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The Status of Marine Megafauna Research in Macaronesia: A Systematic Review

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Marine megafauna serve valuable ecological and economical roles globally, yet, many species have experienced precipitous population declines. The significance of marine megafauna is particularly evident in Macaronesia, a complex of oceanic archipelagos in the Northeast Atlantic Ocean. Macaronesian islands provide important habitats for marine megafauna species, in turn supporting considerable regional economic activity (e.g., ecotourism and fisheries). Despite this, concerted efforts to manage marine megafauna throughout Macaronesia have been limited. This systematic review provides the first description of the trends in marine megafauna research in this unique insular ecosystem, to provide a better understanding of taxa-specific research needs and future directions for conservation. We identified and validated 408 peer-reviewed publications until 2021 following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) criteria. Literature was dominated by marine mammal research conducted in the northern archipelagos (Azores, Madeira, and Canary Islands) and marine turtle research conducted in Cabo Verde. Much less research focused on large-bodied fish, especially in Madeira and Canary Islands, leaving some of the most vulnerable species regionally data deficient. Research across scientific disciplines focused more on biological studies than management and policy, and anthropogenic impacts were quantified more frequently on mammals or turtles and less on fishes. By identifying gaps in our knowledge of megafauna in relation to threats faced by these organisms, we offer taxa-specific recommendations for future research direction. Although, overall our results indicate that determining population level connectivity should be a major research priority among many marine megafauna species as this information is vital to numerous management strategies, including marine protected areas. In this review, we present a basis of understanding of the current work in Macaronesia, highlighting critical data gaps that are urgently needed to guide the next steps toward establishing conservation priorities for marine megafauna in the region.

Keywords: Atlantic, insular systems, marine mammal, sea turtle, elasmobranch, conservation, predators, large fish

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INTRODUCTION

Marine megafauna are broadly defined by their large size and important ecological functions, including animals such as mammals, large fishes, and sea turtles (Moleón et al., 2020; Pimiento et al., 2020). Most notably, marine megafauna are key components to their environment as they help shape ecosystems (and the related functional processes), many of which are considered ecosystem engineers and act as sentinels for ecosystem health (Bossart, 2006). For example, baleen whales contribute to the horizontal transfer of limiting nutrients throughout the water column (Roman et al., 2014), and stingrays alter the benthic morphology as bioturbators which increase localized nutrient fluxes (Lohrer et al., 2004). Moreover, many species of megafauna are considered apex and meso-predators across pelagic and coastal food-webs (Temple et al., 2018). The loss or depletion of such species may limit their current ecological impacts (Pimiento et al., 2020), and potentially result in trophic cascades with consequent loss of community structure and dynamics (Heithaus et al., 2008; Kiszka et al., 2015) and subsequent nutrient cycling (Burkholder et al., 2013). In addition to the biological and ecological consequences of megafauna extirpation, commercial and social relationships also rely on marine megafauna as a source of income in terms of fisheries (Morato, 2012; González et al., 2020; Martinez-Escauriaza et al., 2021) and ecotourism (O'Connor et al., 2009; Mazzoldi et al., 2019; Gonzáles-Mantilla et al., 2021).

Despite their commercial and ecological importance, many species of marine megafauna are of high conservation concern, of which nearly one-third are considered at risk of extinction (Pimiento et al., 2020; Dulvy et al., 2021). This is primarily due to the shared k-selected life history traits that these groups possess, notably high longevity, slow growth, late maturity, and low fecundity (Temple et al., 2018). The increase of waterborne anthropogenic activities has led to an increase in potential threats to marine megafauna, notably fisheries, marine traffic, pollution, and climate change (Halpern et al., 2008). The threats associated with humans often overlap with ecologically important areas for marine megafauna, consequently, a multitude of species have been impacted globally which continues to rapidly intensify (McCauley et al., 2015). Without protective measures, international cooperation, and management of threatened species, marine megafauna populations are expected to face global, local, and functional extinction within the next century (McCauley et al., 2015; Pimiento et al., 2020).

Successful conservation is dependent on quantifying certain biological aspects of marine megafauna, such as species distributions, habitat use, and connectivity (Sequeira et al., 2019). Yet, there are many challenges associated with conservation and research for these threatened groups, such as low detectability and encounter rates, in addition to the high costs associated with accessing the, often remote, marine environment which they inhabit (Afonso et al., 2020). Furthermore, the wide-scale migratory nature of many marine megafauna has made it challenging to acquire descriptive information for many species, and as such, their decline or loss may go unnoticed due to lack of knowledge and poor management (He et al., 2017; Temple et al., 2018). Insular systems, such as oceanic island systems, are particularly vulnerable regions that warrant increased attention as marine megafauna are often in closer proximity to anthropogenic threats (Fernández-Palacios et al., 2021). Management strategies for marine megafauna in these systems are largely based upon existing research conducted on these organisms. Consequently, there is a need to identify research areas lacking in such knowledge to help provide actionable conservation goals and better manage marine megafauna groups within oceanic insular ecosystems.

In this context, this review specifically focuses on the status of marine megafauna research in the Macaronesia region. Macaronesia lies in the Northeast Atlantic Ocean and is historically composed of four oceanic archipelagos of volcanic origin, in decreasing order of latitude: the Azores, Madeira, Canary Islands, and Cabo Verde. The northern archipelagos of the Azores, Madeira and Canary Islands are interconnected by oceanic currents and are considered temperate or sub-tropical, whereas Cabo Verde is considered a tropical ecosystem (Spalding et al., 2007). The Macaronesian biogeographic unit has been subject to years of some debate where, depending on the taxa of study, archipelagos have either been subdivided or grouped into smaller and distinct ecoregions (e.g., Lloris et al., 1991; Spalding et al., 2007). For example, the most recent study proposed the complete exclusion of Cabo Verde based on a multi-taxon approach to redefine the region (i.e., coastal fishes, invertebrates and macroalgae; Freitas et al., 2019c). Owing to the migratory nature of many marine megafauna species, Macaronesia is herein considered inclusive of all four archipelagos. Although there are taxa specific reviews on an archipelago scale (e.g., Das and Afonso, 2017), and few throughout the region (e.g., Valente et al., 2019; Cartagena-Matos et al., 2021), the current study presents the first comprehensive multi-taxa review across Macaronesia. Collecting information on such a wide-scale enables an assessment of current marine megafauna research status including gaps among archipelagos and key taxa.

The combination of high regional diversity and lack of comprehensive understanding of marine megafauna calls for a synthesized documentation of the research conducted in the region as a crucial step toward establishing conservation priorities for Macaronesia. The main objectives of this study were to (I) quantify the relative magnitude of research that has been conducted on key marine megafauna groups in Macaronesia, (II) compare the trends of research among the Macaronesian archipelagos, and (III) describe the advances and future direction of marine megafauna research within Macaronesia. Finally, this review aims to contribute in guiding future research, management, and evidence-based conservation of vital taxonomic groups for the marine ecosystem of Macaronesia.

GENERAL METHODOLOGY

This study followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA; Moher et al., 2016) guidelines (**Figure 1**). All analyses were performed after the characterization of suitable studies (**Supplementary Table 1**).

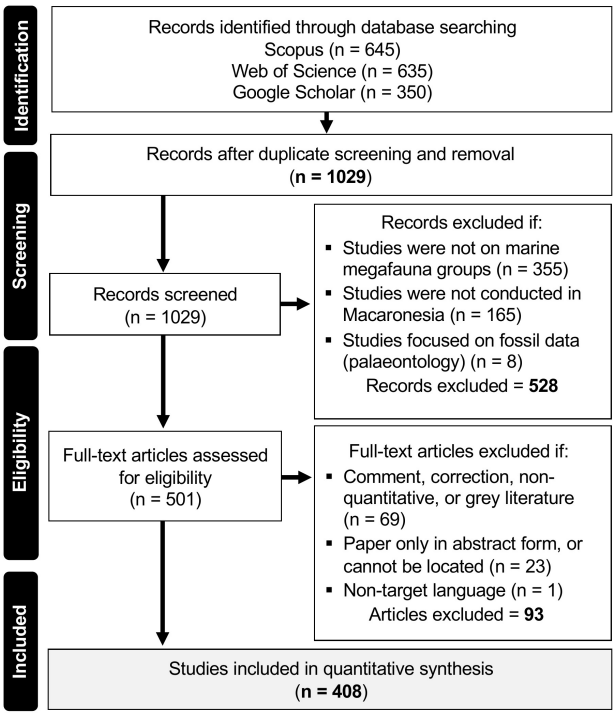

FIGURE 1 | Flow diagram of the Preferred Reporting Items for Systematic Reviews (PRISMA; Moher et al., 2016) methodology and selection process used, indicating the number (n) of studies included in this review. The bold numbers are key numerical values associated with the number of studies included in the review.

