors, photoperiod, and internal cues (Bauer et al., 2011). Species that rely on such fine-scale changes to initiate migration may experience discrepancy between optimum habitat and presence. A common example is the movement of migrant birds between breeding and feeding grounds (Mayor et al., 2017). Different rates of environmental change between the two habitats create a mis-match. For example, migration arrivals no longer match up with peak insect production, generating a negative fitness consequence for migratory birds (Dobson et al., 2017; Mayor et al., 2017). Long-term monitoring is essential to understand trends in migration arrivals and departures, along with the environmental factors that influence presence. Many terrestrial migrants are well studied and show vulnerability in the face of climate change; yet, comparatively little research has been dedicated towards susceptibility of migrants in a changing marine environment (Balbontín et al., 2009; Mayor et al., 2017; Rickbeil et al., 2019).

The humpback whale (*Megaptera novaeangliae*) annually migrates to access quality habitats with optimum environmental conditions. Specifically, the animals migrate from polar, higher-latitude feeding grounds in the summer months to lower-latitude, temperate/tropical breeding grounds in the winter months (Fossette et al., 2014; Andrews-Goff et al., 2018). In the Southern Hemisphere, populations of humpback whales have been divided into different stocks, dependent upon their genetic structure and feeding grounds in Antarctic waters (IWC, 2007). The population migrating through Western Australia (WA) belongs to the Southern Hemisphere population known as Breeding Stock D (BSD) (IWC, 2007). These animals spend November to May in Antarctica feeding on Antarctic krill (*Euphausia superba*) and taking advantage of the highly productive upwellings (Jenner et al., 2001; Bestley et al., 2019). Historic whaling records and satellite tags show that this population resides in the Antarctic International Whaling Commission (IWC) Management Area IV during this time (Jenner et al., 2001; Matsuoka et al., 2011; Bestley et al., 2019). Amongst others, the Southern Kerguelen Plateau is a hotspot for phytoplankton blooms, which consequently attracts high densities of humpback whales during the feeding season (Schallenberg et al., 2018; Bestley et al., 2019). Once this resource is depleted, the population disperses north and is found from June to November in Australian waters (Jenner et al., 2001). But not all humpback whales migrate simultaneously.

The humpback whale migration is staggered into a progression of cohorts. This behavior is known as “temporal segregation” and is recognized in humpback whale populations around the world (Dawbin, 1997; Recalde-Salas et al., 2020). Migration starts with the resting females (not lactating or with year-old calves) travelling from Antarctic waters to South-West Australia (Dawbin, 1997). Sequentially, the following cohorts are the male and female juveniles, females that are not pregnant or lactating, then males, and the last to arrive in Australia are the heavily pregnant females (Dawbin, 1997). The population travels north along the WA coast to reach the high-latitude breeding grounds in the Kimberley region in North-West Australian waters (Jenner et al., 2001). The 6000 km structured migration is reversed when the population begins the journey back to Antarctic waters (Jenner et al., 2001). Resting females are followed by juveniles and mature males (Dawbin, 1997). Females with newborn calves are last to leave the continent (Dawbin, 1997). In some instances, male humpback whales will linger to travel with mothers and act as an “escort” for breeding advantages or protection against killer whales (Smith et al., 2008).

Aside from predators, humpback whales face many threats throughout their migration including pollution (e.g., noise or plastic), entanglement, and ship collisions (Prideaux, 2003). Lesser known are the impacts of environmental change on the fitness of humpback whales. Sea surface temperature (SST), particulate organic carbon (POC), chlorophyll *a* (Chl-*a*), and sea ice concentration (SIC) have seasonal fluxes that impact the distribution and abundance of whales (Doney et al., 2012; Cheung et al., 2013; Melbourne-Thomas et al., 2016; Chavez-Rosales et al., 2019; Szesciorka et al., 2020). Some population studies have found long-term trends of humpback whales arriving earlier to breeding grounds, with strong influences from environmental variables (Avila et al., 2020; Davis et al., 2020; Szesciorka et al., 2020). Temporal shifts in arrival and departure dates have not been studied in the BSD population. Migration timing discrepancies between optimum Antarctic feeding grounds and Kimberley breeding grounds may pose an additional threat to the population. However, collecting long-term data on whale migration can be expensive and prohibitive (Nowacek et al., 2016). Therefore, we used passive acoustic detections as a proxy for whale presence to investigate migration timing.

Passive acoustic monitoring has identified humpback whale presence since the 1950s, when musical tones in Hawaiian waters were attributed to their seasonal migration (Schreiber, 1952). The humpback whale vocal repertoire is exhaustive and can be broken down into recognizable components that distinguish them from other vocal marine species (Payne and McVay, 1971). Humpback whales produce song and non-song sounds (Payne and McVay, 1971; Recalde-Salas et al., 2020). The complexities of songs can be dissected into smaller components. Discrete sounds are referred to as a "unit", units make up a "phrase", and repeating phrases compose a "theme". Humpback whale songs are sequenced themes that can last from minutes to days (Payne and McVay, 1971). Song is heard in migratory pathways as well as feeding and breeding grounds (Payne and McVay, 1971; Winn and Winn, 1978; Tyack, 1981; Smith et al., 2008; Schall et al., 2021). Humpback whale song is exclusive to males and suggested as being a sexually selected trait (Payne and McVay, 1971). Discrete units may also be uttered as unstructured, stand-alone non-song sounds (Dunlop et al., 2008; Recalde-Salas et al., 2020). All cohorts produce non-song sounds and the function of these discrete units is proposed as social communication or a navigational tool (Payne and McVay, 1971; Winn and Winn, 1978; Tyack, 1981; Mercado and Perazio, 2022). The complex and hierarchical qualities of vocalizations can potentially distinguish males from females, populations from neighboring groups, and humpback whales from any other species in a marine soundscape (Payne and McVay, 1971; Tyack, 1981; Winn et al., 1981)

Based on 16 years of marine soundscape recording in the Perth Canyon, the goals of this study were to: (i) determine past migration arrival and departure dates in the Perth Canyon; (ii) identify any long-term trends or differences in humpback whale presence between years; (iii) evaluate the frequency of occurrence (FO) for humpback whale vocalizations per day and model against environmental variables (SST, Chl-*a*, and POC); and (iv) conduct an exploratory analysis of Antarctic environmental variables against the call FO in the Perth Canyon with a time lag.

2 Methods

2.1 Site description

The Perth Canyon is located on the south-western continental shelf, approximately 50 km west from Perth; it is 120 km long (Trotter et al., 2019). The passive acoustic recorders were deployed on the eastern plateau of the Perth Canyon, in depths between 400 and 490 m (Figure 1). The canyon intrudes on the continental shelf and extends 4000 m in depth. It is home to a variety of deep-sea fauna including deep-sea cnidaria, echinoderms, fish, and cetaceans (Erbe et al., 2015; Trotter et al., 2019). The Leeuwin current runs over the Perth Canyon and contributes to the seasonal upwellings of nutrients. Long-distance migrants take advantage of the seasonally increased primary production (Feng et al., 2009; Rennie et al., 2009). Pygmy blue whales (*Balaenoptera musculus brevicauda*), Antarctic blue whales (*Balaenoptera musculus intermedia*), fin whales (*Balaenoptera physalus*), Antarctic minke whales (*Balaenoptera bonaerensis*), and humpback whales have been identified acoustically while migrating through the Perth Canyon (Erbe et al., 2015). Specifically, the Perth Canyon is a

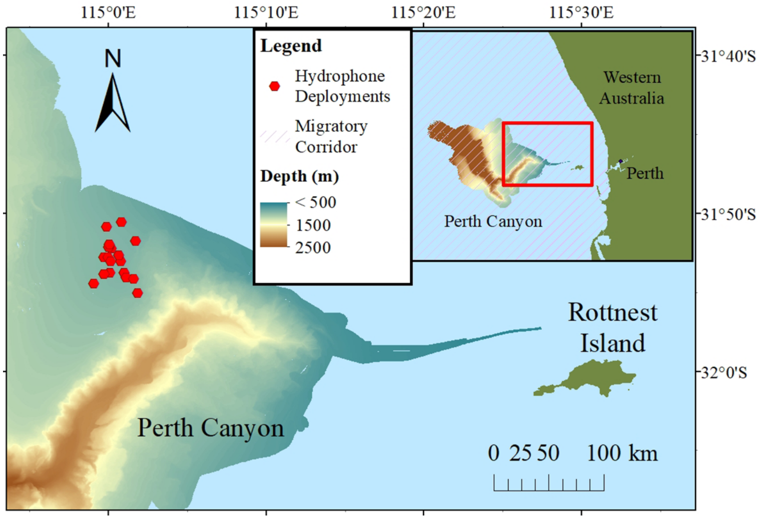

FIGURE 1
Map of the Perth Canyon study site showing the locations of the underwater acoustic recorders (red hexagons). The Perth Canyon bathymetry data was extracted from the Marine Geoscience Data system (MGDS; www.marine-geo.org/tools/datasets/22035; McCulloch, 2016). The migratory corridor shapefile was provided by the International Union for the Conservation of Nature (IUCN) Marine Mammal Protected Areas Task Force (IUCN MMPATF, 2021). Map was created using ArcGIS (Version 10.8.1, Esri, Redlands, CA, USA).

migratory corridor for the BSD population of humpback whales on their northward and southward routes (Jenner et al., 2001).

2.2 Data source

This study investigated humpback whale acoustic presence in the Perth Canyon using underwater acoustic recordings collected by the Centre for Marine Science and Technology (CMST), Curtin University. All recordings were collected with a CMST-built Underwater Sound Recorder (USR; McCauley et al., 2017), using HighTech Inc. HTI-90-U hydrophones (sensitivity −186 dB re 1 V/µPa, 2 Hz – 20 kHz). The recorders were calibrated with input white noise prior to deployment. Deployments were temporally staggered between 2002 and 2017. Recordings from 2009 onwards were collected as part of the Australian Integrated Marine Observing System (IMOS). Refer to Table 1 for deployment set numbers, start and end times, coordinates, sampling rates, and duty cycles.

Daily environmental data for the Perth Canyon (SST, Chl-*a*, and POC) and Antarctic Area IV (SST, Chl-*a*, POC, and SIC) were sourced from 2000 to 2018. A daily mean was calculated for each region utilizing the boundaries of the Perth Canyon Marine Park (Australian Government, 2013) and the Antarctic Area IV waters, south of 60° (IWC, 2007). SST was extracted from a single-sensor multi-satellite system using observations from Advanced Very-High-Resolution Radiometer (AVHRR) instruments on National Oceanic and Atmospheric Administration (NOAA) polar-orbiting satellites with a 0.02° × 0.02° grid cell size. Bias between satellite and buoy matchups is included for every cell. The SST dataset was summarized to only include cells with the level 5 highest quality. Data were obtained using the Australian Ocean Data Network (https://portal.aodn.org.au/ , accessed 6th October 2021). Chl-*a* and POC data were provided by NOAA and obtained from the Environmental Research Division's Data Access Program (ERDDAP; https://coastwatch.pfeg.noaa.gov/erddap/ , accessed 6th October 2021). Data from 2003 onwards were collected in a 4 km grid on the National Aeronautics and Space Administration (NASA) Aqua Spacecraft using a Moderate-Resolution Imaging Spectroradiometer (MODIS). There was Chl-*a* availability prior to 2003 onboard separate satellites and using different equipment. A cross-correlation was used between two satellites for a comparable year, and data prior to 2003 were utilized if $R^2 > 0.7$. Therefore, Antarctic Chl-*a* data from 2000 to 2002 were collected in a 4 km grid on the NASA Orbview-2 satellite using a Sea-viewing Wide Field-of-view Sensor (SeaWiFS). Only Science Quality level 3 data were extracted. Daily Antarctic SIC was obtained from the National Snow Ice and Data Centre (NSIDC; https://nsidc.org/ , accessed 25th March 2022; Fetterer et al., 2017). Data were collected in a 25 km grid using a Scanning Multichannel Microwave Radiometer (SMMR) onboard the NASA Nimbus-7 satellite. Concentration values less than 15% were removed from the SIC mean calculation due to data uncertainty from the passive microwave instruments.

Humpback whale population size for every year of acoustic data was computed based on the 13% annual growth estimate by

TABLE 1 Recorder deployment details for the sets (n = 18) used to detect humpback whale vocalizations in the Perth Canyon.

Set	Start Time	End Time	Latitude (S)	Longitude (E)	fs [kHz]	Duty cycle
2595	01/17/2002	01/24/2002	31° 52.230'	115° 0.180'	10	2/33
2612	10/14/2002	12/20/2002	31° 53.750'	115° 0.110'	10	2/15
2615	02/18/2003	06/07/2003	31° 53.770'	115° 1.000'	4	2/15
2628	06/10/2003	10/06/2003	31° 52.760'	114° 59.720'	5	3/15
2655	11/07/2003	01/07/2004	31° 52.774'	114° 59.990	7	3/15
2656	02/26/2004	06/14/2004	31° 50.864'	114° 59.920'	4	3/15
2672	12/30/2004	07/08/2005	31° 52.124'	115° 0.040'	6	3/15
2724	01/01/2007	04/25/2007	31° 54.083'	115° 1.143'	6	3/15
2802	02/26/2008	08/29/2008	31° 53.858'	114° 59.732'	6	3/15
2823	02/24/2009	19/11/2009	31° 54.466'	114° 59.080'	6	8/15
2825	02/20/2009	10/01/2009	31° 53.046'	115° 0.137'	6	8/15
2884	11/13/2009	07/22/2010	31° 55.039'	115° 1.863'	6	7/15
2962	08/06/2010	05/08/2011	31° 54.139'	115° 1.607'	6	7/15
3006	07/14/2011	06/18/2012	31° 51.980'	115° 0.054'	6	5/15
3154	08/10/2012	06/14/2013	31° 53.053'	115° 0.813'	6	5/15
3376	11/28/2013	11/03/2014	31° 50.530'	115° 0.824'	6	5/15
3444	12/30/2016	08/26/2017	31° 51.767'	115° 1.741'	6	5/15
3445	01/05/2016	12/30/2016	31° 52.656'	115° 0.656'	6	5/15

Start and end times are in mm/dd/yyyy format. Sampling frequency (fs) is in kilohertz. For the duty cycle, the first number is the length of recording (min) for each cycle, and the second number is the total length (min) of each cycle.

Salgado Kent et al. (2012b), who undertook aerial surveys between 2000 and 2008.

2.3 Call detections

Humpback whale vocalizations were identified based on repertoire descriptions of song and non-song catalogues in the literature (Payne and McVay, 1971; Recalde-Salas et al., 2020) and co-authors' prior experience with this population. Humpback whale acoustic presence was visually and aurally determined every hour using spectrograms in Raven Pro (Version 1.6, The Cornell Lab of Ornithology, Ithaca, NY, USA), which were created with 2048-point discrete Fourier transforms, Hann windows, and 50% overlap. Spectrograms were scanned in hourly increments for humpback whale vocalizations between 10 Hz and 2 kHz. Presence per hour was determined by selections of non-song or song within each increment. Raven selection tables were exported to xls format.

2.4 Data pre-processing

Hourly presence/absence of humpback whale vocalizations was calculated in MATLAB (Version R2020b, The MathWorks Inc., Natick, MA, USA). Raven selection tables were read into MATLAB and the frequency of occurrence (FO) of humpback vocalizations was calculated as the number of hours that humpback whales were acoustically present per 24 h day. The FOs for the start and end days of deployment were computed as the number of hours with humpback whale vocalizations divided by the number of hours the recorder was in the water on those days.

The environmental variables in the Perth Canyon and Antarctica were averaged to get a daily SST, POC, Chl-*a*, and SIC value. The datasets were all resourced from satellite imagery, and therefore cloud cover resulted in missing data points.

2.5 Data analyses

2.5.1 Migration arrivals and departures

The date of arrival (A_{25}) of BSD humpback whales in the Perth Canyon was determined as the first day of the year when the call FO exceeded 6/24 hours (25%). This is when the population is ascertained to have begun their northward migration through the Perth Canyon. The departure date (D_{25}) was determined as the last day of the year when the call FO exceeded 6/24 hours. Thus, the departure date is when the BSD population has finished their southward migration through the Perth Canyon. This criterion was arbitrarily selected as a consistent parameter to measure the limits of the BSD's migration, thus removing the early/late outliers of individual whales in the population. We then performed a linear regression to identify trends in A_{25} and D_{25} over the years. We required a 5-day recording buffer before A_{25} and after D_{25}; if fewer than 5 days of recordings were available prior to A_{25} or after D_{25}, then we removed the year from our regression.

2.5.2 Differences in frequency of occurrence

The PERMANOVA+ add-on (Anderson et al., 2015) in PRIMER v7 (Clarke and Gorley, 2015) was chosen to analyze the univariate frequency data. A two-factor PERMANOVA (McArdle and Anderson, 2001) with "Year" and "Week of year" as fixed factors was used to test statistically significant differences in inter-annual and weekly variation in humpback whale FO. The test was based on a Euclidean distance resemblance matrix with Type III partial sums of squares and unrestricted permutation of raw data totaling 9999 permutations. For *post-hoc* pairwise comparisons of significant terms, Monte Carlo *p*-values were computed when the number of permutations was <100 (Anderson et al., 2015).

2.5.3 Influence of Perth Canyon environmental variables

The mean and standard deviation (SD) of the environmental variables in the Perth Canyon (SST, SST bias, Chl-*a*, and POC) were tested for multicollinearity in Draftsman's plots, produced in PRIMER v7. Week of year was correlated with environmental variables in Excel (Version 2019, Microsoft, Redmond, WA, USA) to determine seasonal correlation in the data. Variables with R^2 correlation values >0.7 were removed from the analyses (Ratner, 2009). The correlation tests ensure that the predictor variables will create a parsimonious model. The deployment days with missing environmental values and outliers were removed from the dataset. The predictor variables were input into a DISTance-based Linear Model (DISTLM) (Anderson, 2005) to find the best predictors of variability in humpback whale FO (Euclidean distance resemblance matrix; Type III partial sums of squares; fixed effects sum to zero for mixed terms; unrestricted permutation of raw data; 9999 permutations). The percentage of variation and significance were output for each variable from the marginal tests. The overall best model of the groups was determined by the lowest small-sampled, corrected, Akaike Information Criterion (AICc), which was selected to reduce bias in the smaller sample size (Hurvich and Tsai, 1991). The final model provided the variables that best determined the FO, as well as an R^2 value that described the percentage of variation that the model explained.

A generalized linear model (GLM) was trialed as it provides additional flexibility in exploring non-linear relationships between the predictors and response through the link function. The eight time series of the environmental variables (i.e., means and SDs of SST, SST bias, Chl-*a*, and POC) as well as FO were smoothed with a 7-day moving-average filter to reduce day-to-day variability and rather focus on weekly trends. We linearly interpolated over missing values in any of the variables up to a maximum of 7 days. If more than 7 days of data were missing, we kept the gap in that variable (as NaN). Next, the time series were normalized by subtracting the mean and dividing by the root-mean-square. The GLM was fitted using the *stepwiseglm* function in MATLAB, which performs a stepwise regression, starting with a constant model, adding and subtracting one term at a time, keeping only the relevant terms, until the model cannot be improved further. The terms trialed were the linear terms for each predictor, and all 2-predictor products (i.e., all possible combinations of any two predictors). With predictors and response being of type real, *stepwiseglm* was run with the identity link function.

2.5.4 Exploration of Antarctic environmental variables

As there remained substantial outliers in the Antarctic environmental data, the time series were further pre-processed by removing values deviating more than 3 SDs in a 20-day moving-average window. We linearly interpolated across gaps in the data (from cloud cover and from outlier removal) and smoothed the time series as above.

To determine the BSD northward travel speed from Antarctic Area IV to the Perth Canyon, a literature review was conducted. Modest et al. (2021) tagged humpback whales migrating from Antarctica to South America, across the open ocean and then along the coast. Firstly, the average speed from Antarctica to Cape Leeuwin was derived from the mean speed of the Breeding Stock G (BSG) population travelling across the open ocean from the Western Antarctic Peninsula to Cape Horn. Secondly, the average speed from Cape Leeuwin to the Perth Canyon was estimated using the mean speed of humpback whales travelling along the South American coast from Cape Horn to Peninsula de Paracas. The distance travelled between Antarctica and the Perth Canyon was estimated using the BSD southward migration routes to the Antarctic feeding grounds as determined by tag data from Bestley et al. (2019). The distance-to-speed ratios for the two lags (open ocean and coast) were subtracted from the A_{25} in the Perth Canyon to estimate the environmental conditions in Antarctica when the BSD whales presumably initiated their northward migration. With d representing the travel distance and v the speed, from Antarctica to WA (*Ant*) and along the WA coast (*WA*), the travel duration T was computed as:

$$T = \frac{d_{Ant}}{v_{Ant}} + \frac{d_{WA}}{v_{WA}} \qquad \text{(Eq. 1)}$$

We then investigated what the features of the Antarctic environment were at the time of approximate departure.

3 Results

3.1 Perth Canyon migration arrivals and departures

The FO in the Perth Canyon is visualized in Figure 2. Across the years, whales were acoustically present in the months of May to December. While this period captured two migrations (first northward, then southward), there was no gap in FO in between, so that the migration direction could not be separated at this recording site.

Between 2003 and 2009, migration A_{25} were mid-June, whereas the most recent years (2010-2017) had humpback whale A_{25} in late-May to early-June (Figure 3). The earliest A_{25} was the 23rd May in 2013 and the latest A_{25} was the 13th June in 2005. The rate of change of A_{25} was -1.4 days/year.

The D_{25} were more variable across a longer temporal scale. BSD humpback whales departed the Perth Canyon in early-December to late-November in the early years (2002-2010), except for 2003, which had an unusually early D_{25}. The departures of the population in the later deployment years (2011-2017) were from early to mid-November. The earliest D_{25} was the 16th November in 2003 and 2011 and the latest D_{25} was the 14th December in 2002. The rate of change of D_{25} was insignificant (Figure 3).

3.2 Perth Canyon FO PERMANOVA

The difference of FO between Year, Week of Year, and the interaction between these variables was significant by permutation (p-value ≤ 0.001; Table 2). A *post-hoc* pairwise analysis showed that the weeks of year in which humpback whales arrived differed significantly between years (PERMANOVA: p-value< 0.05). One of the earlier weeks of arrival (week 23) was in early-June and there were significant differences in humpback whale FO between the early years in the study (2003, 2004, 2005, 2008) and the later years in the study (2012, 2013, 2014, 2016, 2017). The last week of departure from the Perth Canyon was in week 50 and FO was significantly different between the earliest year of data (2002) and all other years (2003, 2009, 2010, 2011, 2012, 2013, 2016). There was variable significance in FO between years in the preceding weeks of departures.

3.3 Perth Canyon DISTLM

The Draftsman's plot found positive, approximately linear correlations between Population size and Year (Figure S1), as well as between Mean and SD of POC and Chl-*a* (Figures S2, S3). There was also a sinusoidal correlation between Week of Year

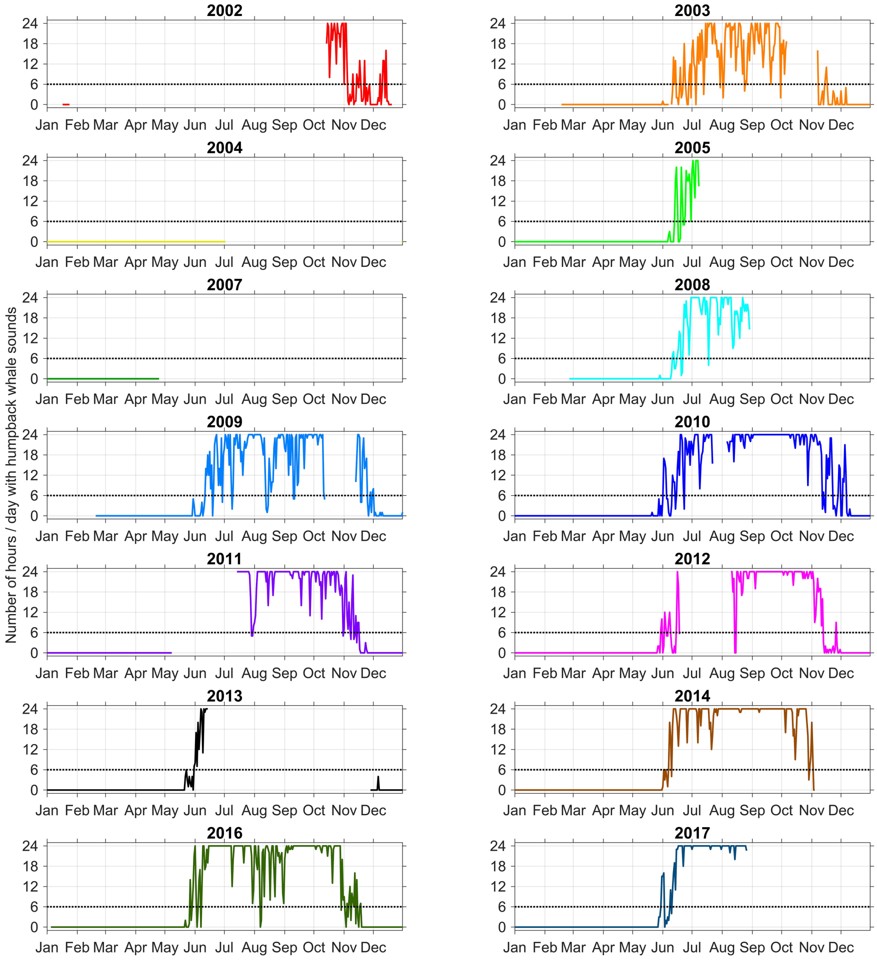

FIGURE 2
Yearly line graphs of humpback whale acoustic FO. Date ticks correspond to the first day of each month. The arrival and departure boundary are indicated by the black dotted line at a FO of 6h/24h = 0.25 (n = 3358).

and SST (Figure S4). The variables POC Mean, POC SD, Population size, and Week of Year were removed from the DISTLM dataset to create the most parsimonious model.

The DISTLM results showed that the highest proportion of the variation in humpback whale acoustic FO was explained by SST Mean, SST SD, and Year (Table 3). These groups were also statistically significant ($p \leq 0.001$). The DISTLM model of best AICc fit utilized all selections, and these predictor variables explained 63.2% of the variation in the humpback whales' vocalizations FO in the Perth Canyon (RSS = 120.65).

3.4 Perth Canyon GLM

Out of the predictors, the GLM identified POC Mean as more significant than Chl-*a* Mean, and so Chl-*a* was dropped from the model. Year was a stronger predictor than Population size, and so the latter was dropped from the model. The effect of SST bias was insignificant, as was the effect of POC SD. The final model retained the variables SST Mean, SST SD, POC Mean, and Year, and the pair products listed in Table 4. The normal probability plot of residuals is shown in Figure S5. In order of decreasing deviance, the model identified SST Mean as the strongest predictor, followed by POC Mean, then the product of SST Mean and POC Mean, then Year (Table 5). Given the predictor variables were normalized to standard Gaussians, the estimated coefficients were comparable; and so, the influence of SST Mean on humpback whale FO was more than four times stronger than that of the other environmental variables. A 1 °C increase in SST corresponded to a 4.4 h/d decrease in humpback whale acoustic presence—according to the model. At the peak of the humpback whale season in the Perth Canyon (when humpback whale sounds were detected 24 h/d), the mean SST was 19 °C.

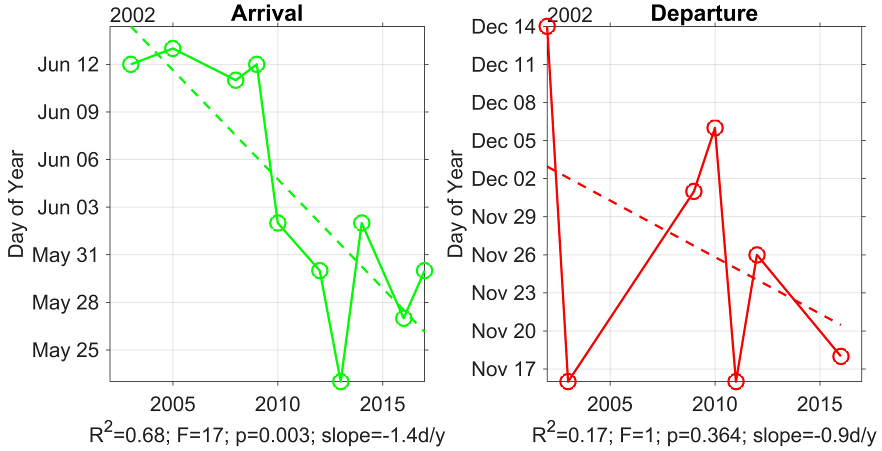

FIGURE 3
Scatter plots of humpback whale arrival (n = 10) and departure (n = 7) dates for the years of available passive acoustic monitoring data in the Perth Canyon. A linear trendline has been fitted; regression statistics (R^2, F, and *p*-value) are noted beneath each plot.

3.5 Antarctic environmental correlations

Based on Eq. 1, with d_{Ant}=5100 km, d_{WA}=300 km, v_{Ant}=5.48 km/h, and v_{WA}=6.48 km/h, the estimated travel time from Antarctica to the Perth Canyon was ~40 days. Figure 4 shows the five time series and the values of the Antarctic environmental variables at the estimated departure dates from Antarctica. SST, Chl-*a*, and POC dropped past their peak in the early months of the year, months prior to the peak of humpback whale vocalizations being detected in the Perth Canyon. Sea ice concentration was lowest when the other environmental variables were at their peak. Humpback whales seemed to depart when SST was, on average, -0.33 °C (higher in recent than earlier years), Chl-*a* was 0.24 mg/m^3, POC 75.0 mg/m^3, and SIC 29.6%.

