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Rebounding marine mammal species and conservation recovery challenges

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Rebounding marine mammal species and conservation recovery challenges

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Editorial: Rebounding marine mammal species and conservation recovery challenges

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Editorial on the Research Topic
Rebounding marine mammal species and conservation recovery challenges

1 Introduction

Marine mammals have been valued for millennia for their cultural significance, cognitive capabilities, ecological role, and resource value. At this complex social-ecological intersection, marine mammal populations worldwide have been shaped by historical exploitation, followed by more recent decades of protection and conservation, enabling the rebound and recovery of numerous (though not all) marine mammal populations (Magera et al., 2013; Roman et al., 2013). Yet, as marine mammals celebrate recent growth in abundance and distribution, conflicts have emerged across diverse ecological, sociological, economic, and political contexts. These conflicts include ship strike, depredation, bycatch, impacts of ecotourism, competition for resources, changing cultural values and political challenges to marine mammal conservation (Nelms et al., 2021). A lack of understanding of historical baselines, differences between ecological and social carrying capacity, and perceptions of "overabundance," whether referring to 1,200 Hawaiian monk seals or 7 million harp seals, fuels discord. While further studies of contemporary and historical marine mammal ecology can address some of the relevant knowledge gaps, these emerging conflicts also require interdisciplinary approaches and the inclusion of social science to address conservation recovery challenges. Despite this need, conflicts in the marine environment are often overlooked in human dimensions of wildlife research (Johnston et al., 2020; Jackman et al., 2023; Wallen et al., 2024).

Our aim with this Research Topic was to further emergent discussions on how to best address complex socio-ecological issues related to marine mammal recovery. The articles in this Research Topic, coming from a variety of disciplinary perspectives, tackle challenging questions such as, how do we measure and document recovery? How do we assess and address social-ecological impacts of recovery? And how do conflicting perceptions of marine mammal population recovery shape "problem" definitions and policy approaches? From this growing body of literature, it is evident that we will need to consider often-opposing values and interests in the development of solutions, and engage diverse stakeholders in decision-making processes.

2 Documenting marine mammal recovery

Marine mammal abundance and distribution have traditionally been surveyed by a combination of visual and acoustic methods. However, established best practices for these survey methods often require significant resources (e.g., vessels, acoustic equipment, time, money) that can limit their broad-scale application. As communities grapple with growing marine mammal populations and the associated conflicts, new methods of documenting marine mammal recovery are therefore emerging, and becoming increasingly accepted in the scientific and management arenas.

Emerging tools (e.g., machine learning, AI, drones, eDNA) and the use of alternative data sources (e.g., opportunistic sightings, historical records, local and traditional ecological knowledge) have the potential to increase accuracy as well as engage a broader audience (Hodgson et al., 2018; Dujon et al., 2021; Suarez-Bregua et al., 2022). Rannankari et al. highlight how long-term data collection archives, combined with the use of contemporary emerging technologies, can elucidate historical ecological shifts with important management implications for species in recovery in areas that now overlap with modern anthropogenic threats. Particularly within a historical context of heavy hunting, tensions between the line of recovering and recovered can fuel concerns about down-listing rebounding marine mammal populations given the modern threats that persist.

Engaging citizen scientists can further increase capacity and public scientific literacy, as well as engage the communities potentially in conflict with rebounding marine mammals (Puskic et al.). Olson et al.'s use of long-term opportunistic sighting records to document spatiotemporal shifts in mysticete presence exemplifies how citizen science can be effectively incorporated into community-driven local monitoring. Their approach not only allows for the tracking of regional trends but also fosters collaboration across geopolitical borders for the collective benefit of ocean stewardship.

3 Marine mammal recovery in a social-ecological context

As top predators or mesopredators in many coastal ocean ecosystems, shifts in marine mammal abundance and distribution as the species recover are likely to have broad-reaching social-ecological impacts. Considering these diverse impacts, including complex interactions between marine mammals, their prey, humans, and the environment in which they all co-exist, is important to both defining the challenges associated with marine mammal recovery and developing solutions.

Across a broad array of diet studies and field observations, we see that the ecological impacts of marine mammal populations are highly context-dependent, they can vary significantly in magnitude and direction, and they are often unexpected. Thus, regional studies that consider the impact of marine mammal recovery on both commercially exploited species (e.g., Lyssikatos and Wenzel) and species or habitats of conservation concern (e.g., Leach et al.) are critical to describing trophic interactions that support ecosystem-based management (Townsend et al., 2019) and can help address misperceptions of marine mammal impact.

While traditionally provided as input to trophic models, novel application of social-ecological systems (SES) models parameterized with trophic interaction data can also be used to predict impacts of marine mammal recovery and identify factors that support and threaten system resilience (García-Castañeda et al.). SES models can consider not only predator-prey interactions, but also impacts of changing environmental conditions, and connections between marine mammals and human activities. Novel insights gained from the SES framework may therefore facilitate the development of adaptive management strategies that can both support recovering marine mammal populations and mitigate associated challenges.

4 Perceptions of marine mammal recovery

In these complex social-ecological systems, understanding how diverse stakeholders perceive rebounding marine mammal populations is critically important. When they return to the marine environments from which they were extirpated, pinnipeds, for example, are often greeted by human populations who have no social memory of their historical presence. This phenomenon of "shifting baseline syndrome" drives conflicts as oceans depleted of large marine predators are viewed as the norm and rebounding populations are perceived as intruders (Pauly, 1995; Roman et al., 2015). The consequences include not only social conflict and dismantling of legal protections, but also direct violence against marine mammals (Konrad et al.).

Social construction and social identity frameworks can help explicate conflict dimensions. Konrad et al. identified the competing social constructions underlying conflicts over rebounding populations of Hawaiian monk seals, where seal rescue volunteers on the Hawaiian Islands view the seals as innocent victims of human-caused destruction in contrast with fishers who see the seals as resource competitors and a proxy for federal fishing restrictions. Because Hawaiian monk seals were extirpated so early in Hawaiian history, they do not play a role in traditional culture and are perceived as invaders and vectors of colonialism by Native Hawaiians. Awareness of these conflict drivers and deliberative management approaches that focus on engagement and communication can be of value to managers.

In the coastal areas of the Northwest Atlantic, stakeholders also hold conflicting views of seals. Still, stakeholder groups are not monolithic; individuals may hold multiple social identities at the same time (Lute and Gore, 2018). In a study of perceptions of residents, tourists and commercial fishers, most commercial fishers simultaneously adhered to non-consumptive (animal protection, environment) and consumptive (angler, hunter) social identities (Bratton et al.). Shared mutualistic values toward marine mammals even among divergent stakeholder groups further suggests some common ground for coexistence with marine mammals and stakeholder collaboration (Jackman et al., 2023).

5 Future directions

The story of the recovery of North Pacific gray whale populations followed by population declines that Garcia-Castaneda et al. relate offers a cautionary tale about the precarious nature of rebounding marine mammal populations, especially in the global context of climate change (Davis, 2022). Even with substantial rebounds in some marine mammal populations, species face anthropogenic threats to conservation gains (Bogomolni et al., 2010; Precoda and Orphanides, 2022). Moreover, in the current political climate, hard-won national and international legal frameworks that protect marine mammals and healthy ecosystems are in jeopardy.

The need for coalitions and collaboration to preserve conservation gains has never been greater. Interdisciplinary research and communication with and among stakeholder groups are critical to this endeavor. Evidence of the historical abundance of marine mammal populations can help address misperceptions about their return to coastal waters (Cammen et al., 2018). Increased awareness of the ecological benefits of marine mammals increases opposition to lethal management (Jackman et al., 2024). Valuing both experiential expertise and empirical data on the extent to which marine mammals interact with fisheries can contribute meaningfully to management conversations, particularly with a community science approach that involves fishermen, managers and scientists together (Bogomolni et al., 2021). Beyond direct benefits to addressing these emerging human-wildlife conflicts, community connection with rebounding populations can further foster empathy, help to mitigate ecological grief, and have broad reaching impacts for our coastal communities.

Author contributions

AB: Conceptualization, Writing – original draft, Writing – review & editing. KC: Conceptualization, Writing – original draft, Writing – review & editing. JJ: Conceptualization, Writing – original draft, Writing – review & editing.

Conflict of interest

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

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Utilizing long-term opportunistic sightings records to document spatio-temporal shifts in mysticete presence and use in the Central Salish Sea

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The Salish Sea supports several baleen whale species, including humpback (*Megaptera novaeangliae*), gray (*Eschrichtius robustus*) and minke whales (*Balaenoptera acutorostrata*). With the exception of minke whales, these species were decimated by commercial whaling in the 1900s. Because recovery of these populations is monitored on broad spatial scales determined by stocks or populations, their use of the Salish Sea ecosystem is not well documented or understood. We collated 17,436 opportunistic sighting reports to assess patterns in mysticete presence and distribution in the Salish Sea (1976–2019). We used the proportion of sightings for each species and spatial models targeting comparisons between species to limit the influence of spatio-temporal variation in reporting efforts. Humpback whale sightings have increased dramatically since the late 2000s, mirroring population-wide increases and suggesting a renewed use of historically important feeding areas. Gray whale sightings increased most notably at two distinct times (1989, 2017), both of which align with periods of high mortality experienced by the delisted Eastern North Pacific stock of gray whales and may reflect individuals straying from their migration routes. Sightings of minke whales remained relatively stable over this study period and were likely driven by a group of 30–40 individuals that forage off shallow banks and bathymetrically complex habitats around the San Juan Archipelago. Though it can be difficult to separate the bias that accompanies public sightings databases, citizen science efforts are invaluable for monitoring the recovery of rebounding populations and can illuminate longitudinal patterns that would otherwise go unnoticed.

KEYWORDS

Salish Sea, citizen science, baleen whales, population recovery, sightings

1 Introduction

The Salish Sea, the inland fjord waters of Washington State USA and British Columbia (BC) Canada, includes the Strait of Juan de Fuca (SJF), Puget Sound and the Georgia Strait and is home to a variety of marine fish, invertebrates, marine mammals and seabirds (Brown and Gaydos, 2007). Marine mammals that are frequently encountered in the Salish Sea include two species of porpoise, two delphinid species, including killer whales (*Orcinus orca)*, three baleen whale (*mysticetes*) species, and four pinniped species [seals (*phocids*) and sea lions (*otariids*)] (Gaydos and Pearson, 2011). The most well-known marine mammals of the Salish Sea are the resident killer whales or orcas (*Orcinas orca)*. Scientists and the public alike track Southern Resident killer whale presence both spatially and temporally documenting their location, movements and population trends (Olson et al., 2018). These whales are arguably one of the most well studied marine mammals in the world (Krahn et al., 2004).

Studies on baleen whales in the region, on the other hand, are less ubiquitous. The baleen whale species known to occur in the Salish Sea include humpback (*Megaptera novaeangliae*), gray (*Eschrichtius robustus*) and minke whales (*Balaenoptera acutorostrata*). Indigenous communities along the outer coasts of Washington and British Columbia traditionally harvested baleen whales, particularly migrating gray whales and humpback whales, for subsistence and cultural practices. While this practice is not thought to have occurred in the inland waters of the Salish Sea (Losey and Yang, 2007; McMillan, 2015), the widespread international commercial whaling of the 19th and 20th centuries led to dramatic population reductions of primarily gray and humpback whales in the region. They were eventually afforded protection from harvest via international law (International whaling convention of 1946) and are also protected by several laws in the US and Canada passed in the 1970s.

Gray whales reach average lengths of about 12 m, weigh up to 40,000 kg and live to be between 40–80 years old (Ford, 2014). They are primarily bottom feeders that consume a wide range of benthic and epibenthic invertebrates (Pike, 1962). Eastern North Pacific gray whales primarily migrate between their breeding grounds in central Baja Mexico to feeding grounds along the nearshore waters from Oregon to Alaska (Pike, 1962). Populations in the eastern North Pacific were declared endangered under the Endangered Species Act (ESA) in 1973 when the act was established. They have since recovered and were delisted in 1994[1], though have experienced large fluctuations in population and mortality events along their entire range (59 FR 31094; Stewart et al., 2023a). Gray whales in the Salish Sea represent a small portion of this overall population that stops to feed during their northbound migration. In recent decades, a small group of gray whales termed "the Sounders" has been documented returning annually each spring to North Puget Sound waters to feed on ghost shrimp (*Callianassa californiensis*; Weitkamp et al., 1992; Calambokidis et al., 2015).

1 https://www.fisheries.noaa.gov/action/delisting-eastern-north-pacific-gray-whale-esa

Humpback whales can reach lengths up to 17 m, weigh up to 40,000 kg and live up to 80–90 years (Ford, 2014). They are mid-water feeders that eat small crustaceans and forage fish using a variety of methods such as bubbles, sounds and barriers to herd large schools of their prey and enhance their feeding efficiency (Clapham, 2000). They were declared endangered worldwide by the ESA in 1973 (35 FR 18319). Based on genetics and movement data, the species was broken into 14 distinct population segments (DPSs), with only four currently listed under the ESA (Calambokidis et al., 2008; Baker et al., 2013; Bettridge et al., 2015). Humpback whales in the Salish Sea come from multiple winter breeding areas and represent the ESA threatened Mexico DPS, ESA endangered Central America DPS, and the non-ESA listed Hawaii DPS (Bettridge et al., 2015; Calambokidis et al., 2017; Wade, 2017; Carretta et al., 2023).

Minke whales are small whales, thought to grow to only around 8 m in the Northeast Pacific, and weigh up to 10,000 kg. Commercial whaling data suggests they have a life span of ~50 years (Ford, 2014). Unlike gray and humpback whales, minke whales have never been commercially harvested in the Northeast Pacific nor were they regularly targeted in historical subsistence hunts (Scammon, 1874; Scheffer and Slipp, 1948; Carretta et al., 2023). This is supported by their absence in middens (McMillan, 2015; Robertson and Trites, 2018) suggesting that minke whales may be naturally rare in the Northeast Pacific. As a result, they are not listed under the ESA. Minke whales are regularly encountered in the Salish Sea from early spring through fall, especially around the San Juan Islands and in the eastern SJF (Dorsey, 1983; Dorsey et al., 1990). Sightings from winter months are rare, raising questions about where minke whales over-winter and breed, though Scammon (1874) suggested that minke whales could be seen year-round in the SJF. Low sighting rates during winter months may be an artifact of sea conditions and low search effort (Dorsey et al., 1990). There are similar knowledge gaps surrounding the population composition of minke whales in the Salish Sea. In the North Atlantic, pronounced sexual segregation occurs on higher latitude feeding grounds with females occurring further north than males (Risch et al., 2019). While this has not been shown in the Salish Sea, the stranding record is almost entirely of female whales (Scheffer and Slipp, 1948; Nikolich and Towers, 2018).

One method that researchers have used to non-invasively document cetacean abundance and presence is through opportunistically collected sightings. These 'presence-only' data from wildlife sightings databases may be useful for monitoring species distribution, movement patterns and critical habitat or hot spots (Olson et al., 2018). For aquatic species like cetaceans that are challenging to monitor consistently, public sightings records significantly increase the scope and geographic range of data available. Databases populated by citizen science reporting are inherently biased by both number and location of observers as well as environmental conditions such as time of day and sea state. Nevertheless, many studies have shown spatial similarities between robust citizen science datasets and systematic surveys, and techniques for effort correction can greatly improve the reliability of the datasets (Hauser, 2006; Embling et al., 2015; Harvey et al., 2018; Olson et al., 2018; Ettinger et al., 2022). Longitudinal databases like the ones used in this study can identify reliable patterns if the potential for error and bias is taken into consideration, and they are invaluable tools for illuminating long-term spatio-temporal patterns (Harvey et al., 2018; Olson et al., 2018).

The recovery and status of baleen whale populations is monitored by the National Oceanic and Atmospheric Association (NOAA) at broad spatial scales determined by populations and stocks. However, the baleen whales' habitat use in the Salish Sea ecosystem and their potential impact on local food webs is not well documented or understood. Here, we report opportunistic sightings records from multiple databases throughout the region to assess patterns in mysticete presence in the Salish Sea from 1976–2019. Our questions were twofold: 1) How have sighting rates of these three baleen whale species changed over time? And 2) How has the spatial distribution and use of the Salish Sea varied between these three species?

2 Methods

2.1 Data sources & characterization

Data were collated from two, long-term marine mammal sightings databases in the Salish Sea region curated by The Whale Museum (TWM) & Cascadia Research Collective (CRC) from 1976–2019. These databases include opportunistically reported sightings by a wide array of sources including non-profit sighting networks (e.g., Orca Network and The Whale Museum Reporting Hotline), research scientists, commercial whale watch operators, trained naturalists, and untrained public citizens. In order to fully leverage the available data, we used all sightings of minke, humpback, and gray whales, regardless of the qualification of the reporting party; however, we removed any sightings of unidentified or unconfirmed baleen whales. When possible, species identifications from non-experts were confirmed through photos, descriptions, other reports (e.g., captain logs, other scientists, etc.), and acoustic data; nevertheless, due to observation bias, weather conditions, and other limitations of opportunistic volunteer reporting there are likely a small portion of sightings that were misidentified (Olson et al., 2018).

We assigned all sightings reports to a 4.6 x 4.6 km quadrant within the study area, a system used by TWM since the onset of their database (Olson et al., 2018). We also assigned sightings to one of seven regions representing divisions by major bodies of water (Figure 1). We removed all sightings that lacked sufficient geospatial information required to assign a quadrant (i.e., either GPS coordinates or anecdotal descriptions) and any sightings that fell outside of the described study area. Only one sighting per day per quadrant was selected in order to reduce duplicate sightings. Furthermore, we assume that the biases in these data are roughly equivalent for all three species studied and aim to tease apart real spatio-temporal trends from reporting bias by using techniques that focus on the differences between species.

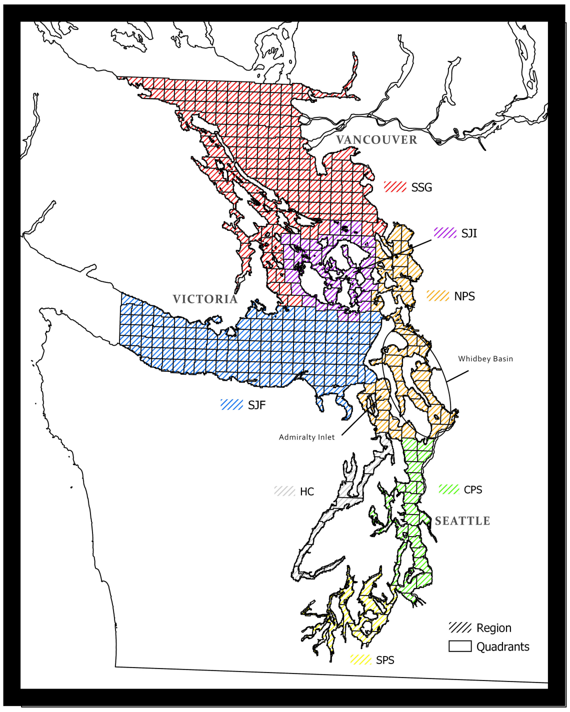

FIGURE 1
The Central Salish Sea study area highlighting the customized quadrant system for quantifying mysticete sightings. Regions include Southern Strait of Georgia (SSG), San Juan Islands (SJI), Strait of Juan de Fuca (SJF), Northern Puget Sound (NPS), Central Puget Sound (CPS), Hood Canal (HC), and Southern Puget Sound (SPS).

