Mammal Review

REVIEW

Sperm Whales—Island Specialists, Are They on the Way to Extinction? Systematic Literature Review in a Global Context

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ABSTRACT

Background: Sperm whale population units, resident off inhabited islands, are an important source of ecosystem services for local communities and may be subject to greater anthropogenic pressures than their oceanic conspecifics.

Aims: The objectives of this review were to identify sperm whale-island specialists' habitats around the world and to assess the level of anthropogenic pressure on such nearshore populations. The hypothesis was that sperm whales with this ecological specialisation are rare and that the negative impacts they experience living close to inhabited shores may be also exacerbated by Anthropogenic Allee effect.

Materials & Methods: This study was conducted using a systematic literature review, following the principles recommended by the PRISMA guidelines, with a scoping of records of the presence of sperm whale social units in the territorial waters of countries around the world published between 2003 and 2023.

Results & Discussion: A review of 422 relevant research papers revealed only two places in the world where sperm whales with an island ecological specialisation exist, and there are negative trends in both. Such population units experience cumulative anthropogenic pressures 1.7–1.8 times higher than oceanic ones. The charisma and media popularity of sperm whales, combined with the rarity of observation sites for this species, may increase pressure, potentially accelerating their extinction (Anthropogenic Allee Effect). The results of the study are presented in the form of a narrative synthesis, tables and a map.

Conclusion: Determining the ecological specialisation of sperm whale population units should be a key component of management at both the local and species level. Exploitation of ecosystem services provided by island specialists should be strictly regulated in favour of sustainability, in order to preserve this rare ecological type.

1 | Introduction

During the whaling era, large whales experienced dramatic population depletion, to the point of exterminating 99% of some species (Clapham 2016). Today large whales survive in geographically and ecologically truncated remnant populations (Letessier et al. 2023). Although whale populations have slowly begun to recover since the moratorium on whaling (Whitehead and Shin 2022), increasing anthropogenic pressure of various origins leave little hope for a full recovery (Clapham 2016; Plön et al. 2024). For example, in the Canaries, ship-strike mortality of whales exceeds the potential natural recruitment rate (Fais

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et al. 2016); in the Mediterranean, entanglement in fishing gear and ingestion of debris have been confirmed as causes of direct mortality (Jacobsen et al. 2010; De Stephanis et al. 2013), and the oil spill in the Gulf of Mexico has had a long-term impact on the reproductive capacity of affected cetacean populations (Marques et al. 2023).

In addition, human population growth and urbanisation have stimulated a demand for ecotourism (Curtin and Kragh 2014). Cetaceans are highly charismatic megafauna (Malinauskaite et al. 2021) and whale-related activities have become hugely popular. This has essentially replaced human use of whale provisioning services with cultural ones, such as ecotourism, education, aesthetic pleasure and entertainment (Cunningham et al. 2012). Operation of these services carve out a niche in a global market with an annual turnover in the billions of dollars (Mallard 2019), both through whale watching in the wild and the production of various photo, video and other art content. The industry provides jobs for local communities in over a hundred countries (O'Connor et al. 2009).

However, continued growth in demand is now leading to overexploitation, negatively impacting cetaceans (Parsons 2012; Gray et al. 2022), although not comparable to those of whaling. Studies show that there are limits on the carrying capacity of whale watching, beyond which the animals experience stress and disturbance, leading to short- and long-term negative effects (Christiansen and Lusseau 2012). The availability of whale habitats to end-users is the factor influencing the intensity of use and the level of cumulative pressure (Oliveira et al. 2022). For example, resident whale populations close to inhabited coasts could be under greater pressure than their migratory relatives, due to the cumulative duration of ecosystem service use, reinforced by continued presence in areas with the high risk of anthropogenic threats. Therefore, to conserve biodiversity and sustainably maintain ecosystem services, conservation and management are required not only at the species level, but also at the population level, identifying units directly providing services (Luck et al. 2003).

The sperm whale (*Physeter macrocephalus*) is a globally distributed cetacean. It can dive to a depth of more than 1000 m and typically inhabits areas with steep bathymetry, along the edge or remote from the continental shelf (Rice 1989; Whitehead 2003). Its distribution is highly gender-segregated. Males, after leaving the maternal pod, mostly have a solitary lifestyle and spend most of the time in cold productive waters (Whitehead 2003). Unlike males, matriarchal groups of females with immatures prefer tropical and subtropical waters and are rarely found at latitudes above 40° (and up to 50° N in the Pacific). Females lead very social lives, typically spending their entire lives in stable family units consisting of several generations of females and their offspring, hunting, caring for young together, periodically joining with other groups (Whitehead 2017).

Their complex social structure and cultural behaviour make sperm whales somewhat similar to human communities (Whitehead 2024b). In particular, like human nations and ethnic groups, sperm whale family units form clans with distinctive dialects and behaviours (Whitehead 2024a). Despite the potential for almost unlimited habitat, as a species sperm whales show ecological diversity, both as ocean nomads and as island specialists (Vachon, Hersh, et al. 2022). The cultural potential may be one of the factors influencing the geographical specialisation of the individual groups of sperm whales, where philopatry to specific small territories may be not simply due to habitat suitability, but to traditions that are transmitted through culture (Vachon, Eguiguren, et al. 2022).