Searches were conducted in English, Portuguese, and Spanish using SciVerse Scopus[1], Thompson's ISI Web of Science[2], and Google Scholar[3] databases (**Table 1**). Results from Google Scholar that exceeded 100 publications were capped at 10 pages, owing to the negligible chance of finding further relevant publications past the 10th results page (Cartagena-Matos et al., 2021). Peer-reviewed research published between 1900 and February 2021 was included to assess general temporal trends. Literature published prior to 1970 was excluded from detailed analysis (i.e., scientific discipline, methodology, general taxa, and anthropogenic impacts) due to the uncertainty of peer-review. Additionally, all gray literature post 1970 and publications in a non-target language were fully excluded. This process provided 1,029 publication records, after removal of duplications.

A screening process was conducted based on a set criterion to filter appropriate studies (**Table 2**). Initially, titles and abstracts were screened for inclusion categories, resulting in 501 publications considered for full-text screening, of which 408 publications were included for full analysis. Validation of every decision to include or exclude a specific paper was confirmed by at least two authors to ensure all appropriate literature was included. The details of the retained literature for this systematic review can be found in the **Supplementary Material**.

TABLE 1 | Search terms used to locate and acquire relevant literature for the systematic review in English, Portuguese (PT), and Spanish (SP).

Search terms	Translation
Marine mammals	
"marine mammal*" OR baleen* OR dolphin* OR whale* OR porpoise* OR cetacean* OR pinniped* OR seal*	**PT:** golfinho, baleia, foca **SP:** delfín, ballena, foca
Chondrichthyes	
"Elasmobranch*" OR shark* OR stingray* OR skate* OR Chondrichthyes* OR chimera*	**PT:** tubarão, raia **SP:** tiburón, mantarraya
Osteichthyes	
"predatory fish*" OR "mobile predator*" OR "game fish*" OR "sport fish*" OR "billfish*" OR sailfish* OR marlin* OR swordfish* OR scombrid* OR tuna*	**PT:** peixe-agulha, peixe-espada, pesca desportiva **SP:** pez espada, marlines, pez vela, pesca deportiva
Sea turtles	
turtle* AND (marine* OR sea* OR ocean*)	**PT:** tartaruga marinha **SP:** tortuga marina

Search terms were combined with a location search using TITLE-ABS-KEY (Macaronesia OR Azores* OR "Canary Islands*" OR Madeira* OR "Cape Verde*" OR "Cabo Verde*").*

TABLE 2 | Inclusion and exclusion criteria for literature in the systematic review.

Inclusion criteria	Exclusion criteria
The study focuses on marine megafauna, i.e., marine mammals, sea turtles, chondrichthyes, and large bodied game fish	The study was conducted on marine birds, or on non-target fish species
The study was conducted in Macaronesia, or the analyses were performed on data derived from the Macaronesian region	The study tagged or reported marine megafauna outside of Macaronesia which was later detected in Macaronesian waters
	The literature is a comment paper, or erratum/corrigendum paper, or only available in abstract form
The literature is in English, Portuguese, or Spanish	Reviews that do not provide quantitative analysis/data (e.g., descriptive books with no extractable data)
	The study of fossils (paleontology)

Data Analysis

Data from publications that passed through all inclusion criteria was extracted using ArcGIS Survey123 (detailed description can be found in **Supplementary Table 2**). The collected data categorized publications by year of publication, author affiliation, archipelago, depth of the surveyed area, research theme (i.e., biology, or management and policy), primary methodology (e.g., extractive, observational, experimental, etc.), primary taxa (i.e., marine mammals, osteichthyes, chondrichthyes, or marine turtles), and if assessed, the type of anthropogenic impact investigated. Although some marine birds might be considered

[1]https://www.scopus.com
[2]https://webofknowledge.com
[3]https://scholar.google.com

marine megafauna, these were excluded for the purpose of this analyses and review. All parameters were compiled into a singular database of marine megafauna research in Macaronesia (**Supplementary Table 3**). For the purposes of comparative assessment, publications that had data from more than one archipelago were represented by each individual archipelago when describing research trends over time (**Figures 2–5**; i.e., single study with data from Madeira and Canary Islands will be represented twice). Original graphical representations and statistical analysis were conducted in R version 4.0.3 (R Core Team, 2020). A linear regression model was fitted to the quantity of publications per year to test for significant trends in publications over time (R base package), excluding 2021 as it was an incomplete year. The threshold for statistical significance was $p \leq 0.05$.

RESULTS

Scientific publications investigating marine megafauna in Macaronesia have significantly increased over time ($r^2 = 0.66$; $p < 0.001$), reaching a peak annual output of 50 publications per year between 2019 and 2020 [maximum recorded annual publications per archipelago: Azores: 15 (2020); Madeira: 12 (2019); Canary Islands: 19 (2019); Cabo Verde: 10 (2019)] (**Figure 2**). Although, current trends of marine megafauna research within Macaronesia are highly variable among archipelagos. The majority of regional studies have been conducted solely in the Azores (33%), followed by the Canary Islands (30%), Cabo Verde (17%), and Madeira (10%). In addition, 10% of studies were conducted in more than one archipelago, and 3% included data from all Macaronesia (**Figure 2**). Of the studies that were conducted in more than one archipelago ($n = 30$), the majority included data derived from both the Azores and other archipelagos ($n = 23$; Azores-Madeira = 16; Azores-Canary Islands = 10; Azores-Cabo Verde = 2[4]). Studies that incorporated data from the Canary Islands and Madeira, and Canary Islands and Cabo Verde were least common ($n = 4$, respectively). From the total number of publications, 79% had at least one author affiliated to a research institution at the archipelago of study. According to our analysis, most publications (68%) were from sea-level or above (i.e., boat, shore, and desk-based). Of the 32% of studies that investigated marine megafauna at depth, 16% collected data from the first 30 m, 6% from between 31 and 200 m, 18% from depths below 200 m, and 65% did not define the depth investigated.

The primary taxa of research conducted in the Azores, Madeira, and the Canary Islands were marine mammals (51%, 51%, and 56%, respectively; **Figure 2**), followed by chondrichthyans (29%, 21%, and 18%, respectively), and an equivalent research output for marine turtles in the Canary Islands (18%). Relative trends in turtle research per archipelago appeared to increase with decreasing latitude (Azores: 8%, Madeira: 17%, Canary Islands: 18%, Cabo Verde: 43%). Research output on large-bodied osteichthyes received the third-most level of relative research effort in the Azores and Cabo Verde (12% and 14%, respectively), yet few studies were found in Madeira and Canary Islands (10 and 8%, respectively). Contrasting trends were observed in Cabo Verde, where the primary output was turtle research, followed by marine mammal (33%), osteichthyan, and chondrichthyan research (10%). Additionally, relative patterns of research effort by archipelago were not consistent among all taxa (**Figure 3**). The majority of research on marine mammals, chondrichthyes, and osteichthyes has been conducted in the Azores archipelago, with a similar, yet fewer number of studies on marine mammals having been conducted in the Canary Islands. Marine turtles have received more research attention in Cabo Verde than any other archipelago in Macaronesia.