2.2 Temporal analyses

We used raw sightings with duplicates removed (henceforth referred to simply as 'sightings') to assess for changes over time. We also used the yearly proportion of the sightings for one species compared to all three species to look for changes over time independent of observer coverage. We conducted a non-parametric change-point analyses to identify the most significant temporal shifts in sightings for each species ('cpt.np' function in the *changepoint.np* R package; Haynes et al., 2022). This method applies a non-parametric cost function and uses the pruned exact linear time algorithm (PELT) to search for optimal segmentations (Killick et al., 2012). In this method, all change points are automatically selected. We used the modified Bayes information criterion penalty term (MBIC) as a penalty function for cost minimization (Zhang and Siegmund, 2007). To further assess the significance of these results, we used a non-parametric Kruskal-Wallace test and pairwise Wilcox tests to compare mean sightings from the distinct time periods as designated by the changepoint segmentations for each species.

2.3 Spatial analyses

We explored spatial trends at the regional level using a heatmap and on a finer scale by creating density plots of sightings using the coordinates for the centroids of each quadrant. We also used SaTScan software (v. 10.1; available at http://www.satscan.org, accessed February 19, 2023) to identify significant space-time clusters for each species. Originally designed for monitoring the spread of diseases, SaTScan is an effective tool for cluster detection and has been widely used in many fields including ecology and environmental monitoring (Kulldorff, 1997; Norman et al., 2012; Adams and Fenton, 2017; Olson et al., 2021). We used the Bernoulli space-time model which pinpoints clusters within a specific geographic region if, at certain time intervals, there was a notable increase in events compared to the surrounding areas.

The Bernoulli model allows designation of both cases and non-cases (i.e., controls). In this study, we applied the approach of cases vs controls as a way to correct for spatial reporting bias in our dataset. Sightings of one focal species were used as "cases," while sightings of the two non-focal species were used as "controls." For example, when looking for gray whale clusters, gray whale sightings were used as "cases" and sightings of both humpback and minke whales were used as "controls." A cluster of gray whale sightings thus represents an area/time with increased gray whale sightings relative to the other two species.

As part of the SaTScan output, we also assessed "relative risk." For the sake of our study, this equates to a measure of how much more common a sighting of a single species is (e.g., gray whale) within a specified space-time cluster, compared to a baseline of sightings for other baleen species (e.g., humpback and minke whales). It is calculated as the observed sightings divided by the expected sightings within a cluster divided by the observed divided by the expected outside the cluster. Any value greater than 1 indicates an increased likelihood hood of that species.

3 Results

We compiled 17,436 baleen whale sightings from 1976–2019. Of the total sightings, 8,008 (45.9%) were of gray whales, 6,235 (35.8%) were of humpback whales, and 3,193 (18.3%) were of minke whales. Sightings spanned all regions, however, less than 2% of combined sightings were reported in Hood Canal (see HC Figure 1).

3.1 Temporal analyses

Annual time series patterns differed by species. Sightings of minke whales were fairly consistent over time with a mild drop-off in late 1990s early 2000s (Figure 2A). Proportionally, sightings of minke whales dominated early in the study period making up 35–82% of yearly sightings from 1976–1989 (Figure 2B). In contrast to the relative consistency observed in minkes, sightings of both grays and humpbacks increased notably over time (Figure 2A). Increases in gray whale sightings took place periodically with substantial stepwise growth initially occurring in the early 1990s and again in the late 2000s. Gray whales dominated the records proportionally from ~1990–2010 making up 47–97% of yearly sightings. Sightings of humpbacks, on the other hand, increased steadily over time with a sharp, exponential increase in recent decades. Since 2011, humpbacks have represented 42–76% of yearly sightings (Figure 2B).

Key change points were identified for gray whales with increases in 1989 and 2017 (Supplementary Figure 1), with mean sightings for those time periods differing significantly from each other (W = 27.948, df = 2, p-value = 8.533e-07; Supplementary Figure 2; p<0.05 for all pairwise comparisons). Change points for humpback whales included increases in the years 2002 and 2013, with means for those time periods differing significantly from each other (W= 31.557, df = 2, p-value = 1.404e-07; p<0.001 for all pairwise comparisons). Changepoints for minke whales included an increase in 1980, a decrease in 1993, and another increase in 2007 with means for those time periods differing significantly from each other (W=34.765, df = 3, p-value = 1.366e-07); however, pairwise comparisons indicated that mean sightings from 1976–1980 did not differ significantly from the 1994–2007 time period (p=0.404).

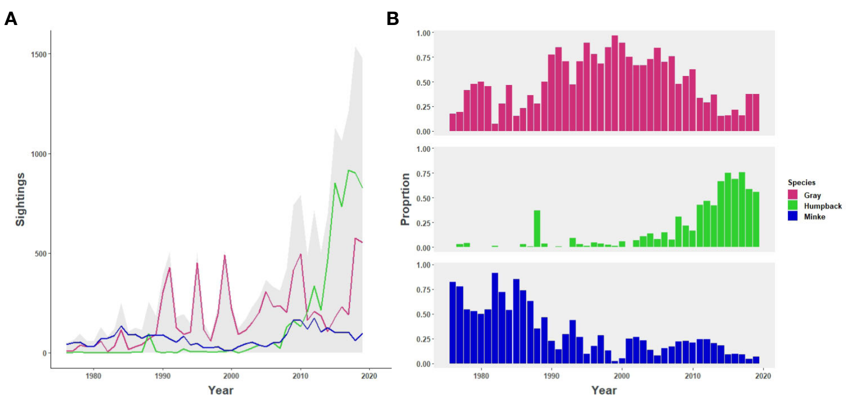

FIGURE 2
Sightings **(A)** and proportion of sightings across the three focal species **(B)** by species in the Salish Sea study area from 1976 - 2019. Total sightings are represented by gray shading and sightings by species are represented by color: gray whales (pink), humpback whales (green) and minke whales (blue).

3.2 Spatial analyses

Sightings of gray whales were reported in all regions throughout the entire study period and were most commonly observed close to shore (Figures 3A, 4). The majority of sightings were concentrated in Northern Puget Sound (NPS) and Central Puget Sound (CPS) regions, with the highest concentration of sightings located within the Whidbey Basin of NPS (Figure 3A). There was a notable increase in gray whale sightings in the NPS region starting in the early 1990s (Figure 4), with the most significant space-time cluster identified by SaTScan located in the Whidbey Basin from 1998–2019 (Figure 3D). Sightings of gray whales in this area and time period were 2.86 times more likely than sightings of minkes of humpbacks (Supplementary Table 1). We also identified two, larger space-time clusters for gray whales in CPS and NPS from 1990 – 2010/2011 and a less significant cluster of 195 sightings near the mouth of SJF from 1986–2007 (Figure 3D; Supplementary Table 1).

Sightings of humpbacks were largely absent in the early years of the study period, but showed sharp increases in all regions after 2010, with the most dramatic increases occurring in the BC, SJF, and CPS regions (Figures 3B, 4). The greatest density of sightings overall occurred off the south end of Vancouver Island in SJF (Figure 3B). We identified five space-time clusters for humpbacks in recent years, beginning primarily in SJF, BC and SJI (2008/2011-2019) and spreading to other areas of Salish Sea and CPS in later years (2013/2014–2019). The most significant cluster indicated humpback sightings were over 4 times as likely as the other species in the northern and western most regions of the Salish Sea from 2008–2019 (Figure 3E; Supplementary Table 1).

Compared to the larger species, sightings for minkes were spread over a smaller geographical area and were primarily concentrated in the San Juan Islands (SJI) and eastern SJF with a mild density spreading into Admiralty Inlet (Figure 3C). Minke sightings were initially concentrated in both SJI and BC and were 8.69 times more likely than other species in these two regions from 1976–1994 (Figures 3E, 4; Supplementary Table 1). In the early 1990s through the early 2000s, we observed a slight drop-off in sightings for in the SJC and BC regions that coincided with an increase in sightings in SJF (Figure 4). Significant space-time clusters support this spatio-temporal shift of minke sightings towards the eastern SJF south of SJI and the entrance to NPS from 2001–2017 (Figure 3E; Supplementary Table 1).

4 Discussion

From 1976–2019, we observed a notable increase in sightings for both gray whales and humpback whales and, in contrast, comparatively stable trends in minke whale sightings. Several distinctions in the spatio-temporal patterns of sightings data highlights the varied use of this Central Salish Sea study area by baleen whales.

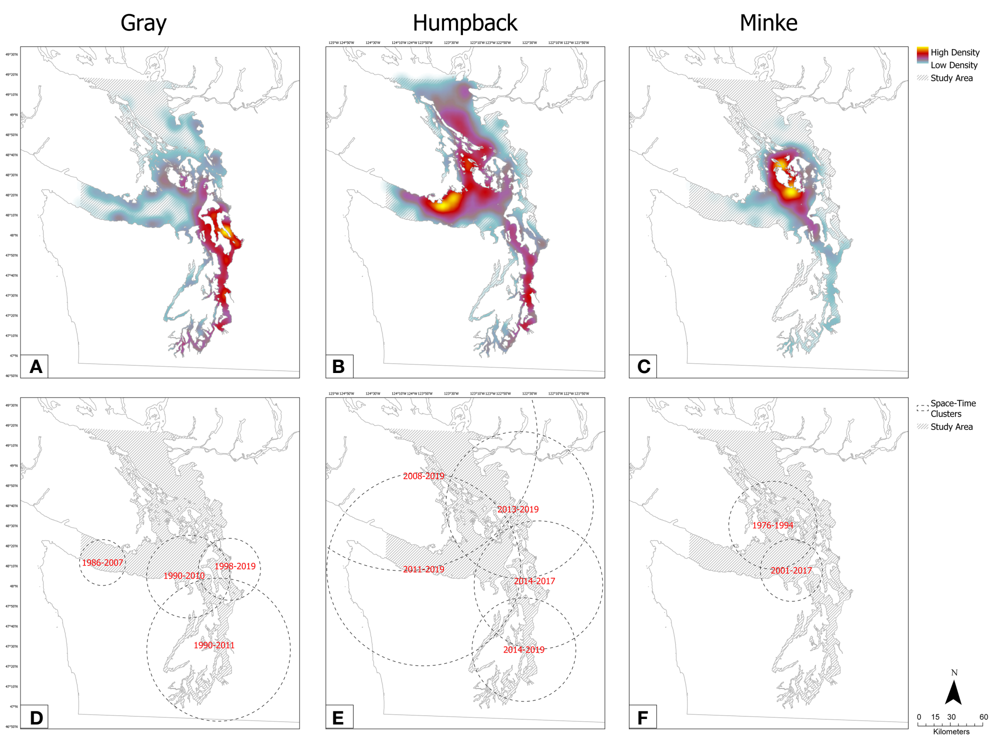

FIGURE 3
Relative sighting density in the Salish Sea study area from 1976–2019 **(A–C)**. Significant clusters identified by Bernoulli space-time model **(D–F)**. Detailed results of SatScan cluster analysis can be found in Supplementary Table 1.

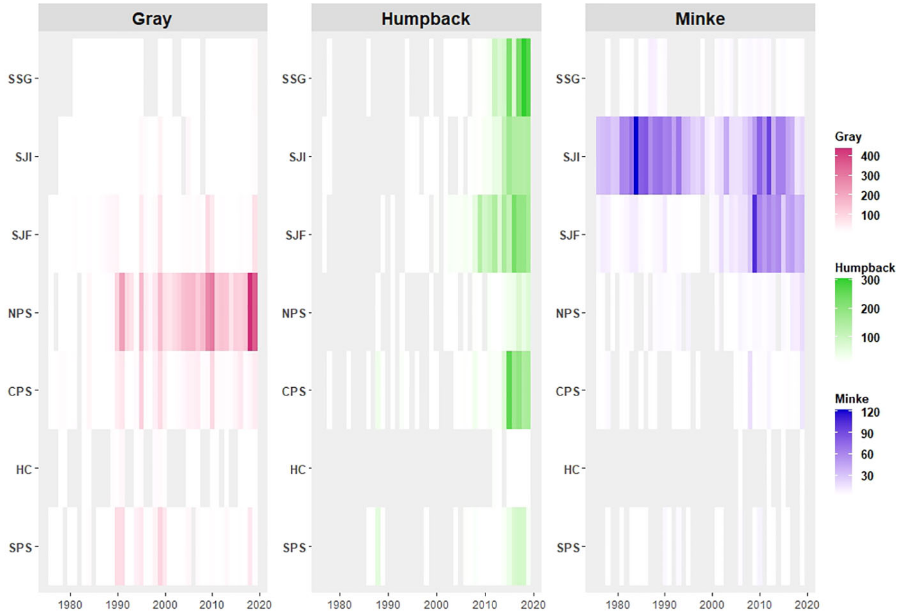

FIGURE 4
Heat map of sightings in the Salish Sea study area (1976–2019) by region and species. Gray shaded areas represent zero reported sightings.

4.1 Gray whales

The high concentration of gray whale sightings in NPS since 1990 reflects the seasonally resident 'Sounders' within the Whidbey Basin which were first documented in 1990 (Weitkamp et al., 1992; Calambokidis et al., 2002, 2015; Clayton et al., 2023; Calambokidis et al., 2024). Increases in gray whale sightings after the 1989 and 2017 change point align well with both the discovery and recruitment of new individuals to this seasonally resident group, which nearly doubled in size in 2018–2019 (Cascadia Research Collective, unpublished data). The change points also align well with periods of high mortality experienced by the Eastern North Pacific gray whale stock (Le Boeuf and Mate, 2000; Christiansen et al., 2021; Stewart et al., 2023a). These seemingly contrasting trends may be a reflection of gray whales straying from migration routes during times of nutritional stress, a small portion of whom are able to establish themselves with the resident foraging group. While a change point was not identified associated with the 1999–2000 gray whale Unusual Mortality Event (Le Boeuf and Mate, 2000), the sightings in NPS did increase during that period.

The benthic foraging behavior of gray whales likely influenced the abundance of nearshore sightings for this species. The significant cluster of sightings from 1989–2007 near the SJF mouth represents a low-use area for both recreational boaters and whale watch operators, particularly in the earlier years of our study period, thus the primary sighting reports are from shore-based observers. This particular cluster appears to be driven by individual gray whales feeding close to shore, with some documented in the area for weeks or months at a time.

4.2 Humpback whales

Though humpback whales were once common in the Salish Sea (Scheffer and Slipp, 1948), sightings of humpback whales were essentially absent for the first 30 years of our study. The dramatic increase in sightings observed since the late 2000s mirrors the rapid population growth rates documented for this species on a larger scale throughout the Pacific (Zerbini et al., 2010; Calambokidis et al., 2017). It also corresponds to a period when the overall abundance of humpback whales along the US West Coast up into BC has been increasing (Calambokidis and Barlow, 2004, 2020; Miller, 2020).

Humpback sightings were spread throughout the study area but were particularly prevalent in SJF starting in about 2008. While this does represent an area of high whale watch activity, it is also an area where large groups of humpbacks are documented. Furthermore, researchers have documented the foraging behaviors of humpback whales in this high use area, which may be influenced by connections to the productive waters off the continental shelf (Reidy et al., 2023). An expansion of humpback sightings into additional areas of the Central Salish Sea (e.g. SJI and SSG, see Figure 1) and Puget Sound beginning in 2013 coincided with the increase in overall sightings at this same time. In addition to sighting records, photo identification studies in the area have matched whales in the Salish Sea to individuals previously observed in offshore waters (Cascadia Research Collective, unpublished data). All of these results highlight the renewed use of historical feeding grounds in the Salish Sea as the population recovers to pre-whaling numbers.

4.3 Minke whales

Sightings of minke whales exhibited more subtle magnitudes of change relative to that of gray and humpback whales, which is not surprising given the lack of commercial or indigenous harvest of the species in the region (Scammon, 1874; Scheffer and Slipp, 1948). Considered rare in this region, photo identification studies suggest that the population in the SJI region is likely driven by a group of approximately 30–40 individuals that comes to forage in the bathymetrically complex habitats (Hoelzel et al., 1989; Dorsey et al., 1990; Salish Sea minke whale project, unpublished data).

Despite the seemingly stable numbers of individuals documented, we did observe a notable decrease in sightings in the early 1990s. Concurrent with this decrease, significant spatial clusters of minkes shifted from a large (40 km radius) cluster encompassing the SJI region (1978–1994) to a smaller (29 km radius) cluster concentrated in eastern SJF, south of SJI (2001–2017). This shift in habitat use is consistent with photo identification studies that documented a decline in the use of two historically preferred foraging areas in the SJI region, including San Juan Channel and the waters off of Waldron Island (Dorsey et al., 1990). Though minkes are known for having small-scale site fidelity in the Salish Sea, some of the individuals who previously specialized at these sites were observed using sites further south after a presumed lack of prey availability in their usual feeding range or were never seen in the area again (Dorsey et al., 1990). This shift in habitat use continued to be evident during focal follow foraging studies conducted during 2005–2011 (Salish Sea minke whale project, unpublished data).

With no evidence of an increasing population size from photo identification studies, the increase in sightings observed after 2007 may be representative of increased search efforts. The onset of both social-media based sightings platforms and the establishment of shore-based whale watching education programs in the Salish Sea in 2008 may have been a contributing factor. Furthermore, as Southern Resident killer whales spent less time in the inland waters during this time period (Stewart et al., 2023b), commercial whale watch operators may have conducted more dedicated search efforts in the shallow banks south of the San Juans where there can be a degree of predictability around minke whale presence if active bait balls and associated feeding seabirds are observed.

4.4 Limitations

Though it can be difficult to separate the inherent bias that accompanies public sightings databases, citizen science efforts are invaluable for monitoring the recovery of rebounding populations and fostering environmental stewardship (Embling et al., 2015). We recognize that the technological advancements and outreach initiatives of sightings networks, which have contributed to the datasets presented here, are known to have increased over time (Olson et al., 2018). Geographical biases also exist, such as population density and proximity to the home ports of whale watch operators. Furthermore, the feeding ecology of some species (e.g., gray whales) may expose them to high reporting areas more often.