Physeter macrocephalus is listed as "Vulnerable" on The International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Taylor et al. 2019). Even several decades after the end of whaling, sperm whales inhabiting areas off populated coasts are showing negative trends (Gero and Whitehead 2016; Somerford et al. 2022). Sperm whales are one of the most popular wild species in social media (Willemen et al. 2015), but there are not many known observation sites in the world for this species due to its preference for a deep-sea lifestyle. Social units with island-specific habitats in climatically favourable tourism regions may be susceptible to the Anthropogenic Allee effect. The Anthropogenic Allee effect is based on the public's pursuit for rare/charismatic or simply trendy species, which increases exploitation of these species and may ultimately lead to accelerated extinction (Courchamp et al. 2006). In the face of increasing anthropogenic pressures and climate change, sperm whale island specialists should be the focus of special management attention, both locally and globally, in order to maintain intraspecies ecological, genetic and cultural diversity.

The objectives of this review were (1) to identify current sperm whale island-specialists' habitats around the world; (2) to assess the level of anthropogenic pressures on such inshore populations. The hypothesis was that sperm whales with this ecological specialisation are rare, and that the negative impacts they experience living close to inhabited coasts and being used as providers of ecosystem services may be also exacerbated by the anthropogenic Allee effects.

2 | Methods

According to the IUCN, sperm whales occur in the waters of 132 countries worldwide (Taylor et al. 2019), of which 121 territories are within the range of females (between 40° N in the Atlantic, 50° N in the Pacific and 40° S). Sperm whales are a relatively data-rich species (Kaschner et al. 2012) and this study was undertaken by systematic literature review following the principles recommended by the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Page et al. 2021).

2.1 | Study Characteristics and Literature Search Strategy

The literature search was made using multidisciplinary academic search systems SCOPUS from Elsevier and Bielefeld Academic Search Engine (BASE) by Bielefeld University Library. A fairly broad search was undertaken using keywords "Sperm Whale" AND/OR "*Physeter macrocephalus*". In addition, a keyword search was conducted for "Ecosystem services

AND Whales/Cetaceans/Marine mammals/Sperm whales", in case any research on cetacean's ecosystem services had been conducted with or without being species-specific. In addition to period and keywords, the literature search on SCOPUS had no restrictions; on BASE it was limited to the following document types: books and parts of books, journals and newspaper articles, conference objects, reports and reviews. Once articles were identified, duplicate removal was performed using free version of Rayyan (Ouzzani et al. 2016) and MS Excel software.

Given that the focus of interest was on current sperm whale habitats, the literature review included records for the period from 2003 to 2023. The last search was conducted on 1 January 2024. A manual literature search was also conducted using references in relevant articles (during January and February 2024). Unique entries were then screened by titles and abstracts, and full text if the title and abstract were insufficient. In case the articles were in a language other than English, Google Translator was used for translation. The inclusion criteria for the review were records containing data on sightings of sperm whales in the 2000s, with the study area encompassing latitudes below 40° (and below 50° in the North Pacific). For the purposes of this study, the limit of distance from shore was taken as the boundary of the respective countries' territorial waters (12 nautical miles or 22 km). Records that were off-topic, based only on stranding data, on encounters that occurred before 2000, studies that were not geographically specific or for which no papers have been located, were excluded. In the end, 422 records were included in this review (Figure 1; Appendix S1).

2.2 | Data Extraction and Synthesis

2.2.1 | Definition of Island Specialists

All included studies were grouped geographically by ocean, Western and Eastern part of the world, hemispheres, countries/region, location. Given that the Mediterranean sperm whale population is considered to be isolated from the Atlantic (Rendell and Frantzis 2016), studies on the Mediterranean were classified as a separate group. Within each group, the following information was extracted from the records and included in order to identify locations relevant to this study: the fact of sperm whale presence in territorial waters, the sex composition, the frequency of occurrence in territorial waters. Rare occurrence was recognised when sperm whales were encountered sporadically and opportunistically, periodic occurrence was recognised when sperm whales were encountered in half or less of the field effort, regular/frequent occurrence was recognised when sperm whales were encountered predictably and/or in more than half of the field effort.