Research across scientific disciplines was not evenly distributed, with more biological studies ($n = 346$ *c.f.* 62) than management and policy publications. The majority of biological research was conducted within the sub-disciplines of biodiversity and behavior yet was highly variable among taxa (**Figure 4**). Biological studies involving marine mammal research was composed mainly of pathological studies (19%), followed by population (18%), and biodiversity assessments (16%). There were less marine mammal publications focusing on life history (1%) and none on reproduction, similar to chondrichthyan research (1%, respectively). Chondrichthyan research was dominated by biodiversity research (34%), followed by trophic ecology (11%), whereas osteichthyan research had primarily behavioral (25%), and biochemical (17%) related studies. Within the sub-disciplines of osteichthyan research, there were no available publications on either reproductive of pathological assessments. Marine turtle research was predominantly focused on biochemistry studies (23%), pathology (14%), and genetic assessments (11%), with no publications on behavior or taxonomy, and few on their life history (1%). Within management and policy related sub-disciplines, the majority of marine mammal, chondrichthyan, and osteichthyan research was based on fisheries (38%, 62%, and 56%, respectively), whereas marine turtle research focused on environmental impacts assessments (EIAs; 47%). There were few publications on EIAs or marine protected areas (MPAs) for either chondrichthyes (5% and 6%, respectively) or osteichthyes (5% and 6%, respectively).

The number of sub-disciplines investigated within the primary thematic lines (i.e., biological studies; management and policy) have increased considerably over the past two decades (2000–2020; **Figure 5**). Biological studies, specifically biodiversity research, appears to be the earliest occurring sub-discipline per taxa, and is also one of the fastest growing research themes for marine mammal, chondrichthyan, and osteichthyan research. Marine mammal research on pathology, behavior and movement have seen recent increases in publication output, whereas chondrichthyan and osteichthyan trophic ecology have also shown recent increases. Marine turtle research has increased in almost all sub-disciplines in the past decade, especially within biochemistry, movement, and population ecology. Management and policy related disciplines have lagged in comparison with the first publications for marine mammal and osteichthyan research surfacing in 2003, then in 2010 for chondrichthyes, and 2011

[4]Sum of individual products are greater than that of the total due to instances where data were derived from more than two archipelagos.

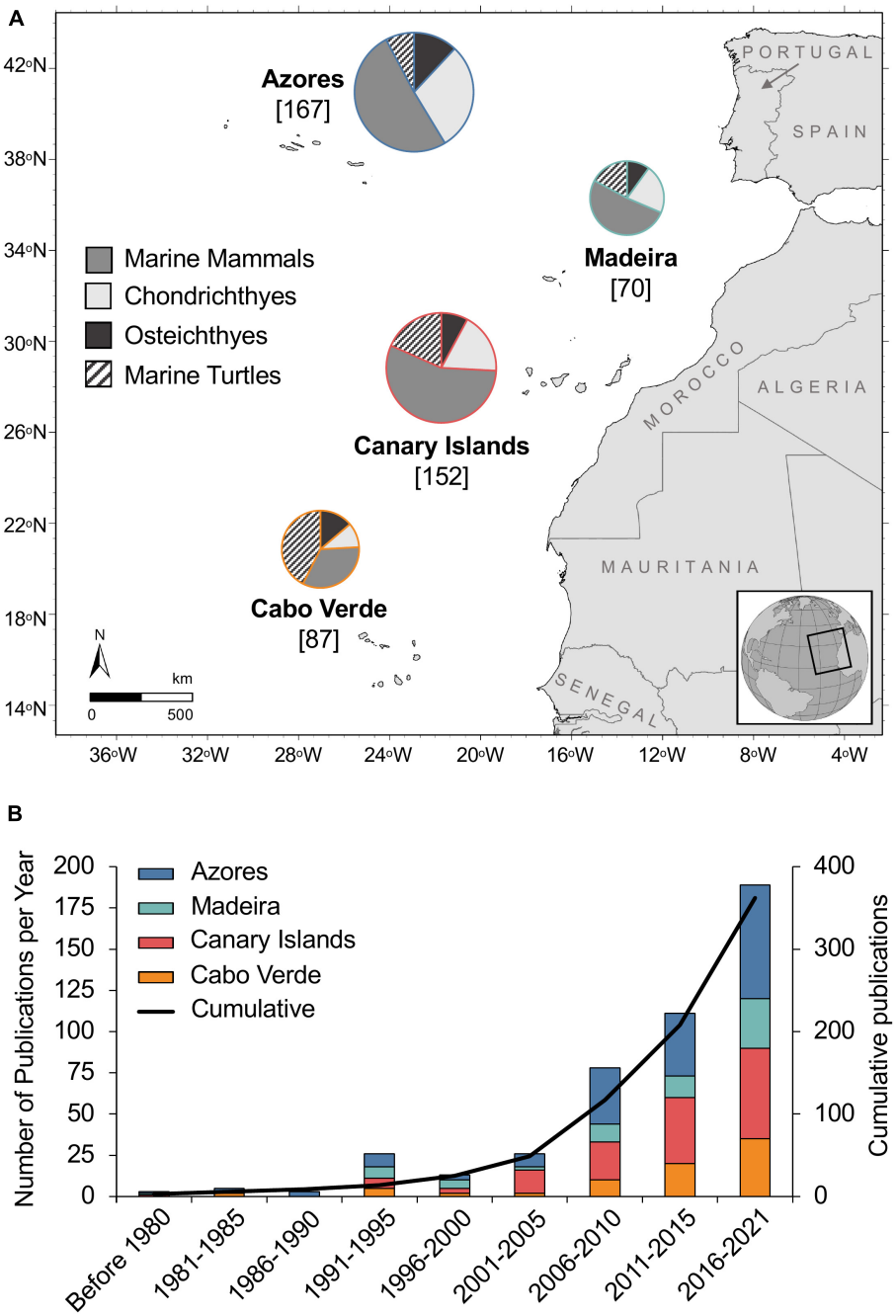

FIGURE 2 | Quantitative representation of reviewed publications by Macaronesian archipelago in relation to **(A)** composition of focal taxa (size of chart scaled to relative number of publications) and **(B)** publication trends over time.

for marine turtles. Research into MPAs has seen the most recent increase in publications for all taxa, except for osteichthyes. Notable increases in publication output have recently been observed in EIA research for osteichthyes and marine turtles, and in fisheries research for chondrichthyes.

The majority of publications did not attempt to quantify anthropogenic impacts (73%). Of the publications that quantified risk to the focal taxa, most focused on fishing related impacts, followed by marine pollutants and maritime traffic (**Figure 6**). Specifically, the majority of impacts assessments in marine mammal and chondrichthyan research focused on fishing related impacts, whereas osteichthyan and marine turtle research had a greater emphasis on impacts from marine pollution. Papers which assessed the impacts of pollution and climate change in Macaronesia were primarily focused on marine turtles, while the majority of marine traffic research was conducted in