In this study, the ability to examine changes in the yearly proportion of sightings for different species helps to adjust for some of the temporal bias due to changes in reporting effort. Furthermore, the lack of similar change points across species suggests the temporal shifts are not purely due to reporting effort. The application of the Bernoulli space-time model also allows us to identify species specific space-time clusters that are less likely to be driven by reporting bias (e.g., heavily populated or frequently observed areas). While this approach is advantageous for comparison between species, it may have the potential to under-report areas that were heavily used by two or more species. Finally, cross-referencing results with smaller systematic datasets and insights from the literature is an important step to discern real patterns from the background noise.

4.5 Conclusions

We analyzed differences between three baleen whale species to highlight long-term patterns of presence and use in the Central Salish Sea and have identified locations for targeted data collection, monitoring and mitigation efforts. Whidbey Basin, the Strait of Juan de Fuca, and the shallow banks south of the San Juan Islands may be important habitats for gray, humpback, and minke whales, respectively. The results presented here are not meant to represent true population or density estimates, but rather to highlight regional trends that may be overlooked when limited by the availability and financial constraints of systematic population survey efforts. Our findings support larger population recovery trends documented for humpback and gray whales. Furthermore, consistencies with regional studies for all three species highlight the value of these opportunistic sightings as a tool for monitoring large whale species in this area. As the Salish Sea region continues to see development and population growth with the associated increases in demand for international maritime freight (Sobocinski, 2021), all three species of baleen whale are at risk, especially as humpback and gray whale populations rebound and expand their use of the Salish Sea. Continued monitoring of these species through opportunistic public reporting efforts is essential for their continued conservation.

Data availability statement

The data analyzed in this study is subject to the following licenses/restrictions: Sightings data can be requested by The Whale Museum. Requests to access these datasets should be directed to sightings@whalemuseum.org.

Author contributions

JO: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. SL: Conceptualization, Methodology, Writing – original draft, Writing – review & editing. FR: Conceptualization, Writing – original draft, Writing – review & editing. HM: Conceptualization, Writing – review & editing. AM: Data curation, Writing – review & editing. SB: Data curation, Writing – review &

editing. JC: Conceptualization, Data curation, Writing – review & editing.

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Conflict of interest

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

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1401838/full#supplementary-material

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What bycatch tells us about the diet of harbor and gray seals and overlap with commercial fishermen

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Northwest Atlantic harbor (*Phoca vitulina vitulina*) and gray (*Halichoerus grypus atlantica*) seal populations are recovering from early to mid-20th century exploitation, increasing their biological interactions and bycatch in Northeastern US commercial fisheries. We evaluated the seals' diet composition and compared their prey to commercial catches to assess trophic overlap and potential competition with commercial fisherman target catches. We obtained 148 harbor and 178 gray seal stomach samples from bycatch events that occurred between 2004 and 2018. We learned from the hard part remains that the majority of seals bycaught are young-of-the-year (≤12 months old) that consume a wide breadth of prey across three trophic groups. There was a general dichotomy in extrinsic factors associated with seal diet in which 45% trophic niche separation was explained by non-overlapping harbor and gray seal phenology and pup haul-out locations that are adjacent to active fishing areas. Prey size estimated from fish otoliths and squid beaks recovered from stomach contents showed that gray seals consumed larger prey than harbor seals and prey sizes from both seals showed limited overlap with prey sizes caught by commercial gillnet fishermen. The most important prey to both seals included large (>20 cm) and small (≤20 cm) silver hake (*Merluccius bilinearis*), (≤40 cm) red hake (*Urophycis chuss*), gulf stream flounder (*Citharichthys arctifrons*), medium (21–40 cm) white hake (*Urophycis tenuis*), and (<50 cm) Atlantic cod (*Gadus morhua*). Important prey to harbor seals that did not overlap with gray seals were Acadian redfish (*Sebastes fasciatus*), Atlantic herring (*Clupea harengus*), longfin (*Doryteuthis pealeii*), and shortfin squid (*Illex illecebrosus*). They contrasted with prey important to gray seals that did not overlap with harbor seals: yellowtail flounder (*Limanda ferruginea*), sand lance (*Ammodytes* spp.), *Urophycis* spp., and fourspot flounder (*Hippoglossina oblonga*). Despite the potential bias associated with opportunistic bycatch sampling, this study demonstrates the importance and value of utilizing carcasses retained from bycatch events, is complimentary to newer methodologies (i.e., DNA meta-barcoding), and fills data gaps in our understanding of the role recovering harbor and gray seal populations have on Northeastern US regional food webs.

KEYWORDS
harbor seal, gray seal, bycatch, diet, prey, commercial fishermen

Introduction

Fishery bycatch is broadly defined as the incidental capture or discard of any living marine organism, including unobserved mortality, due to direct encounters with fishing vessels and gear (NMFS, 2016a). Bycatch of seals has been documented in several Northeastern US commercial fisheries where bycatch events can provide temporal and spatial context for analysis of seal distribution (Chavez-Rosales et al., 2018; Hayes et al., 2021; Precoda and Orphanides, 2022). Time and space are important factors in evaluating the diet of seals because of their life history where foraging patterns are largely dictated by the timing and location of reproduction and movements of their prey (Beck et al., 2007; Russell et al., 2015; Scharff-Olsen et al., 2018).

The western North Atlantic gray and harbor seal populations extend from eastern Canada to the mid-Atlantic US. Due to the semi-aquatic and wide-ranging movements of harbor (*Phoca vitulina vitulina*) and gray seals (*Halichoerus grypus atlantica*), utilizing dead specimens retained opportunistically from fishery bycatch events is a valuable resource because they provide rare insight to marine mammal trophic ecology that is otherwise difficult to obtain (Craddock et al., 2009; Wenzel et al., 2013; Orphanides et al., 2020). Williams (1999) and Ampela (2009) presented the first accounts of Northwest Atlantic harbor and gray seal diet utilizing stomach sample hard part remains obtained from Northeastern US incidental bycatch events (1991–2008). Our research will expand the time series by building off later research completed by Wenzel et al. (2015, 2017) including additional sampling from bycatch collected through 2018.

Cape Cod, coastal Maine, and nearby islands are home to several harbor and gray seal breeding colonies. These regions are adjacent to some of the most productive fishing grounds in the Northeastern US (NEFSC, 2023). Consequently, the resurgence of these transboundary seal populations has led to perceived competition for economically valuable prey between commercial fishermen and seals (Guerra, 2019; Behnke, 2021). While gray seals are exhibiting exponential rates of growth, there is increasing evidence of interspecific competition with gray seals outcompeting harbor seals for mutually desirable habitat and prey resources (Pace et al., 2019; Hayes et al., 2021; Wood et al., 2022). This could be contributing to an apparent decline or slowed growth of the Northwest Atlantic harbor seal population (Bowen et al., 2003; Johnston et al., 2015; Russell et al., 2015; Ampela et al., 2018; Jones et al., 2018; Pace et al., 2019; Wilson and Hammond, 2019; Hayes et al., 2021; Sigourney et al., 2022). Improving our understanding of forage diversity and consumption supporting the population growth of Northwest Atlantic harbor and gray seals is necessary to evaluate the magnitude of competition for both managed and protected resources in the Northeastern US region (Kusnierz et al., 2014; Hui et al., 2015; Swain and Benoît, 2015; Chasco et al., 2017). It is also necessary to improve our knowledge on key predator–prey linkages fundamental to the development of ecosystem-based fisheries management plans (Yodzis, 2001; Plaganyi and Butterworth, 2009; Fogarty, 2013; Free et al., 2021).

The success of the US Marine Mammal Protection Act of 1972 as amended (MMPA) has created a new set of challenges for natural resource managers (Gazit et al., 2013; Roman et al., 2013; Ferretti et al., 2015; Marshall et al., 2015; Jackman et al., 2018; Cammen et al., 2019; Guerra, 2019). Since the implementation of the MMPA, the US Northwest Atlantic harbor and gray seal populations have been recovering from near extirpation status. These species were considered extirpated from New England waters in the 1960s due to bounty hunting and overharvesting from legal hunting practices in coastal New England and Canadian provinces (Lelli et al., 2009). With the moratorium on the hunting of seals implemented under the MMPA, the recolonization of harbor and gray seals has been documented on several coastal beaches and islands throughout the Northeastern US and Canadian maritime region (Gilbert et al., 2005; Pace et al., 2019; den Heyer et al., 2020; Wood et al., 2020; Hayes et al., 2021; Sigourney et al., 2022).

The recovery of seals in Northeastern US waters has led to unintended negative interactions with stakeholder groups that range from landowners concerned about perceived impact on water quality around seal haul-out/pupping sites and beachgoers heightened awareness of sharks foraging in waters in search of seal prey adjacent to popular tourist beaches (Skomal et al., 2012; Bass et al., 2016; Jackman et al., 2018). Northwest Atlantic gray seal bycatch was over 2,000 individuals in 2019, the highest recent marine mammal bycatch in the US (Martins et al., 2019; Hayes et al., 2021). Increasing bycatch has also contributed to evidence of depredation due to apparent competition for resources that fishermen target for commercial and personal consumption and seals target to support their growth (Kaschner and Pauly, 2005; Konigson et al., 2009; Plaganyi and Butterworth, 2009; Rafferty et al., 2012; Gruber, 2014; Cosgrove et al., 2015; Sirak, 2015; Trull, 2015; Byron and Morgan, 2016).

The increasing interactions between recovering seal populations and fishermen are not unique to the Northeastern US. On the West Coast of the US, recovering seal populations have been blamed for impeding the recovery of protected salmon species (Chasco et al., 2017; Nelson et al., 2019). In Atlantic Canada, the Atlantic cod (*Gadus morhua*) has not recovered after two decades of moratorium on commercial harvest, and some of this decline has been attributed to predation by seals (Trzcinski et al., 2006; O'Boyle and Sinclair, 2012; Hammill et al., 2014; Neuenhoff et al., 2019; Rossi et al., 2021). In the Northeast Atlantic, Cook et al. (2015) stated that gray seal predation on Atlantic cod could impede recovery from overharvest by commercial fishing practices. In the Baltic Sea, researchers have documented economic losses to fishermen due to depredation and whole consumption of cod and salmon catches (Konigson et al., 2009, 2013).

The perceived increase in competition between marine mammal populations and fisheries has spurred new debate to legalize culling of seals in Northeastern US waters (Butterworth et al., 1988; Yodzis, 2001; Bowen and Lidgard, 2011; Schakner et al., 2016). However, contrasting studies suggest that changing environmental conditions and high fishing mortality outweigh the impact of natural mortality by predation from increasing higher trophic level predator populations (Kaschner and Pauly, 2005; Nye et al., 2013; Costalago et al., 2019). Furthermore, there is also evidence that marine mammal recovery has a positive impact on ecosystem health and trophic interactions potentially benefiting commercial fisheries (Trites et al., 1997; Morissette et al., 2012; Roman et al., 2013; Bass et al., 2016; Byron and Morgan, 2016). Thus, improving our understanding of the diversity and magnitude of seal prey consumption will move society further down the roadmap of an ecosystem-based approach to fisheries management (NMFS, 2016b; Gaichas et al., 2018).

Direct measurement of feeding by marine mammals in the wild is limited due to the nature of their habitat and how they interact with their environment (Boyle, 1997; Heithaus and Dill, 2009). Although pinnipeds spend a portion of their lives hauled out on land, they generally spend that time resting, mating, giving birth, and providing natal care. Consequently, scientists are mostly limited to indirect sampling approaches (e.g., hard part remains, stable isotopes, DNA, and fatty acids) to estimate the diet of marine mammals (Bowen and Iverson, 2013). There has been a growing body of literature from the Northeastern US region utilizing stable isotope and DNA techniques to infer the diet of US Northwest Atlantic gray seals. Hernandez et al. (2019a, 2019b) and Lerner et al. (2018) report the difficulty in obtaining taxonomic prey resolution using stable isotopes for a generalist predator. Ono et al. (2019) and McCosker et al. (2020) found several prey items present in Northwest Atlantic gray seal diet utilizing DNA techniques. However, obtaining estimates of prey abundance and biomass from DNA is still in the developmental stages (Deagle et al., 2018; Shelton et al., 2023). Consequently, there is uncertainty in 1) the relative magnitude of consumption and changes over time among prey types by Northwest Atlantic harbor and gray seals, 2) their interspecies prey foraging patterns, and 3) their competition with commercial fishermen for similar prey. In comparison to stable isotopes and DNA techniques, utilizing hard part remains obtained from seal scat and gastrointestinal samples provides an indirect and relatively inexpensive approach to investigate marine mammal diets. However, they are also not immune to sources of bias (e.g., digestive erosion of hard parts, poor evidence of depredation and scavenging, differential retention rates). Nonetheless, the use of hard part remains to infer the diet of marine mammals is extensively documented in the literature as providing high taxonomic resolution in conjunction with estimates of relative abundance and biomass of prey consumed. Pierce and Boyle (1991) and Bowen and Iverson (2013) provide comprehensive summaries with the pros and cons of indirect methods applied to the study of marine mammal diets.

Our primary aim with this research is to utilize stomach samples obtained opportunistically from harbor and gray seal commercial fishery bycatch events to improve our understanding of the foraging habits of Northwest Atlantic harbor and gray seals and their dietary role in the Northeastern US region ecosystems. The objectives of this study are to 1) quantify the mean length and weight, relative abundance, and biomass of prey consumed by harbor and gray seals using hard parts extracted from the stomachs of bycaught seals; 2) evaluate temporal, spatial, and seal demographic characteristics that may affect diet composition; 3) identify important prey and the magnitude of trophic niche overlap between the two seal species; and 4) compare the size distribution of prey consumed by these seals to the size of prey in commercial catches. Results from this study are expected to improve our scientific understanding of the extent of foraging and harvest competition for commercially important prey resources among these three predators: harbor seals, gray seals, and commercial fishermen.

Materials and methods

Bycatch

The NOAA's Northeast Fisheries Observer Program provides one of the most comprehensive interdisciplinary science at-sea fishery-dependent data collection programs in the Nation (NMFS, 2011; Benaka, 2021). We used contracted fisheries observers to support the opportunistic collection of incidentally captured harbor and gray seal carcasses for subsequent necropsy. Necropsies provide rare and valuable insight into the health and demography of these semi-aquatic animals (Pugliares et al., 2007). All specimens obtained from bycatch events were collected and sampled in accordance with regulations pursuant to the Marine Mammal Protection Act.

Stomach sample collection and processing

From 2004 to 2018, 326 seals were retained from observed bycatch events by the observers (94%) and incidental to cooperative industry-government research studies or agreements (6%). Whole fresh dead seals returned to shore were either put in a chiller and subsequently necropsied within 24–72 h or put in a freezer for necropsy at a later date.

Necropsies were primarily conducted at the Woods Hole Oceanographic Institute Marine Research Facility. During necropsy sessions, whole stomachs were extracted from the seal carcasses, and animal sex, weight, length, and overall body condition (e.g., robust, thin, and emaciated) were recorded. Stomachs were initially tied off at both ends of the stomach; the esophagus, the (top) entrance to the stomach, and the pyloric region near the bottom of the stomach and at the intersection of the large intestine were subsequently frozen at −10°C for future analysis. Intestinal and colonic contents were not examined. Stomachs were thawed and cut open over a large container to prevent loss of content, the stomach lining was rinsed, and all contents were emptied into a small plastic tub and eluted with hot water for analysis. Prior to eluting stomach contents, any evidence of non-trace (whole or semi-intact prey with skulls) prey items was removed, separated, identified, and measured (standard length for fishes). Otoliths were removed from the skull of non-trace and trace (free floating otoliths and cephalopod beaks) fishes, cleaned, and dried. The eluted stomach content samples were continually rinsed separating soft tissue from hard part remains (Craddock et al., 2009). All otoliths and cephalopod beaks found were separated and dried for identification using Campana (2004); McBride et al. (2010), and in-house reference guides. All non-trace and trace prey remains were identified to the lowest taxonomic group possible. Evidence of elasmobranch species (i.e., sharks, skates, and rays) was noted as either present or absent. Cephalopod beaks were not stored in an air-tight or oil-based solution and, consequently, were subject to shrinkage due to dry storage conditions. As a result, cephalopod beaks were not measured, and they were counted (uppers versus lowers) with the higher number of the two as the minimum number of cephalopods consumed (see steps 1–4 of Supplementary Figure S1).

Otolith sorting, subsampling, measurements, and other hard part remains

Fish otoliths (by species, family, or genus) were sorted into four condition categories: 1) pristine or near pristine otoliths [pristine otoliths come from non-trace prey items (whole fish or intact skulls)]; 2) trace otoliths with only mild/moderate degradation margin erosion; 3) trace otoliths with advanced erosion, with tips or margins worn down; and 4) broken trace otoliths. Within-sample (i.e., stomach) otoliths with minor erosion (within prey species) were subsampled if there were >30 but fewer than 120 structures. If there were ≥120 otoliths with minor erosion, 25% of those structures were randomly selected for measurement. Pristine otoliths and those with minor erosion were measured with digital calipers to the nearest 0.01 mm. Broken otoliths and those with major erosion were not measured. Broken otoliths were counted only if uniquely identified as belonging to one structure. Multiple broken pieces that could not be pieced together were not counted (Bowen and Harrison, 1994, 1996; Hammill et al., 2007; Wilson and Hammond, 2019); see steps 5–9 of Supplementary Figure S1). A total of 5,499 otoliths were processed. Fewer than 10% of otoliths were unmeasurable (Supplementary Table S1).

Estimating the minimum number of individual prey consumed

The count of individual prey consumed by individual seals in this study is treated as a minimum number of individuals because it does not 1) include the number of elasmobranch species consumed when found present, 2) account for possible loss due to digestion (e.g., fragile and highly digestible *Clupeid* spp.) or otoliths not located due to stomach processing procedures (e.g., digestive tracts were not processed) or missing small otoliths (e.g., sand lance), 3) account for depredation where heads of prey are not consumed, and 4) account for evidence of prey based on fish bones and soft tissue that were not enumerated for this study (Pierce and Boyle, 1991; Bowen and Harrison, 1994; Orr et al., 2004; Hammill et al., 2007; Bowen and Iverson, 2013).