TABLE 2 Results of PERMANOVAs examining the effects of year, week of year, and the interaction between these factors on humpback whale FO (n = 3358).

Factors	df	SS	Pseudo-F	*p*-value	Permutations
Year	13	7.1591	35.892	<0.0001*	9933
Week of Year	51	403.32	515.42	<0.0001*	9871
Year × Week of Year	425	43.143	6.616	<0.0001*	9659

*denotes a significant *p*-value from 9999 permutations.

TABLE 3 DISTLM marginal test results between group and humpback whale FO showing the proportion of the variation explained by the predictor variable (n = 1798).

Selection No.	Group	SS (trace)	Pseudo-F	*p*-value	Proportion
1	SST Mean	175.07	2062.9	<0.001*	0.535
2	SST SD	32.619	198.68	<0.001*	0.010
3	Bias Mean	18.668	108.57	<0.001*	0.057
4	Bias SD	6.490	36.314	<0.001*	0.020
5	Chl-*a* Mean	6.162	34.443	<0.001*	0.019
6	Chl-*a* SD	0.033	0.17993	0.667	1.00×10^{-4}
7	Year	35.399	18.027	<0.001*	0.108

*denotes statistical significance by 9999 permutations.

TABLE 4 GLM specifications estimating the effects of Perth Canyon environmental variables on humpback whale acoustic presence: Predictor variables and their combinations, estimated coefficients, standard errors, t-statistics and *p*-values.

Predictor	Estimated coefficients	Standard error	t-statistic	*p*-value
(Intercept)	0.12	0.012	10	1E-24
SST Mean	-0.68	0.011	-62	<1E-100
SST SD	0.1	0.012	9	2E-17
POC Mean	0.17	0.012	14	2E-44
Year	0.17	0.011	15	9E-50
SST Mean × SST SD	-0.05	0.011	-5	1E-06
SST Mean × POC Mean	-0.17	0.013	-13	7E-38
SST Mean × Year	-0.08	0.012	-7	5E-11
SST SD × POC Mean	-0.05	0.01	-5	3E-07
SST SD × Year	0.11	0.012	9	1E-18

4 Discussion

The long-term acoustic examination of the humpback whale BSD population while travelling through the Perth Canyon provided insight into their migration timing. The study revealed thresholds of the north- and southward migrations, determined shifts in migration timing between years, provided environmental predictors of humpback whale acoustic FO in the Perth Canyon, and explored Antarctic environmental conditions at the time when the population likely departed their feeding grounds, heading for WA.

4.1 Temporal shifts in migration

This study showed a gradual change in humpback whale acoustic arrival dates in the Perth Canyon over the years 2002-2017. Both arrival and departure dates in the later years of the study were weeks premature compared to those in the earlier years. However, departure dates exhibited great variability and there were fewer years with acoustic recordings at the time of departure, so that the shift in departure dates was statistically insignificant. These results, which are entirely based on passive acoustic monitoring, are consistent with visual observations in Geographe Bay, WA, finding an earlier shift of the humpback whale season by approximately four weeks over the last 15 years (C. Burton, personal communication, 21st October 2021). The shift of humpback whale presence in the Perth Canyon alters the migration periods described in Jenner et al., (2001): Original estimations of northbound and southbound migrations were mid-late June and mid-October, respectively. The later years in our study estimate that the boundaries of the migration are now late-May to early-June for the arrivals and possibly early to mid-November for the last departures (pending further data collection to increase statistical power). These migration shifts are concurrent with the literature of humpback whale populations elsewhere, with varying rates of change or suggested influences (Ramp et al., 2015; Avila et al., 2020).

4.2 Predictors of Humpback Whale presence

Extrinsic factors are posed as potential triggers for these shifts in migration. Different predictors for humpback whale

TABLE 5 Stepwise GLM estimating the effects of Perth Canyon environmental variables on humpback whale acoustic presence: Order of predictors added to the model in decreasing deviance, showing F-statistic and *p*-value for each step.

Step	Added predictor	Deviance	F-statistic	*p*-value
1	SST Mean	1445	4555	<1E-100
2	POC Mean	1365	195	3E-43
3	SST Mean × POC Mean	1287	203	8E-45
4	Year	1229	160	9E-36
5	SST SD	1201	78	2E-18
6	SST SD × Year	1158	125	2E-28
7	SST Mean × Year	1146	34	7E-09
8	SST SD × POC Mean	1136	30	5E-08
9	SST Mean × SST SD	1128	23	1E-06

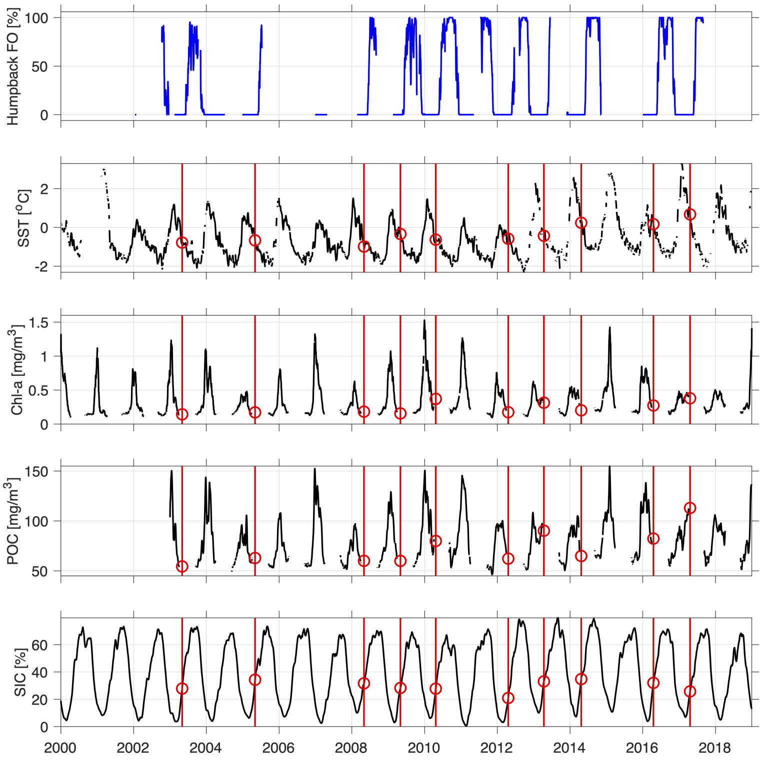

FIGURE 4
Time series of environmental variables in Antarctic Area IV between 2000 and 2019 with the humpback whale acoustic presence in the Perth Canyon. Red vertical lines indicate dates 40 days before humpback whale arrival in the Perth Canyon. Red circles indicate the environmental conditions when humpback whales possibly departed Antarctica.

presence have been found for different populations and geographic regions. At a summer feeding ground in the Gulf of St Lawrence (Canada), earlier arrivals related to sea ice extent and SST (Ramp et al., 2015). Avila et al. (2020) found no correlation to SST but instead suggested ice sheet mass as a predictor for an earlier migration arrival at breeding grounds in Gorgona National Park (Colombia). Possible predictors of humpback whale presence are not consistent in the literature and may be population or site specific.

Our model showed humpback whale acoustic FO in the Perth Canyon was largely driven by Year and SST. Call FO was temporally predicted by Year in the DISTLM, meaning the acoustic presence of humpback whales was not consistent between years. This could be influenced by population densities or behavior. The population growth was estimated as 13% per year by Salgado Kent et al. (2012b) based on population counts between 2000 and 2008, and this may be reflected in the species' earlier (and ultimately longer) acoustic presence over the years. Others have speculated that a growing population shows earlier migration arrivals (Beazley, 2022). Alternatively, fluctuations in acoustic FO might reflect variability in the proportion of humpback whales migrating from Antarctica each year. Van Opzeeland et al., (2013) found pervasive acoustic detection of humpback whales in Antarctic waters year-round, suggesting that not all individuals complete a full migration each year, and the proportion of the population that undertakes long-distance travel may fluctuate between years based on environmental factors on their feeding grounds (van Opzeeland et al. 2013; Ramp et al., 2015; Avila et al., 2020). A high percentage of the migrating humpback whale population are males, implying that females might circumvent departure in particular years if they cannot afford the energy cost of long-distance travel (Brown et al., 1995; Alerstam et al., 2003). Humpback whales rely on high volumes of krill during the feeding season to build energy reserves for migration (Riekkola et al., 2020). Krill abundance is heavily influenced by SST, thus, environmental variability between years may affect their fitness for migration (Alerstam et al., 2003; Kawaguchi et al., 2013; Melbourne-Thomas et al., 2016; Riekkola et al., 2020).

SST was the strongest environmental predictor for humpback whale presence in the Perth Canyon and this finding aligns with observations elsewhere (Ramp et al., 2015; Chavez-Rosales et al., 2019). For example, along the eastern coast of Australia, humpback whales departed weeks earlier than normal during years of higher temperatures (Meynecke et al., 2017). Consequently, the parameters around migration timing and the presence of the BSD population in the Perth Canyon would be affected by future trends in SST and, on a larger scale, climate change. The southwest Australian waters have experienced an increase in SST over the last few decades (Foster et al., 2014). Coupled with our study results, the rising SST will likely impact the BSD migration in the future. The shifting arrival dates may already be an adaptation to climate change as hypothesised by Ramp et al. (2015). Looking at other taxa, pied flycatchers showed flexibility in migration timing, possibly to keep up with climate change (Both, 2010). Specifically, the birds shifted their migration to more closely align with a shifting food peak. Similarly, in our study, the shifting arrival dates of humpback whales in the Perth Canyon may be a behavioral response to triggering environmental variables on their Antarctic feeding grounds.

4.3 Environmental variables on Antarctic feeding grounds

Assuming a constant (over the years) migration duration from Antarctica to WA, humpback whales would have left Antarctica when SST, Chl-*a*, and POC were well past their peak and SIC had started to increase again. We hypothesize that shifts in arrival in the Perth Canyon (during northward migration) may be linked to environmental conditions on the feeding grounds. Tsujii et al., (2021) found that the annual migration timing of bowhead whales was linked to both SIC and SST in the Arctic. Antarctic SST may be slowly increasing on the feeding grounds and acting as a trigger for the population to leave earlier (Mintenbeck, 2017).

Once again, the increasing population may create a natural temporal expansion of the migration parameters and pressure more individuals to initiate migration earlier. Conversely, a theorized earlier departure from Antarctica may be in relation to temporal shifts in the peak availability of food. Krill abundance may not thoroughly nourish the entire population sufficiently; an exhaustion of the food supply may encourage earlier departures from the polar waters. Antarctic krill populations are predicted to be negatively impacted by climate change in the future and this could lead to a negative fitness consequence for humpback whales undertaking their long-distance migration (Tulloch et al., 2019). Grey whales (*Eschrichtius robustus*) on their feeding grounds exhibited overall decreased body condition over a three-year period between the beginning and end of the study (Soledade Lemos et al., 2020). An earlier departure from Antarctica may therefore be indicative of diminishing food availability on the Antarctic feeding grounds.

4.4 Drawbacks of the study

This study was strictly focused on the acoustic presence and trends of the BSD population in a migratory corridor. While it seems plausible that changes in environmental conditions of the Antarctic feeding grounds send them on their way northward (and similarly, changes in environmental conditions of their breeding grounds send them on their way southward), no concurrent observations were available of humpback whale presence (arrival and departure) on feeding or breeding grounds. Acoustic recordings on the feeding grounds could substantiate theories of earlier migration shifts beginning in Antarctica. Otherwise, the humpback whale population could still be spending the same amount of time in each region but travelling at different speeds each year on their journey between the two (Zerbini et al., 2006; Andrews-Goff et al., 2018). For instance, humpback whales stagger their migration between travel and rest in the Australian coastal waters (Jenner et al., 2001; Bejder et al., 2019)—possibly differently in different years, leading to changes in overall migration duration. From this study, it is uncertain if the humpback whales' feeding and breeding grounds are facing a similar temporal shift in arrivals and departures as the Perth Canyon migratory corridor. An acoustic comparison with Antarctica and northwest Australia would determine whether inter-annual shifts in arrival and departure also occur on feeding and breeding grounds and ultimately enable an investigation of the distribution of the BSD population throughout the entire migratory cycle.

The long-term nature of this study had shortcomings in the early acoustic datasets. Technology constraints at the beginning of the study condensed the available recordings to be much shorter in length and temporally sporadic. For the total 15 years of passive acoustics, there were only 10 years of arrival data and seven years of departure data. Additionally, only five years had both arrival and departure data. A more complete dataset with arrival and departure recordings every year would legitimize how migration patterns may develop (Laake et al., 2012). Hence, more long-term passive acoustic data for this region can better project future shifts in migration.

In addition, monitoring at a different location within the migratory corridor, where the northward and southward migrations are temporally separated, would be beneficial and provide both arrival and departure dates for both migration legs. In the Perth Canyon, the two legs were not separable acoustically; meaning that some vocalizing humpback whales were still migrating north when others were already on their return journey, migrating south. So we missed the departures of the northward migration from the Perth Canyon, and the arrivals of the southward migration. At a different location, such as Cape Leeuwin (the whales' first contact with Australia on their northward migration and last contact with Australia on their southward migration), we expect the two migration legs to be temporally separated, but acoustic recordings with a sampling frequency appropriate for humpback whale sounds are unavailable.

During migration, all humpback whales can vocalize non-song sounds, but males also produce song (Recalde-Salas et al., 2020). Songs are much easier to detect because they run for longer periods of time and create recognizable patterns (Payne and McVay, 1971). We may have missed individuals in the population if they were not vocalizing when travelling within range of the recorder. Moreover, some cohorts (i.e., the mother-and-calf cohort) vocalize very quietly and far less frequently than the males (Félix and Haase, 2005; Salgado Kent et al., 2012a). These particular cohorts would likely be largely missed by the Perth Canyon recorders.

4.5 Ecosystem impacts

Migration timing is important to maximize presence in suitable habitat and needs to match up with environmental variables that inform desirability (Dingle, 2014). There is evidence of some migrant species adapting their behavior with climate change to maintain temporal and spatial synchronicity (Both, 2010; Sanders and Mennill, 2014; Mayor et al., 2017). Under increasing environmental pressure, short-distance migrants are more successful at balancing opportune habitats than long-distance migrants (Jenni and Kéry, 2003; Both et al., 2006). Long-distance migrants might struggle to keep arriving at their functionally different habitats at the optimum time (i.e., when habitat features are optimum). Furthermore, if the different habitats change out-of-sync, it might become impossible to be present in each at the optimum time. Some long-distance migrant birds are compensating for such environmental mis-match by leaving breeding grounds sooner to align with the phenology of insects on their feeding grounds (Jenni and Kéry, 2003). Similarly, a shift in humpback whale migration presence in Australian waters may be an indicator of shifting parameters elsewhere. Marine mammal migrants are less studied than their terrestrial counterparts and it remains undetermined whether a shift in humpback whale migration is detrimental to the population's survivability. However, larger shifts increase the likelihood of habitat mis-match and may negatively affect the survivability, as witnessed with other long-range migrants (Both et al., 2006; Sanders and Mennill, 2014; Mayor et al., 2017).

Studies with similar shifts in migration arrivals and environmental predictors are also finding that the rates of change in migration are not the same between migrant species that occupy the same habitat (Ramp et al., 2015). For example, the increasingly earlier humpback whale northbound migration may temporally and spatially overlap migrant species that do not usually co-exist (Ramp et al., 2015). Another migrant whale species in the Perth Canyon is the pygmy blue whale (McCauley and Jenner, 2010). Although this species is listed as data deficient on the IUCN Red List of Threatened Species, other studies on a range of marine mammals have shown that shifting migration arrivals is not limited to humpback whales (Szesciorka et al., 2020; Huang et al., 2022). Therefore, the pygmy blue whales that utilise the Perth Canyon for feeding during summer could be affected by interspecific competition, should the humpback whale presence increasingly overlap their own. The humpback whale BSD population has recovered significantly over the last few decades; however, resource competition may add another threat to the growing number of concerns for the species.

This study was able to determine the arrival and departure parameters of the BSD population, identify a significant temporal shift of humpback whale migration, and provide supporting evidence of SST predicting their presence in the Perth Canyon. This research is novel for the BSD population in determining long-term trends of their presence. Future research should further investigate the Antarctic Area IV to determine the population's geographic distribution and the contributing extrinsic factors in initiating their migration. Similar trends on the feeding grounds may pose additional threats to the BSD population in the face of climate change.

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 the study relied entirely on archival data, which were collected passively and remotely.

Author contributions

CG, CE, and EH contributed to the design of the study. RM collected the acoustic data. The environmental data was sourced by CG and MLF. The data was analyzed by CG, CE, EH, and MLF. CG wrote the first draft of the manuscript. CE contributed to sections of the manuscript. All authors contributed to manuscript edits, read, and approved the submitted version.

Acknowledgments

Data was sourced from Australia's Integrated Marine Observing System (IMOS), Passive Acoustic Observatories; https://imos.org.au/facilities/nationalmooringnetwork/acousticobservatories. – IMOS is enabled by the National Collaborative Research Infrastructure Strategy (NCRIS). It is operated by a consortium of institutions as an unincorporated joint venture, with the University of Tasmania as Lead Agent.

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.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.1086763/full#supplementary-material

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frontiers | Frontiers in Marine Science

TYPE Original Research
PUBLISHED 20 March 2023
DOI 10.3389/fmars.2022.850162

La Niña conditions influence interannual call detections of pygmy blue whales in the eastern Indian Ocean

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Oceans across the globe are warming rapidly and marine ecosystems are changing as a result. However, there is a lack of information regarding how blue whales are responding to these changing environments, especially in the Southern Hemisphere. This is because long term data are needed to determine whether blue whales respond to variability in environmental conditions. Using over 16 years of passive acoustic data recorded at Cape Leeuwin, we investigated whether oceanic environmental drivers are correlated with the migration patterns of eastern Indian Ocean (EIO) pygmy blue whales off Western Australia. To determine which environmental variables may influence migration patterns, we modelled the number of acoustic call detections of EIO pygmy blue whale calls with broad and fine scale environmental variables. We found a positive correlation between total annual whale call detections and El Niño Southern Oscillation (ENSO) cycles and the Indian Ocean Dipole (IOD), with more whale calls detected during La Niña years. We also found that monthly whale call detections correlated with sea surface height around the hydrophone and chlorophyll-a concentration at a prominent blue whale feeding aggregation area (Bonney Upwelling) where whales feed during the summer before migrating up the west Australian coast. At the interannual scale, ENSO had a stronger relationship with call detections than IOD. During La Niña years, up to ten times more EIO pygmy blue whale calls were detected than in neutral or El Niño years. This is likely linked to changes in productivity in the feeding areas of the Great Australian Bight and Indian Ocean. We propose that in lower productivity years whales either skipped migration or altered their habitat use and moved further offshore from the hydrophones and therefore were not detected. The frequency and intensity of ENSO events are predicted to increase with climate change, which is likely to impact the productivity of the areas used by blue whales. These

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

RECEIVED 07 January 2022
ACCEPTED 23 November 2022
PUBLISHED 20 March 2023

CITATION
Truong G and Rogers TL (2023) La Niña conditions influence interannual call detections of pygmy blue whales in the eastern Indian Ocean.
Front. Mar. Sci. 9:850162.
doi: 10.3389/fmars.2022.850162

changes in productivity may affect the physical condition and reproductive success of individual whales. A reduction in reproductive success could have a significant impact on blue whale recovery from historical whaling and their ability to adapt to a changing environment.

KEYWORDS

pygmy blue whales, passive acoustic monitoring (PAM), El Niño southern oscillation, chlorophyll-a, long-term data, environmental drivers, La Niña, Indian Ocean

Introduction

Global temperatures have been steadily increasing over the past few decades due to the burning of fossil fuels and the emission of greenhouse gases such as carbon dioxide and methane. The ecological impacts of climate change are evident in terrestrial and marine systems, spanning from the warm tropics to the cold polar regions (Walther et al., 2002; Parmesan, 2006). Overall, marine environments are changing at a much faster rate than terrestrial systems (Burrows et al., 2011). Ocean circulation has changed considerably due to increased water temperatures and changes to major ocean currents. Poleward western boundary currents are strengthening, bringing warmer water further south towards mid to high latitude regions (Wu et al., 2012; Yang et al., 2016). In the Southern Ocean, the Antarctic Circumpolar Current is predicted to strengthen and shift its overall position southward (Saenko et al., 2005). At the same time, other abiotic climate stressors in temperate and southern oceans (e.g., shifts in sea surface temperature and acidification, and decreases in winter sea-ice cover) have been found to drive change for marine fauna (Kroeker et al., 2013; Post et al., 2013; Stuart-Smith et al., 2015). To date, abiotic factors have resulted with biotic changes at lower trophic levels. These include decreases in primary productivity and changes in phytoplankton community structure (Montes-Hugo et al., 2009), which in turn influence the structure of grazer communities such as krill and salps (Atkinson et al., 2004). Some of these changes have transferred to higher trophic level species. However, a better understanding of how these lower trophic changes will impact higher trophic levels in the context of climate change is necessary, especially for conservation efforts.

Climate change can increase the risk of extinction of already endangered megafauna with depleted populations. The change in environmental conditions can disrupt the reproductive success of large whales, by affecting resource availability, survival, and growth (Post and Forchhammer, 2008; Molnár et al., 2010; Auer and Martin, 2013). Food availability is strongly correlated with body condition and fecundity in female fin, humpback, and sperm whales (Lockyer, 1986; Wiley and Clapham, 1993; Whitehead, 1996; Braithwaite et al., 2015), as well as in odontocetes, pinnipeds, and sirenians (Read and Gaskin, 1990; Boyd, 1996; Learmonth et al., 2006). A reduction in prey availability can result in increased competition for resources and a decrease in body condition and fecundity during periods of low productivity. Thus, climate change can indirectly threaten the recovery of large whales by influencing their prey. Some of these greatly depleted whale populations have recovered since the banning of commercial whaling, while others have shown little to no signs of recovery (Magera et al., 2013).

Long-term data is required to identify the historical and potential future impacts of climate change on higher trophic marine species (Rosenzweig et al., 2008). This is because cyclic/periodic climatic events such as the El Niño-Southern Oscillation (ENSO) and the Indian Ocean Dipole (IOD) can mask the underlying effects of long-term climate change. These large-scale, ocean basin-wide environmental drivers influence climatic factors such as rainfall and temperature to the point of affecting the likelihood of extreme events such as heatwaves, droughts, and floods. In the ocean, ENSO events can lead to marine heatwaves, changes in primary productivity, and the excessive runoff of nutrients, sediments, pollutants (McPhaden et al., 2006). Few studies have examined how the interannual climatic variability caused by ENSO and the IOD affects marine megafauna, because long-term studies at decadal scales are expensive and logistically difficult to conduct.

Antarctic blue whales, in particular, are likely to be vulnerable to environmental change in the Southern Ocean (Atkinson et al., 2004; Montes-Hugo et al., 2009; Mulvaney et al., 2012; Wijffels et al., 2016; Yang et al., 2016; Turney et al., 2017) because they feed predominantly in the euphausiid-rich waters for a relatively brief period (three to four months) each year in the austral summer. (Branch et al., 2007; Gill et al., 2011). During this time, a high rate of fat layer development is essential for the whales to prepare for long-distance migration to and from low-latitude breeding grounds, a journey which may require fasting for months at a time (Brodie, 1975). Pygmy blue whales, on the other hand, may not be able to build up large blubber stores like Antarctic blue whales as they do not feed in the euphausiid-rich waters surrounding Antarctica. As their reproductive success in linked with their migration, tracking the movement of these animals can reveal how they are responding to environmental changes. The primary methods of studying the movement patterns of whales include visual surveys, satellite tagging, acoustic tracking, and more recently satellite imagery. Visual surveys require high levels of effort, are restricted to daylight hours, and are hindered by adverse weather conditions. Satellite tagging provides precise movement tracks but is expensive and tags only work for a limited duration before falling off. More recently, with improved resolution, satellite imagery has been used to survey whales, but this method requires high levels of image processing and computing power. Passive acoustic monitoring (PAM), on the other hand, provides a relatively cost-effective method and can be effective for monitoring vocal species. PAM can be used to generate long-term data and requires less effort than other methods as the data are collected passively. Therefore, PAM could be used to detect variability in biological signals due to environmental changes.

Blue whales are ideal candidates for using PAM because they produce stereotypical, simple, and low frequency calls (McDonald et al., 2006). In addition, their cryptic nature and distribution in remote areas means that visual surveys are ineffective. Blue whales are traditionally thought to move each year between mid-to-high latitude productive feeding grounds in summer and low-latitude oligotrophic breeding areas to overwinter (Branch et al., 2007). Eastern Indian Ocean (EIO) pygmy blue whale calls are detected across mid-latitude southern Indian Ocean waters, including off the Crozet Islands (Samaran et al., 2010), Amsterdam Island, Reunion Island (Samaran et al., 2013), and in southern Australian waters. Within Australian waters, blue whale aggregations have been observed feeding in the Great South Australian Coastal Upwelling System (GSACUS) near the Bonney coast in the eastern Great Australian Bight (Figure 1, Gill, 2002; Gill et al., 2011), as well as in the subtropical convergence zone (Garcia-Rojas et al., 2018). The GSACUS is a wind-driven coastal upwelling system active from November to May during which upwelling of nutrient-rich water makes the area an important marine biodiversity hot spot (Ward et al., 2006; Kämpf, 2010). The EIO pygmy blue whales are present within the GSACUS from November to May, coinciding with the period that upwelling occurs (Gill, 2002; Gill et al., 2011; Balcazar et al., 2015; Tripovich et al., 2015). Satellite-tracking studies show EIO pygmy blue whales migrate from the south of Australia (starting their migration in March/April), moving past the West Australian coast to reach Indonesia from June after which they return south between the months of October and December (Double et al., 2014; Möller et al., 2020; Thums et al., 2022).

The aim of this study is to investigate the environmental drivers that are correlated with, and therefore potentially influence, the migration patterns of EIO pygmy blue whales detected off Cape Leeuwin, Western Australia. We use acoustic detections of pygmy blue whales calls as a proxy for whale presence and analyse large-scale oceanic climate drivers such as ENSO and IOD. We hypothesise that fewer whales migrate (indicated by fewer acoustic detections) during years of low

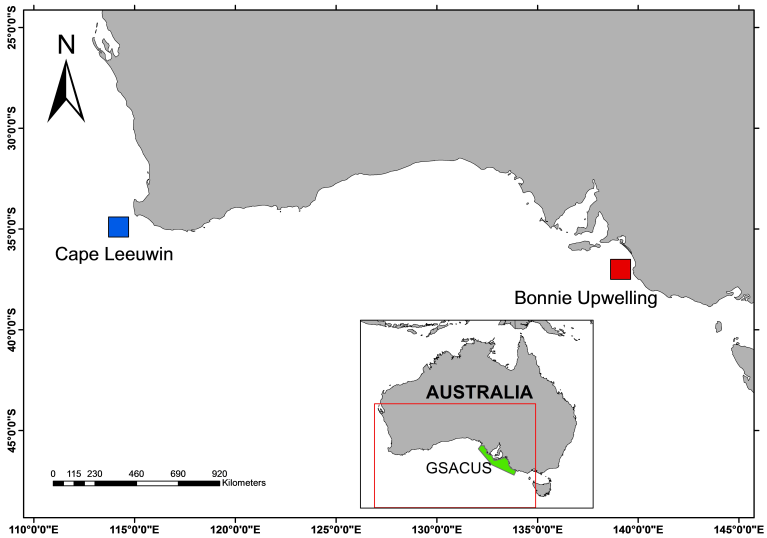

FIGURE 1
Map of the Australian Bight. The hydrophone H01W1 is located approximately 105 km from the shore at Cape Leeuwin, Western Australia (blue square). The Bonney Upwelling (red square) is the largest and most predictable upwelling location and also a known blue whale feeding aggregation area within the Great South Australian Coastal Upwelling System (GSACUS; highlighted in green).

productivity in known feeding areas. We examined whether environmental variables such as chlorophyll and ocean temperature and height correlate with changes in whale presence. Establishing a link between environmental variables and whale presence could be used to predict the occurrence of baleen whales in the future and provide valuable information for the conservation and management of these threatened species.

Methods

Acoustic data collection

Passive acoustic data from a hydrophone recording station at Cape Leeuwin was obtained from January 2003 to December 2018. The monitoring station is maintained by the Comprehensive Nuclear Test Ban Treaty Organisation (CTBTO) and forms part of the International Monitoring System. The hydrophones at Cape Leeuwin are moored to the bottom of the ocean in a triplet array with the hydrophones positioned at a depth of 1,063 m. Acoustic data were recorded continuously with a sampling rate of 250 Hz for a flat frequency range of 1-100 Hz. The noise floor of the hydrophones was ≤ 60 dB per µPa (1-Hz band) and ≤ 81 dB per µPa (wide band). Data from a single hydrophone (H01W1; Figure 1; 34.9° S, 114.2° E) were analysed in this study. H01W1 is located approximately 72 km from the nearest point of land at Cape Leeuwin.