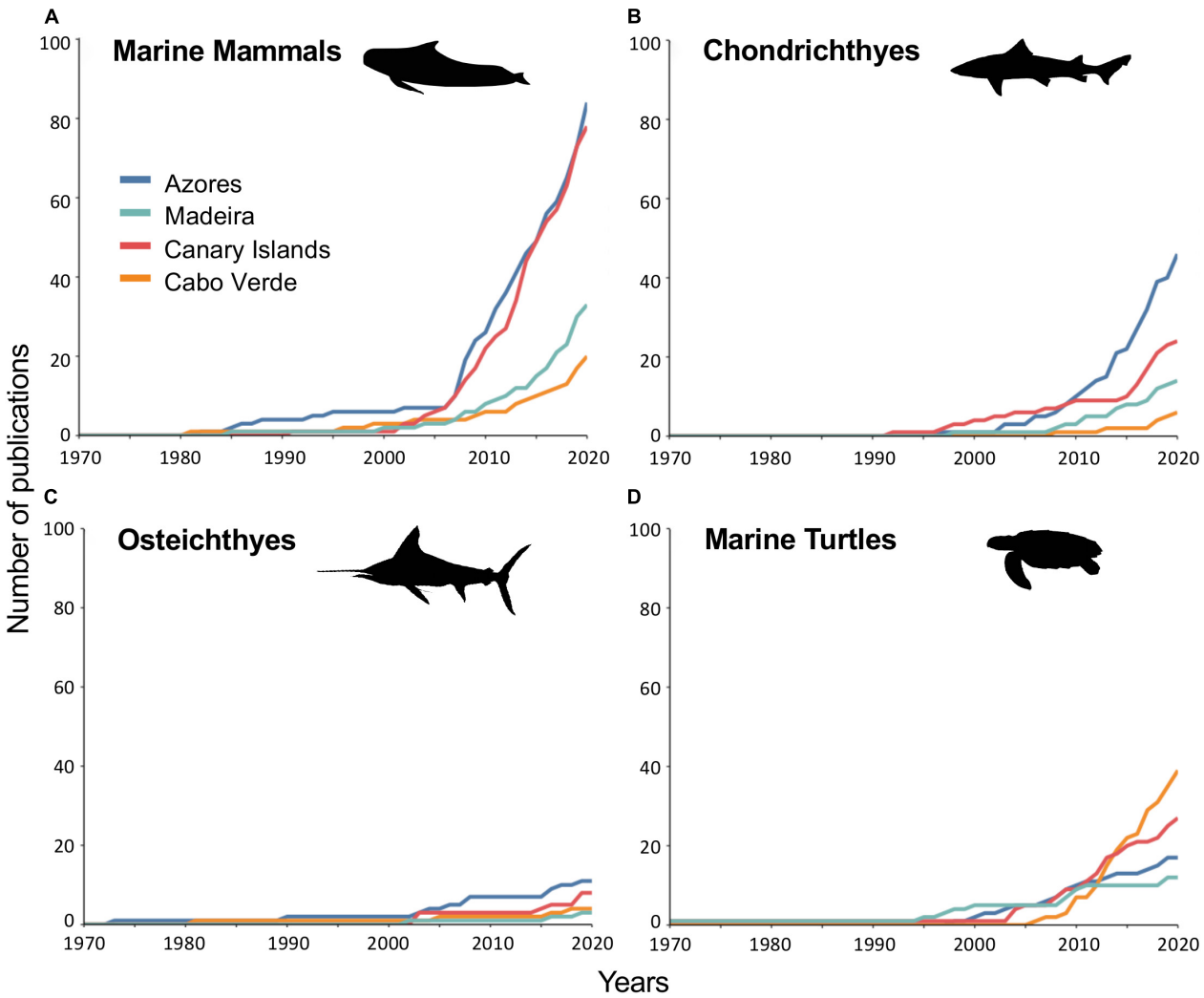

FIGURE 3 | Cumulative number of publications in marine megafauna research per archipelago through time: **(A)** marine mammals, **(B)** chondrichthyes, **(C)** large-bodied osteichthyes, and **(D)** marine turtles. Silhouettes derived from Phylopic (http://phylopic.org).

relation to marine mammals. Overall, anthropogenic impacts were quantified more frequently in publications that focused on marine mammals or marine turtles, and less likely in fish (**Figure 6**).

DISCUSSION

This study provides the first quantitative representation of relative trends in marine megafauna research throughout Macaronesia. Research output has increased annually, yet the reviewed studies are currently dominated by marine mammal research in the northern archipelagos (Azores, Madeira, and Canary Islands) and by marine turtle research in Cabo Verde. There is less fish-related research, especially within the Canary Islands and Cabo Verde, leaving some of the most vulnerable species regionally data deficient (Pimiento et al., 2020; Dulvy et al., 2021; **Supplementary Table 4** and **Supplementary Figure 1**). The majority of research is conducted from boats/land, and only 24% of research explored depths >30 m, highlighting a serious knowledge gap regarding pelagic and deep-sea ecology in this oceanic system. Although overfishing and direct harvesting are commonly referred to as the main global anthropogenic threats to marine megafauna (McCauley et al., 2015; Dulvy et al., 2021), our findings reveal that other significant threats (e.g., marine pollutants, climate change, etc.; **Figure 6**) remain largely unexplored in Macaronesia and require further research attention to fully-understand their impacts across marine megafauna taxa.

Marine Mammals

Macaronesia hosts a variety of resident marine mammals [e.g., short-finned pilot whale *Globicephala macrorhynchus* (Alves et al., 2013; Servidio et al., 2019), common bottlenose dolphin *Tursiops truncatus* (Dinis et al., 2016), and Mediterranean monk seal *Monachus monachus* (Pires et al., 2008)] as well as migratory species [e.g., rough-toothed dolphin *Steno bredanensis* (Steiner, 1995; Alves et al., 2018) and Bryde's whale *Balaenoptera edeni*

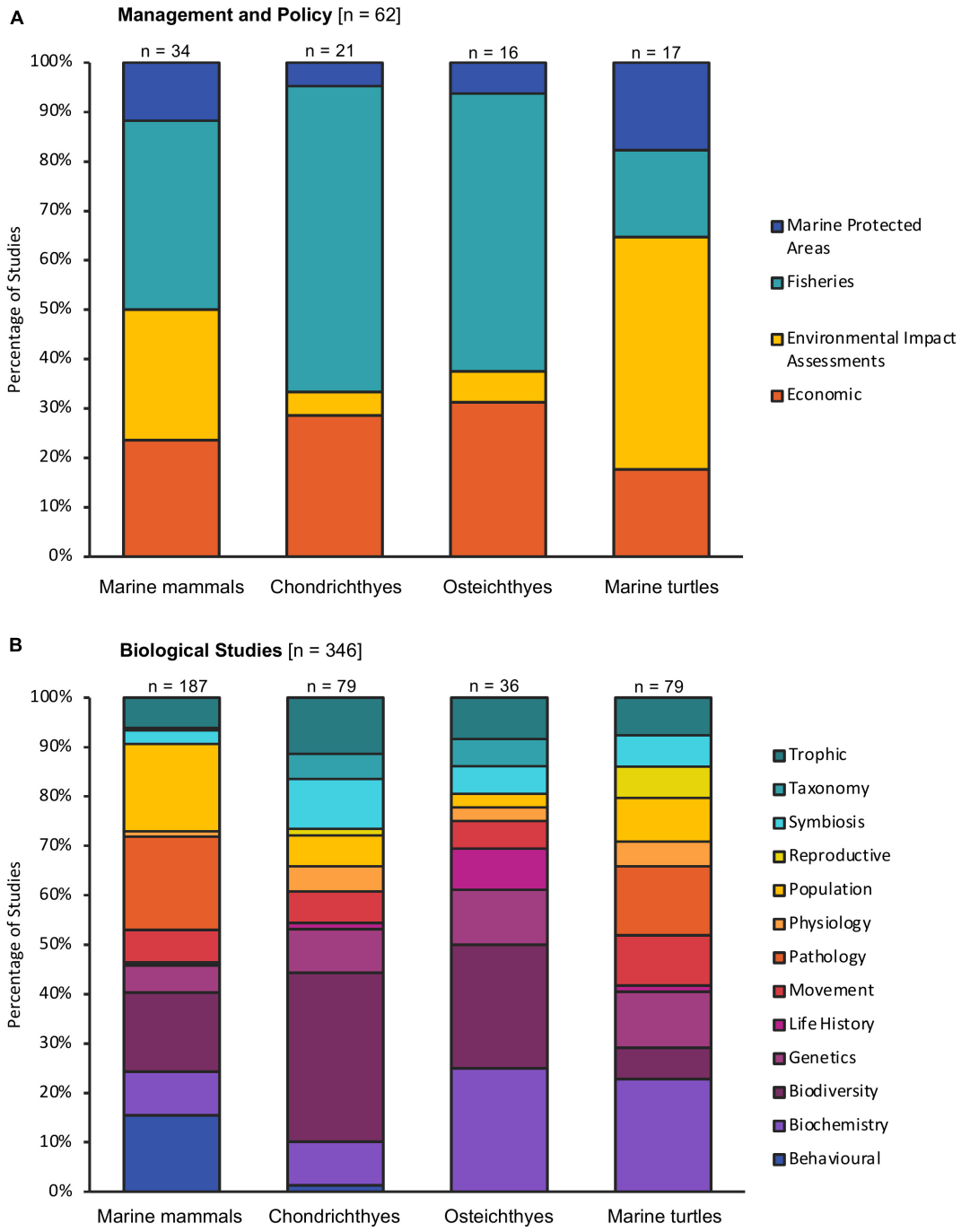

FIGURE 4 | Trends of sub-disciplines among reviewed papers corresponding to: **(A)** management and policy and **(B)** biological studies.

(Ferreira et al., 2021)]. Marine mammals are typically seen as charismatic animals that receive a lot of support from the public and conservation entities, which often refer to them as flagship species (Mazzoldi et al., 2019). There has been a corresponding shift in perspectives of marine mammals from a consumptive to an ecological resource. Following the end of industrial whaling in the Azores and Madeira (1984 and 1981, respectively; Brito, 2008; Mazzoldi et al., 2019), cetacean eco-tourism has become an important regional industry that has promoted their conservation (Mazzoldi et al., 2019). However, the expansion of anthropogenic activities in Macaronesia brings with it associated pressures that may require novel management strategies.