For each seal stomach (sampling unit), pristine otoliths and those with minor erosion were paired (left and right) to the extent possible. The minimum number of individual (minimum number) prey present was determined by counting the number of pairs and single (left or right) otoliths (assumed to be unique individuals; Bowen and Harrison, 1996; Hammill et al., 2007; Wenzel et al., 2013). For unpaired subsampled otoliths with minor erosion, the Microsoft Corporation (2016) Excel Data Analysis ToolPak (sample function) was used to reconstruct a full sample of otolith lengths from the subsampled data (10% of stomach samples included subsampled otoliths). Reconstructed otolith lengths were randomly reduced by 50%, and those individual (not paired) otolith lengths were used to infer the minimum number of otoliths with minor erosion and prey sizes from the subsampled data. This step was necessary because, unlike the non-subsampled data, the subsampled otoliths with minor erosion were not paired so an estimate of the minimum number of prey could not be determined and subsequently not available to estimate prey length for this group of otoliths. For broken otoliths and those with major erosion, the aggregate counts of otoliths within sampling units and prey species were divided in half to estimate the minimum number. The minimum number of prey species consumed by each seal is the sum of the minimum number across all four otolith condition categories and cephalopods. See Supplementary Figure S1 for a detailed flowchart of the methodology estimating the minimum number consumed by harbor and gray seals.

Estimating seal prey size and weight

Prey sizes are an important consideration given the size of prey that harbor and gray seals are able to consume and for comparison to mean prey size from commercial catches (Sirak, 2015; Ono et al., 2019). The mean otolith length (from pairs) or individual lengths from pristine otoliths or those with minor erosion were used to estimate individual prey length (cm) and weight (kg) using equations compiled from the literature and other data sources (Supplementary Appendices 1–2). Pristine otoliths or those with minor erosion recovered from stomach samples spend less time subject to erosive factors compared with otoliths with major erosion or fully passed through the digestive tract (e.g., recovered from scats), and thus, no otolith size correction factors were applied to the measured otolith lengths (Olesiuk et al., 1990; Bowen and Harrison, 1994, 1996; Hammill et al., 2007).

Reconstructing harbor and gray seal diets

Prey weight for the minimum number from all four otolith categories and cephalopod minimum number was required to estimate prey biomass consumed by harbor and gray seals (heretofore "seals"). Prey weight for the minimum number of pristine otoliths or those with minor erosion was directly estimated (see section above). However, the minimum number counted from broken otoliths or those with major erosion was aggregated by seal and prey species. Consequently, to estimate biomass consumed by each seal, a three-tiered matching system was used to multiply mean prey weight from pristine otoliths or those with minor erosion by the minimum number from broken otoliths or those with major erosion. Tier 1 match multiplied mean prey weight by the minimum number of broken otoliths or those with major erosion where sampling unit (seal stomach sample) and prey species match; tier II match multiplied mean prey weight from the same prey species over all sampling units within the same seal species and season by the minimum number of broken otoliths or those with major erosion from the same seal species and season; and tier III match multiplied prey weight from the same prey species over all sampling units within the same seal (ignoring season) by the minimum number of broken otoliths or those with major erosion from the same seal and prey species. The prey weight of squids was estimated by multiplying the mean prey weight (within species) derived from Ampela (2009) and Williams (1999) by its minimum number. For unidentifiable flatfish, hakes, and gadids, the mean prey weight from the same taxonomic family found within the same sampling unit (stomach sample) was applied to the unidentified flatfish, hakes, and gadid minimum number. If no match was found within the same stomach, the mean prey weight from the same taxonomic family with the same seal species, sex, age, and season was used where applicable. For unidentified species, the mean prey weight from all identified prey within the same stomach sample was applied to the unidentified minimum number. Total biomass consumed for each predator is the sum of prey weight estimated from pristine otoliths or those with minor erosion plus the sum of prey weight estimated from all three tiers of broken otoliths or those with major erosion plus prey weight from all unidentified prey categories (<1% of all identified prey items).

The reconstructed seal diet data were categorized by season (spring = March–May, summer = June–August, fall = September–November, winter = December–February), geographic region (Gulf of Maine, Georges Bank, Southern New England/Northern Mid-Atlantic), sex, and age class (pup, young-of-the-year, juvenile and adult: Table 1). Geographic regions were defined from ecological production units, which are defined areas within the Northeastern US continental shelf containing all or the majority of an ecosystem with unique biological, chemical, and physical characteristics supporting various assemblages of marine life (Gamble et al., 2016; NEFSC, 2023). The frequency of occurrence (the number of times a prey item was found in a stomach sample), abundance, and biomass consumed, as well as mean prey size (cm) and weight (kg), were summarized by the trophic guild for both harbor and gray seals. Trophic guild refers to a group of prey species that feed on similar items or have similar dietary requirements and, therefore, have a similar ecological function within the structure of an ecosystem (Adams, 1985). Organizing seal diet data by trophic guild is important to support the development of predator–prey linkages, a critical need in furthering the application of ecosystem-based fishery management in Northeastern US (Fogarty, 2013).

Commercial catch length data

Fish length data from commercial gillnet catches (both kept and discards) obtained from NOAA's observer program were compared to the length distribution for some of the most important prey consumed by harbor and gray seals. We used catch length data from 2004 to 2018 to match the time period of stomach samples collected. The observer program manuals detail fish biological sampling procedures on board observed commercial fishing trips (https://www.fisheries.noaa.gov/resource/document/fishery-monitoring-and-research-supplemental-documents). The reconstructed diet and commercial catch length data were prepared for subsequent statistical analyses using SAS (2016).

Statistical methods

We used the BiodiversityR (ver. 2.15-1; Kindt and Coe, 2005) and vegan (ver. 2.6-4; Oksanen et al., 2022) packages in R (ver. 4.2.2; R Core Team, 2022) to generate stomach prey community data sets and prey species accumulation curves as a function of stomach sample size, respectively. This was done to determine if we had sufficient sample sizes to evaluate diet composition (Gosch et al., 2014; Matić-Skoko et al., 2014). The relative importance of prey resources consumed was determined by the index of importance (iIMP) defined by Garcia-Rodriguez and Aurioles-Gamboa (2004) as:

$$iIMP_i = \frac{1}{U}\sum_{j=1}^{U}\frac{x_{ij}}{X_j}$$

where i = taxon or species, j = stomach sample, U = total number of stomach samples with prey (harbor seal U = 144; gray seal U = 143), x_{ij} = number of prey i in stomach j, and X_j = total number of prey in stomach j. The iIMP was chosen over prey occurrence: $(\Sigma Oi\ /U)^{*}$ 100, where O is the presence/absence of prey$_i$, and prey abundance: $(\sum_{j=1}^{U}\frac{x_i}{X}) * 100$, to identify important prey in the diet. The iIMP takes both prey occurrence and abundance into account and is thereby less sensitive to large numbers of an individual taxon or species found in only a few stomachs and vice versa (Garcia-Rodriguez and de la Cruz-Aguero, 2011). Values of iIMP that were greater than 1/S (S = species richness; total number of taxa or species identified) were considered important prey (Krebs, 1999). The proportion of diet overlap and diversity were evaluated using Morisita's (C) and Shannon–Wiener (H') measures, respectively (Krebs, 1999).

Generalized additive models (GAMs) were used to explore temporal, spatial, seal species, sex, age, and diet diversity effects on seal consumption. The minimum number of prey items consumed is inherently variable (Supplementary Figures S2–S2A). Rather than transforming and eliminating real data outliers, a GAM with the quasi-Poisson log-link family allowed for the estimation of a dispersion parameter and non-linear effects (mgcv package; Wood, 2017).

Finally, to evaluate evidence of biological interactions for the same resources targeted by commercial fishermen, the length frequency distribution sampled from observed commercial gillnet catch composition data was compared to prey length frequency distribution estimated from the stomach contents of bycaught harbor and gray seals. Chi-square and permutation hypothesis tests were used to test differences in diet composition, meal size, and size of prey consumed by the seals and caught by commercial gillnets. All statistical analyses were performed in R-Studio (Posit Team, 2022).

TABLE 1 Demographic, spatial, and temporal characteristics associated with gray (top panel) and harbor (bottom panel) seals bycaught in commercial gillnet and bottom trawl gear, years 2004–2018: GoM, Gulf of Maine; GB, Georges Bank; SNE/NMA, Southern New England/Northern Mid-Atlantic; Spring, March–May; Summer, June–August; Fall, September–November; Winter, December–February; Unk, Unknown.

		Season (%)				Sex (%)			Region (%)				Age classes [length range, (%)]				
Species	*N*	Spring	Summer	Fall	Winter	♂	♀	Unk	GoM	GB	SNE/ NMA	Unk	Pup [≤ 131 cm and ≤3 months old]	YoY [>3 months old and ≤131 cm]*	JUV [>131–<160 cm]	Adult [≥160 cm]	Unk
Gray seal (*Halichoerus grypus atlantica*)	178	105 (59)	22 (12)	12 (7)	39 (22)	90 (50)	83 (47)	5 (3)	41 (23)	21 (12)	114 (64)	2 (1)	29 (16)	122 (69)	16 (9)	7 (4)	4 (2)
		Season (%)				**Sex (%)**			**Region (%)**				**Age classes [length range, (%)]**				
Species	***N***	Spring	Summer	Fall	Winter	♂	♀	Unk	GoM	GB	SNE/ NMA	Unk	Pup [≤ 90 cm and ≤3 months old]	YoY [>3 months old and ≤ 115 cm]†	JUV [>115–<145 cm]	Adult [≥145 cm]	Unk
Harbor seal (*Phoca vitulina vitulina*)	148	10 (7)	51 (34)	44 (30)	43 (29)	86 (58)	54 (37)	8 (5)	106 (71)	0 (0)	38 (26)	4 (3)	31 (21)	101 (68)	4 (3)	4 (3)	8 (5)

Age classes based on length ranges (cm) differ between gray seal and harbor seals: gray seals bycaught between December and February and ≤131 cm = pup, harbor seals bycaught between June and August and ≤90 cm = pup.
YoY, young-of-the-year (≤12 months old excluding pups); JUV, juvenile.
*Hammill (unpublished), McLaren (1993), and Ampela (2009).
†Boulva and McLaren (1979) and McLaren and Smith (1985).

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Results

Seal sample characteristics

Of the 326 processed stomach samples, 148 were from harbor seals, and 178 were from gray seals (Supplementary Table S2). For both seals, sex ratios were equal (50% male harbor seal, 58% male gray seal, Table 1). Nearly 70% of stomach samples came from young-of-the-year seals followed by pups (16%–21%). Juvenile and adult sample sizes were small (<10%). The majority of gray seal samples were obtained during the spring (59%) followed by the winter, summer, and fall seasons, whereas harbor seal samples were more evenly distributed among summer, fall, and winter seasons. The majority of gray seal samples (64%) were obtained from the southern region, whereas the majority of harbor seal samples (71%) came from the Gulf of Maine region (Table 1 and Figure 1).

Diet composition, diversity, important prey, and trophic overlap

From 2004 to 2018, 31 prey species plus another 9 unidentified taxonomic groups were identified from otoliths and squid beaks, representing at least three prey trophic groups (benthivores, planktivores, and piscivores) in the diet of Northwest Atlantic harbor and gray seals (Table 2). Species accumulation curves showed diet richness leveling off for both harbor and gray seals at ~90 stomach samples (Supplementary Figure S3). Benthivorous prey occurred more frequently in gray seal stomachs, and the only planktivorous/piscivorous prey (Acadian redfish; *Sebastes fasciatus*) was rarely found in gray seal stomachs (χ^2 = 88.71; P = 0.000; Figure 2). However, the number of prey species and trophic groups present in individual stomach samples was not affected by seal species (prey: χ^2 = 10.29; P = 0.24, trophic groups: χ^2 = 9.32; P = 0.05).

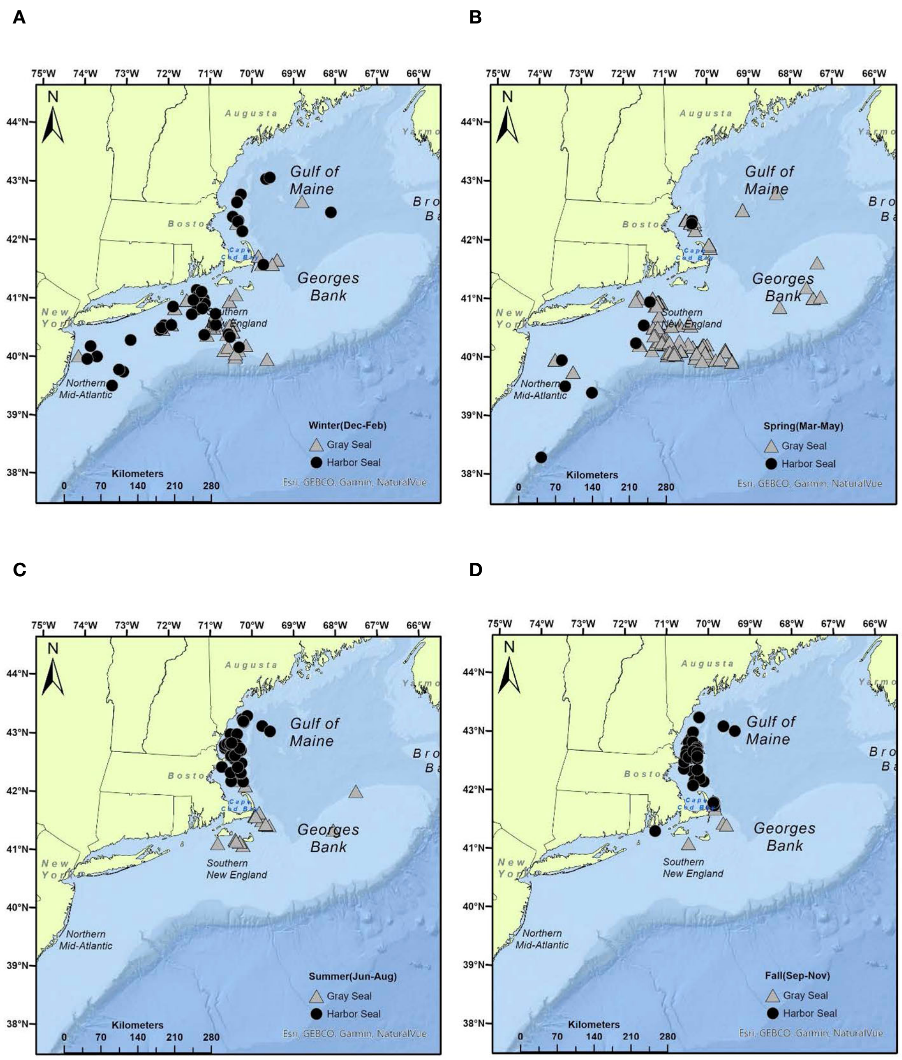

FIGURE 1
Seasonal distribution of harbor and gray seal stomach samples obtained from bycatch events in NEUS commercial fisheries, 2004–2018: **(A)** winter, **(B)** spring, **(C)** summer, **(D)** fall (see Supplementary Table S3 for additional details).

TABLE 2 Diet composition of harbor (*Phoca vitulina*) and gray (*Haliochoerus grypus*) seals collected from observed incidental bycatch events in NEUS Gulf of Maine, Georges Bank, and Southern New England gillnet and bottom trawl fisheries (Figure 1) between 2004 and 2018 (*n*, number of stomach samples; kg, kilograms; g, grams; cm, centimeters; s, standard deviation; mni, minimum number of individuals; unk, unknown).

		Harbor seal (*n* = 144)					Gray seal (*n* = 143)				
Trophic group	Prey	Frequency of occurrence (PO%)	Numerical abundance (PN%)	Biomass kg (PB%)	Mean length† (cm, s)	Mean weight† (g, s)	Frequency of occurrence (PO%)	Numerical abundance (PN%)	Biomass kg (PB%)	Mean length† (cm, s)	Mean weight† (g, s)
Planktivore	Sand lance	1 (0.7)	2 (0.1)	0.04 (0.02)	18.66 (1.12)	20.93 (2.19)	14 (7.9)	152 (7.1)	1.93 (0.73)	13.55 (4.64)	12.85 (7.56)
Planktivore	Silver hake (≤20 cm)	18 (12.2)	302 (10.0)	11.19 (4.16)	16.21 (2.82)	29.37 (11.93)	18 (10.1)	65 (3.0)	1.25 (0.48)	13.30 (4.54)	18.36 (17.00)
Planktivore	White hake (21–40 cm)	27 (18.2)	94 (3.1)	11.19 (4.17)	25.59 (3.78)	129.61 (66.49)	37 (20.8)	94 (4.4)	16.92 (6.43)	29.36 (4.25)	173.25 (84.01)
Planktivore	Pollock (21–50 cm)	2 (1.3)	4 (0.1)	1.35 (0.50)	27.24 (7.18)	255.07 (181.00)	–	0	–	–	–
Planktivore/ piscivore	Redfish	48 (32.4)	539 (17.9)	10.71 (3.99)	10.04 (3.57)	19.65 (19.65)	2 (1.1)	5 (0.2)	0.26 (0.09)	15.23 (0.02)	51.01 (0.19)
Planktivore	Butterfish	14 (9.4)	42 (1.4)	0.97 (0.36)	10.33 (2.25)	24.97 (13.78)	1 (0.6)	1 (<0.1)	0.01 (0.00)	9.27 (.)	12.90 (.)
Planktivore	Alewife	5 (3.4)	7 (0.2)	0.32 (0.12)	15.57 (4.10)	47.16 (42.93)	1 (0.6)	1 (<0.1)	0.03 (0.01)	15.13 (.)	32.92 (.)
Planktivore	Blueback herring	4 (2.7)	14 (0.5)	1.37 (0.51)	20.67 (3.46)	99.79 (50.50)	2 (1.1)	2 (0.1)	0.10 (0.04)	16.14 (4.93)	47.93 (41.47)
Planktivore	Atlantic herring	23 (15.5)	62 (2.1)	6.33 (2.36)	22.02 (4.35)	103.77 (47.40)	3 (1.7)	3 (0.1)	0.31 (0.12)	22.74 (4.84)	104.38 (63.49)
Planktivore	Atlantic mackerel	5 (3.4)	12 (0.4)	1.63 (0.61)	23.37 (4.14)	133.69 (79.51)	1 (0.6)	1 (<0.1)	0.13 (0.05)	–	–
Planktivore	Clupeidae	3 (2.0)	8 (0.3)	0.50 (0.19)	13.38 (.40)	21.36 (1.92)	1 (0.6)	1 (<0.1)	0.10 (0.04)	–	–
Planktivore/ benthivore	Gadid spp. (cod, haddock, pollock)	–	0	–	–	–	5 (2.8)	17 (0.8)	0.34 (0.13)	4.45 (0.65)	0.78 (0.43)
Planktivore/ benthivore	*Urophycis* spp.	11 (7.4)	97 (3.2)	13.10 (4.87)	–	–	13 (7.3)	120 (5.6)	10.57 (4.02)	20.78 (4.64)	58.64 (37.19)
Benthivore	Gulf stream flounder	15 (10.1)	109 (3.6)	0.31 (0.12)	9.41 (2.56)	2.93 (5.44)	42 (23.6)	226 (10.55)	0.69 (0.26)	9.98 (2.16)	3.09 (1.75)
Benthivore	Smallmouth flounder	–	0	–	–	–	3 (1.7)	5 (0.2)	0.03 (0.01)	12.42 (1.90)	5.88 (3.17)