To detect EIO pygmy blue whale calls, we used an automated detector with the spectrogram correlation method in the bioacoustics analysis program Ishmael 3.0 (Mellinger et al., 2018). The EIO call typically consists of three units that are repeated, as described in McCauley and Jenner (2010). Our spectrogram correlation detector targeted the third harmonic (66 – 71 Hz) of the second unit of the EIO call using the same parameters described in Truong and Rogers (2021). Variations in the three-unit call have been described recently for this population, with some of the units being either excluded or inserted into the song, leading to different song structures and detection rates (Jolliffe et al., 2019). The second unit was the only unit present in all the song variations described, which is why it was targeted for detection. The proportion of the song variations differed slightly between years that were sampled, but overall, the relative proportions of each song variant were mostly consistent across years (Jolliffe et al., 2019).

Individual calls were verified visually using Raven Pro 1.6 and false positives were removed. False negative rates were quantified by randomly selecting a subset of recordings and manually counting the calls. Our detector was designed to be conservative by using a relatively high detection threshold. This resulted with low false positive rates (0.84%) and high false negative rates (81.35%) as we targeted loud calls produced by whales closer to the hydrophone and excluded fainter calls produced by whales further away. We analysed the whale detection data for EIO pygmy blue whale calls at two temporal scales: an annual scale to assess the relationship between ENSO and whale call detections; and a monthly time series to examine the link between environmental covariates and whale call detections at a finer temporal scale.

Environmental data

The southern oscillation index (SOI) quantifies the atmospheric pressure difference between Tahiti and Darwin and is used as an indicator of ENSO status. Monthly SOI values between 2003 and 2018 were obtained from the Australian Bureau of Meteorology (http://www.bom.gov.au/climate/enso/soi/) and yearly averages were calculated for the interannual analysis. The strength of the IOD is measured using the Dipole Mode Index (DMI). The DMI is represented by an anomalous sea surface temperature (SST) gradient between the western and eastern Indian Ocean. DMI values were obtained from the Global Climate Observing System Working Group on Surface Pressure (https://psl.noaa.gov/gcos_wgsp/Timeseries/DMI/). Satellite-derived environmental variables included SST, sea surface height (SSH), and sea surface chlorophyll-a (SSC), all of which were obtained for 2003 to 2015. SST data were from the NOAA Optimum Interpolation SST V2 from NOAA's Physical Sciences Lab based in Boulder, Colorado, USA (https://psl.noaa.gov/). SSH data were obtained from the AVISO multi-satellite mission and SSC data from MODIS-Aqua, both acquired from the NOAA Ocean Watch – Central Pacific program (https://oceanwatch.pifsc.noaa.gov/). SSC was measured at the location of the hydrophone (SSC.HP) and at a major upwelling and feeding location, the Bonney Upwelling (SSC.BU) (Figure 1). We wanted to test SSC as it is a proxy for primary productivity which would then likely influence krill abundance. The Bonney Upwelling (37.2° S, 139.5° E) was selected as it is one of the most prominent upwelling locations within the GSACUS in the Great Australian Bight and also a known blue whale feeding aggregation area (Ward et al., 2006). All environmental variables were sampled monthly and averaged over a 1° x 1° latitude and longitude grid (approximately 10,000 km^2).

Data analysis

Yearly models

We analysed the interannual variability of whale call detections and yearly average SOI and DMI. In our yearly models, the response variable was the total number of EIO pygmy blue whale detections within each year and the explanatory variables were SOI and DMI. We used a generalised linear model (GLM) with a negative binomial distribution as part of the analysis at a yearly scale to assess the correlation between the interannual variability of whale call detections and yearly averaged SOI values for data up to and including 2018. SST, SSH and SSC were not analysed at the yearly scale as they are highly seasonal and averaging at an annual scale would result in the loss of seasonal variation.

Monthly models

At the monthly scale, we assessed the relationship between environmental covariates and the number of monthly call detections, examining data up to and including 2015. Total monthly detections were used as the response variable in the monthly models. To determine which environmental variables were correlated with the detection of EIO pygmy blue whale calls we used a time series analysis with count data following generalised linear models using the tscount package (Liboschik et al., 2017) in R version 4.0.2 (R Core Team, 2020). The environmental variables used in the models included SOI, SST, SSH, SSC.HP, and SSC.BU. A variance inflation factor was used to check for collinearity and none of the variables were highly correlated (i.e., no values exceeded ten). The time series approach accounted for possible serial dependence (autocorrelation) with past observations. The highly cyclic, seasonal nature of whale call detections and the potential increase in the number of whale calls through time (since this is a recovering population) meant time was an important consideration for this analysis. To account for autocorrelation in the data a first order autoregressive term (β1) was used to capture short-range serial dependence, whereas a 13th order autoregressive term (α13) was used to capture the annual seasonality. The models were fitted using a negative binomial distribution and a "log" link function due to high overdispersion of the data where the variance far exceeded the mean. Model selection was used to identify the best fitting model using a forward stepwise selection approach. The best fitting models were assessed using AIC values.

Results

Interannual and monthly variability in call detections

A total of 74,812 EIO pygmy blue whale calls were detected from Cape Leeuwin between 2003 and 2018, with the highest number of calls being detected in 2008 (Figure 2). The number of calls detected per year between 2008 and 2012 was 9,112 ± 1,324 (mean ± SE). This was substantially higher than in the preceding and following years, where an average of 1,164 ± 403 calls were detected each year between 2003 and 2007 and an average of 3,906 ± 746 calls were detected each year between 2013 and 2018. The monthly whale call detections were seasonal in nature, with calls peaking in April for most years and occasionally peaking in March or May in other years (Figure 3A). The highest monthly detection occurred in June 2011 with 5,950 calls, despite the highest yearly call detections being in 2008. The high number of yearly call detections between 2008 and 2012 was due to increased call detections during the peak months in those years (Figure 3A). Monthly time series of the environmental variables are presented in Figures 3B, C, 4.

Statistical analysis

Yearly models

The negative binomial GLM showed a positive relationship between yearly-averaged SOI values and yearly EIO whale call detections (Figure 5; Coefficient estimate = 0.08, SE = 0.03, $p = 0.0078$, $R^2 = 0.567$), where more calls were detected in years of higher SOI values corresponding to La Niña conditions. There was also a positive relationship with DMI and yearly call detections (Figure 6; Coefficient estimate = 2.85, SE = 1.24, $p = 0.02$, $R^2 = 0.124$).

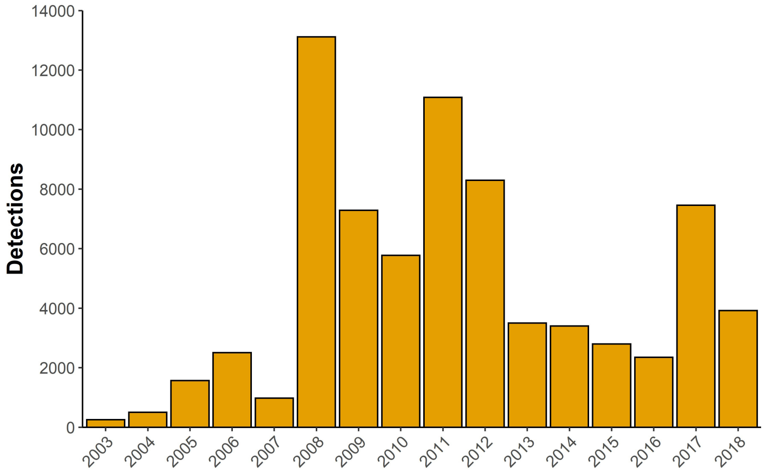

FIGURE 2
Total yearly number of eastern Indian Ocean (EIO) pygmy blue whale calls detected between 2003 and 2018 at Cape Leeuwin.

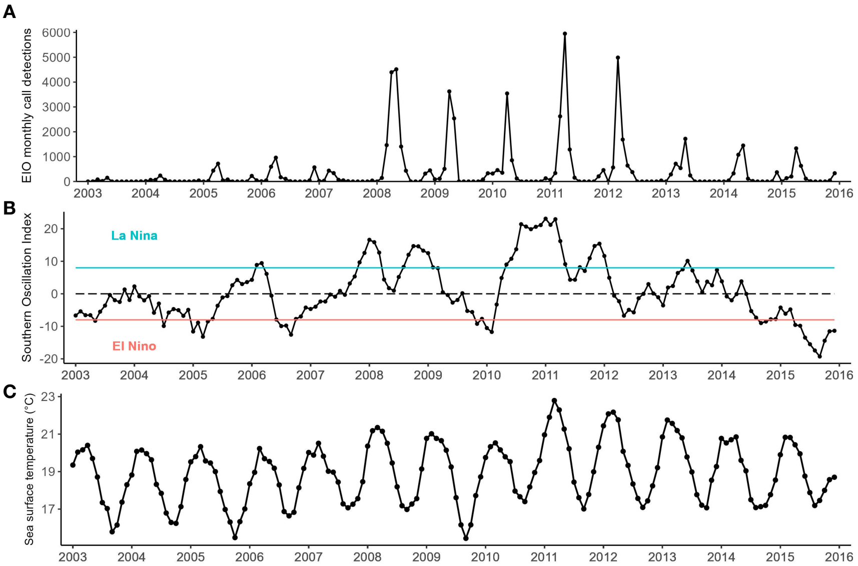

FIGURE 3
Monthly time series of **(A)** eastern Indian Ocean (EIO) pygmy blue whale call detections between 2003 and 2016 at Cape Leeuwin, Western Australia, **(B)** Southern oscillation index (SOI) obtained from the Australian Bureau of Meteorology calculated as a three-month running average between 2003 and 2016 SOI values above the green line indicate La Niña conditions; SOI values below the red line indicate El Niño conditions, **(C)** mean sea surface temperature measured across a 1° x 1° latitude and longitude grid centred around the Cape Leeuwin hydrophone.

Monthly models

The time series analyses accounted for possible autocorrelation with observations through time due to seasonality and possible population increase. The univariate models identified SOI as the best explanatory variable (Table 1). The multivariate model with the best fit included the variables SOI, SSH, SSC.HP, and SSC.BU (AIC = 1558.8, Table 2), with SST dropped from the final model. The next best model contained SSH, SSC.HP and SSC.BU (AIC = 1561.2,

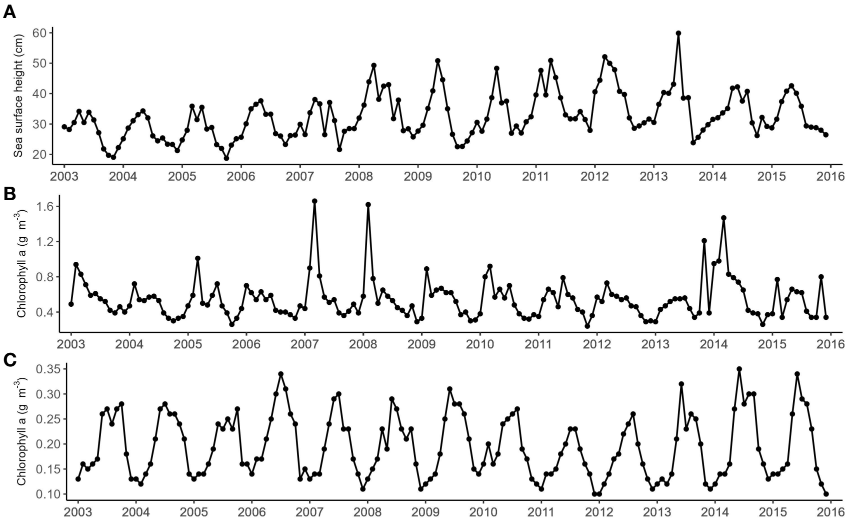

FIGURE 4
Monthly time series of **(A)** Sea surface height measured at Cape Leeuwin obtained from the AVISO multi-satellited mission. Chlorophyll-a obtained from Modis Aqua from the NOAA Ocean Watch - Central Pacific Program **(B)** measured at Cape Leeuwin, and **(C)** measured at the Bonney Upwelling. All variables were averaged from a 1° x 1° latitude and longitude grid at each location.

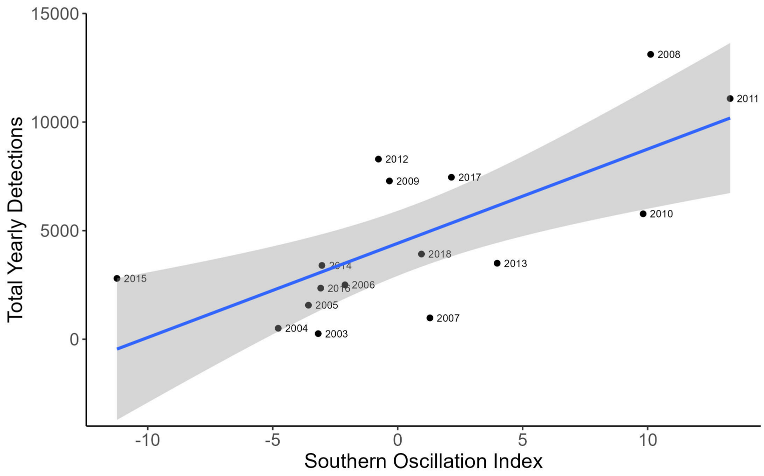

FIGURE 5
A scatterplot showing the correlation between the total yearly EIO pygmy blue whale call detections and yearly average southern oscillation index. The blue line represents line of best fit and the grey shaded area is estimated 95% confidence interval.

Table 2). Under the principle of parsimony, the second model with three explanatory terms would be the better model as the difference in AIC is only 2.4. Based on the second model SSH (Figure 7A, Coefficient estimate = 0.08, SE = 0.05) and SSC.BU (Figure 7B, Coefficient estimate = 1.15, SE = 1.0) were positively correlated with monthly whale call detections, while SSC.HP (Figure 7C, Coefficient estimate = -10.4, SE = 5.2) was negatively correlated with monthly whale call detections.

Discussion

ENSO events were correlated with, and so likely had influence on, the number of EIO pygmy blue whale calls detected in the southeast Indian Ocean. The IOD was also correlated with the total number of yearly pygmy blue whale detections. Increased numbers of detected whale calls between 2008 and 2012 coincided with La Niña events over multiple consecutive years, with the highest number of calls detected in

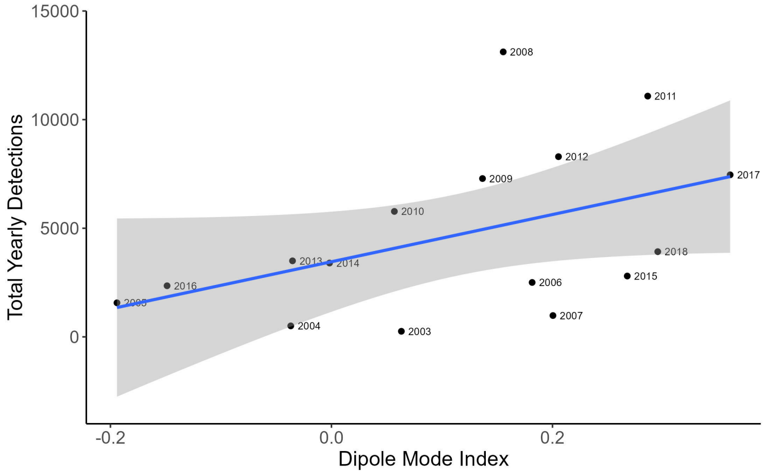

FIGURE 6
A scatterplot showing the correlation between the total yearly EIO pygmy blue whale call detections and yearly average dipole mode index. The blue line represents line of best fit and the grey shaded area is estimated 95% confidence interval.

TABLE 1 Univariate models obtained from the monthly time series analysis with whale call count data.

Variable	AIC	β1	α13	Coefficient estimate	σ^2
SOI	**1582.6**	0.55 ± 0.21	-0.07 ± 0.28	0.04 ± 0.05	7.79
SSC.BU	1589.2	0.54 ± 0.22	-0.05 ± 0.28	1.20 ± 1.54	8.46
SSC.HP	1609.7	0.52 ± 0.10	-0.04 ± 0.16	-10.57 ± 3.71	2.47
SST	1634.7	0.33 ± 0.34	0.06 ± 0.21	0.66 ± 0.59	16.82
SSH	1644.6	0.37 ± 0.13	-0.14 ± 0.19	0.08 ± 0.04	2.21

Models are ranked by AIC values. AIC is the Akaike information criterion, β1 and α13 are measures of autocorrelation, and σ2 is a measure of overdispersion. Values are coefficient estimates ± SE.

2011 during the strongest La Niña event. The 2010/2011 La Niña, one of the strongest on record, was associated with unprecedented warming and strengthening of the Leeuwin Current (Feng et al., 2013). If we use the number of whale calls as a proxy for the number of migrating whales, the greater number of whale calls detected suggests that more whales migrate past the west coast of Australia during La Niña years, as our study area represents a corridor through which whales move between feeding areas and low-latitude breeding grounds. We propose that the tenfold increase in the number of blue whale calls detected from 2007 to 2008 and sustained through to 2012 is due to more whales migrating during this period. The increase in the number of whale calls detected after 2008 suggests that the whales change their behaviour, responding quickly to shifts in climatic conditions. The IOD is also correlated with blue whale call detections, but the relationship is not as strong as ENSO. There was no lag observed between the timing of increased whale call detections and the onset of the sustained La Niña conditions which commenced in 2008. Although the EIO population is believed to be recovering (McCauley et al., 2018), the increased number of call detections is likely not due to an increase in EIO blue whale population numbers, as a shift of this magnitude over such a short period is unrealistic. Rather, it likely represents a higher proportion of the whale population migrating past Cape Leeuwin.

La Niña and El Niño conditions likely affect ocean productivity and food availability within the southern Indian Ocean feeding grounds of EIO pygmy blue whales as it affects other oceanic regions (Wang and Fiedler, 2006; Messié and Chavez, 2012). Therefore, we speculate that there are at least two possible explanations for the change in the number of blue whale calls detected during La Niña years. The first is that more whales underwent the yearly migration from the Great Australian Bight past Cape Leeuwin during highly productive La Niña years, while fewer whales migrated during years of lower productivity. Monthly chlorophyll-a concentrations at the important GSACUS foraging location of the Bonney Upwelling were

TABLE 2 Multivariate model selection with all variables and whale call detection counts as the dependent variable using a count time series analysis.

Model	AIC	β1	α13	σ2	SST	SSH	SOI	SSC.HP	SSC.BU
SSH + SOI + SSC.HP + SSC.BU	**1558.8**	0.39 ± 0.2	0.08 ± 0.3	3.5	–	0.06 ± 0.06	0.02 ± 0.04	-9.3 ± 5.5	1.26 ± 1.0
SSH + SSC.HP + SSC.BU	1561.2	0.36 ± 0.2	0.09 ± 0.3	3.3	–	0.08 ± 0.05	–	-10.4 ± 5.2	1.15 ± 1.0
SOI + SSC.HP + SSC.BU	1571.2	0.56 ± 0.2	0.04 ± 0.3	7.1	–	–	0.04 ± 0.05	-7.03 ± 6.9	1.58 ± 1.5
SSH + SOI + SSC.BU	1583.9	0.41 ± 0.2	-0.06 ± 0.2	3.6	–	0.05 ± 0.06	0.03 ± 0.03	–	1.1 ± 1.0
SST + SSH + SOI + SSC.HP	1584.6	0.3 ± 0.3	0.05 ± 0.2	9.6	0.53 ± 0.8	0.03 ± 0.1	0.01 ± 0.06	-0.54 ± 14.4	–
SST + SSH + SOI + SSC.HP + SSC.BU	1604.9	0.32 ± 0.4	0.07 ± 0.2	11.9	0.46 ± 0.9	0.03 ± 0.1	0.01 ± 0.07	-1.76 ± 16.9	0.73 ± 2.0
SST + SSH + SSC.HP + SSC.BU	1621	0.3 ± 0.4	0.06 ± 0.2	14.1	0.52 ± 1.0	0.03 ± 0.1	–	-1.47 ± 18.2	0.61 ± 2.1
SST + SSH + SOI + SSC.BU	1626.8	0.3 ± 0.4	0.06 ± 0.2	14.8	0.53 ± 0.6	0.02 ± 0.1	0.013 ± 0.08	–	0.64 ± 2.1
SSH + SOI + SSC.HP	1630.1	0.38 ± 0.1	-0.003 ± 0.2	1.8	–	0.08 ± 0.04	0.02 ± 0.03	-8.95 ± 4.1	–

Models are ranked in order of AIC values, with better fitting models having lower AIC values. AIC is the Akaike information criterion, Beta1 and alpha13 are measures of autocorrelation and σ2 is a measure of overdispersion. Values are coefficient estimates ± SE.

seasonal, which reflected the seasonal call detections of EIO whale calls at Cape Leeuwin. Chlorophyll-a concentrations at the hydrophone location were also seasonal, but out of sync with the number of whale call detections, explaining the observed negative relationship. Sea surface height at the hydrophone was also higher during La Niña conditions due to the strengthening of the Leeuwin Current. The variability in chlorophyll-a suggests that changes in food availability affect blue whale migratory behaviour. Firstly, the blue whales likely use partial migration strategies (Širović et al., 2004; Širović et al., 2009; Thomisch et al., 2016), typical of other migratory species (Chapman et al., 2011), so that only a proportion of the population migrates each year. Moving away from productive feeding grounds where krill are in high densities can be a risky strategy, as blue whales require large amounts of food to sustain their large body size and high energetic requirements (Goldbogen et al., 2011). The great distances that blue whales travel during migration are assumed to be energetically demanding. Therefore, individuals that are not in good body condition may skip migration altogether. In this case, the larger number of whale call detections suggests that a higher proportion of whales may have developed better body condition and underwent migration during La Niña years.

A second possible explanation is that a higher proportion of whales foraged within the GSACUS and subtropical convergence regions south of Australia during La Niña years, while during lower productivity years they foraged in areas away from Australia. Alternatively, EIO pygmy blue whales that typically feed in other regions within the Indian Ocean (Samaran et al., 2010; Samaran et al., 2013) may shift to feed in the Great Australian Bight in years when there are strong, sustained La Niña conditions, resulting in more whales migrating past the Cape Leeuwin hydrophone. Conditions within the Indian Ocean in La Niña years may make the GSACUS in the eastern Great Australian Bight a more favourable feeding site. Conversely, when conditions are not favourable and productivity is low, the whales may move to feed in other areas of the Indian Ocean (as far west as Amsterdam Island) and would therefore not be detected as they no longer pass by Cape Leeuwin during their northbound migration. A recent study of EIO pygmy blue whales in the central Indian Ocean showed an increase in the number of call detections from 2012 to 2016 near Amsterdam Island (Torterotot et al., 2020). This complements our results, where the number of call detections decreased after 2012 following the period of sustained La Niña conditions. This suggests that a higher number of EIO pygmy blue whales may have moved away from the Great Australian Bight towards the central Indian Ocean after 2012, potentially because of ENSO driven environmental conditions and altered prey availability. Further studies are needed to determine whether the whales detected in the central Indian Ocean are from the same population as those found in the GSACUS.

The monthly covariates that were examined had varied degrees of seasonality which to an extent was correlated with

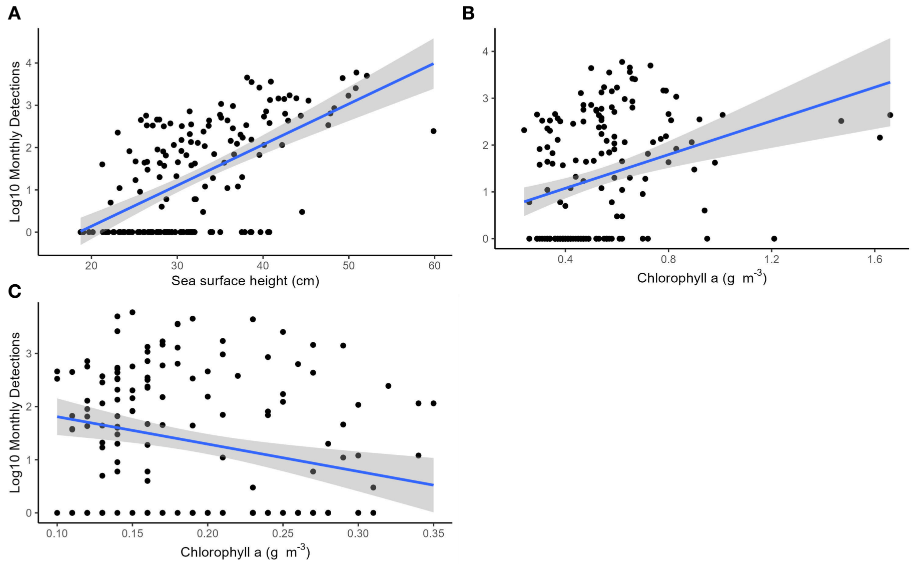

FIGURE 7
Scatterplots showing the correlation between the $\log_{10}$ monthly EIO pygmy blue whale call detections and **(A)** monthly average sea surface height at the Cape Leeuwin, **(B)** chlorophyll a measured at the Bonney Upwelling and **(C)** chlorophyll a measured at the Cape Leeuwin hydrophone. All environmental variables were averaged across a 1° x 1° latitude and longitude grid. The blue lines represent the lines of best fit and the grey shaded areas are estimated 95% confidence intervals.

the seasonality of EIO pygmy blue whale call detections. SST had the most regular and predictable seasonality. SST and SSH peaked in autumn and were lowest in early spring. These patterns reflected the seasonal dynamics of the Leeuwin Current (Feng et al., 2009). During La Niña years, the Leeuwin Current experiences warming, and the southward flow strengthens (Feng et al., 2013). This too is reflected in the SST and SSH measured off Cape Leeuwin, where the annual peak temperature and height are elevated during La Niña years. Despite SSH and SST being influenced by La Niña conditions, models containing SST did not perform very well. A possible reason for SST not being a good predictor could be due to its highly predictable seasonality which does not correlate well with the less seasonally predictable blue whale calls. SSH is unlikely to directly influence blue whale movement patterns but may have an indirect relationship. SSH at Cape Leeuwin is largely driven by the strength of the Leeuwin Current, but SSH can also be influenced by upwelling and eddies which can change the availability of nutrients. Chlorophyll was also seasonal in nature, albeit not as regularly so as SST. Overall, chlorophyll levels at the Bonney Upwelling exceeded the levels measured at Cape Leeuwin. This supports the idea that feeding was more likely to occur along the Bonney coast then it was to occur at Cape Leeuwin. Furthermore, chlorophyll at Cape Leeuwin peaked during winter when the whales were further north, while chlorophyll peaked during summer at the Bonney Upwelling which is when the whales would be feeding. We used chlorophyll as a proxy for productivity, however it may not necessarily translate to krill availability or abundance. Satellite-measured chlorophyll also only reflects what is on the surface, so *in-situ* measurements at other depths could improve our models. The Bonney coast is not the only known feeding aggregation area within the GSACUS. Pygmy blue whales have also been observed feeding in the subtropical convergence zone (Garcia-Rojas et al., 2018). However, the subtropical convergence covers a large area and is highly variable in terms of upwelling and productivity, therefore analysis using the subtropical convergence was too broad and out of the scope for this study.

There are limitations in using acoustics to infer population level changes in migration patterns, as it can be difficult to differentiate whether calls come from multiple vocalising whales or a single, highly vocal individual. In addition, only singing individuals (i.e., males) are represented, as non-singing whales cannot be detected (Croll et al., 2002; Oleson et al., 2007). This means that the sampling could be biased towards male individuals and may not reflect the behaviour of female and non-vocalising whales. The conservative detector with a high detection threshold that we used meant that a substantial proportion of calling animals were missed. This was intentional, since we took a conservative approach for this study and aimed to capture whales closer to the hydrophone, rather than detecting faint calls from individuals much further away. To identify if there were changes in whale behaviour through time, our sampling design sampled in a standardised, continuous fashion, using a conservative acoustic detector that would be less influenced by changes in ambient sea noise. Whales were also only sampled as they migrate past the Cape Leeuwin hydrophone site, decreasing the likelihood of resampling the same animals over extended periods which would increase if we had also sampled within a feeding or breeding site. Additionally, it is also possible for individual whales to migrate further offshore and be out of range of the hydrophone. However, studies using satellite telemetry to track pygmy blue whales have shown that tagged individuals migrated close to the Cape Leeuwin hydrophone (Double et al., 2014; Möller et al., 2020).

ENSO events are predicted to become more intense under further climate change (Cai et al., 2014). The feeding success of baleen whales is dependent on synchronisation with planktonic production, which often occurs in pulses (Edwards and Richardson, 2004). Marine plankton has shown varied responses to climate change at different levels, leading to either a temporal or spatial mismatch between different trophic levels and their functional groups (Edwards and Richardson, 2004). Small animals with short life cycles and large population sizes will probably adapt to the longer growing seasons and be able to persist. However larger animals with longer life cycles and smaller population sizes are more likely to experience population decline (Bradshaw and Holzapfel, 2006). Extreme climatic events are predicted to disrupt phenotypic plasticity in marine birds (Lescroël et al., 2014), which means that the adaptability and resilience of other marine vertebrates should be called into question. Rates of observed shifts in the distribution and phenology (timing) of marine species are comparable to, or greater than, those for terrestrial systems (Poloczanska et al., 2013). The recovery of endangered whale populations would be influenced by their ability to adapt to these environmental changes.

This study of 16 years of whale acoustic presence, though covering a small subset of time in comparison to climate modelling studies, suggests that large-scale changes in environmental variability due to ENSO are potentially influencing the migration behaviour of blue whales. This period contained only two La Niña events and further sampling of additional La Niña events would provide a clearer picture of the impacts of ENSO events on whale migration. Our study highlights the importance of capitalising on archived, calibrated, long-term acoustic data (such as the CTBTO data) to examine the influence of periodic climatic signals such as ENSO in addition to long-term warming trends on whale migratory behaviour.