The majority of research in Macaronesia has been conducted in the Azores and Canary Islands. Marine mammal research

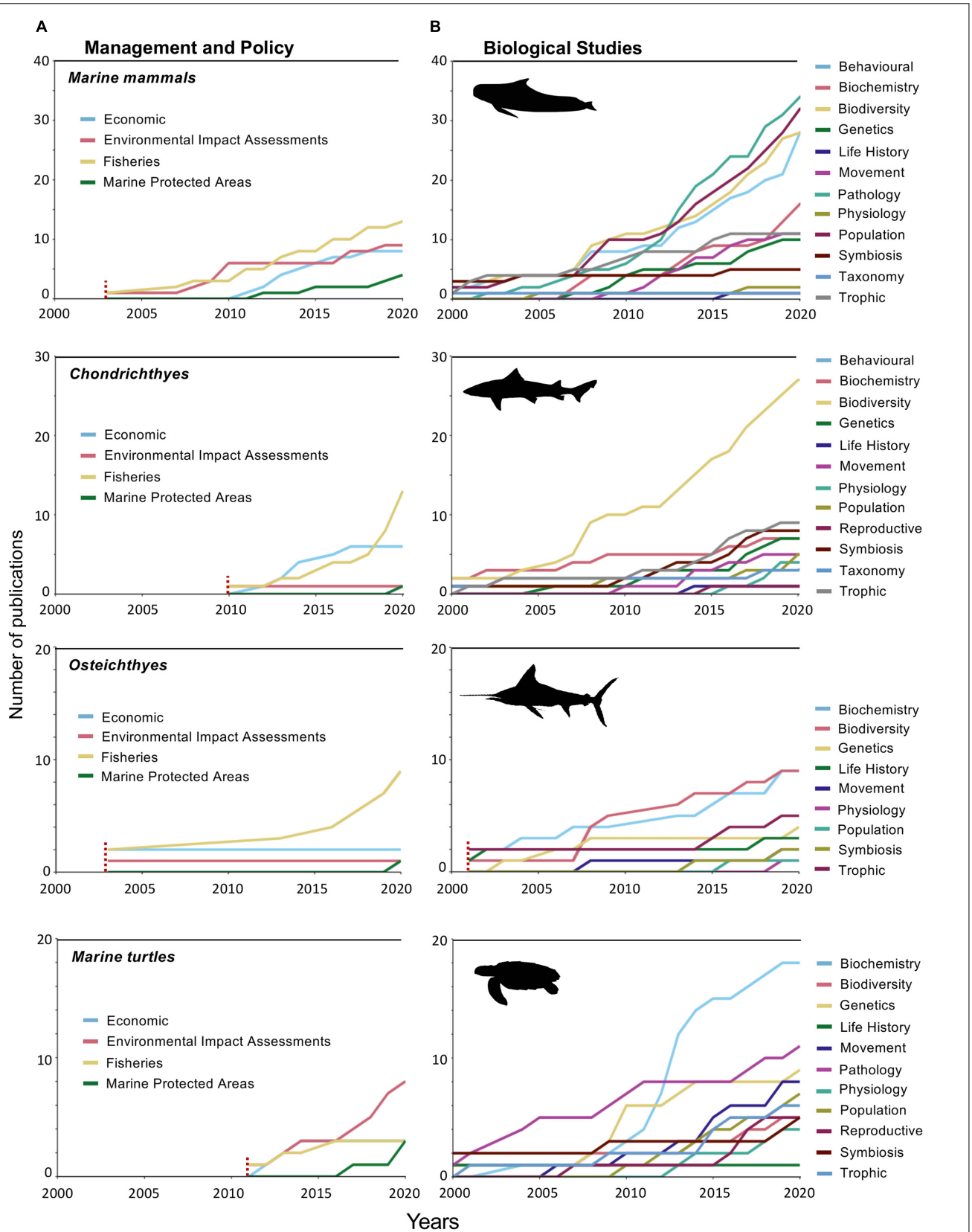

FIGURE 5 | Sub-topic evolution of **(A)** management and policy, and **(B)** biological studies per marine megafauna group, over the past two decades (2000–2020). Dashed red line indicates the first research article published within the respective topic. Note differences in scale per taxa.

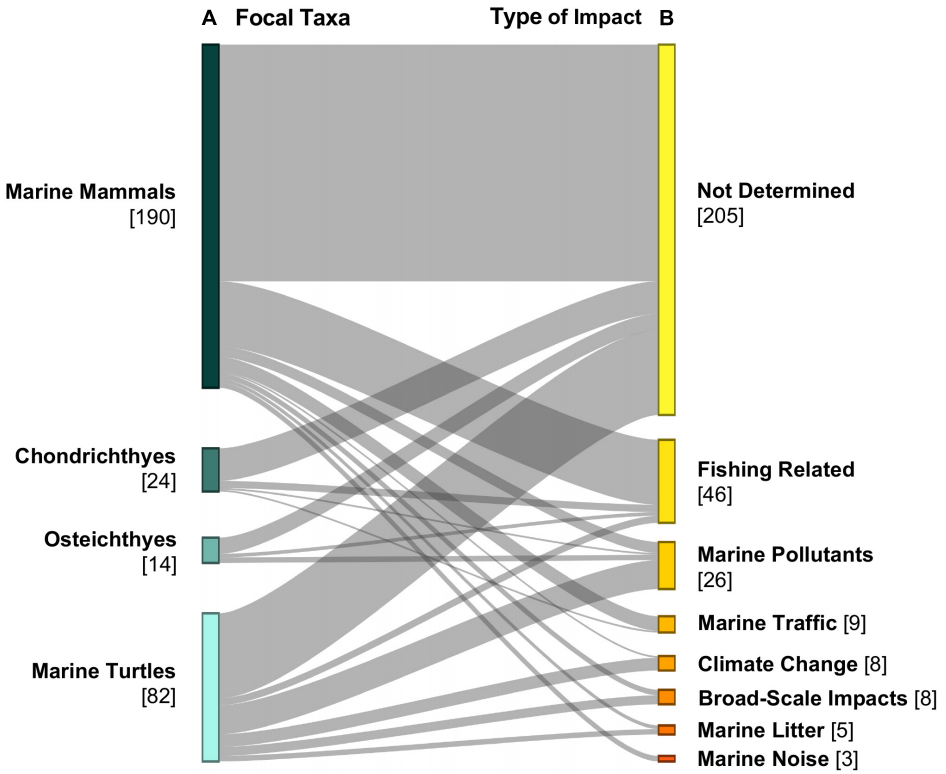

FIGURE 6 | Sankey diagram depicting **(A)** the number of publications that quantify **(B)** anthropogenic impacts on Macaronesia marine megafauna in relation to the focal taxa of study.

is the main research output for the Azores, Madeira, and the Canary Islands, and second largest output in Cabo Verde. Early exploitation of marine mammals in Macaronesia allowed preliminary research to grow (e.g., sperm whales *Physeter macrocephalus* in the Azores; Clarke et al., 1993) and has been steadily increasing since the 1980s. The primary focus of cetacean research in Macaronesia has been biodiversity/biogeography studies, population assessments [i.e., abundance and distribution (Alves et al., 2015; Wenzel et al., 2020)], and pathological research [e.g., necropsy/clinical reports, virology (Fernández et al., 2017)]. The high volume of pathological research is related to established stranding networks throughout Macaronesia, for which the majority has been conducted in the Canary Islands. In line with previous research, our review highlighted species specific biases in which research primarily focused on three main species (i.e., short-beaked common dolphin *Delphinus delphis,* sperm whale, and common bottlenose dolphin; Cartagena-Matos et al., 2021).