(Continued)

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TABLE 2 Continued

Trophic group	Prey	Harbor seal (*n* = 144) Frequency of occurrence (PO%)	Numerical abundance (PN%)	Biomass kg (PB%)	Mean length† (cm, s)	Mean weight† (g, s)	Gray seal (*n* = 143) Frequency of occurrence (PO%)	Numerical abundance (PN%)	Biomass kg (PB%)	Mean length† (cm, s)	Mean weight† (g, s)
Benthivore	Flatfish spp.	3 (2.0)	1 (<0.1)	<0.01 (0.00)	–	–	14 (7.9)	29 (1.3)	5.14 (1.95)	–	–
Benthivore	Gulf stream/ smallmouth	1 (0.7)	11 (0.4)	0.01 (0.00)	6.34 (1.48)	0.66 (0.49)	1 (0.6)	3 (0.1)	0.01 (0.00)	8.16 (4.23)	2.22 (2.21)
Benthivore	Red hake (≤40 cm)	54 (36.5)	258 (8.6)	25.83 (9.62)	23.59 (5.37)	95.15 (58.97)	82 (46.1)	704 (32.8)	78.05 (29.67)	25.98 (4.31)	110.80 (53.31)
Benthivore	White hake (≤20 cm)	3 (2.0)	6 (0.2)	0.32 (0.12)	17.33 (2.29)	36.73 (12.34)	3 (1.68)	3 (0.14)	0.08 (0.03)	16.37 (3.90)	26.68 (17.15)
Benthivore	Pollock (≤20 cm)	3 (2.0)	9 (0.3)	0.58 (0.22)	17.60 (2.58)	58.13 (22.36)	–	0	–	–	–
Benthivore	Yellowtail flounder	1 (0.7)	1 (<0.1)	<0.01 (0.00)	7.51 (.)	2.78 (.)	28 (15.7)	61 (2.8)	12.19 (4.63)	26.52 (7.51)	202.82 (156.35)
Benthivore	American plaice	2 (1.3)	2 (0.1)	0.02 (0.01)	10.49 (4.10)	8.50 (8.83)	9 (5.1)	14 (0.6)	2.94 (1.12)	26.59 (7.27)	181.16 (149.21)
Benthivore	Atlantic cod (<50 cm)	23 (15.5)	47 (1.6)	6.10 (2.27)	21.24 (7.07)	121.61 (129.13)	9 (5.1)	13 (0.6)	3.41 (1.30)	22.70 (13.19)	247.22 (523.30)
Benthivore	Ocean pout	3 (2.0)	3 (0.1)	0.10 (0.04)	21.15 (2.50)	33.44 (11.84)	9 (5.0)	13 (0.6)	1.55 (0.59)	30.00 (3.68)	110.23 (53.30)
Benthivore	Haddock (<80 cm)	9 (6.1)	115 (3.8)	3.46 (1.29)	14.11 (3.40)	31.15 (32.92)	9 (5.0)	21 (1.0)	8.68 (3.30)	26.17 (13.41)	331.54 (487.54)
Benthivore	Cunner	3 (2.0)	3 (0.1)	0.05 (0.02)	11.25 (4.04)	17.25 (17.19)	3 (1.7)	4 (0.2)	0.74 (0.28)	24.13 (2.07)	184.47 (56.83)
Benthivore	Scup	–	0	–	–	–	4 (2.2)	17 (0.8)	5.40 (2.05)	23.61 (2.61)	327.02 (98.53)
Benthivore	Winter flounder	–	0	–	–	–	11 (6.2)	13 (0.6)	7.41 (2.82)	33.56 (8.88)	540.49 (295.70)
Benthivore	Windowpane flounder	–	0	–	–	–	7 (3.9)	30 (1.4)	1.24 (0.47)	13.68 (4.87)	41.43 (39.95)
Benthivore	Fawn cusk-eel	2 (1.3)	4 (0.1)	0.01 (0.00)	9.94 (5.32)	3.26 (4.66)	–	0	–	–	–

(Continued)

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TABLE 2 Continued

		Harbor seal (*n* = 144)					Gray seal (*n* = 143)				
Trophic group	Prey	Frequency of occurrence (PO%)	Numerical abundance (PN%)	Biomass kg (PB%)	Mean length† (cm, s)	Mean weight† (g, s)	Frequency of occurrence (PO%)	Numerical abundance (PN%)	Biomass kg (PB%)	Mean length† (cm, s)	Mean weight† (g, s)
Benthivore	Cusk-eel	–	0	–	–	–	13 (7.3)	26 (1.2)	0.32 (0.12)	17.00 (3.65)	12.01 (7.01)
Benthivore	Tautog	3 (2.0)	3 (0.1)	0.40 (0.15)	17.78 (5.40)	132.41 (118.92)	4 (2.2)	4 (0.2)	0.64 (0.24)	19.42 (4.27)	160.64 (94.75)
Benthivore	Spotted hake	1 (0.7)	3 (0.1)	0.25 (0.09)	21.70 (2.31)	81.93 (25.31)	4 (2.2)	10 (0.5)	0.76 (0.29)	21.05 (2.68)	76.10 (26.56)
Benthivore	Fourbeard rockling	3 (2.0)	4 (0.1)	0.05 (0.02)	20.67 (1.96)	12.04 (3.79)	–	0	–	–	–
Benthivore	Snakeblenny	2 (1.3)	2 (0.1)	0.04 (0.01)	26.41 (0.94)	19.05 (1.66)	–	0	–	–	–
Benthivore	Wrymouth	4 (2.7)	5 (0.2)	0.50 (0.19)	29.26 (3.62)	100.37 (42.67)	2 (1.1)	3 (0.1)	0.16 (0.06)	24.54 (2.80)	54.93 (19.25)
Benthivore	Eel spp.	–	0	–	–	–	1 (0.6)	1 (<0.1)	0.01 (0.00)	18.19 (.)	(.) (.)
Benthivore/ piscivore	Weakfish	2 (1.3)	2 (0.1)	0.32 (0.12)	22.47 (12.76)	160.62 (193.21)	1 (0.6)	2 (0.1)	0.26 (0.10)	23.92 (.)	131.84 (.)
Piscivore/ benthivore	Conger eel	1 (0.7)	3 (0.1)	6.76 (2.52)	104.70 (.)	(3,378.67) (.)	–	0	–	–	–
Piscivore	Silver hake (>20 cm)	91 (61.5)	892 (29.7)	95.93 (27.11)	24.72 (4.02)	107.36 (64.95)	55 (30.9)	303 (14.1)	37.47 (14.25)	26.35 (4.35)	123.56 (75.21)
Piscivore	Red hake (>40 cm)	2 (1.3)	2 (0.1)	0.86 (0.10)	41.34 (0.81)	448.88 (26.67)	1 (0.6)	1 (<0.1)	0.43 (0.16)	41.34 (.)	429.88 (.)
Piscivore	White hake (>40 cm)	–	0	–	–	–	3 (1.7)	5 (0.2)	8.22 (3.13)	53.99 (13.70)	1,434.5 (1,213.8)
Piscivore	Fourspot flounder	2 (1.3)	3 (0.1)	0.34 (0.13)	20.92 (11.76)	111.98 (165.68)	37 (20.8)	91 (4.2)	37.40 (14.22)	35.92 (8.08)	425.63 (276.38)
Piscivore	Summer flounder	1 (0.7)	4 (0.1)	0.20 (0.08)	18.10 (2.61)	50.92 (21.96)	6 (3.4)	16 (0.7)	6.76 (2.57)	33.75 (9.30)	451.46 (327.08)
Piscivore	*Illex* squid	25 (16.9)	87 (2.9)	12.44 (5.27)	19.60* (32.00)	143.00* (70.00)	2 (1.1)	15 (0.7)	2.15 (0.82)	19.60* (32.00)	143.00* (70.00)

(Continued)

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TABLE 2 Continued

		Harbor seal (*n* = 144)					Gray seal (*n* = 143)				
Trophic group	Prey	Frequency of occurrence (PO%)	Numerical abundance (PN%)	Biomass kg (PB%)	Mean length† (cm, s)	Mean weight† (g, s)	Frequency of occurrence (PO%)	Numerical abundance (PN%)	Biomass kg (PB%)	Mean length† (cm, s)	Mean weight† (g, s)
Piscivore	*Loligo* squid	18 (12.2)	154 (5.1)	38.96 (14.56)	23.20* (8.40)	259.00* (180.00)	13 (7.3)	30 (1.4)	6.81 (2.59)	20.10** (6.18)	227.00** (–)
Piscivore	Squid spp.	14 (9.4)	78 (2.6)	13.87 (4.47)	19.8* (–)	174.00* (–)	3 (1.7)	5 (0.2)	0.87 (0.33)	19.8* (–)	174.00* (–)
Unknown	Unidentifiable spp.	10 (6.7)	14 (0.5)	2.24 (0.83)	–	–	7 (3.9)	12 (0.6)	1.24 (0.47)	–	–
Planktivore/ benthivore	Elasmobranch spp.	2 (1.34)	Unk	Unk	Unk	Unk	17 (9.24)	Unk	Unk	Unk	Unk
		Total MNI	3,007	268.67	17.12 (7.63)	59.27 (66.86)	Total MNI	2,142	263.03	22.64 (9.11)	120.99 (185.96)
		Richness—*S****	30				Richness—*S****	31			
		Diversity *H′*	0.65				Diversity *H′*	0.66			

Percent frequency of occurrence (PO%), relative abundance (PN%), and biomass (PB%) consumed, mean prey size (cm), and weight (kg) are summarized by the trophic guild. Seal stomachs with no otoliths or squid beaks present were removed from the sample size (n). Prey highlighted in blue reflect numerical abundance ≥1%.

†Mean length and weight calculations from measured otoliths (codes 1 and 2) only. Urophycis spp.—silver hake length equation used for harbor seal; red hake length equation was used for gray seal diet; gadid spp.—haddock length equation was used for gray seal diet—see Supplementary Appendix 1.

*Harbor seal—Illex, Loligo, and squid spp. length and weight from Williams (1999).

**Gray seal—Loligo squid length and weight from Ampela (2009).

**Gray seal—Illex and squid spp. length and weight from Williams (1999).

***Excludes taxonomic groupings: Clupeidae, eel spp., flatfish spp., Gadidae spp., gulf stream/smallmouth spp., squid spp., Urophycis spp., Unidentifiable spp., and elasmobranch spp.; species with more than one size category were only counted once (i.e., silver hake, red hake, white hake, and pollock).

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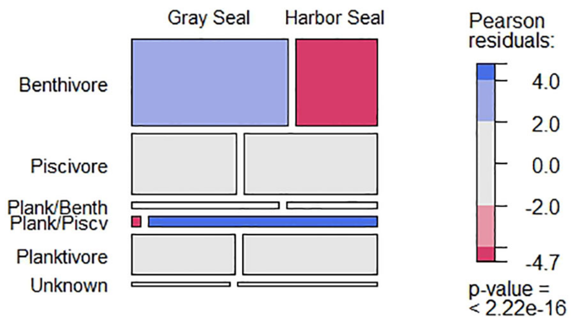

FIGURE 2
The frequency of occurrence among trophic groups present in harbor and gray seal stomach samples between 2004 and 2018. Block width (columns) reflects the frequency of occurrence by the seals and block height (rows) reflects the frequency of occurrence by guild. Pearson residual scale based on the chi-square test. Elasmobranch spp. and empty stomachs (i.e., stomachs with no otolith or squid beak remains) were removed.

The breadth of both seal diets was similar between harbor (H' = 0.65) and gray seals (H' = 0.66). Fourteen prey contributed to >1% of prey abundance consumed by harbor seals. Two size categories of silver hake (*Merluccius bilinearis*; ≤20 cm + >20 cm; 40% of prey abundance), redfish (18% of abundance), and ≤40 cm red hake (*Urophycis chuss*; 9% of abundance) were the most abundant, frequently present, and collectively contributed to 45% of the biomass consumed by harbor seals. Fourteen prey also contributed to >1% of prey abundance consumed by gray seals. Red hake (≤40 cm; 30% of prey abundance), two size categories of silver hake (≤20 cm + >20 cm; 17% of abundance), and gulf stream flounder (*Citharichthys arctifrons*: 11% of abundance) were the most abundant, frequently present, and collectively contributed to 45% of the biomass consumed by gray seals (Table 2).

Over the study period, the mean reconstructed harbor seal meal size (minimum number of individuals = 21) was significantly more than the reconstructed gray seal meal size (14; T_{obs} = 7, P = 0.003; Figure 3). However, among all the prey and their respective trophic groups consumed by both seal species, the mean prey size consumed by harbor seals was significantly smaller (18 cm) than the prey consumed by gray seals (26 cm; T_{obs} = −8 cm; P = 0.000; Supplementary Figures S4, S8A). This was also true for individual prey biomass where mean harbor seal prey biomass (0.06 kg) was significantly less than the mean individual prey biomass consumed by gray seals (0.15 kg; T_{obs} = −0.09 kg; P = 0.000; Supplementary Figure S5). Consequently, even though harbor seals consumed more individual prey, their mean meal size measured in mass (1.82 kg) was similar to gray seals (1.84 kg; T_{obs} = 0.02kg; P = 0.525; Figure 3 and Supplementary Figure S6). Although consumed elasmobranch species abundance and biomass could not be determined in this study, they occurred more frequently in gray seal diets compared with harbor seals (z-score = −3.06; P = 0.001; Table 2).

When sorted by importance, the most important prey consumed by harbor and gray seals were species that had iIMP ≥2.6% (11 species) and 2.4% (10 species), respectively (Figure 4). Among these most important prey, approximately half of them overlapped between the two seals (C = 0.55). They included large (>20 cm) and small (≤20 cm) silver hake, (≤ 40cm) red hake, gulf stream flounder, medium (21–40 cm) white hake (*Urophycis tenuis*), and (<50 cm) Atlantic cod (Figure 4). The other half of prey with high iIMP for harbor seals that did not overlap with high iIMP to gray seals were redfish (15.4%), Atlantic herring (*Clupea harengus*; 4.8%), longfin squid (*Doryteuthis pealeii*; 4.4%), and shortfin squid (*Illex illecebrosus*; 4.3%). These

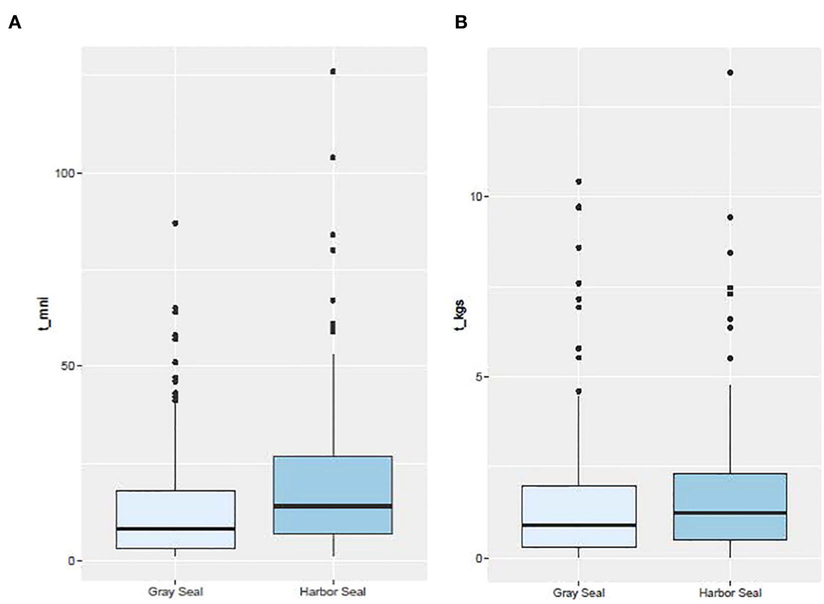

FIGURE 3
Box plot distribution of meal size based on **(A)** the minimum number of individual prey (t_mni) and **(B)** the biomass of those individual prey (t_kgs) by seal species. Number of stomach samples = 138 and 121 for harbor and gray seals, respectively.

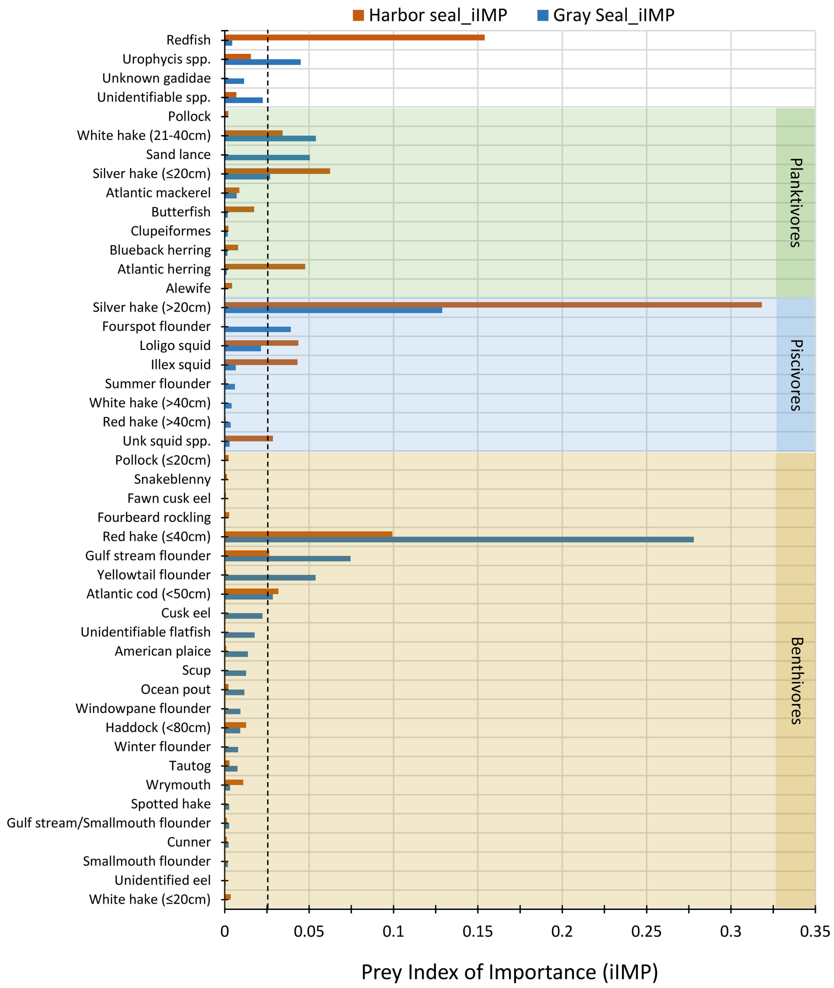

FIGURE 4
Prey index of importance (iIMP) consumed by harbor (brown bars) and gray (blue bars) seals. Prey species are organized and shaded by trophic groups: benthivores (tan), piscivores (blue), and planktivores (green). Unshaded prey species or groups belong to more than one trophic group: redfish = planktivore/piscivore, *Urophycis* spp. and Unknown Gadidae = planktivore/benthivore, and unidentifiable spp. the trophic group is unknown. Prey species with no length category shown belong to only one trophic group regardless of their size, whereas prey species with a length category belong to more than one trophic group. The vertical dashed line marks the minimum iIMP that identifies important prey to the seals. Morisita index of diet overlap (*C*) between harbor and gray seals = 0.55.

contrasted with yellowtail flounder (*Limanda ferruginea*; 5.4%), sand lance (*Ammodytes* spp.; 5.0%), *Urophycis* spp. (4.4%), and fourspot flounder (*Hippoglossina oblonga*; 3.9%) prey with high iIMP to gray seals that did not overlap with high iIMP prey to harbor seals (Figure 4).