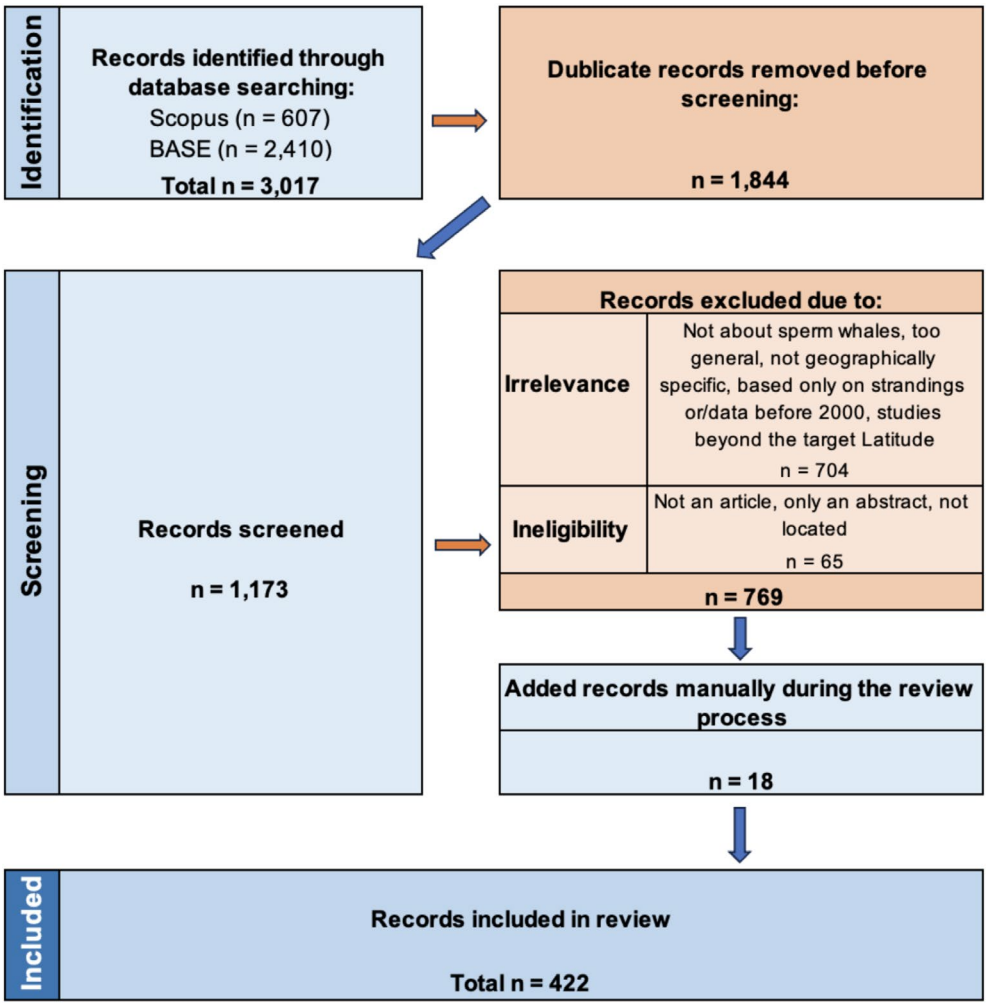

FIGURE 1 | Flow diagram of the literature search in this study according to PRISMA.

For locations with regular/frequent occurence, additional information was extracted: evidence and parameters of fidelity/residency, if any population trends were identified and the causes thereof, information on anthropogenic threats to the species in these regions. A region was recognised as habitat of sperm whale with island specialisation if it simultaneously met two criteria: (1) frequent/regular presence of sperm whales throughout the year and most of the year within the regions territorial waters (22 km or 12 nautical miles from the coast); (2) presence of populations/part of populations, with confirmed high intra- and inter-annual recapture rates, not only in the region, but also off specific islands. The analysis of the results in each oceanic group on locations with the presence of sperm whale social units in the territorial waters was presented in the form of a narrative synthesis, tables and map.

2.2.2 | Assessment of Anthropogenic Stress Level

To understand the level of anthropogenic pressure depending on habitat, an estimate of the cumulative effects of anthropogenic threats was made for the average ocean habitat and for locations with frequent sperm whale presence. For each location, information on the presence of threats and their intensity was categorised according to the following categories: direct use of sperm whale provision (whaling) and cultural (whale watching) ecosystem services, entanglement in fishing gear, habitat degradation, pollution, acoustic disturbance, vessel strikes. The impact level scoring was made on a modified scale (Hammar et al. 2020) according to the effect on the species on individual and population level to each of the seven categories of anthropogenic threats in the respective region:

- *0.0 No or negligible impact.*
- *0.2 Low stress or risk of incidental occurrence.*
- *0.4 Stress with implications for the survival or reproduction of individuals with possible long-term adverse effects on the population.*
- *0.6 Very significant impact or occasional direct mortality with a probability of adverse effect on the population.*
- *0.8 Frequent mortality leading to population decline.*
- *1.0 Pressure leading to imminent extinction of the population.*

The cumulative effect was calculated as the total impact, that is, the sum of the effect scores of overlapping anthropogenic stressors in the region (Foley et al. 2017). If no records for a specific stressor were found in the region, the species average score for open ocean was taken. The maximum cumulative impact was calculated, that is, without taking into account residency (duration of exposure of individuals to stress in a particular region).

3 | Results

3.1 | Sperm Whale-Island Specialists' Locations Worldwide

For this review, 422 relevant research papers concerning sperm whales were assessed, published between 2003 and 2023 (Figure 2).

As a result, records of sperm whale occurrences in the territorial waters of 52 countries located in the study area were identified (Appendix S2), of which only eight from five regions of the world where sperm whales are frequently encountered throughout the year (Figure 3).