Data availability statement

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

Ethics statement

Ethical review and approval was not required for the animal study because acoustic data was obtained passively with no direct impact on the animals.

Author contributions

Both authors conceived and designed the project, revised, and approved final manuscript. GT conducted blue whale acoustic analysis, statistical analysis and wrote the first draft of the manuscript. All authors contributed to the article and approved the submitted version.

Funding

GT was funded by an Australian Government Research Training Program Scholarship. Additional funding was also provided by the Winifred Violet Scott Estate Charitable Trust.

Acknowledgments

We thank Gordana Popovic for providing advice on the statistical analysis. We also thank members of the Mammal Lab for their comments on the manuscript. We greatly appreciate the comments provided by the reviewers. Their feedback has greatly improved the manuscript. Data was made available *via* a vDEC contract with the CTBTO. The findings and conclusion in this manuscript are those of the authors and do not necessarily represent the views of the CTBTO.

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.

Publisher's note

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frontiers | Frontiers in Marine Science

TYPE Hypothesis and Theory
PUBLISHED 05 June 2023
DOI 10.3389/fmars.2023.1117409

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OPEN ACCESS

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RECEIVED 06 December 2022
ACCEPTED 24 April 2023
PUBLISHED 05 June 2023

CITATION
Meynecke J-O, Samanta S, de Bie J, Seyboth E, Prakash Dey S, Fearon G, Vichi M, Findlay K, Roychoudhury A and Mackey B (2023) Do whales really increase the oceanic removal of atmospheric carbon? *Front. Mar. Sci.* 10:1117409. doi: 10.3389/fmars.2023.1117409

Do whales really increase the oceanic removal of atmospheric carbon?

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Whales have been titled climate savers in the media with their recovery welcomed as a potential carbon solution. However, only a few studies were performed to date providing data or model outputs to support the hypothesis. Following an outline of the primary mechanisms by which baleen whales remove carbon from the atmosphere for eventual sequestration at regional and global scales, we conclude that the amount of carbon whales are potentially sequestering might be too little to meaningfully alter the course of climate change. This is in contrast to media perpetuating whales as climate engineers. Creating false hope in the ability of charismatic species to be climate engineers may act to further delay the urgent behavioral change needed to avert catastrophic climate change impacts, which can in turn have indirect consequences for the recovery of whale populations. Nevertheless, whales are important components of marine ecosystems, and any further investigation on existing gaps in their ecology will contribute to clarifying their contribution to the ocean carbon cycle, a major driver of the world's climate. While whales are vital to the healthy functioning of marine ecosystems, overstating their ability to prevent or counterbalance anthropogenically induced changes in global carbon budget may unintentionally redirect attention from known, well-established methods of reducing greenhouse gases. Large scale protection of marine environments including the habitats of whales will build resilience and assist with natural carbon capture.

KEYWORDS

blue carbon, whales, carbon export, ocean carbon cycle, climate change

Introduction

Baleen whales (mysticetes) are present in all oceans and are among the largest marine animals to have ever existed. From studies of terrestrial megafauna, evidence has emerged that various species can modify their environment and indirectly influence landscape carbon dynamics. For example, the presence of forest elephants (*Loxodonta cyclotis*) favors the emergence of fewer and larger trees with higher wood density (Berzaghi et al., 2019). White rhinos (*Ceratotherium simum simum*) help maintain short grass communities which result in smaller more patchy fires (Waldram et al., 2008), and dugongs (*Dugong dugong*), large aquatic grazers, can alter seagrass communities affecting carbon sequestration and storage (Scott et al., 2018). Theories have emerged that baleen whales may also act as ecosystem engineers by influencing the ocean carbon cycle on regional and large basin scales as part of the marine food web (Willis, 2014) even bringing the idea of 'carbon credits' into the debate (Hagger et al., 2022; Pearson et al., 2023).

Whales amongst other marine life contribute to the biological carbon pump providing a secondary transfer pathway (Bowen, 1997; Mariani et al., 2020; National Academies of Sciences and Medicine, 2022). The biological carbon pump involves a number of processes through which inorganic carbon such as CO2 is fixed into organic matter via photosynthesis and then transported into deeper ocean away from the atmosphere (Claustre et al., 2021). Whales mediate transfer of carbon from inorganic to organic forms through marine biota activity and its export into the deeper ocean. Carbon export may eventually add to the carbon pool of the global ocean circulation or sequestration into marine sediments, which implies much longer recycling time scales (millennia) of inorganic carbon back to the atmosphere (Strand and Benford, 2009; Legge et al., 2020). Marine organic carbon travels through nested cycles operating on temporal scales of orders of magnitude difference and are subsystems of the global ocean carbon cycle (Figure 1).

The following examples from the literature can give indications of carbon volumes but need to be understood within a context of complex systems and are provided to give a better understanding of how some theories were derived. The global ocean net primary productivity has been estimated at 53 Pg carbon annually (Johnson and Bif, 2021). Ocean export production ratios (i.e., export from the surface ocean to deep ocean as a fraction of primary production) have been estimated to range from 0.02–0.96 (Jo et al., 2021). This organic matter decomposes at depth and drives the biological pump. However, of the organic matter raining out of the surface ocean, only 1% (0.05 Pg carbon out of 4 Pg carbon annually; Hain et al., 2014) is incorporated into the surficial sediments and potentially sequestered for scales longer than the global ocean circulation. Latest estimates put the ocean carbon sink at 9-11% higher than previously estimated (Terhaar et al., 2022). A carbon sink is defined as any form of carbon accumulation and storage for long periods of time (millennia) that removes CO_2 from the atmosphere (Alexandrov, 2008). The carbonate pump is estimated to be larger than the soft-tissue pump; some organisms construct inorganic hard parts from CaCO3 of which ~25% (~0.25 Pg C out of 1 Pg C annually) sinks to the seafloor and is preserved and buried in the sediments. The total amount of carbon permanently sequestered from the atmosphere is therefore approximately 0.3 Pg carbon annually (Honjo, 2004; Hain et al., 2014).

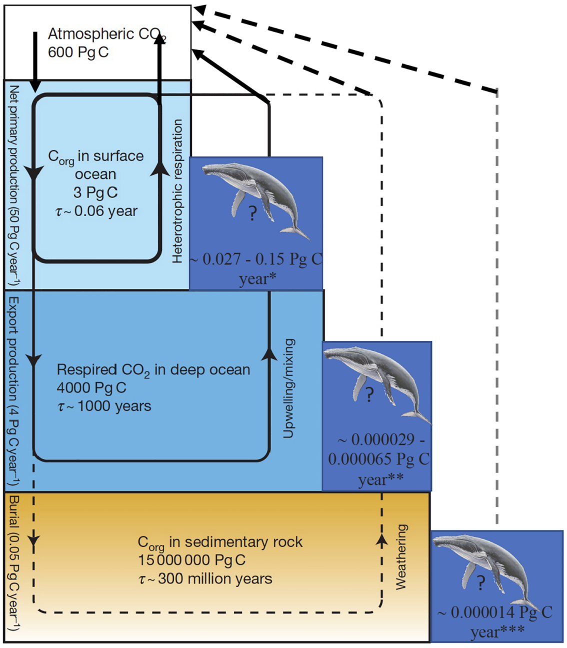

FIGURE 1
The nested cycles of marine organic carbon (C_{org}), including (1) net primary production and heterotrophic respiration in the surface ocean, (2) export production from the surface ocean and respiration in the deep sea followed by upwelling or mixing of the respired CO_2 back to the surface ocean (the soft-tissue component of the biological pump); and (3) the burial of sedimentary organic carbon. Also shown are the indicative residence times (*r*). Note that carbon reservoirs shown refer solely to the fraction affected by organic carbon cycling; for instance, the deep-ocean value shown is of carbon dioxide produced by respiration, not the carbon released from $CaCO_3$ dissolution. Adapted from Hain et al. (2014). *Southern Ocean estimates, Savoca et al., 2021 **All oceans estimate, Pershing et al., 2010 and Pearson et al., 2023 ***Southern Ocean estimates, Pershing et al., 2010.

To summarize the main aspects, about 20-32% of anthropogenic CO_2 is transferred from the atmosphere to the ocean through the biological, carbonate and solubility pumps (Sabine Christopher et al., 2004; Khatiwala et al., 2009; Hauck et al., 2020; Kim and Kim, 2021). For instance, in the period 2009-2018, 48 ± 3% of anthropogenic emissions (18.0 ± 0.07 Pg CO_2/yr) remained in the atmosphere, 29 ± 6% (11.7 ± 2.2 Pg CO_2) were taken up by terrestrial ecosystems, and 23 ± 5% (9.1 ± 2.2 Pg CO_2) were taken up by the ocean (Friedlingstein et al., 2019), of which approximately 40% were absorbed in the Southern Ocean (Terhaar et al., 2021).

For whales to play a role in reducing atmospheric CO_2 concentrations, they need to influence the biological pump such that there is an increase in (i) the export of organic carbon from the surface to the deep ocean and/or (ii) the amount removed from the ocean and entering the slower sediment circuit (Figure 1). In the following section, we outline the contrast between available data on whales and carbon export and coverage of the topic by media, often portrait as climate savers.

We then present an overview of the role of baleen whales relative to the global ocean carbon cycle, and frame their potential effects in the light of existing literature. We further review the knowledge of whale ecology in the context of the ocean carbon cycle, to provide a better understanding on baleen whales' claimed role as climate engineers and propose a range of fundamental research requiring further investigation.

The gap between science and media

The topic of whales as carbon sinks has received much media attention combining two popular subjects: whales and climate change. A non-representative search in ProQuest using the terms "whales" and "carbon" revealed 352 newspaper articles from over 45 countries between 2012 and 2022, with a strong increase of interest in the topic in the past three years (Figure 2). An online search in Google Scholar and ProQuest on peer-reviewed studies in international journals over the same 10-year period resulted in six studies providing observations or modelling studies on whales as carbon sinks mostly focusing on the Southern Ocean (Figure 2, Supplementary Table 1). A report that triggered a strong outreach in media was published by the World Monetary Fund in 2019 by Chami et al. (2019) (e.g., "Protecting whales to protect the planet" UNEP, 2019; "Restoring whales to their pre-hunted numbers could capture 1.7 billion tons of CO_2 a year", EuroNews, 2021). The report used data from research publications analyzed in the following sections (Lavery et al., 2010; Pershing et al., 2010; Roman and McCarthy, 2010) to calculate a potential carbon uptake by whales. An opinion published by (Pearson et al., 2023) further underlined the gap between available scientific evidence on this topic and also triggered a strong media response (e.g., "Whales can have an important but overlooked role in tackling the climate crisis, researchers say" CNN News 15/12/2022) with many news stories continuing to claim whales as climate savers or climate engineers. The phenomenon of simplifying complex relationships to gain readers attention is particularly common in the "post-truth" era (Gobo and Marcheselli, 2022) amplified by the increased use of social media.

A search of social media posts on varies platforms that contained the key words "whales" and "carbon" using the analyst tool keyhole (https://keyhole.co) showed that this topic has a high retention within the social media domain (Figure 2). Over 10 days between 18th-27th February 2022, 677 posts were reported, showing a sharp increase of posts during and after World Whale Day on the 20th February. However, it is important to notice that 88% of these were reposts and only 10% had original content related to whales and carbon further underlining the high retention of this topic from original posts. Retention of popular topics is high across social media platforms even if the original content is not updated (Kapoor et al., 2018). The sharing of content is often driven by believes over

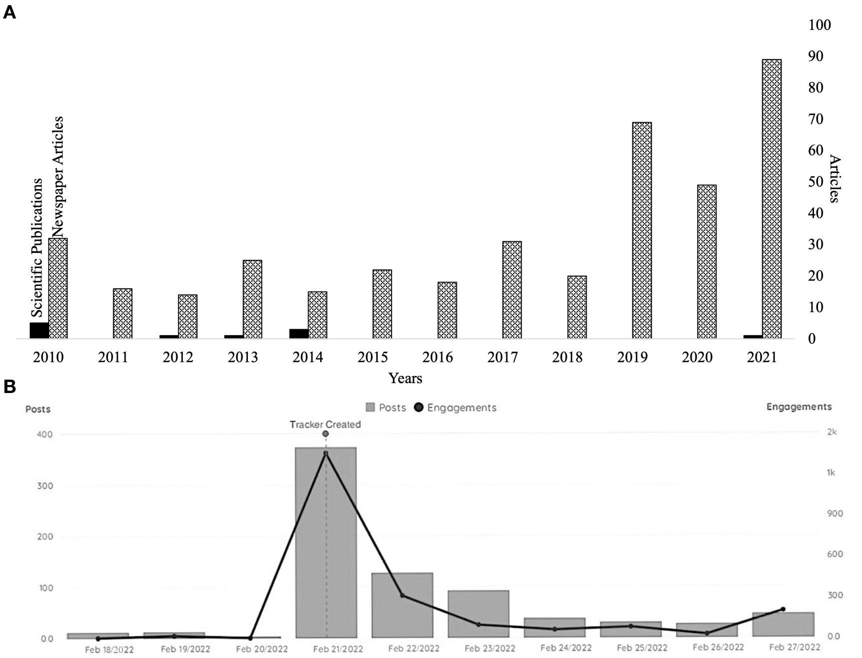

FIGURE 2
(A) Number of published newspaper articles in English and number of peer reviewed scientific studies based on a ProQuest online database search for entries between 01/01/2010 and 01/01/2021. Search term "whales and carbon" and **(B)** Results from a search for the keywords "whales" and "carbon" in social media posts over a 10-days period showing the increased posting on this topic for "World Whale Day" on the 20th February 2022. Engagements refer to number of interactions with a post e.g., comments and reactions such as likes.

accuracy (Pennycook et al., 2021). The implications of a believe-driven process can result in a diversion of attention towards well-established methods of carbon sequestration. It can result in attention and resources drawn away from proven, effective nature-based solutions to climate change.

Limitations of whale mediated carbon removal

There are five pathways identified by Roman et al. (2014) and further outlined by Pearson et al. (2023) in which whales can potentially enhance the removal of carbon from the atmosphere into the deep ocean and/or deposition. They are summarized in Figure 3 and discussed in the next paragraphs in the context and order of contribution to global carbon export. There are difficulties and limitations in quantifying the impact of whales on carbon sequestrations with the estimated contribution of each pathway being hypothetical. Estimates are presented to provide a guidance and support the theory that whales have a limited contribution to global carbon export. Processes in the euphotic zone are generally faster and short lived (days to weeks), whereas processes in deeper parts of the ocean take much longer (years to millennia).

Primary production is generally limited in macro-nutrient depleted oligotrophic oceans. Despite macro-nutrients (nitrate and phosphate) are abundant in the in the Southern Ocean (Marinov et al., 2008), micro-nutrients, prevalently iron (Fe), are scarce in the so-called high-nutrient-low-chlorophyll (HNLC) regions of the Southern Ocean, and in the equatorial and northern Pacific. This results in a limited primary production in vast region of the global oceans and associated CO_2 drawdown from the atmosphere.

In theory, the whale conveyor belt, whale pump, and whale bioturbation are linked to the biological pump by increasing the availability of nutrients and enhancing phytoplankton primary production, thereby driving a positive feedback loop in the oceanic carbon pump (Smetacek and Naqvi, 2008; Roman et al., 2014; Pearson et al., 2022). Primary production in the sunlit surface ocean is limited by nutrient availability. Macro-nutrients (nitrate and phosphate) are abundant in the deep ocean and in the Southern Ocean (Marinov et al., 2008), while micro-nutrient, prevalently iron (Fe), are scarce in the so-called high-nutrient-low-chlorophyll (HNLC) regions of the Southern Ocean, and in the equatorial and northern Pacific. For example, Roman et al. (2014) suggested that blue whales (*Balaenoptera musculus*) in the Southern Ocean transported an estimated 88 t of nitrogen per year (estimated for 2001) from Antarctic feeding grounds to tropical breeding grounds *via* nitrogen-rich urea released through catabolism of lipids and proteins during fasting. Although it is difficult to demonstrate the excess production in lieu of the large natural variability, this flux can be considered new production and could lead to a carbon flux of up to 2,100 tons of CO_2 per year (equivalent to 572 tons of carbon) by phytoplankton (Martin et al., 2021). However, this quantity is then released in the upper ocean where respiration processes may rapidly release it back to the atmosphere (Bolaños et al., 2020). Respiration of whales during their migration also add to release of CO_2 back to the atmosphere (Lavigne et al., 1986; Huntley et al., 1991). While nutrients directly recycled by whales within the upper water column from distant regions support primary production, they do not necessarily stimulate downward particle flux, which is required for carbon sequestration (Lavery et al., 2014; Martin et al., 2021).

The key micro-nutrient iron that is translocated via whales is generally scarce in open oceans, especially in the Southern Ocean (de Baar et al., 2005; Tagliabue et al., 2017). Whale-dependent recycling and relocation of iron is suggested to play a key role in increasing primary productivity, and in turn enhancing the biological pump and possibly carbon export (Smith et al., 2013; Ratnarajah et al., 2016). Generally, the contribution of baleen

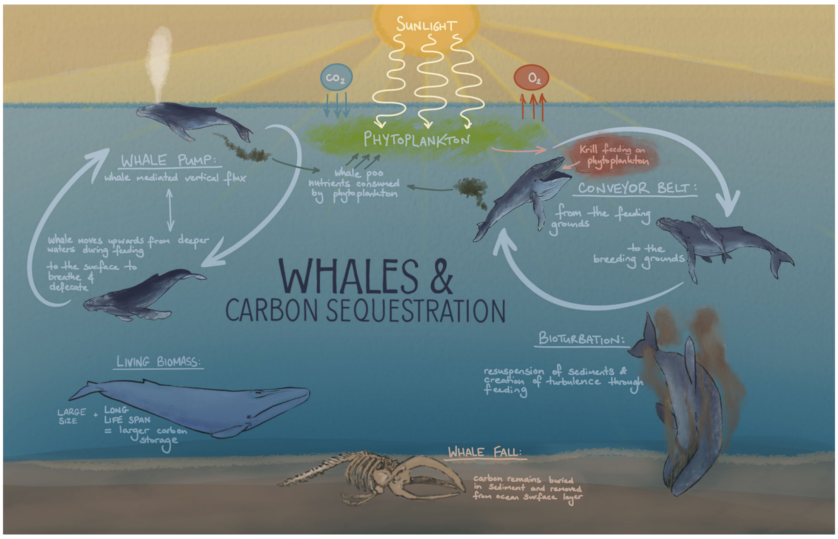

FIGURE 3
Illustration of five different ways in which whales can contribute to an increase in oceanic removal of atmospheric carbon: whale pump, whale conveyor belt, whale biomass and known long life span, whale falls, and whale bioturbation (artist impression based on Roman et al., 2014).

whales to the iron flux is through the spatial redistribution of iron in surface waters rather than through the recycling of iron. Given the extent of ocean where primary production occurs, internal cycling of iron by phytoplankton degradation is much larger than whale contribution (Maldonado et al., 2016). However, whale feces do supply and distribute both macro- and micro-nutrients to areas where external sources are limited (Roman and McCarthy, 2010), for instance when crossing the Southern Ocean HNLC region in the meridional migration. Whale feces are known to have high iron concentration (146 ± 134 µg/g) (Nicol et al., 2010; Ratnarajah et al., 2014) compared to Antarctic krill (65 ± 41 µg/g, Supplementary Tables 2, 3). Whales provide biomagnification because they preferentially store carbon in their muscles, but do not need all the Fe found in the ingested krill biomass (e.g., 147 mg Fe/kg dry weight of krill; Nicol et al., 2010). It is suggested that foraging whales concentrate carbon in their muscles and release a majority of ingested iron in a more bioavailable fraction through feces. Ideally bioavailable iron stays at +2 stage, which is soluble. In contrast, iron +3 is insoluble. Inside the whale stomachs digestion is an acidic (HCl) and oxygen depleted environment, which would favor the reduction reaction, i.e. Fe^{+3} to $Fe^{\ +2}$ (Ratnarajah et al., 2014; Ratnarajah et al., 2017; Ratnarajah et al., 2018), however, further evidence on the bioavailability of whale feces is required. The iron concentration in whale feces reaches ten million times that of the Southern Ocean surface waters (Nicol et al., 2010) and can contribute 3 to 5 orders of magnitude higher iron concentrations than that required for phytoplankton growth (Wing et al., 2014). For instance, compared to surface seawater dissolved iron concentration of ~ 0.1 – 0.5 nmol/L in the Southern Ocean (Tagliabue et al., 2012), humpback whale (*Megaptera novaeangliae*) feces iron concentration ranges from 186 - 754 nmol/L and from 5,026 – 22,526 nmol L in dissolved (<0.2 µ) and particulate (>0.2 µ) phases, respectively (Ratnarajah et al., 2017). Other factors, such as the differences between soluble and colloidal iron, fraction of lithogenic iron, and available organic matter, may also influence bioavailability and ocean primary production (Ratnarajah et al., 2016; Ratnarajah et al., 2018). Fin (*B. physalus*) and blue whale species are likely the largest contributors to iron supply, due to their higher prey consumption, and thus having a greater potential for enhanced carbon fluxes (Durfort et al., 2020). Whether this contribution to the natural ocean iron cycle would lead to enhanced sequestration of carbon is however not demonstrated. Iron relocation is one of the most likely components of the biological pump that can be enhanced by whales' activity in open ocean that otherwise lie barren. Modelling based on the latest baleen whale prey consumption estimates suggested that in some areas such as the Scotia Sea, iron from whale feces may have stimulated more than 20% of net primary production prior whaling (Savoca et al., 2021). Given that phytoplankton uptakes one quarter of iron released by whales (Ratnarajah et al., 2016), for four whale species (blue, fin, humpback and Antarctic minke whales - *B. bonaerensis*) in the Southern Ocean could capture up to 0.215 Pg carbon annually during pre-whaling period (Savoca et al., 2021) However, whale feces driven carbon capture is likely to vary among the global oceans based on the nutrient availability in surface ocean and bioavailable fraction of nutrients in whale feces. For instance, unlike the Southern Ocean, the Southern Benguela upwelling system in the Southeast Atlantic is a nutrient rich oceanic sector in a low latitude feeding area. Hence, the carbon capture potential through the whale pump in the Southern Benguela feeding ground is likely lower compared to the estimations made in the Southern Ocean.

Similar considerations can be made for the whale pump, which describes the process of whales moving up and down the water column for feeding, and transferring nutrients to surface waters in the process (Nicol et al., 2010; Pearson et al., 2022). Spatial and temporal scales are much smaller in this case than for regional migrations, and there is no quantification in the literature whether this process may have an annual effect on the duration of the blooms or on net ecosystem production. For instance, there is no evidence of how more effective whales could be in relocating iron from the deeper Southern Ocean to the surface when compared to the typical mixing rates. It has been reported that sperm whales (*Physeter macrocephalus*) feeding in depth of 1,000 m can make nutrients available when defaecating at the surface, coinciding with phytoplankton blooms (Roman et al., 2014). Based on a population estimation from the year 2000, Lavery et al. (2010) estimated that an additional 240,000 t of CO_2 (0.000066 Pg carbon) annually were exported into the Southern Ocean through the promotion of phytoplankton growth (of which one quarter is recycled by phytoplankton) from the nutrients provided by sperm whale feces. These estimates are indicative of the contribution exerted by whales to ecosystem functioning, but do not give a comparative view of their role with respect to the background physical-biogeochemical dynamics and also exclude the respiration of whales during this process.

Whale bioturbation (Figure 4) is the process by which whales resuspend bed sediments into the water column, when feeding on mollusks and other organisms on the ocean floor. It is conceptually similar to the whale pump, but involves a pool of nutrients that are assumed to be less readily available to marine degradation. This process is commonly observed in feeding of demersal fish, the main difference is their smaller size compared to whales (Mariani et al., 2020). For example, gray whales (*Eschrichtius robustus*) have been shown to remobilize nutrients into the Bering Sea when foraging for amphipods (Nelson and Johnson, 1987; Alter et al., 2007). However, this is non-selective bioturbation, and the same process could release organic matter previously buried in the sediments, thus enhancing the recycling of carbon back to CO_2. The overall whale bioturbation contribution to carbon export or sequestration has not been quantified to date and may prove difficult to be disentangled from other bottom biogeochemical processes but its contribution to carbon export if any is likely smaller than the whale pump contribution. Bottom feeding is only known for a few whale species such as gray whales restricted to small areas.

The long-life span and large body size of whales can contribute to carbon storage over decades. Using whale populations of eight baleen whale species from the year 2001, the living biomass stock of carbon was estimated to be about 0.002 Pg (Pearson et al., 2023). Commercial whaling has reduced the size of baleen whale populations by an average of 70% since 1900 (Tulloch et al., 2019). Prior to whaling, the carbon in living biomass was estimated to be five times higher (0.01 Pg). Other marine

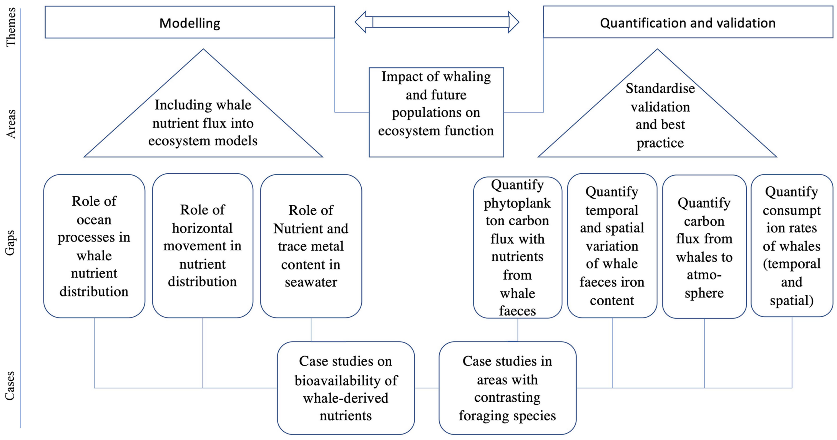

FIGURE 4
Main research areas, gaps and possible case studies that fall under modelling, quantification and validation themes to better define the role of whales as carbon sinks.

organisms like fish also accumulate carbon but over shorter times scales with the removal of fish from the ocean causing an estimated 0.00034 Pg of carbon release per year since 1950 (Mariani et al., 2020). The overall contribution of whales living tissue to carbon storage is limited by their lifespan (at least several decades) and their own respiration as for all animals. However, the value of animals to carbon sequestration in general also needs to be assessed in the context of their ecosystem function ((Schmitz et al., 2023).

Whales can fall into the deep sea after death, where their carcasses can take hundreds of years to decompose, or millennia if buried in sediments, which depends on sedimentation rate and available oxygen (Pershing et al., 2010). However, the overall contribution of whale falls to carbon sequestration could be relatively small and might be in the range of only 2% of estimated carbon export by whales (Durfort et al., 2020). The amount of biogenic carbon is species specific and depending on the region. Whale species vary in size and some species, such as southern right whales (*Eubalaena australis*), have a tendency to float after death and are less likely to sink. The effect would be more marked in regions supporting larger whale populations e.g. on the west coast of North America where a study from marine sanctuaries off San Francisco claimed that whale falls represent roughly 60% of the estimated total annual carbon removal of the area equivalent to about 10 890 tons of carbon or 0.00001 Pg (Hutto et al., 2021). Should the population recover to pre-whaling numbers, Pearson et al. (2023) estimated for baleen whale species (blue, fin, humpback, southern right, gray and Antarctic minke whales) a carbon sequestration potential through sinking carcasses of 0.000062 Pg carbon annually. Respiration rates of whales to atmospheric CO_2 would need to be subtracted from this calculation as well as any CO_2 release during decomposition.

Carbon buried under marine sediment within the deep sea is generally a long-term (millennia) removal of carbon from the atmosphere (Teng and Zhang, 2018). However, the burial rate of organic carbon is a function of sedimentation rates (Betts and Holland, 1991), which is less than 0.01 cm k per year for major ocean basins and the Southern Ocean; (Restreppo et al., 2020). Scavengers remove whale soft tissue at high rates (40–60 kg per day), and then the exposed bones are colonized by dense assemblages of polychaetas and crustaceans (Smith and Baco, 2003). Anerobic bacteria decomposes bone lipids. The scavenging process can last up to 50 years (Smith and Baco, 2003), which prevents whale carcasses from being buried under falling sediment. Therefore, burial of organic carbon (sequestration) associated with whale falls is expected to be the least effective pathway of carbon sequestration by whales will make only a small contribution to carbon sequestration.

Discussion

Based on the literature presented in the previous sections, there is a common understanding that baleen whales contribute to carbon uptake, as done by other marine life in the marine ecosystem. The challenge remains to quantify whether this uptake at the whale's population level translates into an effective enhancement of carbon export and subsequent sequestration that is comparable with the known scales of the global ocean. A lack of comparable global data for different regions and species, has led to generalized estimations based on few observations with extrapolations based on numerical models. Our analysis has demonstrated that only relatively few studies so far have provided direct observations on the baleen whales contribution to the ocean carbon cycle on a locally limited scale, and that the majority of the carbon sequestration potential estimates are obtained through model parameterizations. Currently there is a lack of evidence showing that whales make a significant contribution to global carbon export to alter climate change. We looked at whale carbon sequestration pathways and available knowledge for each pathway suggests that the influence of whales on carbon flux is small compared to the global carbon flux. Nevertheless, public interest on this topic has steadily increased over the past decade underlining the need for more research in this field. The gap between media and available science to support the theory of whales influencing global climate may distract falsely portraying the role of whales as important to increase carbon sequestration from the atmosphere may distract policy from other important issues.