Diet patterns by age, sex, time, and area

Diet overlap was highest in the southern region (*C* = 0.71) and in the winter season (*C* = 0.68) when young-of-the-year harbor and gray seals co-occur. Diet overlap was also high in the spring (*C* = 0.93), but the harbor seal sample size was limited. Diet overlap was lowest in the Gulf of Maine (*C* = 0.34) and in the summer season (*C* = 0.32) when young-of-the-year harbor and gray seals are the most segregated (Table 3 and Figures 1, 5). Approximately half of the diet overlapped for young-of-the-year and both sexes. Weaned pups do not overlap in space and time, so their dietary overlap is low (*C* = 0.27; Table 4 and Figure 5). Harbor seal adult and juvenile sample sizes were too small to make reliable comparisons to adult and juvenile gray seals. Several prey species were important to both seal species in the southern region. This contrasts with the Gulf of Maine where redfish and large silver hake were important prey to harbor seals in comparison to the importance of yellowtail flounder and sand lance to gray seals (Supplementary Figure S7A). Silver and red hakes were important to both seals across all seasons. Gulf stream flounder was important to both seal species during the winter and spring. Sand lance was important to gray seals, whereas redfish was most important to harbor seals during the summer and fall. Atlantic cod was important to both seals but mostly to harbor seals during the spring and both seal species during the summer. Yellowtail flounder was important only to gray seals mostly during the fall, and herring was important only to harbor seals year-round except

TABLE 3 Morisita index (*C*) of trophic niche overlap between gray and harbor seals by season (winter=december-february, spring=march-may, summer=june-august, fall=september-november) and region (georges bank=gb, gulf of maine=gom, southern new england/mid-Atlantic=mab).

Season	Region	Gray seal		Harbor Seal		*C*
		Prey Species	Samples	Prey Species	Samples	
winter	gom	11	4	14	11	
	mab	26	24	22	30	
	Winter Total		28		41	0.68
spring	gb	9	3	0	0	
	gom	18	14	6	2	
	mab	29	71	17	7	
	Spring Total		88		9	0.93
summer	gb	15	8	0	0	
	gom	15	9	28	51	
	Summer Total		17		51	0.32
fall	gb	1	1	0	0	
	gom	16	9	20	42	
	mab	0	0	1	1	
	Fall Total		10		43	0.47
Region Totals	gb		12		0	na
	gom		36		106	0.34
	mab		95		38	0.71
Grand Total			143		144	0.55

Prey species = the number of prey species recovered from stomach samples; Samples = the number of stomach samples; na = not applicable.

for the summer season (Supplementary Figure S7B). The regional and seasonal patterns of important prey to harbor and gray seals applied to both sexes, pup, and young-of-the-year age classes. Sample sizes were too small to make meaningful comparisons for the adult and juvenile age classes (Supplementary Figures S7C, D).

Modeling effects on prey consumption

Sample sizes were too limited to simultaneously evaluate the effect of seal, region, season, sex, and age on consumption (Supplementary Table S3). However, univariate models showed that 1) the variety of prey in seal diets and 2) the location of bycatch samples explained a significant portion of variability in the minimum number of prey consumed. The minimum number consumed increased when prey species richness (*S*) and the number of trophic guilds increased. Geographic region was not as important, but there was a significant longitude effect on seal consumption with less consumption observed east of 70.5° (Supplementary Table S4 and Supplementary Figure S2). The effect of seal age, sex, season, region, and trophic group on the mean prey size consumed by each seal was not tested. Patterns in prey sizes consumed by these factors are available in Supplementary Figures S8A–F.

Length frequencies of seal prey versus commercial catches

Mean prey size (cm) was compared among some of the most important prey to both harbor and gray seals and Northeastern US commercial gillnet trips. They included silver hake, red hake, and Atlantic cod. Both harbor and gray seals (combined) consumed smaller prey compared with sampled commercial gillnet catches for all three species. The mean length of cod consumed by harbor and gray seals (20 cm) was smaller than the mean cod length caught and sampled on commercial gillnet trips (73 cm; $T_{obs} = -53$ cm; $P = 0.00$; Figure 6). The mean length of red hake consumed by the seals (25 cm) was smaller than the mean red hake length caught and sampled on commercial gillnet trips (43 cm; $T_{obs} = -17$ cm; $P = 0.00$; Figure 7). The mean length of silver hake consumed by the seals (22 cm) was smaller than the mean silver hake length caught and sampled on commercial gillnet trips (36 cm; $T_{obs} = -14$ cm; $P = 0.00$; Figure 8). There were not enough samples to compare the mean sizes of yellowtail flounder.

Discussion

Data available to infer marine mammal diet composition or consumption are often sparse and reflect varying degrees of

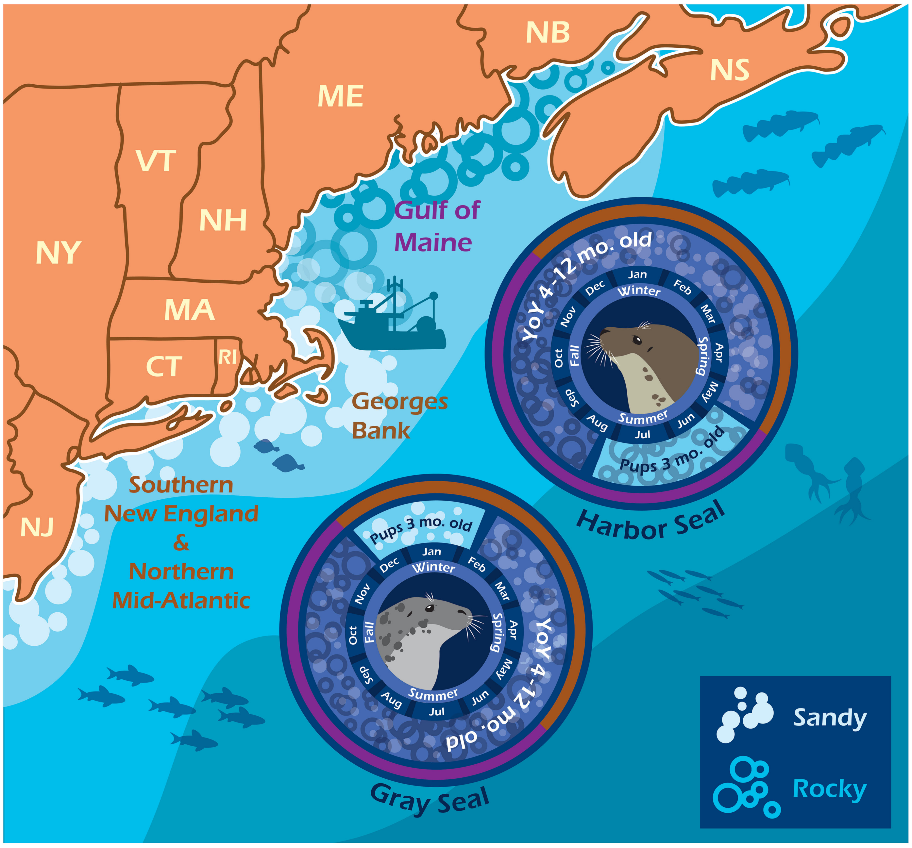

FIGURE 5
Harbor and gray seal bycatch phenology. The infographic depicts when and where pup and young-of-the-year seals generally appear in bycatch given the opposite timing and location of their reproduction cycles and proximity to commercial fishing grounds. Harbor seals are born and weaned along the rocky coastline, ledges, and islands in the Gulf of Maine (purple) during the summer. Gray seals are born and weaned among the sandy islands and beaches of western Georges Bank and into Southern New England (brown) during the winter. Image credit: Ari Morese, https://ariannamorese.wixsite.com/arimorese.

temporal, spatial, and demographic resolution (Smith et al., 2015). This is true of the opportunistic samples obtained from bycatch events for this study (Table 1). In most cases, there were no samples available to make 1:1 comparisons between harbor and gray seal diet that account for both intrinsic (age and sex) and extrinsic (season and region) factors (Supplementary Table S3). However, these samples provide temporal and spatial contexts for analysis of the seals' diet. The imbalance in the temporal and spatial distribution of stomach samples used in this study is explained by non-overlapping harbor and gray seal phenology and pup haul-out locations that are adjacent to high-density large mesh (>20 cm) gillnet fishing regions (Murray et al., 2021; Figure 1). This also explains why the majority of samples are from the pup and young-of-the-year age classes (Table 1). In other words, these age classes appear in bycatch in opposite times and areas given the timing and location of their reproduction cycles. Evidence from tagged animals suggests that most weaned pups and young-of-the-year gray seals forage in Southern New England adjacent to Muskeget Island and Monomoy pupping habitats during late winter into spring and summer (Murray et al., 2021; Wood et al., 2022). On the other hand, most weaned pups and young-of-the-year harbor seals forage in the Gulf of Maine adjacent to coastal bays, ledges, and island pupping habitats in summer into fall seasons (Williams, 1999; Gilbert et al., 2005; Waring et al., 2006; Sigourney et al., 2022). Pup and young-of-the-year age classes from both seals generally overlap in the Gulf of Maine during summer and fall and less so in the southern region in winter and spring (Figure 5). Given this bias toward pup and young-of-the-year age classes, it is not surprising that sex was not an important factor when contrasting patterns in diet between the two seal species (Beck et al., 2007). Both sexes are expected to have limited dive capacity and be equally naive in foraging and consequently subject to higher bycatch rates relative to older more experienced age classes (Frost et al., 2006; Murray et al., 2021).

The differences in important prey, also reflected in 55% overlap in diet, are also a function of when and where the seals show up in bycatch and mostly driven by samples from the pup and young-of-the-year age classes. This trophic niche separation is exhibited by gray seal consumption of more benthivorous prey species compared with harbor seals. The least dietary overlap in the Gulf of Maine during the summer and fall (C = 0.34) appears to be explained by harbor seals' preference for redfish and small silver hake over sand lance, yellowtail flounder, and red hake consumed by gray seals. The most dietary overlap occurs in the southern region (C = 0.71) during winter and spring where both seals consume silver and red

TABLE 4 Morisita index (*C*) of trophic niche overlap between gray and harbor seals by sex (UNK=unkown, F=female, M=male) and age (juv=juvenile, unk=unknown, yoy=young of year, adu=adult, pup ≤ 3 months old).

Sex	Age	Gray seal		Harbor Seal		*C*
		Prey Species	Samples	Prey Species	Samples	
UNK	juv	6	1	0	0	
	unk	2	1	8	5	
	yoy	4	1	1	1	
	UNK Total		3		6	0.53
F	adu	3	2	2	1	
	juv	5	1	0	0	
	pup	16	10	19	12	
	unk	2	1	2	1	
	yoy	27	48	26	39	
	F Total		62		53	0.48
M	adu	18	5	4	3	
	juv	26	13	7	2	
	pup	12	8	18	19	
	unk	0	0	2	1	
	yoy	34	52	31	60	
	M Total		78		85	0.58
Age Totals	adu		7		4	0.03
	juv		15		2	0.42
	pup		18		31	0.27
	unk		2		7	0.24
	yoy		101		100	0.60

Prey species = the number of prey species recovered from stomach samples; Samples = the number of stomach samples.

hake and gulf stream flounder. This is also when most of the squids are present in the harbor seal diet (Table 3 and Figure 9). Pups rarely co-occur which explains low overlap in their diets ($C = 0.27$; Table 4 and Figure 5).

Consistent with Ampela (2009), diet data obtained from the stomachs of bycaught gray seals in our study paint a different picture of the relative abundance of prey in the diet when compared with data obtained from scat samples. Examples of this are shown by Ampela (2009) and Lerner et al. (2018) where a relatively high abundance of sand lance was found in gray seal scat samples obtained from sandbars off the coast of Chatham, Massachusetts. Bowen and Harrison (1994) show a similar pattern with a high proportion of sand lance found in scats collected on Sable Island, a sandy island habitat on the Scotian shelf. In contrast, sand lance relative abundance was low (<10%) in gray seal stomachs examined by Ampela (2009) and this study. We postulate that diet data obtained from Northeastern US bycatch events are more representative of offshore foraging on the continental shelf and banks away from haul-out sites, whereas diet from scats represents more nearshore foraging closer to haul-out sites (Pierce and Boyle, 1991; Ampela, 2009; Hammill et al., 2014; Johnston et al., 2015; Lerner et al., 2018; Hernandez et al., 2019a). These differences may also be confounded by the seal's age and foraging experience (Beck et al., 2007). The majority of data in this study were obtained from young-of-the-year gray seals with limited foraging experience. Scat samples obtained off Chatham sandbars are generally obtained from mixed age groups with a likely bias toward the more numerous older gray seals. Older seals have more foraging experience and are likely more successful in capturing pelagic, fast swimming, or schooling prey. Sand lance are given their name because they burrow in the sand in shallow near-shore habitats (Robards et al., 1999; Staudinger et al., 2020). However, Bowen et al. (2002) documented mature harbor seals' capture of sand lance both burrowed in the sand and as schooling prey in the water column. Although the sample sizes from the adult age class from our study are small, sand lance had the highest importance (iIMP) in the diet of adult gray seals ($n = 7$; Supplementary Table S3 and Supplementary Figure S7C). Hammill et al. (2014) showed that sand lance also rank high in importance and mass consumed by older gray seals collected from digestive tracts obtained from the

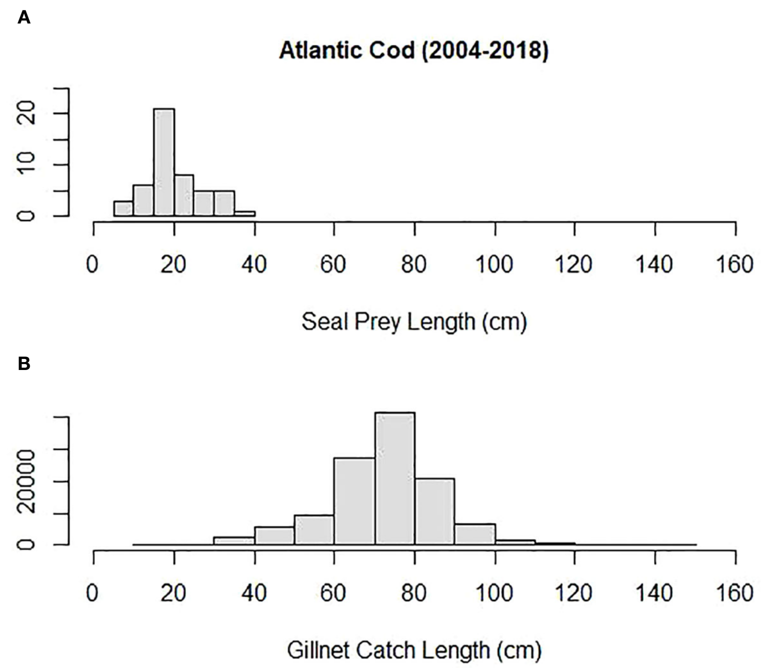

FIGURE 6
Length distribution (cm) of Atlantic cod **(A)** consumed by harbor and gray seals and **(B)** caught by commercial gillnet fishermen.

Cabot Strait and Cape Breton Island off of Canada (mean age ranged 7–12 years old). By comparison, sand lance were rarely found in the stomachs of bycaught harbor seals but historically were found in high abundance when recovered from their scats (Payne and Selzer, 1989). Ignoring all extrinsic and intrinsic factors, the occurrence of cod in gray seal diet (5.1%) is consistent with the findings in Flanders et al. (2020) where the relative contribution of cod (6.7%; resolved to the genus Gadidae spp.) to the diet of gray

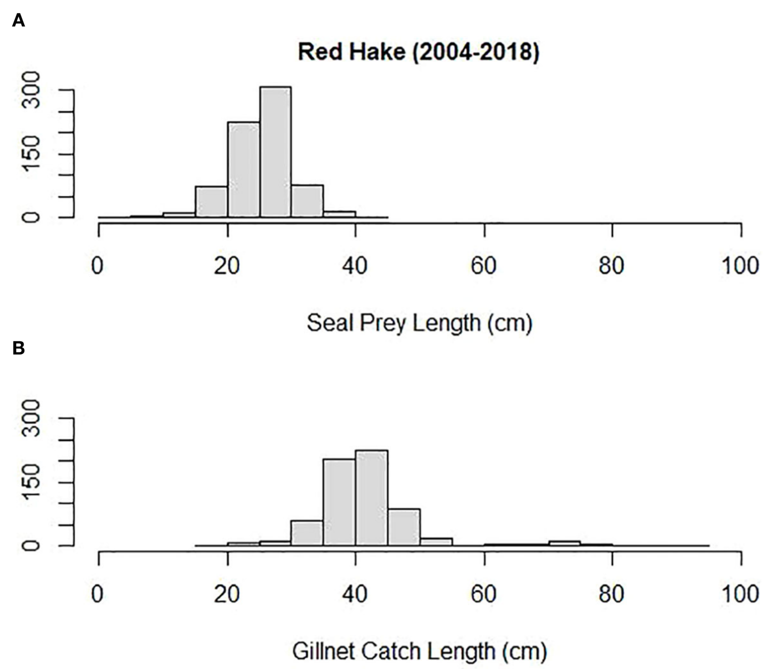

FIGURE 7
Length distribution (cm) of red hake **(A)** consumed by harbor and gray seals and **(B)** caught by commercial gillnet fishermen.