3.1.1 | Pacific Ocean

Based on the reviewed records, the presence of groups of female sperm whales in the territorial waters of at least 21 states in the Pacific Ocean has been detected (Figure 3; Appendix S2). However, except for one location in Japan, these sightings nearshore were rare or occasional, despite the presence of known aggregations, some of which are more or less well studied, for example off the Galapagos Islands (Cantor et al. 2017; Eguiguren et al. 2019), Chile (Bedriñana-Romano et al. 2022), Hawaii (Giorli et al. 2016; Kratofil et al. 2023), Mariana Islands (Wiles 2005; Fulling et al. 2011; Hill and Yano 2021), Gulf of California (Jaquet et al. 2003; Fossi et al. 2014).

The remote sub-tropical islands of Ogasawara, Japan, located approximately 1000 km south of Honshu in the western Pacific Ocean (Ichiki 2003). Groups of sperm whale females with calves were frequently encountered there within 22 km from the shore (Bahl et al. 2004) year-round with a peak in August–September (Aoki et al. 2007, 2012). The only photo-ID study conducted in

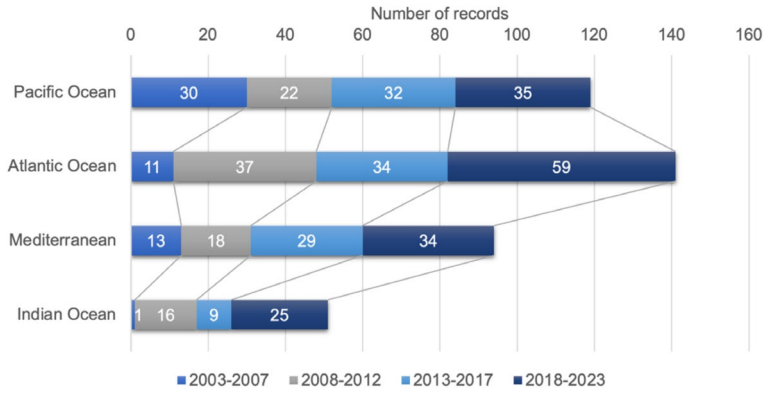

FIGURE 2 | Number of publications for the period 2003–2023 containing data on sperm whales included in this study by year and region.

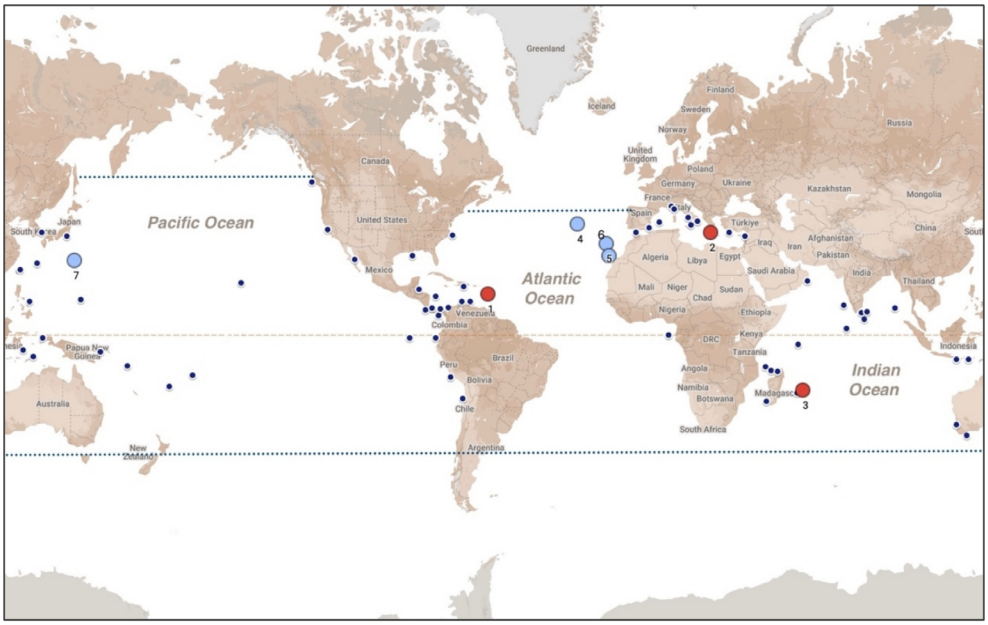

FIGURE 3 | Identified locations of sperm whales occurring within 22 km from shore recorded between 2000 and 2023: Small dots—rare or occasional encounters; light blue circles—frequent encounters, but not resident: 4,5,6—Macaronesian eco-region (4—Azores, Portugal, based on photo ID-studies 1987–2019, 5—Canaries, Spain, based on photo ID-studies 1999–2012, 6—Madeira, Spain, based on photo ID-studies 2001–2019), 7—Ogasawara Islands, Japan, based on only photo ID-study 1994–1999; red circles—locations of the presence of resident sperm whales with frequent occurrence next to the shore: 1—Lesser Antilles (based on photo ID-studies 1984–2020), 2—Hellenic Trench, Greece, based on photo ID-studies 1998–2009, 3—Mauritius, based on photo ID-studies 2008–2023. The blue dashed line separates the target area of the study—the latitudinal boundaries of female sperm whales.

Ogasawara waters between 1994 and 1998 identified at least 129 unique individuals from the 25 groups of females and juveniles encountered (Mori et al. 1999). The low recapture rate led the authors to assume that the whales are not resident to the island waters and that different groups visit the island each year for foraging. Later acoustic studies have shown that most of the whales encountered at Ogasawara belong to one of the vocal clans widely distributed in the South Pacific (Amano et al. 2014).