Although marine mammals have received the most research attention among marine megafauna regionally, certain fields of study remain unrefined. There is a distinct lack of ecological research surrounding species such as the pygmy (*Kogia breviceps*) and dwarf (*Kogia sima*) sperm whale, or beaked whales (Ziphiidae). This is not surprising as many of these species are elusive and difficult to study, and most of the known information comes from stranding-related necropsy reports (McAlpine, 2018). We also found a paucity of peer reviewed research on basic biological aspects of the Critically Endangered Mediterranean monk seal *Monachus monachus* (e.g., diet, movement, pollutants; European Mammal Assessment Team, 2007). The Mediterranean monk seal formerly inhabited the whole of Macaronesia (Monod, 1948; Machado, 1979; Hernandez, 1986; Silva et al., 2009; Brito, 2012; González, 2015), yet is now confined to the Madeiran Archipelago with a single population of ∼20 individuals (Karamanlidis et al., 2005; de Larrinoa et al., 2021). Without adequate information available for certain marine mammal species in Macaronesia, population declines and threats may go undocumented and ineffective species protections may be enacted. Across all marine mammals, population estimates, migratory patterns, and abundance estimates, which underpin many conservation strategies, are currently limited in Cabo Verde and Madeira (**Figure 3**). Understanding species connectivity is another important component of conservation, yet within Macaronesia this information remains scarce. For example, short-finned pilot whale and bottlenose dolphin population structuring is evident between the Azores, Madeira, and Canary Islands (Alves et al., 2019; Dinis et al., 2021), yet has not been expanded to include Cabo Verde (Hazevoet et al., 2010; Correia et al., 2020).

The main potential threats to cetaceans in northern Macaronesia include vessel collision (e.g., Canary Islands; Ritter and Panigada, 2018) and intensive whale watching throughout the Azores, Madeira, and Canary Islands (Arranz et al., 2021a,b;

Sambolino et al., 2022a). Other indirect or difficult to quantify threats, such as by-catch and overfishing, could also pose risks to this taxa, and are of greater concern in Cabo Verde (Visser et al., 2011; Lopes et al., 2016). The increase in marine-based anthropogenic activities is reflected as an increase of pressures faced by marine mammals (Fais et al., 2016; Cunha et al., 2017; Ritter et al., 2019; Schoeman et al., 2020; Sambolino et al., 2022b). This is echoed throughout the literature and has pushed research efforts to investigate the impacts of bycatch, pollutants, and marine traffic, yet future research should also focus on climate induced impacts (Sousa et al., 2021).

Successful conservation of marine mammals in Macaronesia will rely heavily upon a population-level understanding of their ecology and biology. Connectivity and biogeographical patterns of large delphinids and whales among the Macaronesian archipelagos should be prioritized, as managing migratory species often relies upon multi-national cooperation. Facilitating such cooperation requires robust data on species connectivity to guide protections within Economic Exclusion Zones (EEZs) and the international waters in between (Correia et al., 2020; Ferreira et al., 2021). This in turn requires an increased research effort in Macaronesia's offshore areas to attain reliable estimates of species richness and abundance of marine mammals, which may currently be underestimated (Valente et al., 2019; Correia et al., 2020; Cartagena-Matos et al., 2021).

Chondrichthyes

Chimeras, sharks, skates, and rays are especially vulnerable to exploitation owing to their specific life history traits and are experiencing precipitous worldwide declines (Dulvy et al., 2021). Among all megafauna groups, sharks are expected to be most impacted by the decline of taxonomic and functional diversity following species loss (Pimiento et al., 2020). Macaronesia hosts a diverse array of pelagic and demersal species, many of which are of high conservation concern, such as the shortfin mako shark *Isurus oxyrinchus* and angelshark *Squatina squatina*. Species composition differs between archipelagos, except for elasmobranch communities in the Azores and Madeira which are similarly dominated by deep-water Squaliformes (Das and Afonso, 2017). There are very few highly migratory species shared between Cabo Verde and the other Macaronesian archipelagos (Das and Afonso, 2017). Cabo Verde, which exhibits distinct biogeographic features (Floeter et al., 2008; Freitas et al., 2019c), supports a more coastal, tropical elasmobranch assemblage than its temperate counterparts (Wirtz et al., 2013). The majority of chondrichthyan species in Macaronesia are non-migratory, and species richness appears to decrease with latitude (Das and Afonso, 2017).

Within Macaronesia, Cabo Verde and Madeira have the least amount of research conducted on chondrichthyans, with alarmingly no information available for batoids other than within species checklists (Wirtz et al., 2008, 2013; Biscoito et al., 2018; Freitas et al., 2019c) and landings data (Martínez-Escauriaza et al., 2020). The Azores is considered a marine biodiversity hotspot (Afonso et al., 2020), to which many chondrichthyan studies have focused on biogeography and biodiversity, movement, and trophic ecology of the species that utilize local seamounts (Kukuev and Pavlov, 2008; Das and Afonso, 2017). Similar to other archipelagos, the majority of chondrichthyan research from the Azores has primarily focused on sharks and less on batoids or chimeras. Shark-based tourism in the Azores, which in 2014 was estimated to be worth over USD $2 million (Torres et al., 2017), may have facilitated the increase of research effort and long-term datasets from this archipelago. Thus, potential declines in elasmobranchs are more likely to be noticed in the Azores compared to other archipelagos, such as Madeira, where there is very little information on the abundance and distribution of elasmobranchs (Correia et al., 2016). The majority of information available on chondrichthyans from Madeira is derived from commercial fisheries, primarily focusing on species distribution records, check-lists, and taxonomy of deep-water sharks (e.g., Freitas et al., 2017; Biscoito et al., 2018; Stefanni et al., 2021). The Canary Islands have been identified as a unique stronghold for the Critically Endangered angelshark (Barker et al., 2016; Morey et al., 2019) which has led to the increase in chondrichthyan research from the archipelago. Information on elasmobranchs in Cabo Verde is scant, representing merely ∼1% of the reviewed studies.

Many basic biological questions relevant to fisheries management remain unanswered regarding the life-history, reproduction, and drivers of distribution of many chondrichthyes in the region. For example, the scarcity of research conducted on batoids from Madeira and Cabo Verde, with only recent advancements from the Canary Islands (see Tuya et al., 2021), remains a particularly concerning hindrance to the management of these species. Furthermore, there is some evidence of pupping and potential nursery grounds in Macaronesia [e.g., blue shark *Prionace glauca,* Azores (Vandeperre et al., 2014, 2016); smooth hammerhead shark *Sphyrna zygaena*, Azores (Santos et al., 1995; Das and Afonso, 2017) and Madeira (Freitas and Biscoito, 2018); angelshark, Canary Islands (Meyers et al., 2017; Jiménez-Alvarado et al., 2020)], yet there is little information generally on biologically sensitive areas, including nursery grounds, inshore and offshore aggregation, and deep-water skate and ray egg deposition sites. Fisheries-related research only represents 6% of the total research effort in Macaronesia, yet is an essential component to managing populations as there is little evidence that currently legal fisheries are sustainable without adequate baseline information and bycatch statistics (Hareide et al., 2007; EASME, 2017). For example, there is an absence of detailed information regarding species distribution and spatial overlap with regional fisheries, such as those targeting black scabbardfish *Aphanopus carbo* (Veiga et al., 2013), which may further increase the vulnerability of biologically sensitive sites to fisheries. Moreover, inconsistencies between the catch and landing of sharks (i.e., unreported or misreported discards) have been documented in the Azores (Machete et al., 2011; Das and Afonso, 2017) and the Canaries (Pajuelo et al., 2010), yet have not been investigated in Madeira.

Overfishing has been identified as a global driver of extinction for more than one-third of chondrichthyan species (Dulvy et al., 2021), and is likely the largest threat in Macaronesia. Although shark bycatch rates are considered relatively low (Bordalo-Machado and Figueiredo, 2009), they often include

species of conservation concern, specifically deep-sea sharks such as the Portuguese dogfish *Centroscymnus coelolepis*, leaf-scale gulper shark *Centrophorus squamosus*, and kitefin shark *Dalatias licha* (Holley and Marchal, 2004; Ramos et al., 2013; Campos et al., 2019), and pelagic sharks (i.e., blue shark and shortfin mako shark). Other factors that may impact coastal chondrichthyan species, such as the angelshark, include pollution and habitat destruction (Das and Afonso, 2017; Jiménez-Alvarado et al., 2020).