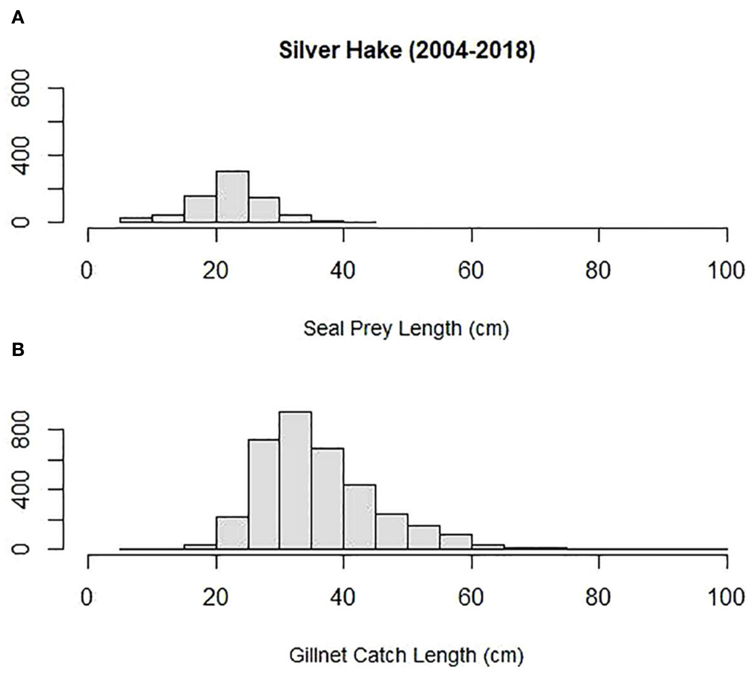

FIGURE 8
Length distribution (cm) of silver hake **(A)** consumed by harbor and gray seals and **(B)** caught by commercial gillnet fishermen.

seals was inferred by DNA meta-barcoding techniques. This is also consistent with the findings in Canadian waters where cod was found to be important in adult gray seal diet (Bowen and Harrison, 1994; Hammill et al., 2014).

Consistent with Williams (1999) and Ampela (2009), prey sizes consumed by both seals in our study showed limited overlap with prey sizes caught by commercial gillnet fishermen. Sørlie et al. (2020) also reported evidence of harbor seal preference for smaller

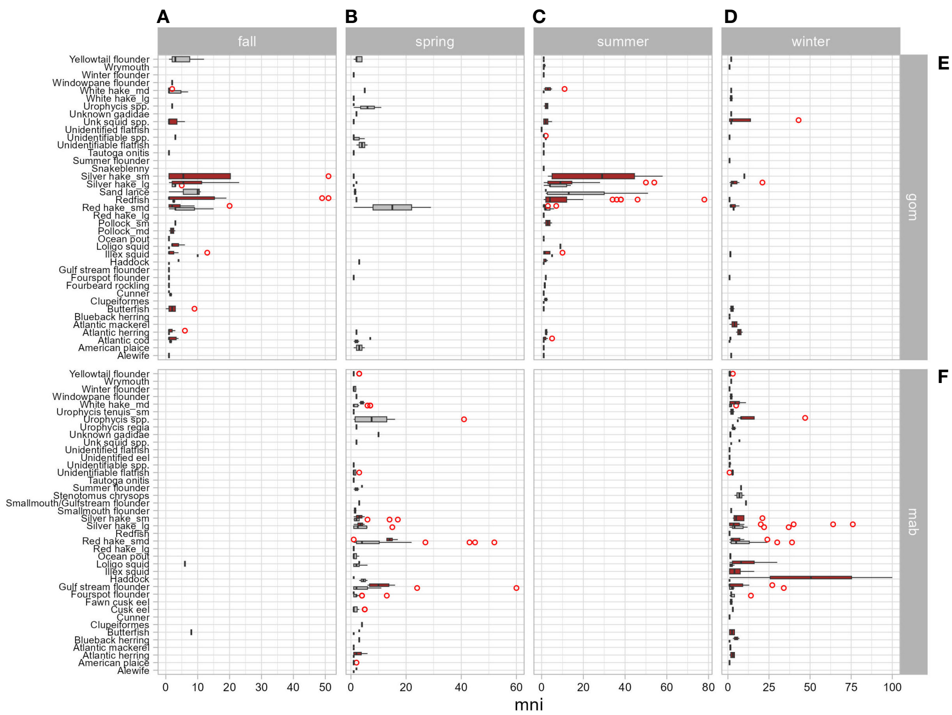

FIGURE 9
Box plots of the number of individual prey (mni) consumed by harbor (red bars) and gray (gray bars) seals by season (**A**: fall = Sep–Nov, **B**: spring = Mar–May, **C**: summer = Jun–Aug, **D**: winter = Dec–Feb) and geographic region (**E**: gom = Gulf of Maine, **F**: mab = mid-Atlantic Bight, including Southern New England). Red circles identify extreme values.

prey compared with the size of some species exploited by commercial fisheries off the coast of Norway and low levels of direct competition between harbor and gray seals and commercial fisheries. However, it is important to note that the majority of seals in our study were young-of-the-year animals, the age class most frequently caught as bycatch in NEUS commercial gillnet fisheries (Murray et al., 2021). It is generally understood that larger seals from the older age classes can consume larger prey. Hammill et al. (2014) showed that adult gray seals in the Cabot Straight and Cape Breton Island off of Canada on average consumed large white hake (29–35 cm) and Atlantic cod (28–39 cm). By comparison, adult gray seals in our study (albeit a small sample size, n = 7) indicate consumption of larger fish (Supplementary Figure S8C). Thus, it is important to consider the age distribution of the seals when utilizing results from seal diet studies to inform fish population and ecosystem dynamic models (Benoît et al., 2011).

If the dietary pattern of harbor seals is correlated to the relative abundance of prey in the ecosystems but also sensitive to gray seal population growth, this can provide insight into the resilience of US Northwest Atlantic harbor seals to gray seal recolonization in New England waters (Smout et al., 2014; Johnston et al., 2015; Russell et al., 2015; Ouellet et al., 2016; Pace et al., 2019; Murray et al., 2021). Consistent with other studies, our research shows that hake species rank at the top of the most important prey to harbor seals, similar to gray seals, regardless of sex and age class (Ampela, 2009; Hammill et al., 2014). Our study also shows that cod occurrence (16%) and abundance (2%) are three times greater in harbor seal diet compared with gray seals (Table 2). The finding of the importance of cod in the diet of harbor seals is consistent with that reported by Williams (1999). The remaining most important prey unique to harbor seals—silver hake, redfish, red hake, herring, and squids—were also identified as the most important prey over 20 years ago by Williams (1999). Bowen and Harrison (1996) also identified cod, herring, and *Illex* squid among the most abundant prey in the diet of harbor seals in the Canadian maritime region. The persistence of important prey to the diet of harbor seals over recent decades provides evidence that they are resilient to the concurrent resurgence of the gray seal population in Northeastern US waters. Finally, mean harbor seal prey size and biomass were 8 cm and 0.09 kg smaller than gray seals, respectively. The significant difference in mean prey size and biomass between the two seal species was expected given the overall difference in body size and mass between the two seals, even at the younger age classes (*Encyclopedia of Marine Mammals*, 2nd ed.; Perrin et al., 2009).

Williams (1999) and Ampela (2009) offer the only empirically based Northeastern US estimates of Northwest Atlantic harbor and gray seal diet composition based on biomass, respectively. In comparison to their research results, our more recent study found similar seal diet compositions, specifically for samples originating from bycatch. In contrast, seal diet composition from our study generally does not align with seal proportional prey composition for the Northeastern US estimated in Smith et al. (2015). There are likely several reasons for the differences. The most notable is that harbor and gray seal mean diet composition among prey groups in Smith et al. (2015) varies widely due to a large number of literature sources used to estimate diet composition. Most of those studies originated from regions outside of the Northeastern US, and several of the sources utilized scats to reconstruct the seal diets.

Using hard parts to evaluate marine mammal diet allows for the estimation of prey biomass consumed at a high taxonomic resolution (Table 2). However, there are three primary shortcomings of using hard parts to estimate diet: 1) a bias toward cephalopod beaks and fish otoliths that have higher retention in the stomach lining and are more resistant to degradation, respectively; 2) underdetection of prey which have no hard part remains (e.g., elasmobranchs, crustaceans, and depredation); and 3) difficulty investigating for evidence of scavenging. Squid beaks have been reported to become lodged in the stomach lining and thereby can be overrepresented in diets inferred from stomach contents (Olesiuk et al., 1990; Bowen and Iverson, 2013). Pristine and otoliths with minor erosion likely reflect prey with more robust otolith size (e.g., gadoid species), but fragile otoliths are more likely to be underrepresented due to breakage, degradation, or fully digested in the stomach before passing through the intestines (e.g., clupeids; Murie and Lavigne, 1986; Pierce and Boyle, 1991; Hammill et al., 2007; Tollit et al., 2007). However, stomach content data are less biased than scats with respect to quantifying the minimum number and size of prey consumed simply because stomach content remains have not cycled through the entire digestive process (Jobling and Breiby, 1986; Olesiuk et al., 1990; Ampela, 2009).

Similar to the findings in Byron and Morgan (2016) and Pitchford et al. (2020), our study found evidence of elasmobranch prey present in gray seal stomach samples but very few in harbor seals. This is likely due to the high incidence of gray seal bycatch events in the southern region that co-occurred with large mesh skate and dogfish gillnet fisheries (Murray et al., 2021). With respect to depredation, only the lower portion or belly region of fish is consumed by predators. Consequently, there generally is no evidence of depredation (i.e., no otoliths consumed or located) in the stomach of the predator unless headless fish remains are found intact within the stomach. In contrast, consumption by scavenging may be detected when only heads of fish are recovered with no further co-occurring evidence of bony or flesh remains. Consumption by scavenging can occur when fishermen dress their fish catch for the market while at sea. The application of fatty acids as trophic markers provides both longer temporal insight into marine mammal foraging patterns and theoretically can limit the depredation source of bias when compared with techniques that involve analysis of hard parts (Kirsch et al., 2000; Dalsgaard et al., 2003; Thiemann and Iverson, 2008; Iverson, 2009; Thiemann et al., 2009; Bowen and Iverson, 2013). The DNA meta-barcoding of prey may also get at this source of bias; however, analytical techniques using DNA to quantify the abundance of prey in the diet are still under development (Jeanniard-du-Dot et al., 2017; Shelton et al., 2023).

In conclusion, this study demonstrates the importance and value of utilizing carcasses retained from bycatch events to fill data gaps in our understanding of the ecological role of recovering harbor and gray seal populations. This includes their impact on the natural mortality of prey important to commercial fisheries providing further insight into the connections between fisheries and protected species management potentially regulating food web dynamics in the Northeastern US region (Kulatska et al., 2021). Given the richness of their diets, these seals may be capable of shifting their diet to species that are predicted to be more abundant in the future as a result of changing environmental or habitat conditions (Nye et al., 2009; Zeppelin and Orr, 2010; Pinsky et al., 2013; Hare et al., 2016; Kleisner et al., 2017; Friedland et al., 2019; Lettrich et al., 2023). Finally, we recommend cross-validation studies comparing results from different diet sample types, locations, and methodologies to minimize bias and provide more robust evidence of the magnitude of natural mortality on commercially important species induced by top-level predators.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: FigShare, https://figshare.com/articles/dataset/Lyssikatos_and_Wenzel_2024/25097213.

Ethics statement

The manuscript presents research on animal diet. No live animals were used or handled during the course of this study. Ethical approval was not required for the study.

Author contributions

ML: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing, Data curation. FW: Data curation, Investigation, Writing – review & editing.

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Conflict of interest

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

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1377673/full#supplementary-material

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Understanding perceptions that drive conflict over the endangered Hawaiian monk seal

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As conservation and management actions facilitate the recovery of threatened and endangered marine species, and human populations expand in urbanizing coastal areas, people are increasingly coming into contact with marine wildlife. These increasing human-wildlife interactions can cause conflict, as has been the case with the endangered Hawaiian monk seal. Since 2009, there have been at least sixteen documented monk seal killings by gunshot or head trauma. Drawing on interviews, surveys, and government and media reports, we explored the underlying drivers behind this conflict, examining how social construction of wildlife, levels of conflict, and ideas from risk communication inform these drivers. Across these sources, we found that most people on beaches where seals are present and other members of the public hold positive perceptions of monk seals and are not engaged in conflicts. Rather, conflict is driven by individuals who have strong feelings about seals and what they represent, which in some cases conflicts with their own values and sense of identity. Many monk seal recovery volunteers saw themselves as protectors of endangered seals, seeing the species as an innocent victim of human-caused environmental destruction. Some fishermen viewed seals as resource competitors, and there were those who also saw them as symbolic of federal government restrictions on access to natural resources. Native Hawaiians who disliked seals saw them as invaders in their native homeland, and perceived federal actions to protect seals as a continuation of colonial restrictions on their rights and access. Social media and other platforms also play an emerging role in escalating the conflict over monk seals. Natural resource managers have engaged in multiple intervention strategies to address conflict, including message framing, education and outreach, and efforts to increase public trust. However, these efforts have not always targeted the people most likely to interact with monk seals as populations recover. Ultimately, it is important for resource managers to articulate their own assumptions and values, and to work to understand the assumptions and values of those who may be affected by successful monk seal recovery efforts, to develop effective strategies that prevent and address conflict over this recovering endangered species.

KEYWORDS

Hawaiian monk seal, human-wildlife conflict, endangered species recovery, social construction, levels of conflict, risk communication, social media, marine management

1 Introduction

As the Endangered Species Act (ESA) and other conservation and management actions facilitate the successful recovery of many threatened and endangered marine species (Valdivia et al., 2019), and human populations expand in urbanizing coastal areas, people are increasingly likely to interact with protected marine wildlife. While these interactions can bring excitement, wonder, and economic benefit to coastal communities (Loomis, 2006; Cisneros-Montemayor et al., 2013), they can also result in conflict, particularly over shared spaces or shared resources (Draheim et al., 2015; Guerra, 2019). In some cases, these types of conflicts have resulted in prolonged legal battles between advocates for marine species and those who want to maintain access to marine and coastal resources (Carswell et al., 2015; Konrad and Levine, 2021). In other cases, conflict has resulted in the death of threatened marine species, such as the recent intentional killings of endangered monk seals in Hawai'i (Harting et al., 2021; Carretta et al., 2022) and the shooting of pinnipeds and sea otters in central California (Baxter, 2015; Barcenas-De la Cruz et al., 2018). While elements of each of these conflicts are species and place specific, they have many common drivers and are often due to differences in values and worldviews between parties in conflict.

To prevent or mitigate conflict related to recovering wildlife populations, including marine species, it is important to understand the underlying factors that drive conflict (Manfredo and Dayer, 2004; Marshall et al., 2007). Human values are critical in shaping how people perceive wildlife (Messmer, 2000; Riley et al., 2002; Dickman, 2010; Madden and McQuinn, 2014; Bennett et al., 2017; Muhar et al., 2018). People from divergent backgrounds and value systems may perceive the impacts of wildlife differently, which may lead to conflicting beliefs about the species and objectives for managing interactions with them (Riley et al., 2002; Jackman et al., 2023). In some cases, the material impacts of wildlife may be less important in shaping people's attitudes than the degree to which people agree with how wildlife is governed and the actions of governing institutions (Merz et al., 2023). Unfortunately, values and perceptions toward wildlife have received less attention in research relating to wildlife conflict when compared with ecological and biophysical factors (Manfredo and Dayer, 2004), though attention to these questions has expanded in recent years (König et al., 2020). The emotional and cultural dimensions of human-wildlife interactions are critical to coexistence (Pooley et al., 2021), and greater attention to how social contexts and material impacts of human-wildlife interactions interplay with approaches to managing conflict are important in designing effective conservation and conflict management programs (Redpath et al., 2013).

The endangered Hawaiian monk seal *(Neomonachus schauinslandi)* is a classic example of a recovering species whose presence evokes predictably diverse responses. In this paper, we explore the underlying drivers of conflict as interactions between people and Hawaiian monk seal populations increase in Hawai'i. This analysis will both (1) inform better management of conflicts about Hawaiian monk seals and, (2) provide insights to help others embarking on marine mammal recovery to proactively anticipate the potential for increased interactions and conflict that paradoxically may be an inevitable outcome of successful recovery.

2 Rebounding species and the potential for human-wildlife conflict

Human-wildlife conflicts are now recognized as largely social conflicts between people about wildlife and how wildlife should be managed (IUCN, 2023). These conflicts may stem from groups of people experiencing different types of interactions with wildlife, for example visitors viewing wildlife in a park for the first time vs. residents near a park interacting regularly with the species in their backyards, as well as different perceptions of the same interactions when the animal is viewed as a pest or pet (Herda-Rapp and Goedeke, 2005; Jerolmack, 2008; Leong, 2009). When animals have become rare enough to be protected under the ESA, interactions with them are also infrequent. As populations rebound towards recovery and interactions become more frequent, people will increasingly need to make sense of these novel types of encounters. The encounters themselves are not inherently good or bad; they are weighted through human values that determine their importance and whether the impacts from those interactions are valued on the whole as positive or negative (Riley et al., 2002). A large body of research has demonstrated that many of the conflicts associated with wildlife conservation stem from divergent value systems, worldviews, and histories of the parties in conflict, especially as people learn to make sense of increasing interactions with wildlife that have become intolerable for some (for example, see Hill et al., 2017; Frank et al., 2019; IUCN, 2023). Understanding the specific drivers of these conflicts is necessary for successful recovery and coexistence.

Some core concepts related to drivers of conflict include: social construction of wildlife, levels of conflict, and risk communication. Social construction refers to the process by which people attach meaning to the physical world; the way we understand animals and our interactions with them is based on physical considerations, but they are filtered through the social and cultural symbols and norms that determine how we think about them (Herda-Rapp and Goedeke, 2005; Leong, 2009). Different groups of people may apply different societal norms, leading to conflict. For example, anglers have viewed recovering river otters *(Lutra canadensis)* as "hungry little devils," while protection activists viewed them as "playful, ecological angels" (Goedeke, 2005). This process has also been shown for common species becoming overabundant, where white-tailed deer *(Odocoileus virginianus)* were alternately viewed as pests or pets (Leong, 2009), and for increasing populations of feral domestic species, e.g. outdoor cats *(Felis catus)* seen as invasive species or homeless pets (Leong et al., 2020).