3.1.2 | Atlantic Ocean—Oceanic Waters

In the north Atlantic below 40° N, few well known habitats of sperm whales distributed throughout oceanic waters. In the West, sperm whales inhabit offshore waters in the Sargasso sea, Gulf of Mexico; canyon system of Bahamas (Claridge et al. 2015) and nearshore of Eastern Caribbean (Figure 3; Appendix S2). In the Eastern Atlantic, except for the Macaronesia ecoregion (Ferreira et al. 2022), encounters are mostly outside territorial waters despite the sperm whale being one of the most commonly encountered species in the oceanic waters off southern Europe and the north-west African continent (Correia et al. 2020; Cartagena-Matos et al. 2021). In the South Atlantic, due to the wide extent of the continental shelf on both the western and eastern sides, sperm whales are seldom found in coastal waters (Carvalho et al. 2022).

The Lesser Antilles are a chain of volcanic islands in the eastern Caribbean stretching from north to south for approximately 600 km. Sperm whales are regularly occurring in the region within 22 km from shore, with the highest densities off Guadeloupe, Dominica, Martinique, St. Lucia and St. Vincent and the Grenadines (Vachon et al. 2024). This is probably the most well-studied sperm whale population in the world, also at individual level (Gero and Whitehead 2016). Total population size is about 400 individuals, consisting of about 50 social units/groups. Some social units have shown high residency towards the same specific islands of the Lesser Antilles for many years (Gero et al. 2014; Vachon, Hersh, et al. 2022; Vachon, Eguiguren, et al. 2022). The social units in Dominica and Guadeloupe are best studied, which made it possible to calculate population trends for these areas. Results showed an extremely disturbing population trend, with the annual rates of −4.5% and −6.2%, respectively (Gero and Whitehead 2016; Rinaldi et al. 2021).

Macaronesia ecoregion is situated in the Eastern North Atlantic and includes three oceanic groups of islands—the Azores, Madeira (Portugal) and the Canary Islands (Spain), where groups of females and immatures are present year-round (McIvor et al. 2022; Ferreira et al. 2022). In this region, sperm whales are most abundant in the Azores, where they are one of the most studied species (Cartagena-Matos et al. 2021). Sperm whale social units visiting the archipelago use these areas heterogeneously and move between islands, without island-specific association (Pinela et al. 2009). Photo-ID studies over more than two decades identified about 3000 individuals (Mullin et al. 2022), but, like Madeira with a catalogue of 278 individuals, have shown a low index of fidelity (Ferreira et al. 2022), and no permanent residents (Mullin et al. 2022). Genetic studies have shown that sperm whales visiting Macaronesia could belong to the same larger population (Pinela et al. 2009), about ¼ of which uses the region on a regular basis (Ferreira et al. 2022)

for mating and calving, especially in summer, but spend most of their time elsewhere (Ferreira et al. 2022).

3.1.3 | Atlantic Ocean—Mediterranean

The Mediterranean sperm whale population is segregated from the Atlantic by the Strait of Gibraltar (Engelhaupt et al. 2009). Sperm whales are regularly found in the Strait itself, and in both the western and eastern Mediterranean basins. Despite sperm whales mostly favouring waters beyond the continental shelf (Gnone et al. 2023), they are occasionally found in the territorial waters of many countries, like Spain, France and Monaco, Italy, Turkey, and Syria and resident off the Ionic Islands of Greece (Figure 3; Appendix S2).

The Hellenic Trench is a system with steep bathymetry, 1100 km long, fringing from the west of the Ionian Islands, along south of Crete, until the South and East of Rhodes Island, where sperm whales are regularly encountered all year around along a 1000 m contour that is mostly 3–10 km offshore (Frantzis et al. 2014; Diogou et al. 2019). All age and sex groups represented in the Hellenic Trench with the number about 200–250 individuals (Frantzis et al. 2014). Long-term surveys, although mainly conducted in summer, showed that more than half of the individuals had inter-annual recaptures and at least some social units are probably permanent residents of the Hellenic Trench (Frantzis et al. 2014). However, no evidence has been found to suggest that some units in the Hellenic Trench have an island-specific association. This is also supported by the fact that attempts to develop commercial sperm whale watching happened in some coastal areas of the Hellenic Trench, but the low density and unpredictability of sperm whale presence in a specific location due to their movements along the trench has made small-scale sperm whale watching unprofitable (A. Frantzis, personal communication, 3 June 2024).

3.1.4 | Indian Ocean

At least 11 countries were identified with sperm whales encounters within 22 km from shore (Figure 3; Appendix S2). Sperm whales were rarely or occasionally found in the territorial waters of Oman, India, Maldives, Seychelles, Comoros, Madagascar, Réunion (France), Australia, Indonesia, Sri Lanka, and only in Mauritius they were found frequently.