Whales could enhance primary production through a range of processes (Savoca et al., 2021). If such processes and the precise mechanisms involved can be established, and the mitigation contribution quantified, then additional benefits as ecosystem services be identified, they could be related to some form of 'carbon credits' (Costello et al., 2012), and the corresponding funds be used for marine ecosystem restoration (Hagger et al., 2022).

Enhancing primary production through supply of iron appears to be the most professed contributor to carbon sequestration by whales (Savoca et al., 2021). *In situ* experiments with whale feces have shown diatom growth (Smith et al., 2013) but field conditions are likely highly variable. In the past, iron fertilization experiments have been undertaken with mixed results and also triggering a controversial debate as it has long been criticized for its large-scale impacts (Chisholm Sallie et al., 2001; Martin et al., 2013). Similar experiments are once again underway partially attempting to simulate the effect of whale feces on marine productivity. In late 2021, a group of researchers released a mix of nitrogen, phosphorus and trace elements off the coast of Sydney, Australia simulating the effect of whale feces in the marine environment (The Guardian, 21/12/2021). As part of a similar experiment, led by the Centre for Climate Repair at Cambridge, United Kingdom, researchers are releasing a mix of iron, phosphors, nitrates and silica in the Indian Ocean (New Scientist 22/02/2022). Results from these experiments have not been presented to our knowledge so far.

Smetacek et al. (2012) found a peak of a large diatom bloom in the fourth week after fertilization in an experiment in the Antarctic Circumpolar Current. Half of the diatoms sank deeper than 1,000 m, potentially contributing to carbon removal from the atmosphere. However, significant diatom increase only occurs in HNLC waters when sufficient light conditions occur, which encompass only one-third of the ocean (Boyd et al., 2007). Even the most successful experiment managed to export just 900 t of carbon to the marine environment (Pershing et al., 2010). A larger experiment releasing 100 t of iron sulphate in Canada triggered a debate about the effectiveness and grey areas of ocean fertilisation (Tollefson, 2012). Such experiments are providing us with valuable information about the biological pump but so far have not shown to be effective for climate-relevant CO_2 carbon removal. Achieving this requires long time removal of carbon from the atmosphere with phytoplankton or other forms of carbon stored in sediment (Figure 1). Large-scale fertilisation of marine environments will provide short term removal (100 – 1000-year cycle) of CO_2 but will not provide long-term solutions. Furthermore, it would take hundreds of such events to match the export potential of fully restored whale populations (Pershing et al., 2010).

Assumptions and data gaps

Efforts to model how whales influence the ocean's CO_2 sink capacity have revealed a number of data gaps. The majority of research in this field has concentrated on the Southern Ocean despite the lack of oceanographic data (nutrient transport, circulation) for this region that is required to understand carbon sequestration. Case studies are lacking from most regions, which is particularly relevant given the northern/southern hemisphere dichotomy in micronutrient limitation (Wing et al., 2014). This includes the lack of emerging research on the carbon cycle of all marine vertebrates such as fish and seabirds (Martin et al., 2021; Rhodes-Reese et al., 2021) and the nutrient uptake by bacteria and viruses (Ratnarajah et al., 2018). Viruses are widely distributed in the marine environment, accumulating carbon at an equivalent to over 75 million blue whales (Suttle, 2005).

Also, for precise estimates, it should be considered that the retention of nutrients varies in the whale body with age and reproductive status (Tynan, 1997). The variation in food intake by age and sex also drives iron retention. There are relevant weight variations between breeding and feeding season but some studies assumed defecation of whales in similar amounts between feeding and breeding grounds (Roman and McCarthy, 2010; Roman et al., 2014). Respiration rates of whales would also vary with different behavioral stages (feeding, migrating, socializing or breeding) and regions (tropical versus arctic). For example, Tynan (1997) estimated that humpback whales can contribute up to 34,254 Mt CO_2 (equivalent to 9-71 Mt carbon) to the atmosphere through respiration.

Removal of fixed carbon through whale falls depends on different aspects, such as species, location of death, and season for instance. Also, the carbon levels in different types of tissues (bone, muscle, blubber, visceras) for each species are currently unknown. Although previously it was assumed that 50% of dead whales reach the deep sea (Baco and Smith, 2003) and that biomass-carbon conversion does not change with carcass degradation, now it is clear that all these factors need to be taken into consideration for the evaluation of the contribution of whales falls to deep ocean and sediment carbon stocks.

The whale conveyor belt, whale pump and whale bioturbation potentially increase iron availability for phytoplankton growth. Data on the arrival and departure times of individual whales and their migratory path are crucial to refining bioenergetics models and predictions of iron flux. It is one of the key factors involved in enhancing phytoplankton growth. The amount of biogenic iron (and other elements at the surface waters) released by whales in relation to region, species, prey and time has not been studied in much detail. For example, Ratnarajah et al. (2017) estimated the fractions of lithogenic and biogenic iron in the feces of baleen whales, which showed up to possible 80% biogenic iron for Southern Ocean samples.

The size and nature of iron particles, their reduction or complexation of certain molecular forms allows different phytoplankton classes to access the iron (Ratnarajah et al., 2018; Sutak et al., 2020). There is limited knowledge about whale feces particle size and iron content (Supplementary Table 2) (Ratnarajah et al., 2016; Schlosser et al., 2018). The iron-retention and release rates by baleen whales have also not been measured directly (Savoca et al., 2021). Thus, the complex physico-chemical nature of whale feces influencing phytoplankton blooms on spatial and temporal scales are largely unknown.

Predicting the impact on the carbon sink capacity of oceans from recovering whale populations is being further complicated by the increasing impacts of climate change. Climate change could delay or weaken the carbon sequestration processes (Sigman and Hain, 2012) by whales as their populations are facing food shortages under changing ocean conditions (Seyboth et al., 2016). Some generalist whale species such as humpback whales have the ability to forage on multiple prey types with similar net energy gain and thus can buffer against increased ocean variability under climate change, at least in some periods and regions with potential alternative prey available (Fleming et al., 2016) but other species such as gray whales are more susceptible to the fluctuations in the abundance of specific prey items (Torres et al., 2022). However, this will alter the iron export and carbon capture abilities. There is emerging evidence of altered feeding behavior from humpback whales in the Southern Hemisphere (e.g., supergroups in South Africa) (Findlay et al., 2017). This may result in reduced bioavailable iron content of humpback whale feces in these regions and the large HNLC regions along their migratory paths. Also related to the uncertainties in estimating whales' contribution to carbon uptake from the atmosphere are the confidence intervals associated with abundance estimates of the different species, as for example even for the well-studied Antarctic minke whale (Branch, 2011; Galletti Vernazzani et al., 2017).

Most calculation of carbon export from whales have not included the CO_2 loss to the atmosphere via respiration, therefore not providing whales´ net capacity for carbon removal. Huntley et al. (1991) estimated that marine top predators may transfer as much as 20-25% of photosynthetically fixed carbon back to the atmosphere. The respiration rate of whales can be estimated using the following equation, as previously used by Lavigne et al. (1986): R = 140m^a where *R* represents respiration rate (kcal/day), *m* states the average mass of the whales and *a* being a fixed value of 0.75 for whales (Brown and Gillooly, 2003). The respired carbon is calculated on the assumption that 1 kcal of metabolism produces 0.38 g CO_2 (or 0.10 g C). For an estimated 1.1 million baleen whales (Pearson et al., 2023) of different species and age classes an average weight of 15 ton per whale would result in 0.0079 Pg respired carbon annually, equivalent to 50% carbon stored in whale biomass (Lavigne et al., 1986). A hypothetical number that would also largely fluctuate over time and there is no consensus if respiration rate doubles in marine mammals compared to terrestrial mammals (Sims, 2000). The respired carbon stored in whale biomass could therefore also be much less than 50%. Most of the phytoplankton biomass is respired through consumers and only <1% reaches the sediments (Hain et al., 2014), the whales' contribution to atmospheric CO_2 via respiration likely plays a smaller role in the calculation of their net capacity for carbon removal. However, a thorough understanding of respiration rates and the overall contribution of whales to atmospheric CO_2 is fundamental for the ongoing discussion about whales and carbon export.

Derived from the above discussion, we identified 12 fundamental research areas related to the contribution of whales to atmospheric carbon sink (Figure 4). An overarching topic that applies to all these research fields is the impact of whaling on ecosystem function and future population growth or decline. These areas fall under the overarching themes of modelling, quantification and validation. Future ecosystem models require the inclusion of nutrient flux from whales. There are different aspects of whale nutrient flux that require further investigations including the role of whale mediated nutrient distribution in ocean processes, the role of horizontal movement in nutrient distribution, and the relevance of background nutrient and trace metal content in seawater.

Quantification and with-it validation of ecosystem models, firstly requires standardization for validation and best practice guidelines given the large spatial and temporal scale to be covered with many case studies from different regions. Areas in which further quantification is required are the phytoplankton carbon flux (and intake of recycled nutrients from whale faeces), spatial and temporal variation of whale faeces (nutrient content, iron, trace elements) in relation to prey and estimation of refined consumption rates of whales (according to time on the feeding grounds and prey composition), carbon flux from cetaceans to the atmosphere.

The above research areas should be targeted with case studies on bioavailability of whale-derived nutrients and case studies in particular in the Northern Hemisphere and in areas with contrasting foraging species.

Conclusions

Whales can substantially influence their marine environment and play a part on the global carbon cycle with importance varying regionally depending on the location and species type. However, there is a need for careful evaluation of their impact in the context of climate mitigation, which at present is far from certain and efforts in that direction are somewhat misguided for the lack of corroborative scientific data. Detailed evaluation is needed for different oceanic regimes, and within a comparative context that also accounts for the role of whales in CO_2 mitigation as opposed to other organisms and ecosystems that also contribute substantially to ecosystem functioning.

Combining behavioural observations with bioenergetics, biotic, chemical, and physical features of the marine environment, oceanographic modeling, and nutrient modeling promise to be rewarding. Further exploring the potential contribution of whales to carbon and nutrient cycles and other ecosystem functions if the populations were to recover can add to the conservation value of whales. While some are claiming that baleen whale populations may meet criteria of carbon sequestration to be considered as a natural climate solution (Chami et al., 2020) this should not define the overarching value. Carbon fluxes observed in other marine ecosystems such as mangroves (0.031-0.034 Pg per year) or salt marshes (up to 0.087 Pg per year) are significantly higher than those of baleen whales (Duarte et al., 2005). Competition over carbon credits between whales and marine ecosystems would be counterproductive. Given the uncertainties and lack of data, increased focus on whales and carbon in the public domain bear the risk of inflating the value of whales as carbon sinks. Management measures that help protect marine habitats functioning as carbon sinks including deep see environments will make a significant contribution to mitigate climate change (Simard et al., 2016). Large scale protection of marine environments including the habitats of whales will build resilience and assist with natural carbon capture.

The presence of whales is associated with many other benefits for the marine environment. Whales have economic value through whale-watching (O'Connor et al., 2009), intrinsic cultural value to many societies, they host other species and are an essential source of food for abyssal ecosystems (Baco and Smith, 2003; Sumida et al., 2016). Carbon sequestration may not be the most important contributor to this value, and a further investigation of this role remains a global task.

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 no data was collected as part of this research. Peer reviewed studies are being used.

Author contributions

All authors significantly contributed toward development of the manuscripts. J-OM, SS, JB, ES, SP, GF MV, KF AR and BM contributed to conception and design of study. J-OM, SS, MV, and AR contributed to assessment and organization. J-OM, SS, and AR contributed to model development. SS, JB, ES, SP, GF, MV, KF, BM, and AR contributed to interpretation of results. J-OM wrote the manuscript. All authors contributed to the article and approved the submitted version.

Funding

This work was supported by a grant to Griffith University from a private charitable trust as part of the Whales & Climate Research Program.

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.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1117409/full#supplementary-material

SUPPLEMENTARY TABLE 1
Overview of some scientific studies assessing whales and carbon between 1991-2022.

SUPPLEMENTARY TABLE 2
Iron concentration from whale feces as reported in current literature.

SUPPLEMENTARY TABLE 3
Estimated iron concentration from different Antarctic krill samples.

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frontiers | Frontiers in Marine Science

TYPE Review
PUBLISHED 19 October 2023
DOI 10.3389/fmars.2023.997491

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RECEIVED 19 July 2022
ACCEPTED 28 August 2023
PUBLISHED 19 October 2023

CITATION
Seyboth E, Meynecke J-O, de Bie J, Roychoudhury A and Findlay K (2023) A review of post-whaling abundance, trends, changes in distribution and migration patterns, and supplementary feeding of Southern Hemisphere humpback whales. *Front. Mar. Sci.* 10:997491. doi: 10.3389/fmars.2023.997491

A review of post-whaling abundance, trends, changes in distribution and migration patterns, and supplementary feeding of Southern Hemisphere humpback whales

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Southern Hemisphere humpback whales (*Megaptera novaeangliae*) were heavily targeted during modern commercial whaling operations, with some 216,000 individuals killed between 1903 and 1973. That impacted the abundance of all the seven breeding stocks of the species. Most of these stocks have been recovering from whaling pressure although the understanding of the current growth rates of some stocks, and how the rates compare across stocks are lacking. Updated information is fundamental for understanding the species' current status, and to support the review of management plans promoting its protection and recovery, especially considering current changes in ocean environments due to climate change. This work offers a comprehensive overview of the current knowledge on Southern Hemisphere humpback whales breeding stocks' status. The aim is to provide information on their post-whaling growth trends and changes in distribution and migration patterns. Within that, records of supplementary feeding records (i.e. feeding beyond their formally described feeding grounds) are described. We have also identified knowledge gaps and note that the establishment of research collaborations, as well as standard methodologies for data collection can be important steps for the acquisition of better comparable data sets for the analysis of the current status of humpback whales and to fill such gaps. The compiled information provided can be used as part of an In-Depth Assessment of the species by the International Whaling Commission.

KEYWORDS

abundance estimate, cetacean, climate change, population trends, *Megaptera novaeangliae*, population recovery

Introduction

Humpback whales (*Megaptera novaeangliae*) are a cosmopolitan cetacean species (Clapham and Mead, 1999) and one of the most studied large baleen whales (IWC, 2006). In the Southern Hemisphere, humpback whales generally migrate seasonally between high-latitude feeding grounds typically used during austral summer and mid to low-latitude breeding grounds for late austral autumn and winter (Clapham and Mead, 1999).

Currently, seven humpback whale breeding stocks (hereafter referred to as stocks) are recognized by the International Whaling Commission (IWC) in the Southern Hemisphere (Figure 1; IWC, 1998). These are referred to stocks ‘A’ to ‘G’ by IWC and each is assigned to a specific breeding area. Based on genetic, mark-recapture or whaling data (Findlay, 2000; Rosenbaum et al., 2009; Fleming and Jackson, 2011), some stocks have been subdivided into sub-stocks. The breeding and feeding grounds used by each stock and sub-stock are indicated in Table 1. Given the connectivity amongst sub-stocks from New Caledonia (E2), Tonga (E3), Cook Islands (F1) and French Polynesia (F2), they have been grouped in the so-called Oceania stock (IWC, 2016a). In this review, as for in many publications in the field, we prioritize referring to the stocks based on their breeding ground location. Throughout the text, we refer to specific areas or locations within the breeding grounds that might not be familiar to the reader, so for a better location of the areas mentioned please see the maps included as supplementary information (Figures S1–S5).

The species was severely depleted by modern commercial whaling in the Southern Hemisphere. It is estimated that about 216,000 individuals were killed across the region from 1903 to 1973 (Allison, 2020), which reduced its abundance to a very small fraction of their pre-exploitation levels (Findlay, 2000). Although humpback whales have been protected across the Southern Hemisphere since October 1963 (Tønnessen and Johnsen, 1982), illegal Soviet operations continued until 1973 (Clapham et al., 2009). Further protection for the species came into force in 1986 with the Moratorium established by the IWC (Clapham and Baker, 2002).

Based on catch allocations of blue (*Balaenoptera musculus*) and fin (*Balaenoptera physalus*) whales, the IWC historically identified six main Management Areas (Areas I–VI) within the Southern Ocean for all baleen whales (Figure 1; Mackintosh, 1942; Donovan, 1991). As new information on the distribution of illegal Soviet catches was gained, some of these areas necessitated further longitudinal division of feeding areas in the Southern Ocean(Figure 1; IWC, 1998). The use of these Management Areas by the different stocks of humpback whale is a vexing question that was historically investigated through the analyses of mark-recapture data and catch histories. For example, high-latitude catches were allocated to particular stocks on the basis of longitudinal dispersal (e.g. Paton and Clapham, 2006). With time, information has been gained on the level of mixing between the stocks in high-latitude areas. Reviews of Discovery Investigation’s whale mark-recapture data (collected using stainless-steel tags deployed during the whaling era – please see Rayner (1940)), movement patterns (Bestley et al., 2019), satellite-tag individuals (e.g. Reisinger et al., 2021) and photo-identification data (e.g. Marcondes et al., 2021) suggest a possible greater degree of mixing among stocks on the feeding grounds than originally agreed by the IWC (IWC, 2016a; Jackson et al., 2015).

A Comprehensive Assessment of Southern Hemisphere humpback whales was developed by the IWC was completed in 2014 and results were synthesised in 2015 (IWC, 2016a, 2016b). It was based on a Bayesian statistical approach including a backward projection (Butterworth and Punt, 1995; Jackson et al., 2015), and estimated the pre-modern whaling abundance of the species in the Southern Hemisphere at 137,972 (95% PI = 111,833-197,781) individuals (IWC, 2016b). The sum of the median abundance projected for each stock for 2015 was of 96,675 (95% PI = 78,041-117,527) individuals. An overall recovery of about 70% for all stocks combined is indicated, although there are marked differences in the rates of increase (ROI) across stocks (IWC, 2016b). As a reflection of the recovery of the stocks, the species is currently listed as “Least Concern” on the IUCN Red List, although low numbers of the Oceania stocks have meant

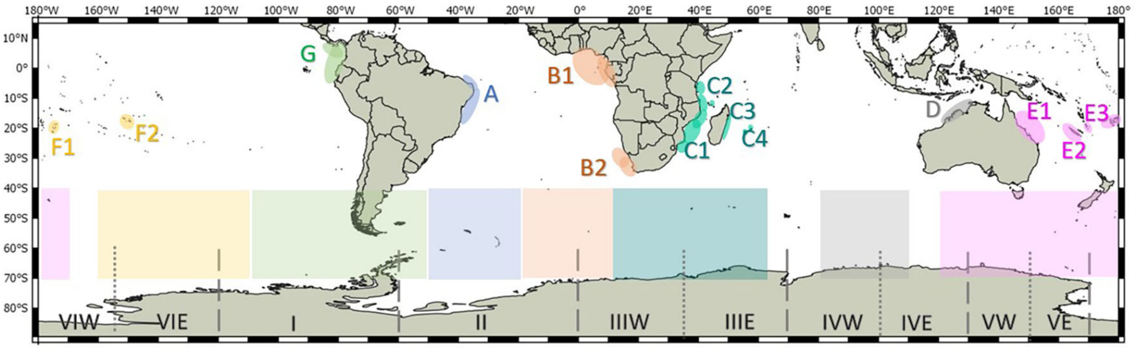

FIGURE 1
Distribution of the core breeding and primary feeding grounds of the Southern Hemisphere humpback whale Breeding Stocks A – G, and Southern Ocean Management Areas I – VI and sub-areas (Donovan, 1991; IWC, 1998; IWC, 2006). Colors are used to indicate the breeding and feeding grounds used by each breeding stock and sub-stock. Dashed lines indicate the limit of the main Management Areas, whereas dotted lines are marking the limits of sub-areas (W = west and E = east). Areas and sub-areas limits are: I = 120°W–60°W; II = 60°W–0°; III = 0–70°E (IIIW = 0–35°E and IIIE = 35°E–70°E); IV = 70°E–130°E (IVW = 70°E–100°E and IVE = 100°E–130°E); V = 130°E–170°E (VW = 130°E–150°E and VE = 150°E–170°E); and VI = 170°E–120°W (VIW = 170°W–155°W and VIE = 155°W–120°W).

TABLE 1 Breeding and feeding grounds of the Southern Hemisphere humpback whale Breeding Stocks A – G and sub-stocks based following the definition by the International Whaling Commission and information from IWC (IWC, 2007; IWC, 2016a, 2016b) and Branch (2011).

Breeding ground	Breeding Stock/sub-stock	Feeding ground
East coast of South America (southwestern Atlantic Ocean)	**A**	**50°W–20°W**
West coast of Africa (southeastern Atlantic Ocean)	**B**	**20°W–10°E**
Gabon	B1	
Namibia and west coast of South Africa	B2	
East coast of Africa and western Indian Ocean	**C**	**10°E–60°E**
Mozambique and southern Tanzania	C1	
Comoros Archipelago	C2	
Madagascar	C3	
Mascarene Islands of Mauritius and Réunion	C4	
West coast of Australia	**D**	**80°E–110°E**
East coast of Australia and western Pacific Ocean	**E**	**120°E–170°W**
Eastern Australia	E1	
New Caledonia	E2*	
Tonga	E3*	
South central Pacific Ocean	**F**	**170°W–110°W**
Cook Islands	F1*	
French Polynesia	F2*	
West coast of South America (northern Peru to Costa Rica)	**G**	**110°W–50°W**

*Combined as the Oceania Breeding Stock.

these are still listed as "Endangered" (Childerhouse et al., 2008; Cooke, 2018).

Despite intense research on Southern Hemisphere humpback whales over the last decades, updated information on their population demographic parameters is essential for stock assessments and evaluation of conservation status (e.g. Rodrigues et al., 2006; Punt and Donovan, 2007). Updated estimates of trends in abundance and of absolute stock sizes are essential for the evaluation of the need for management strategies and for effective measures to be developed, if necessary (e.g. Caughley, 1994; Rockwood, 2015). That is particularly important for humpback whales considering the current pressures faced by the species. Such pressures include climate-driven environmental variabilities affecting both their breeding and feeding grounds, as well as migratory corridors (e.g. Derville et al., 2019; Tulloch et al., 2019; Meynecke et al., 2020; Meynecke et al., 2021; Seyboth et al., 2021; van Weelden et al., 2021), and other threats such as ship strikes (Van Waerebeek et al., 2007; Smith et al., 2020), entanglements (Groom and Coughran, 2012; Ott et al., 2016; Félix et al., 2020a; Santora et al., 2020), underwater noise (Rossi-Santos, 2015; Dunlop, 2019; Dunlop et al., 2020), and pollution (Besseling et al., 2015; Das et al., 2017; Casà et al., 2019; Remili et al., 2020). One example of a climate-driven impact is the influence of sea surface temperature (SST) on the abundance and distribution of prey stocks, which has been identified as a threat to different whale populations (e.g. Simmonds and Isaac, 2007). That is mainly related to the decrease of Antarctic krill (*Euphausia superba*) abundance as a response to warmer ocean conditions (e.g. Loeb and Santora, 2015; Atkinson et al., 2019). This has potential consequences for humpback whale stocks as Antarctic krill is the main prey item in the diet of Southern Hemisphere humpback whales (e.g. Mackintosh, 1965; Santora et al., 2010; Herr et al., 2016) and as food availability may impact their reproductive success (e.g. Seyboth et al., 2021). However, disentangling the effects of these pressures on stock recovery from the effects of exploitation from whaling is complex and requires detailed information on the extent and rates of recovery within and across stocks so their abundance trajectory can be better understood.

Other important aspects to be investigated are potential changes in the distribution of the species including feeding and breeding grounds and migration corridors, and the performance of feeding behaviour in regions beyond the regular feeding grounds. Such changes might be becoming more common as the species increase in abundance, and faces the changes observed in prey populations in the Southern Ocean.

Furthermore, status assessments are important for the understanding of the roles of humpback whales in the trophic ecology of Southern Ocean systems. For example, whales in general may influence both prey populations and community structure through top-down forcing (Croll et al., 2006; Leaper et al., 2008), and the primary production and biogeochemistry of the marine environment through micronutrient fertilisation (Ratnarajah et al., 2014; Ratnarajah et al., 2016). Given the removal of some two million individuals of different whale species from Southern Ocean systems by modern whaling and associated influences on trophic ecology - see for example the krill surplus hypotheses discussion initially introduced by Laws (1977), updated information on population recoveries and status are critical in Southern Ocean management models (e.g. Friedlaender et al., 2006a; Seyboth et al., 2016; Warwick-Evans et al., 2022).

Aiming to contribute to the knowledge of the current status of Southern Hemisphere humpback whale, in this study we review information on their post-whaling abundance and growth rate estimates, and compile information on the stock structure, potential changes in distribution and migration patterns, and records of supplementary feeding (i.e. feeding beyond their regular feeding grounds in high latitudes) for each stock. The information combined in this review may serve as a contribution toward an In-depth Assessment of Southern Hemisphere humpback whale by the IWC.

Methods

We collated information relevant to the review from literature made available online until 01 April 2022 in peer-reviewed papers, books, and IWC or project reports. Online searches were conducted using a different combination of the words/terms 'humpback whale', 'population growth', 'growth rate', 'rate of increase', 'abundance', 'abundance estimate', 'population recovery', 'feeding record', 'distribution', and 'breeding stock' in Google, Google Scholar, and Web of Science platform, and checked references cited in the publications found relevant during this search.

Information found was grouped by stock whenever possible. The cases for which such classification could not be applied were related to circumpolar data and are presented at the end of the following section as complementary data.

Results

General overview

We identified 58 studies in which post-whaling abundance and ROI estimates are presented for Southern Hemisphere humpback whales, published between 1989 and 2022. The number of studies per stock is indicated in Table 2, as well as the number of studies with evidence of feeding beyond the regular feeding grounds of the stocks, which have been reported for the stock related to the east coast of South America, west coast of Africa, east coast of Australia and western Pacific Ocean and west coast of South America. Most studies on abundance were related to stock breeding on the east coast of South America, while most of those investigating ROI were related to eastern Australia.

Information per breeding ground

All the estimates found on abundance and ROI for each breeding ground/stock are presented in Tables 3, 4, respectively, and some studies were chosen to be included in the text to describe the recovering trajectory of each stock. Information on changes in distribution and records of supplementary feeding of each stock is described in the text below.

Southwestern Atlantic Ocean (Breeding Stock A)

Breeding and feeding ground distribution and potential changes in migration

The breeding area for this stock is located along the coast of Brazil the eastern coast of South America, mainly over the Abrolhos Bank (16°40'S–19°30'S) (Andriolo et al., 2006a; Zerbini et al., 2006; Andriolo et al., 2010). Within this area, higher group densities are found between 140 and 236 km from the coast with relatively shallow waters (< 500 m) (Pavanato et al., 2018), and associated to slower currents, sheltered areas and SSTs of between 24 and 25°C (Bortolotto et al., 2017). Areas surrounding oceanic islands such as the Archipelagos of Fernando de Noronha (3°51'S) and Trindade and Martin Vaz (20°30'S) have been included as part of the breeding ground (Lodi, 1994; Siciliano et al., 1999). The breeding period is from June to November, with a peak in August-September (Martins et al., 2001; Morete et al., 2003).

Off the coast of Brazil, there is evidence that the species have been reoccupying regions of the breeding ground that were known to be used before whaling decimated the stocks and subsequently restricted their range in breeding grounds (Zerbini et al., 2004). For example, the increase of encounter rates on the north coast of Bahia State (around 12°S–13°S) between 2000 and 2006 may represent a post-whaling expansion of the area used by the species around Abrolhos Bank (Rossi-Santos et al., 2008). Observations to the

TABLE 2 Summary of the review survey, indicating the number of studies found for each Southern Hemisphere humpback whale main breeding stock/sub-stock on each aspect aimed to be investigated.

Aspect	Breeding stock							Circumpolar
	A	B	C	D	E1	Oceania (E2, E3, F1, F2)	G	
Abundance	16	5	11	8	13	3	9	1
Rate of increase	8	3	6	7	14	1	3	1
Feeding in mid to low latitudes	4	6	0	0	7	0	6	0

TABLE 3 A summary of information on abundance (N) for humpback whales published until 01 April 2022, organized by Breeding Stock (A – G).