Spatial protections often rely upon knowledge of a species' connectivity patterns, information which is currently unavailable for many Macaronesian chondrichthyans. Accordingly, future chondrichthyan research should seek to investigate population structuring and movement patterns across various spatial scales throughout Macaronesia. Moreover, the lack of regional monitoring of fisheries may limit future research efforts, as baseline information needed to examine population trends through time may be unavailable. Establishing regional fisheries observer programs may be one way to address current knowledge gaps for chondrichthyans in certain Macaronesian archipelagos. Observer programs can yield robust estimates of bycatch and discards (e.g., the Azorean Fisheries Observer Program)[5], which could be valuable in understanding the impacts of longline fisheries on deep-sea sharks. Despite this, there are inherent limitations in the types of information that can be determined through observer programs, and the establishment of such programs may be particularly challenging in Cabo Verde given the numerous international fleets that fish their waters (Coelho et al., 2020; González et al., 2020). Further research may be required to propose technical improvements to fishing gear that can minimize the catch of non-target chondrichthyan species, as little has been done to investigate economically viable alternatives in the region. Overall, our findings indicate a pressing need for future investigations of chondrichthyan abundance, distribution and connectivity to inform fishing regulations and implement effective MPAs (Dulvy et al., 2021).

Osteichthyes

The osteichthyan megafauna of Macaronesia is primarily composed of large-bodied tunas (i.e., *Thunnus* spp.) and billfish (i.e., Xiphiidae and Istiophoridae) which are both highly migratory predators. Tunas are a commercially important fisheries resource in the waters of Macaronesia, including albacore tuna *Thunnus alalunga*, yellowfin tuna *Thunnus albacares*, Atlantic bluefin tuna *Thunnus thynnus*, and bigeye tuna *Thunnus obesus*. With the exception of bigeye tuna (Vulnerable; Collette et al., 2021), all other species have recently been re-classified as Least Concern by the IUCN Red List of Endangered Species (**Supplementary Table 4**) owing to decades of reduced catch quotas and successful enforcement in the Atlantic. Billfish are another economically important group regionally and are targeted by commercial and recreational fishers throughout Macaronesia, notably the Atlantic blue marlin *Makaira nigricans*, white marlin *Kajikia albida*, broadbill swordfish *Xiphias gladius*, Atlantic sailfish *Istiophorus albicans*, roundscale spearfish *Tetrapturus georgii*, and the longbill spearfish *Tetrapturus pfluegeri*.

Within this species group, our review only yielded 31 relevant papers, showing that more work has been conducted solely on tunas than on billfish (62 *c.f.* 16%; excluding species checklists). The vast majority of work in Macaronesia has been conducted in the Azores, followed by the Canary Islands, Cabo Verde, and Madeira. Tuna and billfish research have mainly focused on biochemical analysis and genetic work to identify population dynamics, reproductive biology, and to define stock boundaries. This work has been supported by an increase in telemetry studies to understand spatio-temporal connectivity of delineated stocks (Arrizabalaga et al., 2008; Braun et al., 2019). Stock assessment needs appear to be the primary driver for most research conducted on large-bodied osteichthyes in the region. The larger quantity of tuna literature may be due in part to their heavy exploitation and the subsequent efforts to assess population dynamics and reproductive biology in the greater Atlantic. Most work has concentrated on Atlantic bluefin and bigeye tuna in an attempt to identify population differentiation, mixing rates, and natal origins. Of the 14 publications available for billfish from Macaronesia, nine were inclusions in biodiversity assessments and only two quantified tissue contamination in broadbill swordfish. The remaining two relevant papers investigated the movements and connectivity estimates of broadbill swordfish off the Azores, and estimated fishing intensity and spatial use for commercial fleets on the Madeira-Tore seamounts. All non-biodiversity/check-list publications were from the Azores, with the exception of the latter publication in Madeiran waters.

Contrary to the quantity of bluefin tuna work from the Pacific and the south and northwest Atlantic, very few ecological studies have been conducted on tuna movements, reproduction, and foraging ecology from the northeast Atlantic (Azores, Madeira, and Canary Islands; Romero et al., 2021). To date, our knowledge on the spawning periods and locations of Atlantic bluefin tuna in Macaronesian waters is limited, although potential spawning grounds may occur in the waters between the Azores and Madeira, and to the east of the Canary Islands (Natale et al., 2020). Moreover, Cabo Verde has also been suggested to be a spawning area for yellowfin tuna (Kitchens et al., 2018), yet there is very little information available from this archipelago. Nevertheless, fundamental questions regarding stock structure and natal origins within mixing hotspots remain. Despite six species of billfish found throughout Macaronesia, the broadbill swordfish was the only species with dedicated research attention which is most likely owed to their commercial value. There were no publications identified in this review on roundscale spearfish, longbill spearfish, or Atlantic sailfish within Macaronesia.

There were not a sufficient number of studies to examine the specific anthropogenic impacts on this group, yet fisheries exploitation is expected to be the greatest threat to declines of tuna and billfish. Recreational fishing may also have undocumented impacts, as some species are typically landed for personal consumption in Macaronesia (e.g., Atlantic blue marlin; Martinez-Escauriaza et al., 2021), yet there is limited information regarding recreational fishing industries throughout the region. Attention must be given to the roundscale spearfish

[5]www.popaobserver.org

(Data Deficient; Collette et al., 2011), as there have been frequent misclassification of this species in white marlin and longbill spearfish (Beerkircher et al., 2009), which has hindered catch data and population estimates throughout its range.

There is a general lack of information on tunas and billfish in Macaronesia, with strong regional and species biases among what little research is available. Ascertaining primary biological data, such as population structure and life history parameters, would be a logical first step toward adequately managing this species group in Macaronesia. Significant uncertainty surrounds stock delimitations for many species, and more information is needed to understand which Macaronesian archipelagos share stocks of each species. Further examinations of life history characteristics among Macaronesian fish stocks could determine if variation occurs within the region and enable tailored management strategies for each stock. Although establishing fishery regulations for such migratory species is inherently challenging, ongoing research programs (e.g., the Atlantic Ocean Tuna Tagging Program)[6] demonstrate that recovery of Atlantic stocks of historically overfished large pelagic fish species is possible. With many fundamental biological questions currently unanswered future research on osteichthyan megafauna in Macaronesia describing connectivity and life history patterns between archipelagos will likely have a great impact on future management and protections for these species.

Marine Turtles

Six species of marine turtles are known to occur in Macaronesia, the most common being the loggerhead turtle, *Caretta caretta*. The summer occurrence of loggerhead turtles in the Azores, Madeira and Canaries is largely associated with the pelagic phase of the western-Atlantic rookery that feed in oceanic waters (Bolten et al., 1993, 1998; Bjorndal et al., 2000). There are latitudinal correlations between Macaronesian distributions and the natal origin of loggerhead turtles, where those found in the Azores and Madeira typically represent turtles from Florida (United States), and those in Canary Islands from Mexico (Monzón-Argüello et al., 2009). Nesting of the North East Atlantic subpopulation occurs in Cabo Verde and represents the third largest nesting population of loggerhead turtles worldwide (Marco et al., 2011, 2012), with the majority of females (i.e., 60–65%) nesting in Boa Vista Island (Marco et al., 2012). There is evidence of dispersal of Cape Verdean juveniles into northern waters of Macaronesia (Monzón-Argüello et al., 2010c). Hawksbill *Eretmochelys imbricata* and green turtles *Chelonia mydas* have also been documented nesting in Cabo Verde, but more notably use the area for foraging (Monzón-Argüello et al., 2010a,b; Marco et al., 2011). These two species have additionally been recorded in the Azores (Santos et al., 2010), Madeira, and the Canary Islands, albeit relatively less prevalent (Fretey, 2001). Leatherback turtles *Dermochelys coriacea* have been documented in all Macaronesian archipelagos (Doyle et al., 2008; Marco et al., 2011; Correia et al., 2019). Occasional migrations of Olive ridley *Lepidochelys olivacea* have been documented in Madeira, Canary Islands, and Cabo Verde (Fretey, 2001; Marco et al., 2011; Carrillo and Alcántara, 2014; Barcelos et al., 2021), in addition to Kemp's ridley turtles *Lepidochelys kempii* in the Azores and Madeira archipelagos (Brongersma, 1972; Bolten and Martins, 1990; Santos et al., 2010).