Mauritius is an oceanic island of volcanic origin located in the Western Indian Ocean about 1000 km east of Madagascar (Bhagooli and Kaullysing 2018). The sperm whale is one of the most common cetacean species off the main island of Mauritius with a year-round presence (Corbett 1994; Webster et al. 2020; Chambault et al. 2021; Sarano et al. 2021). Mauritius is recognised as one of the most important known feeding and breeding grounds for sperm whales in the Western Indian Ocean (IUCN-MMPATF 2020). The area is mostly inhabited by social groups of females, visited occasionally by adult males for mating. Photo-identification studies conducted from 2008 to 2023 have identified over 250 unique individuals of both sexes (Huijser et al. 2020; Sarano et al. 2022; MMCO unpublished data). Genetic and capture-recapture studies revealed that the matrilineal group totaling about 30 individuals are residents of the main island of Mauritius (Sarano et al. 2021, 2022). Acoustic studies identified the possible presence of two sympatric vocal clans, with some social groups possibly having a wider range and visiting Mauritius periodically (Huijser et al. 2020). The resident groups are present most of the year along the west coast of Mauritius within 22 km from shore, with rare short-term migrations to the neighbouring islands (Chambault et al. 2021). There were no publications on population assessment and population trends at the time of this study.

Therefore, only two regions, the Lesser Antilles and Mauritius, have sperm whale social units that fully met the criteria of island specialists, that is, small-scale geographic specialisation and high residence near specific islands.

3.2 | Cumulative Anthropogenic Impact on Sperm Whales Depending on Habitat

Cumulative anthropogenic impacts were assessed for the average ocean habitat typical of the species and for five selected regions where frequent presence of sperm whales in coastal areas was recorded. The results showed that the level of pressure on sperm whale groups in four of the five regions, without considering residency, was at least 1.6 times higher than the pressure they would have experienced in the open ocean (Appendix S3; Figure 4).

In the Ogasawara Islands in the Pacific, pressures in coastal waters were lower than in the open ocean. This was attributed to the remoteness of the islands, low human population density and limited tourist traffic, as well as the prohibition of whaling in island waters, which remains a risk in oceanic areas. The graph reflects pressure without taking in account the length of residence. Thus, non-resident groups visiting the islands of Macaronesia may, on average, experience less cumulative impact than shown in the graph as they spend most of their time in the open ocean, and visits may not be annual (Ferreira et al. 2022). The resident groups of the Lesser Antilles and Mauritius, which are present in their regions all year round, experience the full range of cumulative pressures, which are 1.8 and 1.7 times higher, respectively, than their oceanic counterparts.

4 | Discussion

4.1 | Island Specialists and Anthropogenic Pressure

The main objective of this review was to identify current habitats where sperm whales are permanent residents in coastal waters, that is, have island ecological specialisation, and to assess the level of anthropogenic pressure on these groups. Given that sperm whales mostly inhabit areas off the continental shelf, the assumption before this systematic review was that there would not be many such locations. Only five regions of the world were identified where population units of the species regularly utilise coastal areas for at least most of the year, but only two of these, the Lesser Antilles and Mauritius, have units meeting the criteria of island specialists.

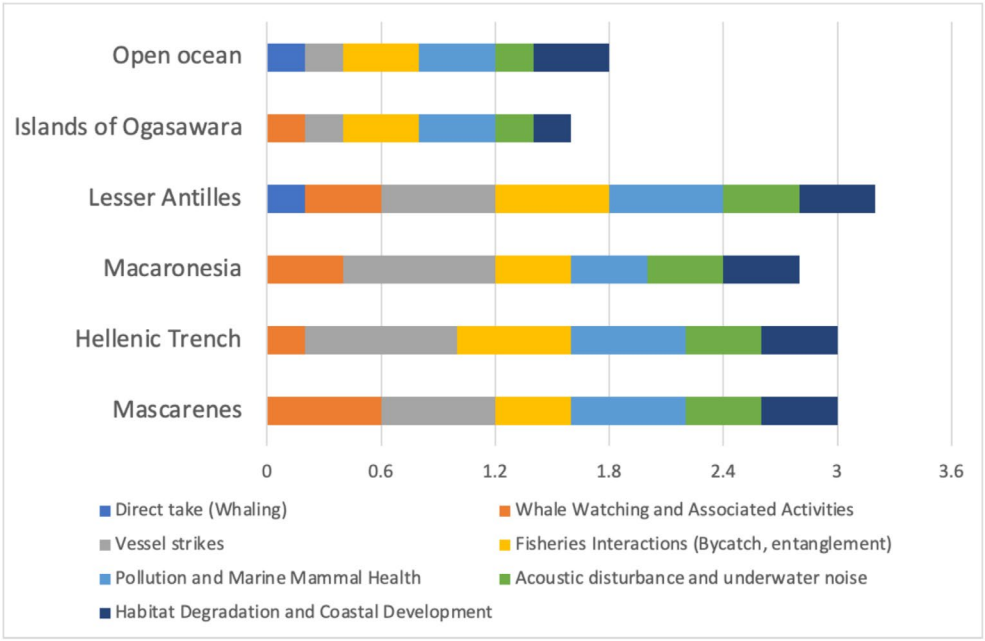

FIGURE 4 | Cumulative anthropogenic pressure on sperm whales by habitat without consideration of residency (duration of presence in the region).