Breeding area/stock	Abundance estimate (*N*)	Year/ Period	Source	Methodology
Southwestern Atlantic Ocean (Breeding Stock A)				
Rio Grande do Norte (4°34'S) to Rio de Janeiro (23°12'S)	7,689 (95% PI = 6,585–8,931)	2008	Pavanato et al., 2017	Aerial survey
Rio Grande do Norte (4°34'S) to Rio de Janeiro (23°12'S)	12,123 (95% PI = 10,811–13,531)	2015	Pavanato et al., 2017	Aerial survey
Natal (5°S) to 10°S in 1999; 5°S to 12°S in 2000	628 (CV = 0.335, 95% CI = 327–1,157)	2000	Zerbini et al., 2004	Ship-based line-transect survey
Natal (5°S) to Cabo Frio (23°S)	16,410 (CV = 0.228, 95% CI = 10,563–25,495)	2008	Bortolotto et al., 2016a	Ship-based line-transect survey
Natal (5°S) to Cabo Frio (23°S)	14,264 (CV = 0.084)	2008	Bortolotto et al., 2017	Ship-based line-transect survey
Natal (5°S) to Cabo Frio (23°S)	20,389 (CV = 0.071)	2012	Bortolotto et al., 2017	Ship-based line-transect survey
Sergipe (10°8'S) to Rio de Janeiro (23°12'S)	8,652 (95% PI = 7,696–9,682)	2011	Pavanato et al., 2017	Aerial survey
Bahia (12°10'S) to Espírito Santo (20°42'S)	2,229 (CV = 0.31)	2001	Andriolo et al., 2006a	Aerial survey
Bahia (12°10'S) to Espírito Santo (20°42'S) in 2002-2004; 5°S to 25°S in 2005	6,251 (CV = 0.16)	2005	Andriolo et al., 2006b	Aerial survey
Bahia (12°10'S) to Espírito Santo (20°42'S)	6,404 (CV = 0.11)	2005	Andriolo et al., 2010	Aerial survey
Salvador (13°S) to Cabo Frio (23°S)	15,332 (CV = 0.243, 95% CI = 9,595–24,500)	2008	Bortolotto et al., 2016a	Ship-based line-transect survey
Salvador (13°S) to Cabo Frio (23°S)	19,429 (CV = 0.101, 95% CI = 15,958–23,654)	2012	Bortolotto et al., 2016a	Ship-based line-transect survey
Abrolhos Bank (16°40'S-19°30'S)	1,634 (90% CI = 1,379–1,887)	1995	Kinas and Bethlem, 1998	Photo-identification capture-recapture data
Abrolhos Bank (16°40'S-19°30'S)	3,871 (CV = 0.18; 95% PI = 2,795–5,542)	2000	Freitas et al., 2004	Photo-identification capture-recapture data
Scotia Arc (~ 52°S–67°S)	2,493 (CV = 0.55)	2000	Hedley et al., 2001	Ship-based line-transect survey
Scotia Arc (~ 50°S–65°S)	24,543 (CV = 0.26; 95% CI = 14,863–40,528)	2019	Baines et al., 2021	Ship-based line-transect survey
South of 60°S, 50°W–20°W	98 (CV = 0.96)	1981/82	Branch, 2011	Ship-based line-transect survey
South of 60°S, 50°W–20°W	336 (CV = 0.55)	1986/87	Branch, 2011	Ship-based line-transect survey
South of 60°S, 50°W–20°W	168 (CV = 0.61)	1997/98	Branch, 2011	Ship-based line-transect survey
Whole stock	6,705 (95% CI = 4,704-9,181)	2006	Zerbini et al., 2011a	Projected using the backwards method of Butterworth and Punt (1995) using previously published data
Whole stock	11,672 (95% PI = 6,649–16,864)	2015	IWC, 2016b	Projected using the backwards method of Butterworth and Punt (1995) using previously published data
Whole stock	24,900 (95% PI = 22,400–27,000)	2019	Zerbini et al., 2019	Bayesian population model integrates catch, abundance, genetics and biological data

(Continued)

TABLE 3 Continued

Breeding area/stock	Abundance estimate (*N*)	Year/ Period	Source	Methodology
Whole stock	14,552 (95% CI = 7,282–19,874)	2019	Bortolotto et al., 2021	Base case model - Zerbini et al. (2011a) (catch data and line transect surveys)
Whole stock	**21,878 (95% CI = 21,377–22,285)**	2019	Bortolotto et al., 2021	Updated model - based on previous estimates and more recent published data
Southeastern Atlantic Ocean (Breeding Stock B)				
Gabon (1°N–4°S), B1	597 (95% CI = 342–1,042)	2002	Rosenbaum et al., 2004	Aerial survey
Gabon (1°N–4°S), B1	1,259 (95% CI = 710–2,333)	2002	Strindberg et al., 2011	Ship-based line-transect survey
Iguela (1°51'S), Gabon, B1	7,196 (CV = 0.15)	2001–2004	Collins et al., 2010	Genotype estimates
Iguela (1°51'S), Gabon, B1	6,432 (CV = 0.18)	2001–2005	Collins et al., 2010	Photo-identification capture-recapture data
Iguela (1°51'S), Gabon, B1	3,810 (CV = 0.34)	2001–2002	Collins et al., 2010	Genotype estimates
Iguela (1°51'S), Gabon, B1	9,301 (CV = 0.40)	2002–2003	Collins et al., 2010	Genotype estimates
Iguela (1°51'S), Gabon, B1	4,672 (CV = 0.23)	2001–2005	Collins et al., 2010	Photo-identification capture-recapture data
Mayumba (3°22'S), Gabon, B1	4,093 (CV = 0.30)	2005–2006	Collins et al., 2010	Genotype estimates
Mayumba (3°22'S), Gabon, B1	3,301 (CV = 0.39)	2005–2006	Collins et al., 2010	Photo-identification capture-recapture data
South of 60°S, 20°W-10°E	246 (CV = 0.85)	1980/81	Branch, 2011	Ship-based line-transect survey
South of 60°S, 20°W-10°E	70 (CV = 0.63)	1986/87	Branch, 2011	Ship-based line-transect survey
South of 60°S, 20°W-10°E	595 (CV = 0.51)	1995/96	Branch, 2011	Ship-based line-transect survey
Whole sub-stock B1	**12,973 (95% PI = 9,709–15,096)**	2015	IWC, 2016b	Projected using the backwards method of Butterworth and Punt (1995) using previously published data
Whole sub-stock B2	**484 (95% PI = 138–860)**	2015	IWC, 2016b	Projected using the backwards method of Butterworth and Punt (1995) using previously published data
East coast of Africa and western Indian Ocean (Breeding Stock C)				
Mozambique Island (14°26'S) to Cabo Inhaca (26°S), C1	5,965 (CV = 0.17)	2003	Findlay et al., 2011b	Ship-based line-transect survey

(Continued)

TABLE 3 Continued

Breeding area/stock	Abundance estimate (*N*)	Year/ Period	Source	Methodology
Mozambique (18°S) to Richards Bay (~ 28°30'S), C1	1,954 (no CI provided)	1994	Findlay et al., 1994	Ship-based line-transect survey
Cape Vidal (28°07'S), C1	1,711 (no CI provided)	1990	Findlay and Best, 1996	Land-based survey
Cape Vidal (28°07'S), C1	695 (no CI provided)	1990	Findlay and Best, 2006	Ship-based line-transect survey
Cape Vidal (28°07'S), C1	1,093 (no CI provided)	1991	Findlay and Best, 2006	Ship-based line-transect survey
Cape Vidal (28°07'S), C1	2,406 (no CI provided)	2002	Findlay and Best, 2006	Ship-based line-transect survey
Whole sub-stock C1	**8,045 (95% PI = 6,756–9,656)**	2015	IWC, 2016b	Projected using the backwards method of Butterworth and Punt (1995)
Madagascar (from 23°0.9'S and 22°S in the wearstern and eastern coasts, respectively), C3	2,532 (no CI provided)	1994	Best et al., 1996	Ship-based line-transect survey
Antongil Bay (15°45'S), C3	5,612 (CV = 0.34; 95% CI = 2,980–10,896)	2003	Cerchio et al., 2008	Photo-identification capture-recapture data
Antongil Bay (15°45'S), C3	5,807 (CV=0.32; 95% CI = 3,452–10,008)	2003	Cerchio et al., 2008	Genotypic data
Antongil Bay (15°45'S), C3	6,737 (CV = 0.31; 95% CI = 3,804–12,229)	2006	Cerchio et al., 2008	Photo-identification capture-recapture data
Antongil Bay (15°45'S), C3	8,348 (CV=0.32; 95% CI = 4,558–15,650)	2006	Cerchio et al., 2008	Genotypic data
Antongil Bay (15°45'S), C3	5,564 (CV = 0.36; 95% CI = 1,646–9,482)	2003	Cerchio et al., 2009	Photo-identification capture-recapture data
Antongil Bay (15°45'S), C3	5,560 (CV = 0.37; 95% CI = 1,556–9,564)	2003	Cerchio et al., 2009	Genotypic data
Antongil Bay (15°45'S), C3	7,406 (CV = 0.37; 95% CI = 2,106–12,706)	2006	Cerchio et al., 2009	Photographic mark-recapture data
Antongil Bay (15°45'S), C3	8,325 (CV = 0.37; 95% CI = 2,323–14,328)	2006	Cerchio et al., 2009	Genotypic data
Whole sub-stock C3	**7,972 (95% PI = 6,409–10,229)**	2015	IWC, 2016b	Projected using the backwards method of Butterworth and Punt (1995) using previously published data
62°S–68°S, 40°E–70°E	4,368 (CV = 0.28)	2006	Peel and Thiele, 2006	Ship-based line-transect survey
South of 60°S, 10°E–60°E	720 (CV = 0.53)	1979/80	Branch, 2011	Ship-based line-transect survey
South of 60°S, 10°E–60°E	700 (CV = 0.46)	1987/88	Branch, 2011	Ship-based line-transect survey
South of 60°S, 10°E–60°E	2,391 (CV = 0.41)	1993/94	Branch, 2011	Ship-based line-transect survey
West coast of Australia (Breeding Stock D)				
Western Australia (20°21'S-20°34'51''S)	2,736 (95% CI = 928–9,928)	1990–1991	Jenner and Jenner, 1994	Photo-identification capture-recapture data
Western Australia (20°21'S-20°34'51''S)	3,878 (95% CI = 1,319–14,108)	1991–1992	Jenner and Jenner, 1994	Photo-identification capture-recapture data

(Continued)

TABLE 3 Continued

Breeding area/stock	Abundance estimate (*N*)	Year/ Period	Source	Methodology
North West Cape (21°S–22°S)	7,276 (95% CI = 4,993–10,167)	2000	Salgado Kent et al., 2012	Aerial survey
North West Cape (21°S–22°S)	12,280 (95% CI = 6,830–49,434)	2001	Salgado Kent et al., 2012	Aerial survey
North West Cape (21°S–22°S)	18,692 (95% CI = 12,980–24,477)	2006	Salgado Kent et al., 2012	Aerial survey
North West Cape (21°S–22°S)	20,044 (95% CI = 13,815–31,646)	2007	Salgado Kent et al., 2012	Aerial survey
North West Cape (21°S–22°S)	26,100 (95% CI = 20,152–33,272)	2008	Salgado Kent et al., 2012	Aerial survey
Shark Bay (~25°S–26°S)	3,302 (no CI provided)	1988	Bannister et al., 1991	Aerial survey
Shark Bay (~25°S–26°S)	8,207–13,640 (95% CI)	1999	Bannister and Hedley, 2001	Aerial survey
Shark Bay (~25°S–26°S)	34,290 (95% CI = 27,340–53,350)	2008	Hedley et al., 2011	Aerial and land-based surveys
Shark Bay (~25°S–26°S)	17,810 (95% CI = 14,210–27,720)	2008	Hedley et al., 2011	Aerial and land-based surveys
~ Shark Bay (24°46'S–26°09'S)	10,300 (95% CI = 6,700–24,500)	2005	Paxton et al., 2011	Aerial survey
~ Shark Bay (24°46'S–26°09'S)	4,700 (95% CI = 2,700–14,000)	2005	Paxton et al., 2011	Land-based survey
South of 60°S, 60°E–120°E	1,033 (CV = 0.44)	1978/79	Branch, 2011	Ship-based line-transect survey
South of 60°S, 60°E–120°E	3,869 (CV = 0.52)	1988/89	Branch, 2011	Ship-based line-transect survey
South of 60°S, 60°E–120°E	17,959 (CV = 0.17)	1997/98	Branch, 2011	Ship-based line-transect survey
Whole stock	**20,337 (95% PI = 18,415–24,918)**	2015	IWC, 2016b	Projected using the backwards method of Butterworth and Punt (1995) using previously published data
East coast of Australia (breeding sub-stock E1)				
Hervey Bay (25°S)	6,246 (95% CI = 5,011–7,482)	2007	Forestell et al., 2011	Photo-identification capture-recapture data
Cape Moreton (27°02'S) and Point Lookout (27°26'S)	1,107 (no CI provided)	1987	Paterson and Paterson, 1989	Land-based survey
Point Lookout (27°26'S),	356 (95% CI = 319–404)	1981	Bryden et al., 1990	Land-based survey
Point Lookout (27°26'S)	396 (95% CI = 338–466)	1982	Bryden et al., 1990	Land-based survey
Point Lookout (27°26'S)	776 (95% CI = 712–850)	1986	Bryden et al., 1990	Land-based survey
Point Lookout (27°26'S)	790 (95% CI = 732–884)	1987	Bryden et al., 1990	Land-based survey
Point Lookout (27°26'S)	1,788 (95% CI = 1,477–2,081)	1991	Brown, 1996	Land-based survey
Point Lookout (27°26'S)	1,896 (95% CI = 1,643–2,149)	1992	Paterson et al., 1994	Land-based survey

(Continued)

TABLE 3 Continued

Breeding area/stock	Abundance estimate (*N*)	Year/ Period	Source	Methodology
Point Lookout (27°26'S)	2,099 (95% CI = 1,759–2,433)	1993	Brown, 1996	Land-based survey
Point Lookout (27°26'S)	3,599 (95% CI = 3162–4,036)	1999	Paterson et al., 2001	Land-based survey
Point Lookout (27°26'S)	4,860 (no CI provided)	2002	Paterson et al., 2004	Land-based survey
Point Lookout (27°26'S)	7,090±660 (95% CI)	2004	Noad et al., 2011	Land-based survey
Point Lookout (27°26'S)	9,683 (95% CI = 8,556–10,959)	2007	Noad et al., 2008	Land-based survey
Point Lookout (27°26'S)	**24,545 (95% CI = 21,631–27,851)**	2015	Noad et al., 2008	Land-based survey
Hervey Bay (25°S), Byron Bay (28°37'S), and Ballina (28°52'S)	7,041 (95% CI = 4,075–10,008)	2005	Paton et al., 2011	Photo-identification capture-recapture data
South of 60°S, 120°E–170°W	995 (CV = 0.58)	1980/81	Branch, 2011	Ship-based line-transect survey
South of 60°S, 120°E–170°W	622 (CV = 0.50)	1985/86	Branch, 2011	Ship-based line-transect survey
South of 60°S, 120°E–170°W	13,300 (CV = 0.20)	2001/02	Branch, 2011	Ship-based line-transect survey
Whole sub-stock E1	19,614 (95% PI = 17,664–21,454)	2015	IWC, 2016b	Projected using the backwards method of Butterworth and Punt (1995) using previously published data
Oceania (breeding sub-stocks E2, E3, F1 and F2)				
French Polynesia, F2	1,057 (CV = 0.24; 95% CI = 700–1,600)	2004	Poole, 2006	Photo-identification capture-recapture data
Whole stock	**6,404 (95% PI = 5,491–7,595)**	2015	IWC, 2016b	Projected using the backwards method of Butterworth and Punt (1995) using previously published data
South of 60°S, 170°W–110°W	3,198 (CV = 0.47)	1983/84	Branch, 2011	Ship-based line-transect survey
South of 60°S, 170°W–110°W	2,801 (CV = 0.53)	1990/91	Branch, 2011	Ship-based line-transect survey
South of 60°S, 170°W–110°W	3,852 (CV = 0.22)	1997/98	Branch, 2011	Ship-based line-transect survey
West coast of South America (northern Peru to Costa Rica) (Breeding Stock G)				
Las Perlas Archipelago, Panama (~8°25'N)	1,041 (95% CI = 664–1,546)	2003–2009	Guzman et al., 2015	Photo-identification capture-recapture data
Coast of Ecuador (2°S)	6,504 (CV = 0.21; 95% CI = 4,270–9,907)	2006	Félix et al., 2011a	Photo-identification capture-recapture data
CCAMLR Subarea 48.1	6,991 (CV = 32.41)	2000	Hedley et al., 2001	Ship-based line-transect survey
Bransfield Strait	865 (CV = 14.13; 95% CI = 656–1,141)	2006	Secchi et al., 2011	Ship-based line-transect survey
Antarctic Peninsula	3,851 (CV = 0.05; 95% CI = 3,666-4,036)	1997	Stevick et al., 2006	Photo-identification capture-recapture data

(Continued)

TABLE 3 Continued

Breeding area/stock	Abundance estimate (*N*)	Year/ Period	Source	Methodology
Western Antarctic Peninsula	12,724 (CV= 0.06; 95% CI = 10,944–14,791)	2020	Warwick-Evans et al., 2022	Ship-based line-transect survey
Bransfield and Gerlache Straits	865 (CV = 14.13; 95% CI = 656–1,141)	2006	Secchi et al., 2011	Ship-based line-transect survey
South of 60°S, 110°W–50°W	683 (CV = 0.63)	1982/83	Branch, 2011	Ship-based line-transect survey
South of 60°S, 110°W–50°W	1,505 (CV = 0.34)	1989/90	Branch, 2011	Ship-based line-transect survey
South of 60°S, 110°W–50°W	3,337 (CV = 0.21)	1996/97	Branch, 2011	Ship-based line-transect survey
Whole stock	9,687 (95% PI = 8,520–10,202)	2015	IWC, 2016b	Projected using the backwards method of Butterworth and Punt (1995) using previously published data
Whole stock	**11,784 (SE = 266)**	2018	Félix et al., 2021	Photo-identification capture-recapture data
Mixed				
Circumpolar	7,100 (CV = 0.36)	1980–1981	Branch, 2011	Ship-based line-transect survey
Circumpolar	10,200 (CV = 0.30)	1987–1988	Branch, 2011	Ship-based line-transect survey
Circumpolar	41,500 (CV = 0.11)	1997–1998	Branch, 2011	Ship-based line-transect survey

Data are ordered in chronological sequence per breeding area, with estimates presented from northern to southern areas used by each Breeding Stock and sub-stocks. Numbers in bold refer to the most recent estimate for each stock/sub-stock.

TABLE 4 A summary of information on stock growth rates (including information found on rate of increase (ROI) and maximum intrinsic rate of increase (r_{max})* - both as % per year) estimates for humpback whales published until 01 April 2022, organized by Breeding Stock (A – G).

Breeding Area/Stock	Growth rate (%/year)	Year/ Period	Source	Methodology
Southwestern Atlantic Ocean (Breeding Stock A)				
Rio Grande do Norte (4°34'S) to Rio de Janeiro (23°12'S)	5.21 (SD = 0.75)	2008–2015	Pavanato et al., 2017	Aerial survey
12°10'S to 20°42'S	12 (CV = 17; 95% CI = 8–16)	2001–2011	Wedekin et al., 2017	Aerial survey
Abrolhos Bank (16°40'S–19°30'S)	7.4 (95% CI = 0.6–14.5)	1995–1998	Ward et al., 2011	Ship-based line-transect survey
Abrolhos Bank (16°40'S–19°30'S)	30.6 (95% CI = 2.6–60)	1996–2000	Freitas et al., 2004	Photo-identification capture-recapture data
Salvador (13°S) to Cabo Frio (23°S)	6.1 (no CI provided)	2008–2012	Bortolotto et al., 2016a	Ship-based line-transect survey
South of 60°S, 50°W–20°W	5.3 (95% CI = -6.9–17.4)	1981–1998	Branch, 2011	Ship-based line-transect survey
Whole stock	6.1 (no CI provided)	2010–2015	IWC, 2016b	Estimated using previously published data
Whole stock	7.6–10.7 (95% CI)*	–	Zerbini et al., 2019	Bayesian population model integrates catch, abundance, genetics and biological data
Southeastern Atlantic Ocean (Breeding Stock B)				
B1	2.9 (no CI provided)	2010–2015	Jackson et al., 2015	Estimated using previously published data
B2	4.1 (no CI provided)	2010–2015	Jackson et al., 2015	Estimated using previously published data
South of 60°S, 20°W–10°E	5.9 (95% CI = -5.9–17.6)	1979–1997	Branch, 2011	Ship-based line-transect survey
East coast of Africa and western Indian Ocean (Breeding Stock C)				
North of Mozambique Island (14°26'S) to Cabo Inhaca (26°S), C1	7.9 (no CI provided)	1991–2003	Findlay et al., 2004	Ship-based line-transect survey
Cape Vidal (28°07'S), C1	12.3 (95% CI = 4.7–19.9)	1988–2002	Findlay and Best, 2006	Land-based survey
Cape Vidal (28°07'S), C1	9.04 (95% CI = -25.6–43.7)	1990–2002	Findlay and Best, 2006	Land-based survey
Cape Vidal (28°07'S), C1	11.5 (SE = 2.8)	1988–2002	Findlay et al., 2011a	Land-based survey
Whole sub-stock C1	1.1 (no CI provided)	2010–2015	IWC, 2016b	Estimated using previously published data
Antongil Bay (15°45'S), C3	6.3 (no CI provided)	2000–2006	Cerchio et al., 2008	Photo-identification capture-recapture data
Antongil Bay (15°45'S), C3	13.6 (no CI provided)	2000–2006	Cerchio et al., 2008	Genetic data
Whole sub-stock C3	0.7 (no CI provided)	2010–2015	IWC, 2016b	Estimated using previously published data
South of 60°S, 10°E–60°E	6.6 (95% CI = -3.8–16.9)	1979–1995	Branch, 2011	Ship-based line-transect survey
West coast of Australia (Breeding Stock D)				
Shark Bay (~25°S–26°S)	10.9 ± 3 (95% CI)	1977–1991	Bannister, 1994	Aerial survey
Shark Bay (~25°S–26°S)	8.8 (95% CI = 3–14.6)	1982–1988	Bannister et al., 1991	Aerial survey

(Continued)

TABLE 4 Continued

Breeding Area/Stock	Growth rate (%/year)	Year/ Period	Source	Methodology
Shark Bay (~25°S–26°S)	10.15 ± 4.6 (95% CI)	1982–1994	Bannister and Hedley, 2001	Aerial survey
Shark Bay (~25°S–26°S)	12.9 (CV = 0.20)	1999–2008	Hedley et al., 2011	Aerial and land-based survey
North West Cape (21°S–22°S)	13 (95% CI = 5.6–18.1)	2000–2008	Salgado Kent et al., 2012	Aerial survey
South of 60°S, 60°E–120°E	14.4 (95% CI = 9.6–19.2)	1978–2004	Branch, 2011	Ship-based line-transect survey
Whole stock	2 (no CI provided)	2010–2015	IWC, 2016b	Estimated using previously published data
East coast of Australia (Breeding sub-tock E1)				
Hervey Bay (25°S)	13.4 (95% CI = 11.6–15.2)	1987–2007	Forestell et al., 2011	Photo-identification capture-recapture data
Point Lookout (27°26'S)	9.7 (95% CI = 6–13)	1981–1987	Paterson and Paterson, 1989	Land-based survey
Point Lookout (27°26'S)	14.4 (no CI provided)	1981–1987	Bryden et al., 1990	Land-based survey
Point Lookout (27°26'S)	11.7 (95% CI = 9.6–13.8)	1984–1992	Paterson et al., 1994	Land-based survey
Point Lookout (27°26'S)	12.3 (95% CI =10.1–14.4)	1981–1996	Bryden et al., 1996	Land-based survey
Point Lookout (27°26'S)	10.0 (95% CI =8.2–11.8)	1986–1993	Brown, 1996	Land-based survey
Point Lookout (27°26'S)	10.9 (95% CI = 10.2–11.6)	1984–1999	Paterson et al., 2001	Land-based survey
Point Lookout (27°26'S)	10.5 (95% CI = 10.0–11.1)	1999–2002	Paterson et al., 2004	Land-based survey
Point Lookout (27°26'S)	10.9 (95% CI = 10.5–11.4)	1984–2007	Noad et al., 2008	Land-based survey
Point Lookout (27°26'S)	10.6 ± 0.5 (95% CI)	1987–2004	Noad et al., 2011	Land-based survey
Point Lookout (27°26'S)	11.0 (95% CI = 10.6–11.3)	1984–2015	Noad et al., 2019	Land-based survey
Byron Bay (28°37'S)	11.0 (95% CI = 2.3–20.5)	1998–2004	Paton and Kniest, 2011	Land-based survey
South of 60°S, 120°E–170°W	13.7 (95% CI = 9.3–18.1)	1978–2004	Branch, 2011	Ship-based line-transect survey
Whole sub-stock	6.8 (no CI provided)	2010–2015	IWC, 2016b	Estimated using previously published data
Oceania (Breeding sub-stocks E2, E3, F1 and F2)				
South of 60°S, 170°W–110°W	1.6 (95% CI = -5.4–8.5)	1982–2001	Branch, 2011	Ship-based line-transect survey
West coast of South America (northern Peru to Costa Rica) (Breeding Stock G)				
South of 60°S, 110°W–50°W	4.6 (95% CI = -3.4–12.6)	1981–2000	Branch, 2011	Ship-based line-transect survey
Whole stock	3.4 (no CI provided)	2010–2015	IWC, 2016b	Projected using the backwards method of Butterworth and Punt (1995) using previously published data
Whole stock	5.07 (no CI provided)	1991–2018	Félix et al., 2021	Photo-identification capture-recapture data

(Continued)

TABLE 4 Continued

Breeding Area/Stock	Growth rate (%/year)	Year/ Period	Source	Methodology
Mixed				
Circumpolar	9.6 (95% CI = 5.8 –13.4)	1978–2004	Branch, 2011	Ship-based line-transect survey

Data are ordered in chronological sequence per Area, with estimates presented from northern to southern areas used by each Breeding Stock and in crescent order for sub-stocks.

south of Abrolhos Bank are also increasing, as it has been reported for the vicinities of Ilhabela Island (23°55'23.2"S, 45°26 53.7"W), São Paulo State, including records of calves and competitive groups, which can indicate the use of the area as a calving and mating site (Morete et al., 2022). There is also a recent discussion on the expansion of the range of the stock or recolonization of broader areas in northern Brazil (at about 5°04'49"S, 45°36'03"W), possibly reflecting the post-whaling recovery of the stock (Ristau et al., 2020).

From late austral spring, whales migrate through offshore areas to the Scotia Sea (Zerbini et al., 2006; Zerbini et al., 2011b) and northern Weddell Ridge (Bedriñana-Romano et al., 2022). Individuals tend to concentrate around the South Georgia and the South Sandwich Archipelago (Stevick et al., 2006; Zerbini et al., 2006; Engel et al., 2008; Horton et al., 2020), within IWC Management Area II. However, there are reports of individuals feeding as far west as 42°W (Stevick et al., 2006) and even matches between the coast of Brazil and the vicinity of Bouvet Island (3°E) (Engel and Martin, 2009). There is also an indication of a potential southerly expansion of the area being used during the 2010s, which can be a response to the increase of the SST during this period, with consequences to food availability for the stock (Bedriñana-Romano et al., 2022). New evidence on the permeability of the boundary between Brazilian and western South America stocks on the feeding grounds has been presented based on photo-identification analysis (Marcondes et al., 2021) and satellite tracking data (Reisinger et al., 2021), the latter also indicating an overlap in the feeding area used by the Southwestern and the Southeastern Atlantic Ocean stocks.

The migration paths of the Southwestern Atlantic Ocean stock are believed to be consistent over time, despite changes in environment conditions over the last decades (Zerbini et al., 2011b; Horton et al., 2020). Such conditions include those related to SST, productivity and currents, for instance, known to influence the species distribution and migration (e.g. Derville et al., 2019; Meynecke et al., 2021). The fact that the migration of this stock does not seem to be affected by changes in these conditions might indicate that humpback whale movement decisions include mechanistic responses to stable and predictable exogenous cues, including gravity (Horton et al., 2020).

Records of supplementary feeding

There is evidence of individuals from this stock feeding in low and mid-latitude waters. For example, the stomach content of a humpback whale stranded on the coast of southern Brazil (29° 45'38"S, 50°00'43"W) in 2002 contained a large amount of the aviu shrimp *Acetes americanus* (Decapoda: Sergestidae) and some Brachyura larvae, with preys assumed to have been eaten about 21 nautical miles from the stranding location (Danilewicz et al., 2009). The presence of humpback whales in this coastal area is unusual, as the migratory corridor of the stock that is located offshore in this area (Danilewicz et al., 2009). The distribution of *A. americanus* ranges from Guayanes Beach, Porto Rico to Rio Grande do Sul State, Brazil, associated with tropical waters (D'Incao and Martins, 2000). A second stranding in southern Brazil (27° 26'27.6"S, 48°22'26.4"W) in 2014 reinforced the use of the area for feeding, with the shrimp *Peisos petrunkevitchi* found in the stomach of the specimen (Bortolotto et al., 2016b). This shrimp species is distributed from Rio de Janeiro, Brazil (22°29'S) to Chubut Province, Argentina (~44°S) (D'Incao and Martins, 2000). Additional feeding evidence for mid-latitude regions come from reports by Siciliano et al. (2019) of plunge-diving feeding behaviour performed by a young individual and other feeding activity by adults of the species in association with gillnet fishery. More evidence has been reported by Pinto de sa Alves et al. (2009), based on observations made in August 2005 from an oil platform located at 19°35'02"S, 39°14'37"W of two likely juvenile individuals performing lunge-feeding behaviour to prey on small fishes of an unidentified species.

Stock structure

There is no evidence of stock sub-structure in the Southwestern Atlantic Ocean. Also, individuals from the stock breeding along the coast of Brazil are genetically significantly differentiated from those breeding on western and eastern coasts of Africa, which can be related to maternal site fidelity and ecological and oceanographic features in breeding and feeding grounds (Rosenbaum et al., 2009).

Stock trajectory

The number of individuals of the stock was estimated to have declined from about 27,000 (95% PI = 22,800–33,000) in 1830 to only 450 (95% PI = 200–1,400) in the mid-1950s (Zerbini et al., 2019). Although this is a substantial decrease in the stock size, studies have indicated no significant decrease in its genetic diversity when analysing samples collected between 1999 and 2007 (Cypriano-Souza et al., 2018).