The majority of turtle research in Macaronesia has been conducted in Cabo Verde, closely followed by the Canary Islands, with relatively fewer studies from the Azores and Madeira (**Figure 3**). This largely is a result of the regional nesting of the North East Atlantic subpopulation of loggerhead turtles in Cabo Verde, and the long-term monitoring efforts from local NGOs and other environmental agencies in this archipelago (e.g., Turtle Foundation, in 2008; Maio Biodiversity Foundation, in 2010). In the Canary Islands, the majority of research has been conducted on dead or stranded turtles, whereas in Cabo Verde research is conducted on nesting individuals. Turtle research in Madeira and the Azores has primarily targeted juveniles in pelagic waters where they forage (Freitas et al., 2018, 2019a). The quantity of turtle research appears to decrease with increasing latitude, most likely due to decreasing water temperatures (i.e., physiological constraints) and distance from the Cape Verdean rookery (i.e., decreased prevalence). The majority of initial publications focused on demographic research, although more recent research on turtles in Macaronesia have focused on biochemistry [e.g., stable isotopes (Raposo et al., 2019), pollutants and contaminants (Orós et al., 2013; Camacho et al., 2014)], and environmental impact assessments (Marco et al., 2021).

There is considerably less research available for hawksbill, Kemp's and Olive Ridley sea turtles relative to other species, as they are less prevalent in the region and thus more challenging to study. Moreover, little information is currently available on the physiology and reproductive ecology of sea turtles in Macaronesia. This is particularly important, as higher environmental temperatures are expected with climate change, which may reduce hatching success, hatchling fitness (Laloë et al., 2014; Santidrián Tomillo et al., 2014; Martins et al., 2020), and increased sporadic nesting events (Carreras et al., 2018) in areas of previously low to no nesting activity (e.g., loggerhead turtles in Malaga, Spain; Gonzalez-Paredes et al., 2021), but also increase parasite abundance (Brunner and Eizaguirre, 2016). There is little information on the causes of the increase in parasite prevalence in Cabo Verde, and the functional links between environmental changes, contaminants, or population density on viral transmission (Lockley et al., 2020; Farrell et al., 2021).

Parasites can be vectors of virus transmission (Greenblatt et al., 2005; Bunkley-Williams et al., 2008; Jones et al., 2016) and have been shown to be correlated with feeding ecology, reproductive success and population dynamics (Lockley et al., 2020), posing as a population level threat. Currently, sea turtle infection has been described in Cabo Verde (Sarmiento-Ramírez et al., 2010; Stiebens et al., 2013), Madeira (Valente et al., 2009), and Canary Islands (Orós et al., 2004; Alfaro et al., 2008). Moreover, among marine megafauna, sea turtles are unique in that they nest on land. This behavior facilitates important ecological connections between terrestrial and marine systems, but also exposes sea turtles to a suite of anthropogenic pressures (Hamann et al., 2010; Pimiento et al., 2020). Wildlife watching tourism (Marco et al., 2021) and the implementation of several

[6] www.iccat.int

environmental protection organizations in Cabo Verde has significantly decreased poaching pressures (Marco et al., 2012, 2021), yet the mass increase in tourism has resulted in a host of other anthropogenic threats such as habitat modification, light pollution (Silva et al., 2017), and beach traffic (Aguilera et al., 2019). In the Azores, Madeira, and Canary Islands, where sea turtle nesting is not known to occur, fisheries and marine litter remain the largest threats to sea turtles, in addition to climate change (Ferreira et al., 2001, 2011; Vandeperre, 2020).

The need to better understand the biological responses of sea turtles to rapid climate change (Hamann et al., 2010) warrants considerable future research efforts throughout Macaronesia so that tailored regional management plans can be established for these organisms. Recently, the Azores has adopted a monitoring program (see COSTA project; Vandeperre, 2020) which is anticipated to result in an increase of scientific research, however, to the best of our knowledge, Madeira does not yet have a dedicated and funded monitoring program in place. The scarcity of long-term monitoring in the Azores and Madeira has made it challenging to document population estimates in the surrounding waters. Without this information it is impossible to identify climate driven changes in abundance and distribution of sea turtles throughout Macaronesia as a whole. In the Azores, Madeira, and Canary Islands specifically, many biological aspects of marine turtles are still unexplored, but future research should focus on immediately pressing areas of study such as documenting mortality rates and quantifying the effect of various pressures (e.g., climate change, fisheries interactions, and marine debris). In Cabo Verde, further investigation into parasite prevalence and mediation is paramount as turtle reproduction, demography, and survival may be significantly impacted.

FINAL REMARKS

The current study provides a comprehensive description of research conducted on marine megafauna in Macaronesia to-date, highlighting the limitations of our knowledge and areas of research that urgently need to be pursued. The literature discussed in this review reflects what is available to the wider scientific community, however, we acknowledge that there is a variety of unpublished works and reports that may not have been discussed owing to their omission in the search engines used. Data availability and accessibility varies between archipelagos (Valente et al., 2019), as such the reporting bias may impact the quantification of records within this review. There is a compelling need to make unpublished work more accessible and to subject regional reports to the peer-reviewed process so that the development of conservation strategies is backed by robust research. Secondly, the absence or presence of literature within the review may have been affected by language. Although searches were conducted in English, Portuguese, and Spanish, the English language may have overrepresented the number of publications which in turn could affect the number of representative publications per archipelago (Mongeon and Paul-Hus, 2016). Inconsistent or non-inclusive language remains a major barrier for regional managers to incorporate research findings into regulations, which may hinder coordinated conservation efforts. Lastly, differences in resource allocation may also play a large role in the output of publications in Macaronesia. Although European countries may be more likely to receive research investment, the majority of research quantified in this review was conducted in the Azores, whereas the least amount of literature was available from Madeira, despite being archipelagos of the same country. This may be a result of different investments and strategy in science from the regional governments, although the results and patterns found in our analysis are more likely to be affected by specific sampling and research effort in each archipelago and the establishment of particular research groups on those archipelagos.

Within Macaronesia, conservation of marine megafaunal groups requires coordinated actions among key stakeholders (i.e., researchers, policymakers, and non-governmental organizations), and in many cases, among national archipelagos. Regional stakeholder cooperation will likely be required to obtain baseline information for many species, which is essential to understand species population trends in addition to their movement and distribution patterns. Without such information, species-specific interactions with the anthropogenic threats or potential range-shifts in response to climate change scenarios cannot be fully quantified (Correia et al., 2020). The implementation of monitoring programs within and beyond national jurisdictions have the potential to significantly contribute to the integrated management of marine megafauna throughout Macaronesia. Tourism development in particular can increase scientific output through data acquisition (e.g., whale watching, sports fishing), but also increase the social and cultural value of marine megafauna to locals (e.g., shark-based tourism can provide a shift from a fisheries-based resource to a more profitable conservation-based resource; Vianna et al., 2011; Cisneros-Montemayor et al., 2013). Future conservation initiatives may benefit to focus on citizen science and ecosystem services based approaches to increase regional scientific knowledge. As the eco-tourism sectors of Macaronesian economies grow, so will the need for marine megafauna conservation.

While our findings represent the current status of marine megafauna research, the field continues to develop. Fundamentally, population level connectivity of marine megafauna species needs to be ascertained so that, among other management strategies, effective MPAs can be implemented, yet climate driven changes in abundance and distribution must also be considered to maintain protection. To prevent regional extirpation of vulnerable species, national and regional governments, and other relevant stakeholders must come together to optimize MPA designs using systematic conservation planning to meet common conservation objectives (Alves et al., 2022a; van Zinnicq et al., 2022). For example, although Madeira has much less research relative to the other archipelagos, it has the support of multiple stakeholders and has subsequently recently implemented Europe's largest MPA, the Selvagens Nature Reserve (Alves et al., 2022b). Critical data gaps identified in this review provide a path forward to better understand the marine megafauna within the complex island system of

Macaronesia, and aid in the development of regional, national, and international conservation strategies.

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.

AUTHOR CONTRIBUTIONS

AM: conceptualization, methodology, formal analysis, investigation, data curation, writing – original draft, review and editing, and visualization. CW: data curation, validation, investigation, resources, and writing – review and editing. FA, AD, MP, and JC-C: writing – review and editing, supervision, and funding. All authors are responsible for and agreed to the publishing of the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.819581/full#supplementary-material

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