Due to their permanent presence and their biomass, these island specialists have significant ecological influence on the habitat region through ecosystem services. First, it shapes the functioning of coastal ecosystems, has significant impacts on lower trophic levels and serves as a natural defence against climate change (Sheehy et al. 2022; Plön et al. 2024). Secondly, both regions are popular whale-watching destinations, precisely because of the high probability of encountering sperm whales. The year-round business has an impact on local communities, providing direct economic benefits (Appendix S3).

Long-term studies in the Lesser Antilles, particularly in Dominica and Guadeloupe, have shown that the population is declining, the precise reasons for which are not clear. In Mauritius, population trends are not known, but the increasing number of stranded sperm whales (Plön et al. 2023, MMCO unpublished data) is a negative sign, especially since actual mortality is usually much higher than the number of reported cases (Gero and Whitehead 2016).

Both the Lesser Antilles and Mauritius are regions with intense anthropogenic activity, where resident sperm whales experience from moderate to severe levels of stress (Appendix S3) from all categories of threats: fisheries interactions, habitat degradation, ship strikes, pollution, acoustic disturbance, whale watching, which is poorly regulated (Gero and Whitehead 2016; Barteneva et al. 2022; Plön et al. 2024). The cumulative impact on island specialists is almost twice the level of stress experienced by oceanic individuals (Appendix S3; Figure 4).

Although it is recognised that major efforts need to be directed at threats that carry fatal risks (Gero and Whitehead 2016), regulating and monitoring the impacts of whale watching should be given as much attention as lethal threats, especially for resident populations that are under constant pressure. There is consensus that whale watching activities are increasingly causing harm to cetaceans. In particular, female sperm whales with calves change their behaviour, increasing energy expenditure and reducing time for suckling and parental care (Williams et al. 2006). Moreover, it is suggested that the cumulative effect on social units that are exposed to whale watching for extended periods of time may lead to long-term disruption of female bioenergetic balance (Boys et al. 2019) and reduction of individual fitness (Lundquist et al. 2013). This puts the population at risk as its future depends on the well-being of adult females (Chiquet et al. 2013). Swimming with whales further exacerbates this effect when the presence of swimmers causes even stronger and long-term negative reactions (Stack et al. 2021), as well as agonistic behaviour (Barra et al. 2020).

No records of sperm whale carrying capacity assessments for sustainable use of their cultural ecosystem services were found in either the Lesser Antilles or Mauritius. At the end of 2023, Dominica announced the establishment of the world's first reserve for sperm whales, covering 788 km^2 (Dominica News Online 2023). The establishment of this reserve is expected to reduce collisions with ships and also to improve the management of whale-watching activities. However, swimming with sperm whales remains a matter of serious concern (Gero and Whitehead 2016). In Mauritius, although banned (Tourism Authority 2012), swimming with sperm whales is still happening. This has already resulted in whales exhibiting more frequent avoidance and defensive behaviour, as well as reducing the quality of the tourist experience (Barteneva et al. 2022).

The rarity and accessibility of these two world-famous populations may also increase demand for the opportunity to see sperm whales in the wild, which could cause an Anthropogenic Allee Effect. For the general public, whales in the wild are an icon of ocean conservation and a source of strong emotional response (Malinauskaite et al. 2021; Suárez-Rojas et al. 2023). For example, the announcement of the establishment of a sperm whale

sanctuary in Dominica was a media event. However, it is worth reflecting on the case of ancient temple complex Angkor Wat in Cambodia, when their declaration as an object of UNESCO World Heritage triggered a tourism boom that the historical heritage was not ready to digest without degradation, giving rise to reflections on whether the UNESCO label is a blessing or a curse (Vecco and Caust 2019).

Excessive pressure can lead to the loss of these subpopulations, either through gradual extinction or by forcing them to move to less stressful habitats, turning them into refugees. This occurred during the whaling era, prior to which sperm whales were not uncommon in coastal areas of the Western Indian Ocean (Letessier et al. 2023), Western Australia (Carroll et al. 2014), Indonesia (Sahri et al. 2020), and off the coast of Peru (Casamayor et al. 2022). However, because of their accessibility, they were the first targets of whaling, which resulted in the physical removal of most of them with the survivors abandoning their habitats, moving deep into the ocean, away from humans (Letessier et al. 2023). Today, sperm whales are found much less frequently or not at all in the same coastal areas, probably because the cultural connectivity of population units to these areas has been lost. This raises the question of whether the island specialists of the Lesser Antilles and Mauritius are just a rare species specialisation or the last remaining ones. Whatever the case, the loss of these island specialist may be irreversible.

To prevent the loss of sperm whale island specialists as an ecological type, threat mitigation measures should be implemented in their habitats, great caution should be exercised in promoting the ecotourism destination (Courchamp et al. 2006; Angulo et al. 2009), and the use of sperm whale ecosystem services should be strictly limited, regulated and monitored to ensure sustainability. The regenerative model, that focuses on natural objects welfare for creation natural capital (Bejder et al. 2022), should be adopted with as little stress on the animals as possible. The demand for underwater observation can be met by providing individual and/or group experiences with an in situ effect using modern technologies, such as virtual reality (Bejder et al. 2022). Such methods can provide a guaranteed and perhaps even higher quality emotional experience, backed up by safety, high accessibility to the general public, and almost zero impact on the animals. The conservation of these sperm whale populations should be a priority, both in the current use of their ecosystem services and any development projects that may influence their health and/or habitat.