The first abundance estimate after the end of whaling is for 1995, when 1,634 (90% CI = 1,379–1,887) individuals were estimated to be in the Abrolhos Bank (Kinas and Bethlem, 1998). A continuous recovery of the stock has been reported since then (Table 3), with an absolute estimate of 3,871 (95% PI = 2,795–5,542) individuals for 2000 in the same area (Freitas et al., 2004). For the main area used by the stock, between Natal, Rio Grande do Norte (~

5°S) and Cabo Frio, Rio de Janeiro (~ 23°S), estimates based on ship-based surveys were of 14,264 (CV = 0.084) individuals for 2008 and 20,389 (CV = 0.071) individuals for 2012 (Bortolotto et al., 2017). Using data from aerial surveys in the same area, abundances of 7,689 (95% PI = 6,585–8,931) individuals for 2008 and 12,123 (95% PI = 10,811–13,531) individuals in 2015 have been estimated (Pavanato et al., 2017). Annual ROIs of 11.08% (2008–2011) and of 1.17% (2011–2015) were estimated for this area, with the difference between periods likely being a result of the stabilization of the population growth towards 2015 (Pavanato et al., 2017). That can also the reason for the decrease in the ROI over a longer period of time, between 1995 and 1998, during which the stock grew at an annual increase of 7.4% (95% CI = 0.5–14.6%) (Ward et al., 2011). A more recent investigation based on combined data from breeding and feeding grounds resulted in the maximum intrinsic rate of increase estimate (r_{max}) ranging from 7.6 to 10.7% (95% CI) (Zerbini et al., 2019). Currently there is no ROI estimate from feeding ground data due to some limitations on data collection during the IWC IDCR/SOWER cruises as indicate by Leaper et al. (2008) and Branch (2011).

Zerbini et al. (2011a) estimated the size of this stock through modelling parameters using estimates from Andriolo et al. (2010) as an index of relative abundance (as the surveys did not cover the whole range of the breeding stock) and on whaling-derived data. They found it to be 6,705 (95% CI = 4,704–9,181) individuals in 2006, which was about 33% of the pre-exploitation levels. Following up, Zerbini et al. (2019) developed models based on results from Bortolotto et al. (2017) and estimated the stock size as 24,900 individuals in 2019 (95% PI = 22,400–27,000), indicating a recovery of approximately 93% of the pre-exploitation levels. Later on, Bortolotto et al. (2021) run an updated model and provided precise estimates for the stock in 2019, with 21,878 (95% CI = 21,377–22,285) individuals.

The recovery of the stock after whaling is also clear from data from the Scotia Sea, within the feeding ground of its stock (Table 3). For example, 2,493 (CV = 0.55) individuals were estimate in the area in 2000 (Hedley et al., 2001), and 24,543 (CV = 0.26; 95% CI = 14,863–40,528) individuals were estimated in 2019 (Baines et al., 2021), although the confidence interval of this last study is considerably large and consideration should be given to the mixing between stocks in the feeding grounds, which can influence such estimates.

Southeastern Atlantic Ocean (Breeding Stock B)

Breeding and feeding ground distribution and potential changes in migration

Individuals from this stock concentrate on the western coast of Africa (IWC, 2006). There is limited information on the overall breeding ground used by this stock (Collins et al., 2010). However, it is known that the sub-stock B1 uses the central West African coast and the northern islands of the Gulf of Guinea for breeding purposes, while the genetically distinct sub-stock B2 uses the west coast of South Africa as a feeding site and migratory corridor (IWC, 2006; Barendse et al., 2010; Barendse et al., 2011). The low numbers of calves and competitive groups observed and the lack of singing activity of sub-stock off Namibia suggests that the area is also not used as a breeding ground, but as a migratory route instead (Elwen et al., 2014). The Gulf of Guinea has generally been considered the northern limit of the distribution of the sub-stock B1, but mixing of individuals from Southern and Northern Hemispheres seem to occur in regions up north. That comes from sightings, satellite track data and strandings of individuals on the coast of Northwest Africa (up to 14°20'N) in January-February and August-November periods, most of them during the breeding season of the Southern Hemisphere humpback whales (Acevedo and Smultea, 1995; Van Waerebeek et al., 2001; Bamy et al., 2010; Van Waerebeek et al., 2013; Rosenbaum et al., 2014). The boundary between the two sub-stocks is not clear but proposed to be around 18°S in the region of the Angola-Benguela Front (IWC, 2011). Some individuals observed on the coast of South Africa have been observed in the areas associated with the Gabon sub-stock, but the breeding ground of the sub-stock feeding on the coast of South Africa remains unknown (IWC, 2011).

Areas such as that off São Tomé (0°20′10”N, 6°43′53”E), known to be used by the Gabon sub-stock from whaling data (Townsend, 1935), have been repopulated by individuals as shown from data collected in the area since 2002 (Carvalho et al., 2011). Considering the relatively high proportion of mother-calf pairs seen, and the limited number of competitive groups (a behaviour typically associated with mating) registered during fieldwork, the authors believe that the area is used primarily for calving and nursing or for resting.

The detection of non-song calls during austral spring in 2019 in the surroundings of Vema Seamount (31°38'S, 8°20'E), an offshore area off the southwestern coast of South Africa may indicate that the region is part of the migratory route of the stock (Ross-Marsh et al., 2022). However, it is recognized that further research is needed for a validation of these results.

Movements between Western South Africa and Gabon in austral spring and summer have been recorded, but whether individuals stay in the former year-round or use the area intermittently during a year is still not confirmed (e.g. Barendse et al., 2011). Genetic and photographic data indicated that individuals that were sighted in the Western South Africa with their mother have returned there as post-weaned, which seems to be evidence of a maternally derived use of the area for feeding (Barendse et al., 2013).

Although information on the connectivity between west African stock and feeding grounds is scarce (IWC, 2006; Leaper et al., 2008), it has been suggested that individuals feed between the longitudes of 20°W and 10°E, within the IWC Management Areas II and IIIW (IWC, 1998). Data from satellite tagged individuals also support the use of this latitudinal band and indicate the importance of the vicinities of Bouvet Island for individuals from the Gabon sub-stock (Rosenbaum et al., 2014). The low number of sightings in this latitudinal band to the south of 60°S during the IWC IDCR/SOWER cruises (Branch, 2011) can also indicate that the species feeds northerly in Areas II and III than in other Areas. However, the cruises did not cover areas north of 60°S to provide evidence on the presence of individuals in such area.

Records of supplementary feeding

Seasonal data from whaling stations located in Saldanha Bay, on the west coast of South Africa, show bimodal trends in the presence of humpback whales in the area (Best and Allison, 2010). That reflects the regular migration of the species. However, there are also data indicating the extended presence of the species in the area through the austral summer (Townsend, 1935), with multiple sources reporting on feeding activity as that time of the year, as detailed below. These are all considered evidence that some individuals suppress migration to feeding grounds in high-latitudes, staying in mid to low-latitude regions year-round.

The first evidence of feeding activity on the west coast of South Africa came from whaling records (Matthews, 1938) and records of stranded or entangled individuals with prey items in their stomachs (Findlay and Best, 1995), including mantis shrimp (*Pterygosquilla armata capensis*). Observation of lunge-feeding behaviour from Cape Columbine (32˚50'S, 17˚51'E) was reported for October–November 1993 at a relative short distance from shore (0.8 to 3.5 km) (Best et al., 1995). During that investigation, the analysis of faecal samples indicated the presence of an unidentified Euphausia species, which was believed to be *E. lucens* given the sample location. No dominant swimming direction among the observed individuals, and a relatively low mean swim speed (2.8 km h^{-1}), and a residency of up to 20 days in the area were reported (Best et al., 1995). The combination of these factors provided evidence of the use of the west coast of South Africa by non-migratory animals during spring.

Further observations of non-migratory behaviour and feeding activity on the west coast of South Africa were made during land and boat-based monitoring from Saldanha Bay in 2001–2007, with feeding activity on crustacean prey being reported (Barendse et al., 2010). Most groups performing feeding behaviour were composed of two or more individuals, but on some occasions (spring 2001, 2002, and 2007) there were loose aggregations of up to 20 individuals (Barendse et al., 2010). Photo-identification and genetic data collected between 1983 and 2008 have indicated that some 500 individuals might have used the area to feed during spring and summer (September-March) during the period (Barendse et al., 2011).

The occurrence of such loose aggregations seems to have grown over time, and the occurrence of the so called 'super-groups' (tightly aggregated groups of 20+ individuals) of humpback whales were recorded during cruises in October and November between Cape Point and St Helena Bay in 2011, 2014, 2015 (Findlay et al., 2017). The origin and destination of the individuals forming these aggregations is unknown. Evidence available so far from satellite tagging data indicate individuals migrating towards the Southern Ocean from early December (IWC, 2016a), but also a considerable spread of the individuals between 15°W and 35°E. It is reported that no calves were encountered within the super-groups, and the relatively small size of the animals encountered suggest a high incidence of non-breeding young animals.

Data on the occurrence of the super-groups have been recorded during cruises, aerial surveys, land and boat-based observations and as citizen-science data every season since 2011, showing consistency on the use of the area as a feeding ground over the last decade (e,g, Findlay et al., 2017; Seafari App, unpublished data). To better understand this behaviour, data from Findlay et al. (2017) was used in association with oceanographic data of the Southern Benguela System. A combination of relatively high chlorophyll-a concentration in the month before the observation of the whales, in association with the decrease in the water export from the area throughout October, seems to support prey availability in the area, composing a scenario favourable to the formation of the super-groups (Dey et al., 2021).

Although no feeding evidence has been reported so far off the coast of Namibia, the occurrence of individuals in the area through austral spring and summer is believed to be a result of the predictable prey availability given the upwelling of the Benguela Current in the region (Papastavrou and Van Waerebeek, 1997). Such evidence comes from catch data (Townsend, 1935) and other observations as described by Best and Shaughnessy (1979). At the same time, an overwinter stay in high latitude areas is also apparent, as the species has been recorded in acoustic monitoring (sounds likely produced by individuals breeding on western Africa given the area of occurrence) for 9 and 11 months over 2008 and 2009, respectively, in the Southern Ocean (70°31'S, 8°13'W) (Van Opzeeland et al., 2013).

Stock structure

Genetic data have indicated substantial (Pomilla et al., 2006; Rosenbaum et al., 2009) to subtle but statistically significant (Carvalho et al., 2014) differentiation between sub-stocks B1 and B2, and there is photographic evidence of interchange between them (Barendse et al., 2011). Potential reasons for the genetic differentiation are maternal site fidelity, the use of two migratory routes (one coastal and other offshore), and spatial or temporal segregation within the Gulf of Guinea breeding ground (Carvalho et al., 2014). More research is needed for the determination of the level of interchange between these stocks and for the identification of the breeding ground used by sub-stock B2. The southeastern Atlantic Ocean stock seems to have an interchange with southwestern Indian Ocean stock (e.g. Best et al., 1998; Rosenbaum et al., 2009; Kershaw et al., 2017), but further investigation is also necessary for the predominant level of connection to be determined.

Stock trajectory

To date, there is no abundance estimate for the whole range of the sub-stock using Namibian and western South African coasts, although some studies have provided numbers for localised areas within the breeding ground. For example, Collins et al. (2010) used two types of data from different locations used by B1 individuals off coastal Gabon, to provide abundance estimates. Numbers based on photographic data indicated 3,225 (CV = 0.39) individuals for 2001–2002, 3,332 (CV = 0.34) for 2002–2003 and 2,814 (CV = 0.28) for 2003–2004 for Iguela area (1°51'S, 9°20'E), and 3,301 (CV = 0.39) for 2005–2006 for Mayumba region (3°22'S, 10°38'E). The analysis of genotypic data resulted in estimates that ranged from 3,810 (CV = 0.34) for 2001–2002 to 9,301 (CV = 0.40) individuals in 2002–2003 for the Iguela area, and of 4,093 (CV = 0.30) individuals for 2005–2006 at Mayumba. The concurrent use of these two areas by the stock is however not well understood and the estimates presented can be biased (Collins et al., 2010).

A further study for the entire Gabon area - from Equatorial Guinea (1°N) to the Republic of Congo (4°S) - indicated that at least 1,259 individuals (95% PI = 710–2,333) utilised the area during the breeding season in 2002 (Strindberg et al., 2011). A projection of abundance at a rate of 2.9% per year between 2010 and 2015 indicated that about 12,973 (95% PI = 9,709–15,096) individuals constituted the sub-stock B1 in 2015 (IWC, 2016b).

Limited abundance information is also available for the sub-stock B2. Evidence suggests that the population size of this sub-stock is small, as 260 individuals were photo-identified on the west coast of South Africa with a relatively high between-year resighting rate (15.6%) (Barendse et al., 2006). That was further evident from the estimate based on photographic and genetic data, of about 500 individuals on the west coast of South Africa during spring and summer (September to March) each year from 1983 to 2008 (Barendse et al., 2011). A similar number, of 484 (95% PI = 138–860) individuals was projected for 2015 for this sub-stock (IWC, 2016b).

These estimates lead to a projected aggregated sum of 13,457 individuals was projected to constitute the stock in 2015 (IWC, 2016b). However, it is important to highlight that the extend of the breeding ground used by the sub-stock B1 is not fully known, and that there are still uncertainties about the use of such ground by individuals from sub-stock B2 (Collins et al., 2010). Therefore, estimates from this stock should be taken with caution.

Data on abundance and ROI estimates are available from IDCR/SOWER cruises from 1979 to 1997 in the Southern Ocean feeding ground between 20˚W and 10˚E. Data from CPIII (using data from seasons 1992–93 and 1996–97) indicate an estimate of about 595 (CV = 0.51) individuals, and the annual increase rate of 5.9% (-5.9–17.6%) (Branch, 2011).

East coast of Africa and western Indian Ocean (Breeding Stock C)

Breeding and feeding ground distribution and potential changes in migration

The overall breeding ground utilized by this stock comprises the eastern coast of Africa and the archipelagos of the Western Indian Ocean (IWC, 1998). The stock has been divided into four sub-stocks, namely C1 (which utilizes the coasts of South Africa, Mozambique and southern Tanzania), C2 (found around Mayotte Island, Comoros Islands and in the Mozambique Channel), C3 (Breeding on the coast of Madagascar, and shown to extend to northern African coastal mainland regions (Cerchio et al., 2016)), and C4 (using the Mascarene islands of Mauritius and Réunion) (IWC, 2006).

Information on the link between breeding and feeding grounds is limited, but the latter is considered to be between 10˚E and 60˚E in the IWC Management Area III (IWC, 2008). One of the few pieces of evidence of this connection come from the animals individually marked in high latitudes at about 54˚S, 10˚E and recaptured south of Madagascar during whaling activities, as part of the Discovery Investigations experiments (Rayner, 1940). Another comes from tagged individuals from the Madagascar sub-stock travelling to Crozet Island (Cerchio et al., 2016).

Based on the review of a combination of data sources, including catch, acoustic, at-sea, land-based and aerial monitoring, three main migratory routes have been proposed for the stock: (i) on the eastern African coast, from South Africa to central Mozambique; (ii) through Madagascar Ridge, with individuals migrating past north Madagascar; and (iii) along the Mozambique Channel (Best et al., 1998).

Although the extents of the feeding ground of western Africa and eastern Africa and western Indian Ocean may suggest that individuals from the west and east coast of Africa might spatially overlap in feeding areas, stable isotope analyses have provided evidence that such mixing does not necessarily happen. Values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios differed significantly between animals from Gabon and Mayotte, Mozambique Channel and Madagascar (Montanari et al., 2020). This can potentially represent a change in the migration patterns of the stocks, or at least of one of them, but this aspect deserves further investigation. Also, as detailed below, individuals from eastern Africa and western Indian Ocean can be mixing with individuals from Namibia and west coast of South Africa sub-stock to feed on the west coast of South Africa. Studies on photo-identification matches and movement tracking of both studies are highly needed for a better understanding of their movement and potential migration changes.

Records of supplementary feeding

There is limited information on supplementary feeding events beyond regular feeding grounds for this stock. Individuals may use the productive waters of the west coast of South Africa, joining individuals from western Africa to form the super-groups seen during spring and summer before continuing their migration to high latitude feeding grounds (Findlay et al., 2017). However, this is a topic that deserves further investigation for conclusions to be made.

Stock structure

The level of connectivity amongst these sub-stocks is variable (Leaper et al., 2008), and genetic studies have shown some level of differentiation between Mozambique and southern Tanzania and both Comoros Archipelago and Madagascar (IWC, 2006; Pomilla et al., 2006; Cerchio et al., 2008; Rosenbaum et al., 2009; Ersts et al., 2011; Kershaw et al., 2017). Photographic and satellite tracking data have also been used to investigate this aspect and suggest that although differentiated, there is an interchange between Comoros, Madagascar and Mascarene Islands sub-stocks, and little interchange between Mozambique and southern Tanzania and the other sub-stocks (Cerchio et al., 2008; Dulau-Drouot et al., 2011; Fossette et al., 2014; Dulau et al., 2017).

Stock trajectory

The recovery of the Mozambique and southern Tanzania sub-stock has been monitored using different methodologies. For example, shore-based surveys of its migration stream were conducted from Cape Vidal, South Africa, from 1988, have indicated a considerable recovery from whaling, as the stock abundance has been increasing over time. For 1990, the estimated abundance of the sub-stock was of 1,711 individuals (Findlay and Best, 1996), while more recent data resulted in estimates of 11,098 (2018) and 13,485 (2019) individuals (Wilkinson et al., 2023). Estimate of ROI are of 12.3% (95% CI = 4.7%–19.9%) (Findlay and Best, 2006), 11.5% (SE = 2.8) (Findlay et al., 2011a) for the period of 1988–2002, and 7.4–8.8% for the period of 1988–2019 (Wilkinson et al., 2023). While the point estimates might suggest a slowdown in the increasing rate of the sub-stock, the range of the estimates overlap and then might not differ significantly from a statistical perspective. In the breeding ground itself, abundance estimate by a line-transect survey along the central-southern coast in August-September 1991 between Quelimane (~18˚S) and Maputo (~26˚S) and from 18.3 to 183 m depths was of 1,954 (CV = 0.38) individuals for that year (Findlay et al., 1994). The authors also found higher densities of humpback whales in the southern region, between 33˚E and 35˚30'E, compared to the northern region. This can be a result of habitat preference considering the orientation of the coast, and wider continental shelf, with the result of the Mozambique Current flowing more offshore in the southern region, meaning individuals can find protection from strong currents closer inshore in this area (Findlay et al., 1994). A second survey in the region was performed during August-September 2003, between Cabo Inhaca (26°00'S) and to the north of Mozambique Island (14°26'S), which allowed the abundance estimation of 5,965 (CV = 0.17) individuals for that year (Findlay et al., 2004; Findlay et al., 2011b), with a ROI of 7.9% per annum for the period of 1991–2003 (Findlay et al., 2004). In both surveys, the high proportion of cow-calf pairs observed confirmed the importance of this region as a breeding area (Findlay et al., 1994; Findlay et al., 2011b). A projection based on a Bayesian multi-stock assessment, resulted in a median abundance estimate of 8,045 (95% PI = 6,756–9,656) individuals across the whole sub-stock C1 in 2015 (IWC, 2016b).

No abundance for the Comoros sub-stock has been estimated to date. For the Madagascar sub-stock, a line-in the southern and eastern portions of the breeding ground resulted in an abundance estimate of 2,532 individuals in 1994 (Best et al., 1996). Later on, Cerchio et al. (2009) estimated the number of individuals using Antongil Bay, northeastern Madagascar, during the 2000–2006 period as 7,406 and 8,325 based on photographic mark-recapture and genotypic surveys, respectively. These numbers were used to project the abundance of the whole sub-stock for 2015, which was 7,972 (95% PI = 6,409–10,228) individuals (IWC, 2016b).

To date, there is no abundance and ROI estimates representative of the stock based on data from the feeding grounds, although numbers are available from IDCR/SOWER cruises as indicated Tables 3, 4.

West coast of Australia (Breeding Stock D)

Breeding and feeding ground distribution and potential changes in migration

Individuals of this stock breed on the west coast of Australia, where the Kimberley coastal region is the main concentration between Camden Sound and Broome (15˚S–18˚S) (Jenner et al., 2001). To the south of this region are areas of intense monitoring of this stock, on the Ningaloo coast (~21°5'S), North West Cape (22˚45'S), and Shark Bay (25˚46'S) (400 km distant from each other), used during their migration. Also, there is evidence of North West Cape being used by females with calves over the last decade, which can represent an expansion of the calving area off the western Australian coast, as the species recovers from whaling (Irvine et al., 2018).

During the summer feeding season, individuals utilize the area between 80˚E and 110˚E, aligned with Antarctic Management Area IV (IWC, 2006), with the southern Kerguelen plateau being highlighted as a main area of concentration through satellite tagging data (Bestley et al., 2019). Such information is well aligned with whaling and Discovery mark-recapture data (Bestley et al., 2019). It has been postulated that some individuals probably also use Area IIIE, where they mix with eastern Australia sub-stock (Pastene et al., 2019).

Records of supplementary feeding

No records of supplementary feeding have been published so far for this stock, but there is evidence that individuals opportunistically do perform such behaviour. When investigating feeding habits of the stock using stable isotope analysis of baleen plates of individuals stranded between 1940 and 2015, Eisenmann et al. (2016) found that the feeding and fasting cycles followed a classical feeding model, with isotope values correlating with those of Antarctic krill. However, one of the individuals sampled showed supplementary discrete feeding in the temperate zone during migration reflected in relatively higher values of δ^{13}C and δ^{15}N in comparison to the other individuals (Eisenmann et al., 2016).

Stock structure

An interchange between individuals from western and eastern Australia sub-stocks has been initially indicated from Discovery Investigation mark-recapture data, based on whales that were marked in the Management Area V and recaptured in Area IV. Two of these ten individuals were also recaptured on the west coast of Australia (Chittleborough, 1965; Dawbin, 1966). Further evidence came from acoustic data suggesting shared songs by whales from western and eastern Australia (Noad et al., 2000). Genetic (Pastene et al., 2019) and photo-identification (Kaufman et al., 2011) evidence reinforce such mixing.

Stock trajectory

This is recognized to be the largest Southern Hemisphere stock of the species. Estimates have indicated a total of 26,100 (95% CI = 20,152–33,272) individuals in the North West Cape area in 2008 using aerial survey data (Salgado Kent et al., 2012), and some 21,750 individuals (95% CI = 17,550–43,000) migrating northward off Shark Bay in the same year from a combination of aerial survey and land-based data (Hedley et al., 2011). Abundance modelling projection of these numbers resulted in projected estimates of 20,337 (95% PI = 18,415–24,918) whales for 2015 for the whole eastern Australian stock (IWC, 2016b).

Previous estimates for Shark Bay from aerial survey data point to- 8,207–13,640 individuals in 1999 (Bannister and Hedley, 2001) and 10,300 (95% CI = 6,700–24,500) individuals in 2005 (Paxton et al., 2011). It is important to note that the estimate from Paxton et al. (2011) has a broader uncertainty (which can be seen from the confidence interval) and is considered conservative as the duration of the survey did not cover the whole breeding season of the species in the study area.

The trend for the North West Cape area shows a relatively high annual ROI (13%, 95% CI = 5.6–18.1%) between 2000 and 2008 (Salgado Kent et al., 2012). That is similar to the ROI observed for Shark Bay – 12.9% (CV = 0.20) – estimated based on the comparison of data from 2008 and those collected in a 1999 survey in the same area (Hedley et al., 2011). Such a relatively high ROI can indicate that the easter Australian stock is increasing at its maximum capacity over the last decade (Jenner et al., 2019). Alternatively, it can arise from sources of error in the abundance estimates for both Shark Bay and North West Cape, including limited accuracy in $g(0)$ estimates, and in precision on the migration direction of the individuals in immigration models when considering data from aerial surveys (Jenner et al., 2019).

Abundance across the feeding ground was estimated to be of 17,959 (CV = 0.17) individuals from CPIII (1991/92–2003/04), with a ROI of 14.4% (95% CI = 9.6–19.2%) per year for the 1978–2004 period (Branch, 2011).

East coast of Australia (Breeding sub-stock E1)

Breeding and feeding ground distribution and potential changes in migration

The sub-stock corresponds to whales breeding in coastal waters off eastern Australia (sub-stock E1) Hervey Bay is considered an important stopover for individuals of the stock coming from the Great Barrier Reef travelling towards the south to Antarctic waters (Forestell et al., 2011), especially for mother-calf pairs (Franklin et al., 2018; McCulloch et al., 2021). The Gold Coast Bay, part of the migratory corridor of eastern Australia sub-stock, has recently been indicated to also potentially be a calving area, as 74 newborns were observed in the area between 2013 and 2016 (Torre-Williams et al., 2019).

The coast of New Zealand is used by individuals of the eastern Australia stock during their migration between breeding and feeding grounds, and there is also evidence of the connectivity with individuals from New Caledonia, Fiji and Tonga has been found from photo-identification, acoustic, satellite tag and genetic data (Chittleborough, 1959; Dawbin, 1964; Franklin et al., 2014; Andrews-Goff et al., 2018; Steel et al., 2018; Warren et al., 2020). Data on the occurrence of the species on the east coast of New Zealand between 1970 and 1999 were compiled (Gibbs and Childerhouse, 2000). Over this 30-year period, only 157 sighting events were made, especially from Kaikoura and Cook Strait with an increase on the numbers over the last four years of the study period (Gibbs and Childerhouse, 2000). Data from annual surveys in the Cook Strait have indicated an increase of 13% (95% CI = 4.9%–21.7%) from 2005 to 2015, which seems to also indicate an influx of individuals from east Australia to this area (Gibbs et al., 2018). Recent acoustic data from 2016 have also supported the use of this migratory corridor between June and August, with song matches with New Caledonia breeding ground (Warren et al., 2020).

Feeding grounds used by the eastern Australian stock have been postulated to be within the longitudes 120˚E and 170˚W, corresponding to the IWC Management Areas IVE, V, and VIW (IWC, 2008). Within this broad area, some specific locations have been identified as important feeding locations for the sub-stock. For example, the Balleny Islands have been indicated to be important for eastern Australia sub-stock through photo-identification data analysis (Franklin et al., 2012). Also, an individual from eastern Australia in Area I during the feeding season, performing one of the longest mammalian migrations ever registered (Acevedo et al., 2022). Another finding relates one individual from the eastern Australia sub-stock to the west of the majority of the stock, widely using Management Area IV during summer (Andrews-Goff et al., 2018). Satellite tracking data of Oceania stock individuals tagged off Raoul Island (29°16′S), Kermadec Islands, New Zealand have shown that females with calves utilized the Ross Sea region during the feeding season, while most adults without calves migrated further east to the Amundsen and Bellingshausen Seas region (Riekkola et al., 2018). Findings indicating a close to year-round presence of the species in the feeding grounds can represent further evidence of possible suppression of migration or adoption of partial migration by some individuals in particular years.

Records of supplementary feeding

Supplementary feeding for this sub-stock was first raised by Dawbin (1956) on the coast of New Zealand, given the presence of prey items such as the coastal krill *Nyctiphanes australis* in the stomach of individuals killed during whaling operations. *N. australis* was also sampled in proximity to two humpback whales feeding on the coast of Tasmania, near Cape Bougainville (~42° 30’S) in November 1996 (Gill et al., 1998). That was after another sighting of individuals feeding on the coast of Tasmania off Blackmans Bay (43°S) in October of the same year (Gill et al., 1998).

Additional evidence of low-latitude feeding occurred some decades later, from the observation of an adult humpback whale in apparent feeding behaviour off Cape Moreton, Queensland, during austral summer in 2004 (Stockin and Burgess, 2005). During this event, observed during a whale-watching trip in the region, the whale was seen expanding and contracting the ventral pleats, and having the mouth partially opened close to the surface, with baitfish (likely sardines *Sardinops sagax*, although not confirmed) seen close to it.

Further south, evidence on feeding in the proximities of Narooma (36°5’S) and Eden (37°16’S), from late September to early November in 2002, 2003, and 2005, also during whale-watching activities, have been described by Stamation et al. (2007). Upwelling does occur in the area (Dawbin, 1956), enhancing marine productivity in the area and possibly contributing to the adoption of feeding activities by the whales of the eastern Australia sub-stock.

The feeding behaviour off Eden has been investigated with the use of digital acoustic recording tagging (DTAGs) of nine individuals between September and October 2011 and 2012 (Owen et al., 2015; Owen et al., 2017). Individuals performed lunge feeding at higher rates when preying upon krill than on fish items. The contribution of energy acquisition from feeding in the area seems significant, especially when individuals prey on N. *australis*, as they were estimated to then consume 1.2–3.4 times their energy requirements (Owen et al., 2017). A lower contribution comes from feeding on fish items, which likely included the jack mackerel *Trachurus declivis*, pilchards *Sardinops neopilchardus*, and redbait *Emmelichthy nitidus*, as they were observed on the surface during the 2012 surveys. Despite such a significant contribution of this low-latitude feeding to the energetic intake of the individuals, it is still not clear if the behaviour is opportunistic or an important aspect of the migration ecology of the sub-stock (Owen et al., 2017).