4.2 | Broader Implications

A synthesis of the known information on coastal use by sperm whales has allowed us to look at the ecological specialisations of the species systematically in a global context and to identify three main types: nomadic and island specialists, and an in-between specialisation—regional residents.

A significant difference in the ecological behaviour of Pacific and Atlantic sperm whale communities was noticed long ago (Whitehead et al. 2012). The Pacific population consists of sympatric clans that may number thousands of individuals. Females appear to have wider ranges (1000–4000 km) than in the Atlantic (on average 200–1000 km) and make long migrations due to climatic factors that cause them to follow prey, such as between the Galapagos and the Gulf of California (Mizroch and Rice 2013). This is consistent with the frequent presence of non-resident groups of females belonging to one of the South Pacific vocal clans in the coastal waters of Japan's Ogasawara Islands, where the bottom topography near the island favours the presence of squid, the main prey of sperm whales (Mori et al. 1999). In addition, groups of females are often seen with calves. It can indicate that sperm whales may be using the islands as nursing grounds with more predictable habitat, which is important during the early periods of offspring rearing. This is similar to the Gulf of California, which is used not only as nursing grounds, but also for breeding (Jaquet and Gendron 2009). This is likely to be a case of nomadic ecological specialisation of sperm whales, which have large habitats and use certain coastal areas for short periods of time during certain seasons and periods of the life cycle.

Apparently, such specialisation is not unique to the Pacific Ocean. It is most likely to be shared by some sperm whales in the North Atlantic that use the Macaronesian eco-region as feeding and breeding grounds. Sperm whales in nearshore waters occur frequently and year-round, but where for several thousand identified individuals, recapture rates are very low and the main habitat of the population remains undefined. It is possible that, on a smaller scale, groups with this specialisation may also be present in some Mediterranean regions, such as the Balearic Islands, where the occurrence of sperm whales is dynamic and recapture rates are low as well (Pirotta et al. 2020). The population structure of sperm whales in the Indian Ocean is still poorly understood, but nomadic sperm whales may occur in Sri Lankan waters. The peninsula and adjacent waters appear to be mating and feeding grounds for both sexes of individuals that spend most of their time somewhere else (Ilangakoon 2012). Sperm whales off Sri Lanka often form large aggregations up to few hundreds, probably under high predation pressure (Nanayakkara et al. 2020), which may be similar to the Pacific.

In general, in the Atlantic, including the Mediterranean, sperm whale populations are more genetically and geographically structured than in the Pacific (Whitehead et al. 2012). There are relatively well-studied populations, with a range of less than 1000 km, that do not overlap with each other (Engelhaupt et al. 2009; Mullin et al. 2022). These include, for example, populations from the Gulf of Mexico, Sargasso Sea, Bahamas and Lesser Antilles in the western Atlantic and the Ionian Islands in the eastern Mediterranean. These regionally resident populations do not appear to extend beyond their limited region. Their range is most often associated with a steep edge of the continental shelf, a system of seamounts and/or canyons containing a more or less stable amount of prey sufficient for foraging, and adult males visit them for mating. Regional residents may also be present in the Pacific. Studies of sperm whales in the East China Sea have shown regular occurrence and suggested possible residency (Liu et al. 2023).

Island specialists as discussed above exhibit high fidelity to particular islands, spending most of their time in a restricted range of about a 100 km, making only short migrations to

neighbouring islands. Resident groups of particular islands appear to be small, consisting of one or more social units, and in both known regions are part of sympatric clans inhabiting the regions. Whether there are units with such specialisation elsewhere is difficult to say. For example, in Atlantic Macaronesia, not all islands are equally studied. In the Pacific, sperm whales are not uncommon in Indonesia, but there is very little research there and direct take of sperm whales still remains.

It appears that units of all three specialisations can be found in some regions, as well as different specialisations in the same vocal clans. For example, in Mauritius waters, long-term studies have shown the presence of not only resident sperm whales, but also units with inter-annual recaptures but short intra-annual residency—possible regional residents of the Mascarenes, as well as groups that have been caught only once and likely have a much wider range (Huijser et al. 2020; Sarano et al. 2022). In the Lesser Antilles, the situation appears similar. Threat analyses showed that all three specialisations are exposed to roughly the same set of threats, but with different risk and intensity depending on the habitat region and length of residency of the population units. Island specialists are subjected to the highest stress. This specialisation is characteristic not only of sperm whales, but also for some other pelagic toothed Whales species, for example melon-headed whales and false killer whales (Aschettino et al. 2012). These groups are integrated into coastal ecosystems and can have a significant impact on local human communities. Therefore, determining the ecological specialisation of population units should be a key component for conservation management at both the local and species level.

Author Contributions

Svetlana Barteneva-Vitry: conceptualization, investigation, methodology, data curation, formal analysis, visualization, writing – original draft, writing – review and editing. **Chandani Appadoo:** writing – review and editing, supervision. **Stephanie Plön:** writing – review and editing, supervision.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.