More recently, the bubble-netting feeding behaviour by humpback whales has been photographed off the east coast of Australia, adopted by individuals of the species feeding between Narooma and Eden and off the coast off Tasmania in September – October 2020 (Pirotta et al., 2021). It is suggested that this represents the second record of a super-group feeding in the Southern Hemisphere, the first being in South Africa. A total of six super-groups were observed, with sizes ranging from 20 to 90 individuals in each (Pirotta et al., 2021). Environmental conditions such as SST and nutrients availability are suggested to might have created a favourable scenario for the increase of the productivity in the area, then leading to large aggregations of individuals for feeding.

Stock structure

There are levels of interchange amongst individuals from the east coast of Australia and the stock using the west coast of Australia (Kaufman et al., 2011).

Stock trajectory

Since 1981, several shore-based survey operations have monitored the relative abundance of east Australian sub-stock (e.g. Paterson and Paterson, 1989; Bryden et al., 1990; Paterson et al., 1994; Paterson et al., 2001; Paterson et al., 2004). The sub-stock abundance was estimated to be 1,107 in 1987, having grown 9.7% (95% CI = 6–13%) yearly between 1981 and 1987 (Paterson and Paterson, 1989). By 1992, the abundance estimate of this stock was of 1,900 (± 250) individuals, growing at a rate of about 11.7% (95% CI = 9.6–13.8%) per year during the 1983-1992 period (Paterson et al., 1994). This is similar to the estimate of 2,099 (1,759–2,433) individuals for 1993 and the ROI of 10.0% (95% CI = 8.2–11.8%) per year between 1986 and 1993 (Brown, 1996) and of 12.3% (95% CI = 10.1–14.4%) per year between 1981 and 1996 (Bryden et al., 1996). By 1999, the abundance was estimated at 3,599 (95% CI = 3,162–4,036), with a ROI of 10.9% (95% CI = 10.2–11.6%) per year between 1987 and 1999 (Paterson et al., 2001), and the numbers increased to about 4,860 individuals by 2002 (Paterson et al., 2004). Later on, an absolute abundance of 9,683 (95% CI = 8,556–10,959) individuals was estimated for 2007 from land-based monitoring in Point Lookout, with a ROI of around 10.9% (95% CI = 10.5–11.4%) per year from 1984 to 2007 (Noad et al., 2008). This is similar to the estimate based on photo-identification data from Byron Bay (northern migration) and Hervey Bay and Ballina (southern migration) of 7,041 (95% CI = 4,075–10,008) individuals for 2005 (Paton et al., 2011).

Based on these data, the abundance of the eastern Australia sub-stock was projected to be of 19,614 (95% PI = 17,664–21,454) individuals in 2015 (IWC, 2016b). Another estimate for 2015 indicates 24,545 (95% CI = 21,631–27,851) individuals (Point Lookout), with a ROI of 11.0% (95% CI = 10.6–11.3%) per year across the period of 1984-2015 (Noad et al., 2019). In this study, the authors state that such estimates indicate the sub-stock can be considered closely recovered from the whaling, but still growing at a relatively high rate. Noad et al. (2019) also modelled future abundance for the sub-stock, and indicate two possible scenarios: (i) continuous growth to an abundance of at least 40,000 individuals, which would represent a new carrying capacity and mean that by 2015 it was actually 62% recovered, or (ii) grow to a peak of about 36,000 to 52,000 individuals at some point between 2021 and 2026, and then potentially face variations over the next decade from there.

On the feeding ground, data from the most recent IDCR/SOWER cruises (CPIII, 1998–2004) indicated an abundance estimate of 13,300 (CV = 0.20) individuals for the whole stock, and a ROI of 13.7% (95% CI = 9.3–18.1%) per year for the 1987–2007 period (Branch, 2011). Although the confidence interval indicates some uncertainty in this estimate, it is believed that the surveys covered most of the stock associated feeding ground.

Oceania (Breeding sub-stocks E2, E3, F1 and F2)

Breeding and feeding ground distribution and potential changes in migration

Here we refer to sub-stock breeding in New Caledonia (sub-stock E2), Fiji and Tonga (sub-stock E3), Cook Islands (sub-stock F1) and French Polynesia (sub-stock F2) (IWC, 2007). There is considerably less information on the different aspects of these sub-stocks in comparison to the others (Tables 2–4). For New Caledonia sub-stock, the use of offshore areas is evident from satellite tag data, with seamounts seemingly important in the distribution of the individuals both during breeding and migration (Garrigue et al., 2015; Derville et al., 2020). For Tonga sub-stock, there seems to be a lack in the description of the habitat use of the species, although it is known that nearshore areas are important, attracting the whale-watching and swim-with-whale tourism industries (e.g. Schaffar and Garrigue, 2007; O'Connor et al., 2009). It has been suggested that the distribution of the French Polynesia sub-stock is expanding as a response to the increase in number or changing distribution in response to environmental changes. That comes from sightings of the species off Pitcairn Islands (25°04'S) during land-based surveys in 2007, with individuals apparently using the area for breeding and calving (Horswill and Jackson, 2012). Later on, the use of the area was confirmed, specifically off Henderson Island, from data collected in 2014 (Irving et al., 2018). This area is in the Central South Pacific, and it is indicated that individuals might be to its sub-stock, migrating from the Southern Ocean through Pitcairn to French Polynesia (Horswill and Jackson, 2012). However, further investigations are needed to confirm if there is a connection between the individuals sighted off Pitcairn and any of the currently recognized stocks. Data from dedicated surveys from areas of the Oceania breeding ground between 1996-2017 suggest the distribution of the individuals using it to be influenced by topography, with a preference for shallowest waters areas close to coast or in lagoons or around seamounts in offshore regions (Derville et al., 2019). In addition, a plasticity in its distribution is indicated as well as the potential use of new habitats as the regular ones become unsuitable due to rising sea temperatures (to greater than 28°C) by the end of the 21st century (Derville et al., 2019).

The migration routes are also poorly understood, but the feeding ground of this stock is suggested to be associated with the area between longitudes 170˚W and 110˚W, within Area VI (IWC, 2004; Hauser et al., 2010). For the Cook Islands sub-stock, there is direct evidence of a connection to Area VI E, based on the migration of a satellite-tagged individual (Hauser et al., 2010). In addition, there is also evidence of the connection of an individual from Tonga sub-stock with Area I (Robbins et al., 2011).

Stock structure

It is worth reminding that there is the Oceania stock is comprised by different sub-stocks from western and south central Pacific considering the level of interchange amongst them (e.g. Olavarría et al., 2007; Clapham et al., 2008; Hauser et al., 2010; Garrigue et al., 2011; Jackson et al., 2012; Pastene et al., 2013; Franklin et al., 2014; Derville et al., 2020).

Stock trajectory

There is limited information on abundance estimates for these sub-stocks, but some studies are available. A preliminary mark-recapture analysis of photo-identification data by the South Pacific Whale Research Consortium provided estimates for the period of 1999–2004 of 472 (CV = 0.18) for New Caledonia sub-stock and 2,311 (CV = 0.22) individuals for Tonga sub-stock (SPWRC et al., 2006). There is additional information on abundance for the Tonga sub-stock based on photo-identification mark-recapture data, indicating that some 1,057 (CV = 0.24) individuals utilized the area of French Polynesia between 1999 and 2004 (Poole, 2006). The Oceania stock as a whole was estimated to be of 4,329 (95% CI = 3,345–5,313) individuals in 2005, based on photo-identification and microsatellite genotype data (Constantine et al., 2012), and predicted to be of about 6,404 (95% PI = 5,491–7,595) individuals in 2015, considering a ROI of 8.2% per year during the 2010-2015 period (IWC, 2016b). These numbers indicate that BSO is the least abundant stock in the Southern Hemisphere.

The only estimated ROI for BSF comes from ICDR/SOWER cruise data and indicates an annual increase of 1.6% (95% CI = -5.4%–8.5%) for the 1982-2001 period (Branch, 2011). Considering the broad confidence interval, there is limited evidence for an actual increase (Leaper et al., 2008). The cruises in the Southern Ocean are also the source of the abundance estimate for BSF feeding grounds of 3,852 (CV = 0.22) individuals (Branch, 2011).

West coast of South America (northern Peru to Costa Rica) (Breeding Stock G)

Breeding and feeding ground distribution and potential changes in migration

The breeding area for this stock is located on the east coast of Central and South America, including the coasts of Peru, Ecuador, Colombia, Panama, and Costa Rica (Flórez-González, 1991; Clapham and Mead, 1999; Félix and Haase, 2001; Stevick et al., 2004; Pacheco et al., 2009; Guidino et al., 2014; Acevedo et al., 2017; Albertson et al., 2018). Although the breeding ground encompasses a relatively large area, there is not enough current evidence for its sub-division into sub-stocks.

Possible extension of the breeding ground has also been reported, e.g. the presence of the calves in northern Peru potentially indicating the use of new areas with suitable environmental conditions (Guidino et al., 2014), as it increases in number (e.g. Félix et al., 2021). in the use of the Galapagos Archipelago (1°S, 91°W), with evidence of a genetic connection to western South America stock (Félix et al., 2011a), can also be an example of the post-whaling expansion of the area used by the species.

Individuals breeding between the Peruvian and Colombian coasts have been shown to feed in the Southern Ocean at longitudes between 110°W–50°W, mostly in the vicinities of the Western Antarctic Peninsula (e.g. Mackintosh, 1942; Stone et al., 1990; IWC, 2007; Rasmussen et al., 2007; Caballero et al., 2021). A second feeding ground has been identified in the Fuegian Archipelago, in the Magellan Strait (~53°30'S), with connection to individuals breeding on the coast of Panama (Acevedo et al., 2017). Magellan Strait is believed to have been repopulated as the stock recovers from whaling. Although there are historical records of whales using the area for the last six centuries (Gibbons et al., 2003 and references therein), there is evidence of the increase in the use of the area over the last few decades. It is indicated that individuals utilising this area generally do not migrate to the Antarctic Peninsula (Acevedo et al., 2017), although a few photo-identification matches have been found between this area and the Antarctic Peninsula (Acevedo et al., 2021). A third feeding location has been identified in the Gulf of Corcovado, Chilean Patagonia (41–44°S) (Hucke-Gaete et al., 2006), where the number of individuals encountered each year has been increasing since 2000 (Hucke-Gaete et al., 2013). Little is known about the breeding area of whales utilising this region.

There is also evidence that some individuals can suppress migration. In some cases, both evidence of feeding and breeding behaviour was seen in the same area, as in Chile, a feeding area beyond the regular feeding grounds (e.g. Hucke-Gaete et al., 2013), and there are also records of feeding observations were made during austral winter in the Magellan Strait, Chile (Gibbons et al., 2003), or individuals appeared to stay in the breeding ground year-round (e.g. Acevedo et al., 2017).

Although the connection of breeding and feeding grounds of this stock is well known (Stevick et al., 2004), the migratory corridors used by individuals remained unknown until recently. Satellite telemetry has been used for the investigation of this aspect, with the tagging of 16 whales in Antarctic waters between 2012 and 2017 (Modest et al., 2021). Results show two points of convergence of the migratory routes, one from the southern portion of Chile, and another off Peru, towards Colombia and Ecuador and into Panama. The authors indicate that such information provides a baseline for future studies to investigate the potential impacts of climate change and other stressors on the migration of humpback whales breeding on the east coast of South America.

Records of supplementary feeding

The stock uses two feeding grounds in mid latitudes. Gibbons et al. (2003) provided evidence of the post-whaling use of the Magellan Strait (in the area between 48°50'S and 54°18'S) based on the record of 128 individuals in the area between December and June from 1997-2001, including the performance of lunge and 'flick' feeding behaviour. Another investigation on feeding behaviour in the area has demonstrated the adoption of bubble-net feeding, some of which were single straight-line bubble curtains (Acevedo et al., 2011). Gibbons et al. (2003) have indicated the presence of schooling fish as Fuegian sprat *Sprattus fueguensis* as potential prey, and more recently stable isotope analysis confirmed these to be the main food item of humpback whale individuals in the area (Haro et al., 2016), especially of adults in comparison with juveniles (Haro et al., 2021).

The second additional feeding ground of the stock is recognized to be also in Chilean waters, in the northern Chilean Patagonia (mostly between 41.5°S and 44°S), where aerial, land, and boat-based surveys performed between 2000 and 2010 (Hucke-Gaete et al., 2013) provided data on feeding activities in the area, mainly from 2006 onwards. Observations of group lunge feeding behaviour during boat-based surveys with concurrent prey sampling allowed the identification of krill *Euphausia valentinii* and lobster krill *Munida* spp. (*M. subrugosa/gregaria*).

In addition to these feeding grounds in mid latitude regions along the coast of Chile, feeding behaviour has been observed in low latitudes in the Southeast Pacific Ocean, including lunge and trap feeding behaviour by two humpback whales in Mejillones Bay (~23°S), northern Chile, in March-April 2019, preying upon Peruvian anchovy (*Engraulis ringens*) (García-Cegarra et al., 2021). One of the two individuals was resighted feeding in the same area in April 2020. In addition, two humpback whales are reported to have performed lunge feeding behaviour in June 2005 off Machalilla National Park (1°18'S), Ecuador, and feacal matter was observed on the surface on different occasions in 2008, 2011, 2016 and 2017. One of the individuals seen in Mejillones Bay in 2019 was also observed feeding on krill *Euphausia* sp. in the Gulf of Corcovado (42°S), Chile, in 2017, and further resighted at Machalilla National Park in 2020 feeding on *E. ringens*. García-Cegarra et al. (2021) state that the feeding activities can be a result of a higher competition for food in high latitudes given the increase in the stock's abundance, changes in prey distribution, or more intense research efforts in regions that were previously poorly investigated.

Stock structure

To date, there is no evidence of stock division. Genetic data from the stock were found to be significantly different from other stocks, which can be related to a high site fidelity to the Antarctic Peninsula feeding ground (Amaral et al., 2016).

Stock trajectory

Humpback whales have been studied off the coast of Ecuador since 1991 (e.g. Félix et al., 2011a; Félix et al., 2011b). The abundance of the species visiting the area has been estimated to be of 6,504 (CV = 0.21; 95% PI = 4,270–9,907) individuals for 2006, based on photo-identification data collected from 1991 to 2006 (Félix et al., 2011a).

In an investigation around Las Perlas Archipelago, Panama, a stock size of some 1,041 (95% CI = 664–1,546) adults was estimated to have utilized the area across the 2003-2009 period (Guzman et al., 2015). On the coast of Colombia, the Gorgona Natural Park is an important area for breeding and nursing of humpback whales (Ávila et al., 2020). The analysis of a long-term dataset (1988-2018) revealed that the residency of the species in the area during the breeding season has extended over time, with individuals arriving from May and staying until December (Ávila et al., 2020). To date, there is no abundance estimate specific to this area.

An estimated abundance projection of 9,687 (95% PI = 8,520–10,202) individuals was made for 2015 (IWC, 2016b). An updated capture-recapture estimate using data from both feeding and breeding grounds across a 27-years period (1991–2018) indicated an abundance of 11,784 (SE = 266) individuals in 2018 and an estimated ROI of 5.07% (no CI provided) per year (Félix et al., 2021). In comparison to the ROI of other stocks, this increased rate is relatively low, which is attributed to different factors, including potential past overestimates and mixing of different stocks within the feeding grounds (Félix et al., 2021).

Based on the IDCR/SOWER cruises, an abundance of 3,337 (CV = 0.21) individuals was estimated for the Antarctic feeding ground (110°W–50°W) for 1999/2000 season, a number that increased about 4.6% (95% PI = -3.4–12.6%) per year over the period between 1981 and 2000 (Branch, 2011). Also, this feeding ground showed a very high pregnancy rate from sampled females, of 63.5% (95% CI = 57.14–69.57%), of which a considerable number (54.5%) were females with calves, indicating short post-partum periods as part of the reproductive cycles (Pallin et al., 2018). It is stated that such high pregnancy rates are not consistent with the current ROI of this BS, and that environmental factors may be playing a role in its demography. The correlation between the number of calves observed in the breeding area and the density of krill in the feeding area of the stock in the previous summer (Seyboth et al., 2021) can be an indication of this role. This is because food availability for sexually mature individuals is essential for them to be able to breed successfully and sustain a pregnancy (e.g. Reeves et al., 2001).

Circumpolar data

The IWC developed the International Decade of Cetacean Research (IDCR) and the Southern Ocean Whale Ecosystem Research (SOWER) programmes with the main aim of estimating minke whale abundance in the Southern Ocean (south of 60°S). However, sightings of all baleen whales were recorded during the cruises, between 1978 and 2004, so data have been used for other purposes (e.g. Branch and Butterworth, 2001). The initiative completed three circumpolar surveys (CPs) in 1978/79–1983/84 (CPI), 1985/86–1990/91 (CPII), and 1991/92–2003/04 (CPIII) (Branch, 2011).

Abundance estimates for the approximate mid-point of each CV were 7,100 (CV = 0.36) for 1980/81; 10,200 (CV = 0.30) for 1987/88; and 41,500 (CV = 0.11) for 1997/98, with an average ROI of 9.6% (95% CI = 5.8–13.4%) per year (Branch, 2011). The author states that these abundances are underestimates considering that some surveys did not cover the entire feeding grounds of the stocks. In the Southern Ocean, the area of higher encounter rates of humpback whales is in the Western Antarctic Peninsula (Kasamatsu et al., 1996), which can be related to the considerable amount of prey availability in the area, as indicated by the high density of krill in the area (e.g. Murphy et al., 2017).

Discussion

Overview of the estimates found and comparisons among breeding stocks and sub-stocks

This review highlights the successful recovery of humpback whale stocks in the Southern Hemisphere after being subjected to decades of human exploitation. The level of recovery, however, varies amongst different stocks. Most recent data suggest western Australian stock to be the most abundant, followed, in decreasing order, by the stocks and sub-stocks related to the east coast of South America, western Australia, Mozambique and southern Tanzania, west coast of South America, and Madagascar, Gabon, and French Polynesia. The simple sum of latest mean estimated and projected numbers from each sub-stock result in an abundance of around 114,422 individuals (the numbers considered are highlighted in bold in Table 3). Considering the estimate of around 140,000 whales individuals in the early 1900s (IWC, 2016b), current estimates of abundance suggest that Southern Hemisphere humpback whales recovered to nearly 80% of their abundance prior to the onset of modern whaling operations. Based on most recent growth estimates, the stock related to the east coast of South America ($r_{\max}$ = 7.6-10.7%) and Mozambique and southern Tanzania sub-stock (ROI = 7.4-8.8%) seem to be the ones growing at highest rates in comparison to other stocks and sub-stocks. These are however just broad evaluations of the most recent estimates, and we emphasize that in-dep analyses are needed for estimates and comparisons to be conclusive. Therefore, it seems to be important that a possible In-Depth Assessment for humpback whales in the Southern Hemisphere takes into consideration the updated estimates and the influence of modern threats (as climate change, ship-strikes, entanglements, underwater noise, and pollution – please see the Introduction section).

Lacks and limitations of the estimates

Although information on abundance, ROI, and distribution is available for all Southern Hemisphere humpback whale stocks, it can be very limited and not available at the sub-stock level in some cases. Since the last IWC Comprehensive Assessment (IWC, 2016a), little progress has been made to fill important gaps for most of the sub-stocks. The need for new estimates of abundance and trends for some sub-stocks (Namibia and west coast of South Africa, Comoros Archipelago, Madagascar, New Caledonia, Cook Islands, and French Polynesia) as indicated in such assessment remains relevant to date. Gathering information for the evaluation of both the absolute abundance and the growth rate of each sub-stock will require a collaborative approach and would be ideally based on the use of the same methodology and protocol for data collection so the numbers are highly comparable and the growth estimates more precise. Estimates based on data from feeding grounds are also limited, and as indicated throughout the text, some from IDCR/SOWER cruises should not be considered representative of the whole stock they refer to considering the area covered during the cruises (Miyashita et al., 1995; Ensor et al., 2006).

It is also worth mentioning that some of the growth rate estimates presented in Table 4 for different stocks are not statistically different even though the point estimate is different. It is also important to remind that while most of the values refer to ROIs, one of them, as highlighted on the table, refers to the maximum intrinsic rate of increase ($r_{\max}$), which needs to be taken in consideration when evaluating the values. Also, the data for their estimation were not necessarily collected using the same protocol and then some comparison should be made with caution. However, they are informative, and we believe they contribute to the knowledge of the stocks trends and therefore are considering such information during the review of the publications.

The methodology adopted for data collection for abundance estimation can impact on the results found (e.g. Cerchio et al., 2008; Paxton et al., 2011). Aerial surveys, with the use of distance sampling methodology (Buckland et al., 2001), have been indicated as one of the most effective methods for the estimation of population abundance and growth, once adequate protocols are established (Andriolo et al., 2006b). In some cases, however, as for the investigation of migration of the western Australia stock using land-based and aerial surveys (Jenner et al., 2019), the combination of methodologies for data collection can increase confidence in the results. Therefore, it seems important that the method applied consider the characteristics of each stock and the resources available for estimating their size and trends. Furthermore, the importance of standardization of data collection in a specific area over time so changes can be properly evaluated has been highlighted by Andriolo et al. (2006b).

Working on the standardization and improving the quality of citizen science data (e.g. Downs et al., 2021) is also important. Although coming with limitations and biases, this type of data has been increasingly used in marine science (e.g. Kelly et al., 2020) and can be highly valuable to provide updated information from different humpback whale stocks and sub-stocks (e.g. Tonachella et al., 2012;

Bruce et al., 2014; Lodi and Tardin, 2018; Pirotta et al., 2020). Initiatives to connect the public with research groups, and to increase the use of established platforms such as Happywhale (Cheeseman et al., 2022) are encouraged.

Factors potentially influencing estimates

The interchange among breeding stocks and sub-stocks is another relevant factor for the investigation of stock parameters such as abundance and ROI and ignoring this aspect can lead to a misinterpretation of the recovery of stocks (Amaral et al., 2016). There are different levels of interchange between stocks and sub-stocks, and they tend to be higher in the feeding grounds (e.g. Butterworth and Johnston, 2009; Pastene et al., 2013; Stevick et al., 2013; Rosenbaum et al., 2017; Félix et al., 2020b; Marcondes et al., 2021). It is also worth noting that the increase in the number of individuals as the stocks recover from the whaling era is expected to lead to an increase in the mixing between stocks in feeding grounds, suggesting that feeding ground boundaries between stocks might need to be revised (Marcondes et al., 2021), with potential implications to catch allocation. Although in a lesser extent, the connection between breeding sub-stocks in breeding grounds and the different residency patterns of the individuals in such areas should be considered for the development of management and conservation actions in both regional and local scales (Dulau et al., 2017).

A potential factor contributing for relatively high ROI estimates can be an increased reproductive capacity of the individuals (e.g. through a shorter calving interval), as observed for the Oceania stock (Chero et al., 2020). It is important to note that some of the ROI estimates presented are higher than the maximum biologically plausible rate estimated for the species (11.8% per year, Zerbini et al., 2010), which can be a result of measurement errors and/or faulty sampling methods. For the Oceania stock, immigration amongst sub-stocks seems to be an important aspect contributing to relatively high estimates observed and for the relatively low rates estimated for areas that are known to have a substantial abundance before whaling (Clapham and Zerbini, 2015). Also, some abundance and ROI estimates presented have considerable large confidence intervals, and in some cases the ROI range includes the value of 11.8% per annum, so can also be considered with caution as it then falls in values not considered biologically plausible for the species and can indicate limitations in data collection and/or analysis. That also adds uncertainty to some numbers, and the continuity of data collection and investigation of potential causes for the large confidence interval are necessary for a more precise investigation of the status of the species in some areas.

How the recovery of the species might impact prey populations is an additional aspect to be addressed, especially considering the variabilities in biomass that the main prey item of the species is already subjected to under the current climate change scenario (e.g. Atkinson et al., 2019; Veytia et al., 2020; Sylvester et al., 2021). That can influence not just the relationship between humpback whales and krill, but also the interaction of humpback whale and other species that rely on krill as their main prey item. For example, resource partitioning of humpback and minke (Friedlaender et al., 2006b) and fin (Herr et al., 2016) whales has been observed in the Western Antarctic Peninsula, and can potentially be affected as whale species recover from whaling and krill development tend to decrease over time given environmental changes (e.g. Atkinson et al., 2004, Atkinson et al., 2019). Supplementary feeding beyond the Southern Ocean has been reported for baleen whales for a long time (e.g. Kawamura, 1975) but it can potentially increase with the changes being observed in the Southern Ocean and the consequences for krill availability, so the compilation of the records so far for humpback whales might serve as a baseline for comparison in the future. The formation of feeding aggregations (super-groups) in feeding grounds and/or migratory routes in lower latitudes, as on the west coast of South Africa (Findlay et al., 2017) and off Tasmania (Pirotta et al., 2021), might also be a response of some stocks to environmental changes. On this topic, it is worth indicating that information coming from stranded animals should be taken with caution as those animals might not be healthy and not performing their expected behaviour, then providing misleading information.

Another point to be considered in future studies is how the different threats to the species will affect current numbers and possible interaction between stocks, as well as the challenging task of disentangling the effect of each of these multiple stressors. A multidisciplinary approach focused on the understanding of the effects of climate change on humpback whale stocks can be essential for such achievement, as proposed by Meynecke et al. (2020), a process that can also be benefitted from crossdisciplinary analysis (Pirotta et al., 2022). Analysing potential changes in the distribution of the species, considering the multiple environmental drivers of habitat selection (e.g. SST, bathymetry, chlorophyll-a concentration – Meynecke et al., 2021) is also necessary to better evaluate the conservation status of different stocks and the need for their management. That would help in the identification of potential new areas to be used by the species, as well as areas under such a high level of stress that might become unsuitable, which is relevant for the better protection of humpback whales (Meynecke et al., 2021).

The more information gathered on the distribution and behaviour of the species, the more viable it is for researchers to start relating changes to specific causes or threats. Finding the causes of changes in distribution, migration and/or behaviour for the species can be an important aspect for the management of the different stocks. In addition, the adaptability shown by the species, for instance by the return to areas used prior to whaling and the expansion of historical breeding grounds into both breeding and feeding grounds are aspects that can impact the abundance found in these areas, as well as management planning. Such plasticity shown by different stocks makes the investigation of the recovery of the species and interpretation of estimates even more challenging. For example, data collection that has been performed for some time in specific places within the breeding area where individuals tended the concentrate can indicate a decrease in the numbers, but that does not necessarily mean the growth rate decrease, but be a reflect of the stocks expanding their distribution in breeding grounds, spreading out as their return to areas previously used and/or explore new areas. It is also important to note that the inclusion of pre-modern whaling catches (e.g. Zerbini et al., 2019) and the use of correction factors to account for struck-and-lost animals (Baker and Clapham, 2004; Vighi et al., 2020) is critical for the whaling data to be more accurate and the habitat use of the stocks to be better understood. That can influence for instance on the evaluation of catch data when investigating humpback whale plasticity and potential response to climate change in breeding areas.

Despite research efforts on humpback whales in the Southern Hemisphere since the cessation of the commercial whaling activities, there are a number of unknowns. This review may help in updating trends of the different stocks and in giving direction to further efforts to fill current knowledge gaps that affect the conservation of the species.

Author contributions

ES and KF contributed to the conception and design of the study. ES performed the literature review, organized data and information found, and wrote the first draft of the manuscript. All authors contributed to the manuscript revision, read, and approved the submitted version.

Funding

This work was supported by a grant to Griffith University from a private charitable trust as part of the Whales & Climate Research Program.

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.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.997491/full#supplementary-material

SUPPLEMENTARY FIGURE 1
Map with the indication of specific locations/areas withing the breeding area of the Southwestern Atlantic Ocean stock, along the coast of Brazil.

SUPPLEMENTARY FIGURE 2
Map with the indication of specific locations/areas withing the breeding area of the west coast of Africa stock.

SUPPLEMENTARY FIGURE 3
Map with the indication of specific locations/areas withing the breeding area of the east coast of Africa and western Indian Ocean stock.

SUPPLEMENTARY FIGURE 4
Map with the indication of specific locations/areas withing the breeding area along the west coast of Australia.

SUPPLEMENTARY FIGURE 5
Map with the indication of specific locations/areas withing the breeding area of the stock using the west coast of South America.

References

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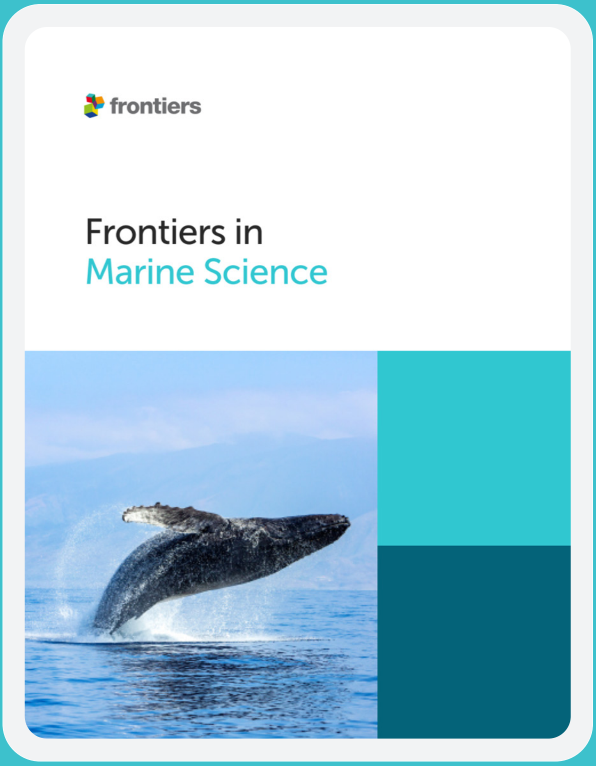
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