When differing constructions of wildlife are based on identities, conflict becomes even more difficult to manage. The levels of conflict framework illustrates how resolving a surface level dispute can appear to be relatively straightforward, but conflicts with a long history or that impact the sense of identity or values of the parties involved can become intractable (Madden and McQuinn, 2014; Zimmermann et al., 2020). In these instances people may only voice surface level concerns, when they actually care more about threats to their identity or values. The nature of the conflict thus informs the type of resolution needed, where deep-value identity conflicts require reconciliation techniques that transform dialogue from a focus on the visible disputes about how to manage physical interactions with wildlife to addressing the harms to identity or values that may stem from the way management priorities or methods are applied and perceived.

Approaches to communication also may drive conflict when they are not targeted to the appropriate level of conflict. While education and outreach may be helpful in addressing surface-level disputes, these approaches are not well-suited to addressing the deeper level drivers. For example, it is well known that experts and the public perceive risk differently, with experts more focused on probability of harm (hazard) and the public focused on characteristics of the risk (outrage), such as whether it is a known or new risk, natural or man-made, chronic or catastrophic, and whether it approaches everyone equally or if some people are more affected than others (Slovic et al., 1979; Morgan et al., 2002; Sandman, 2021). For each of those dimensions, the former is perceived as less risky than the latter, regardless of probability of harm. Perceptions of risks and benefits also may differ between managers and publics, further driving conflicts (Bruskotter and Wilson, 2014). In addition, public risk perceptions are formed within a social context, where entities such as news media, cultural groups, or interpersonal networks can amplify or attenuate perceptions of risk and may not be aligned with expert perspectives (Kasperson et al., 2022).

The majority of research to date on human-wildlife conflict has focused on terrestrial species where wildlife encroaches on what are viewed as human spaces. More recently, scholars have begun exploring human wildlife-conflict in coastal and ocean systems (Denkinger et al., 2014; Draheim et al., 2015; Guerra, 2019; Konrad and Levine, 2021). Notably, Sprague and Draheim (2015) apply the Conflict Conservation Transformation framework (Madden and McQuinn, 2014) to better understand how levels of conflict influence the emerging conflict over monk seals in Hawai‘i. Using a largely theoretical approach, they describe how issues of government mistrust, perceptions of monk seal origin, disputes over resources and regulation, and underlying conflict relating to Hawaiian history have sparked debate over monk seals and their management. Our research uses primary data to expand on their theoretical work to improve our understanding of factors influencing the continuing conflict over the Hawaiian monk seal.

2.1 Hawaiian monk seals

The Hawaiian monk seal can be found throughout the Hawaiian archipelago and is native and endemic to the Hawaiian Islands, with some evidence of monk seal remains found in Hawaiian middens in archeological studies (Watson et al., 2011). While little is known about their population prior to 1950, those who study this species assume that they had broad distribution across the archipelago prior to the arrival of humans (Baker and Johanos, 2004; Littnan et al., 2017a). Hawaiian monk seals spend most of their lives at sea and come to shore only to pup, nurse, molt, and rest (Antonelis et al., 2006). Monk seals are opportunistic feeders, preying on a variety of fish, cephalopods, and crustaceans. They forage both nearshore and offshore, diving to significant depths to find food (Cahoon et al., 2013). Mating occurs at sea and is rarely observed. Females may give birth as early as age five after an estimated 10–11 months gestation (Johanos et al., 1994). Mothers nurse their pups for about six weeks before weaning them. Hawaiian monk seals are solitary animals, though they may occasionally form small groups (Robinson et al., 2022).

Unlike many other marine mammals, monk seals do not play a strong role in traditional Hawaiian culture (Watson et al., 2011; Kittinger et al., 2012), and it is likely that populations were extirpated from the main Hawaiian Islands (MHI) shortly after the arrival of the first Polynesian colonists on the islands (Baker and Johanos, 2004). The remaining monk seal population was limited to the Northwestern Hawaiian Islands (NWHI) which remained largely uninhabited by people. Monk seal populations were reduced dramatically in the 1800s due to hunting, and their numbers were further depleted in the early 1900s, likely caused by human disturbance (fishing and military activity) and/or ecological shifts (associated with the Pacific Decadal Oscillation) in the NWHI (Baker et al., 2012; Littnan et al., 2017a).

Based on critically low population estimates of 1000 ± 500 seals and ongoing population decline, the species was listed as depleted under the Marine Mammal Protection Act (MMPA) and endangered under the ESA in 1976 (Littnan et al., 2017b). In addition, Hawaiian monk seals have been protected by the State of Hawai‘i since 2010 under Hawai‘i State law HRS §195D-4.5 (NMFS, 2015). Despite the protections granted to monk seals under these acts, monk seal populations continued to decline; the first official stock assessment found that Hawaiian monk seal populations decreased at a rate of 5% annually from 1985–1993 (Antonelis et al., 2006). At this time, the majority of the monk seal population was still located in the NWHI. The terrestrial habitat remained uninhabited by people during this time, except for a few government employees, although Native Hawaiians and fishers were able to access the waters of the NWHI for fishing, voyaging, and other purposes, as allowed. Since the early 2000s, the total population has shown stability or even increases, with a significant increase in monk seals in the MHI from 2010–2020 and a consistent annual growth rate of 2% from 2013–2020 (Antonelis et al., 2006; Carretta et al., 2022) (Figure 1). Estimates of monk seal populations from the National Marine Fisheries Service (NMFS) based on 2020 data were around 1,465 seals rangewide with the large majority of the population found in the NWHI and only 25% of the population located in the MHI (Carretta et al., 2022).

At the same time, the human population on the MHI has continued to grow steadily, increasing by 20% across all islands between 2000–2020 (Gove et al., 2022), while tourist arrivals to the islands increased by nearly 50%, from just under 7 million visitors per year in the year 2000 to just over 10 million in 2019 (Hawaii DBEDT, 2000; Hawaii Tourism Authority, 2019). Given the monk seal population's growing numbers in areas of higher human density, encounters with humans on populous islands such as ʻOahu are increasing. The first documented birth of a monk seal on a popular Waikīkī beach in 2017 was extensively covered in the press (McKenzie et al., 2020), and marked the start of an emerging trend. Monk seals now consistently haul out on highly visited ʻOahu beaches for resting and occasionally also pupping; four additional pups have been born (to two mothers) on the same beach in 2021, 2022, 2023, and 2024 (NOAA Fisheries, 2024). Encounters between people and monk seals have, in a few instances, resulted in physical harm and have been well documented in the news media, for instance when a swimmer has been bitten by a monk seal or a monk seal has been found shot in the head (McKenzie et al., 2020). As both monk seal and human populations continue to expand in the MHI, it is critical to understand the social factors driving conflict over marine wildlife in order to anticipate and prevent future conflicts.

3 Materials and methods

A mixed methods approach was used to explore the perceptions and values driving conflict over monk seals and their management. To understand historical and contemporary monk seal management, human-monk seal interaction in Hawaiʻi, and the potential conflict associated with these, we reviewed literature including peer-reviewed publications, gray literature, and NOAA technical memos, reports, and internal documents related to monk seals and conflict. This included projects that involved both formal and informal interviews with diverse stakeholders, including members of the Native Hawaiian community. We also reviewed media coverage of monk seals to create a timeline of interactions

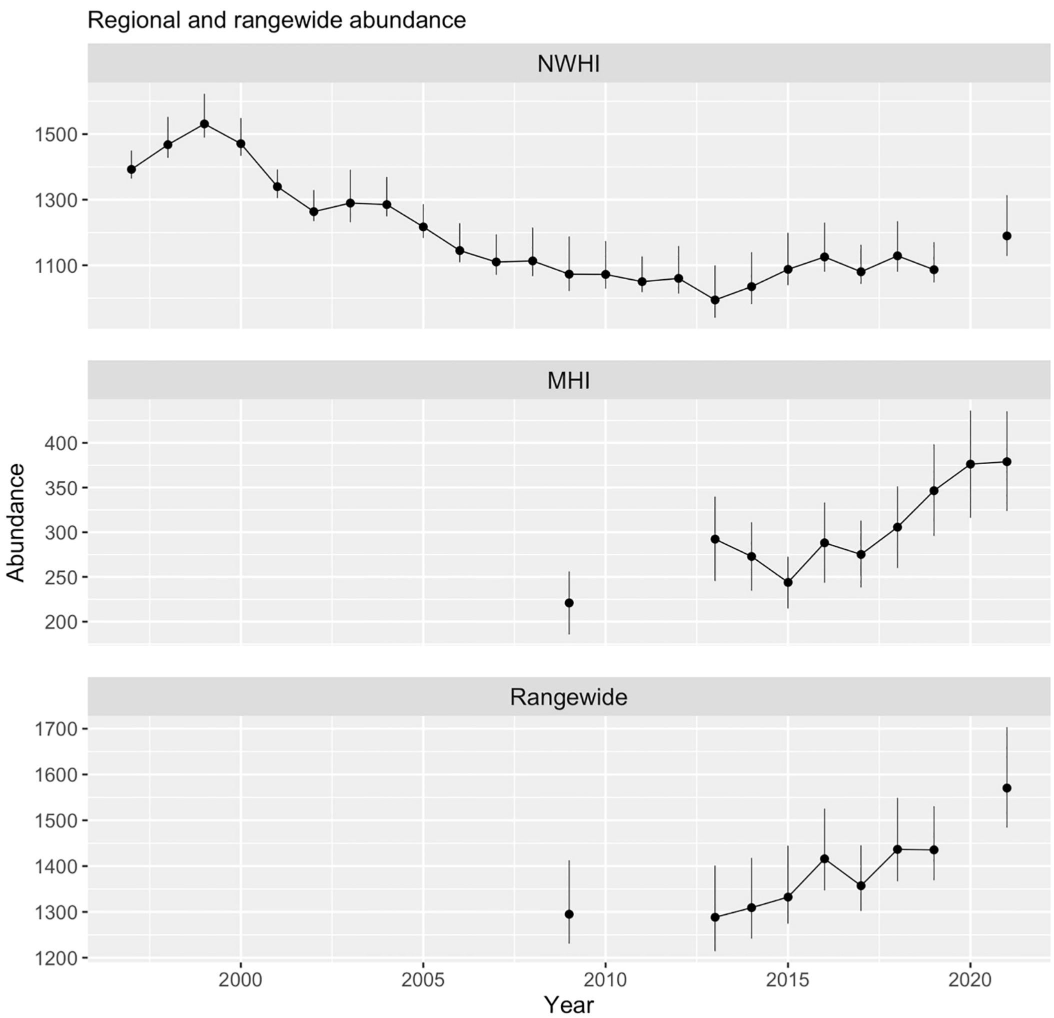

FIGURE 1
Regional and rangewide abundance trends for the Hawaiian monk seal population to 2021 (NOAA Fisheries, 2022).

between people and monk seals that resulted in physical harm, as well as to better understand how monk seals are portrayed in popular media.

In addition, we conducted semi-structured interviews between August and November of 2018. NOAA project partners identified initial interviewees and organizations based on their involvement with monk seal recovery in the past. They suggested state resource managers, federal resource managers and researchers, as well as representatives from volunteer organizations including Hawai'i Marine Animal Response (HMAR) and the Monk Seal Foundation, both of which have been involved in monk seal monitoring and outreach. Representatives from fisherman groups and lifeguards were also interviewed to understand a range of perspectives associated with monk seal conflict in the MHI. Where contact information for individuals was not known, public agency contact information was used, and snowball sampling was used to identify additional interviewees. A total of 20 interviews were completed with state managers (2), federal managers or researchers (9), fishermen (2), lifeguards (2), and monk seal volunteers (5). Interviews ranged from 30–70 minutes in duration. Interview questions focused on the interviewee's involvement and experiences with monk seals, observed interactions between people and monk seals, perceptions of reasons for conflict over monk seals, as well as their perception of the role monk seals should play in Hawaii and how they are personally affected by monk seals. Interviewees who were managers were also asked additional questions relating specifically to monk seal management. Fifteen of the interviews were recorded (with the subject's approval), transcribed, and analyzed using NVivo v12.5 software. Detailed notes were taken during interviews when the respondent did not agree to be recorded. Interview responses were analyzed using an inductive approach (Thomas, 2006), where initial themes were generated and then refined through iterative review of the data. Transcripts and notes were reviewed to identify themes relating to values and perceptions relevant to monk seals and their management. The first author conducted all coding for internal consistency using NVivo software. After three iterations of transcription analysis, preliminary codes were refined in consultation with the second author and condensed to reduce redundancy and focus on themes most relevant to the research objectives. Codes were also analyzed using NVivo to identify frequencies.

To gauge the broader public's perceptions of monk seals and their management, surveys were conducted on beaches where seals were present on the island of O'ahu, the most populous of the MHI. Beaches where seals were actively hauled out (and thus target sites for surveys) were identified by coordinating with NOAA and HMAR, the local non-profit that currently monitors the monk seal population throughout four sectors in O'ahu (North, South-East, South-West, and West). HMAR sector managers respond to a sighting hotline that is utilized for the public to report any sightings of monk seals across the island. Once monk seal presence was confirmed at a beach location, HMAR sector managers relayed the location of a hauled-out monk seal via phone call or text message, and an attempt was made to go to that beach and opportunistically survey any individual who was present at a beach while the seal was also present.

People at beaches with a monk seal present were approached and asked to take a paper survey, with the goal of surveying as many people as possible. Surveys were conducted in English, which limited our ability to include some international visitors in the sample. Surveys included Likert-type scale and multiple-choice questions including basic demographics, reasons for beach visitation, reactions to seal's presence on the beach, and opinions of potential management responses to limit human interaction with monk seals. A total of 132 surveys were completed between July 19th and August 16th, 2018 at ten different beaches with seals present (Figure 2). All survey data were imported and normalized in a database using PSQL and analyzed using Excel and R v2023.03.1 + 466 software. All information collection and informed consent procedures were reviewed by the Institutional Review Board at San Diego State University and deemed exempt under protocol number HS-2018–0097.

As an author group, we also drew on our own expertise as individuals working to support the recovery of endangered marine species and as academics with a long history of studying conflict over wildlife. We have all been directly involved in efforts to understand and reduce conflict over seals and other forms of wildlife for multiple years and have engaged directly with diverse stakeholder groups on different sides of these conflicts as a part of participatory management processes. These experiences informed our analysis of the findings, provided insight into how our findings relate to broader themes in the human-wildlife conflict literature, and guided our discussion of paths toward addressing emerging conflicts.

4 Results and discussion

Here we present findings based on our review of government and media reports, stakeholder interviews, and beach-based surveys to better understand the drivers of conflict relating to the endangered Hawaiian monk seal in the MHI. We organize the results and discussion of this study by thematic areas relevant to conflict that have emerged from this research: emerging signs of conflict, polarized views of seals and what they represent, the role of media and social media platforms, and management intervention to prevent and address conflict. Within each of these thematic areas we discuss how values, environmental beliefs and perceptions, and other factors contribute to existing and future conflict.

4.1 Emerging signs of conflict

As both monk seal and human populations have increased in the MHI, so too have human-seal interactions (Figure 3). These interactions began to be documented in the media as early as 2004 with the report of a monk seal biting a tourist swimming off of the Island of Kauai and a few other incidents of monk seals

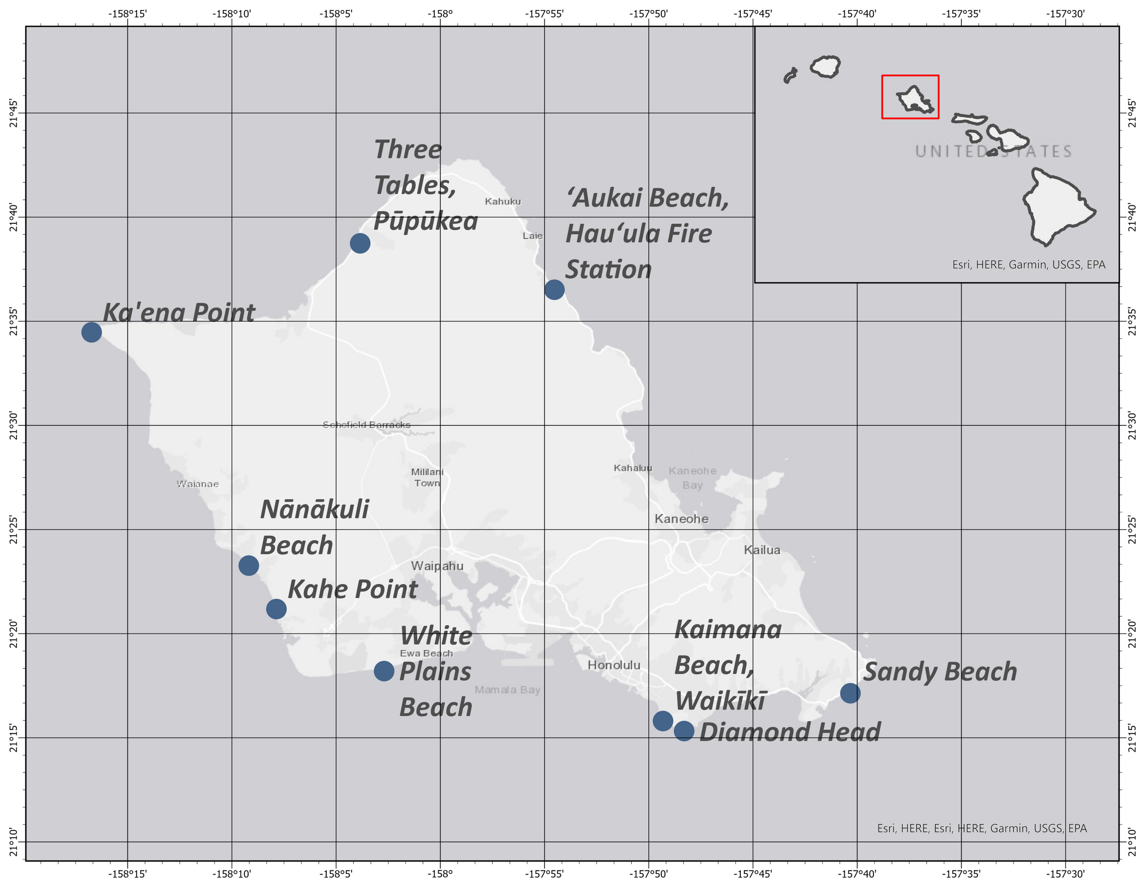

FIGURE 2
Survey locations on O'ahu, Hawai'i.

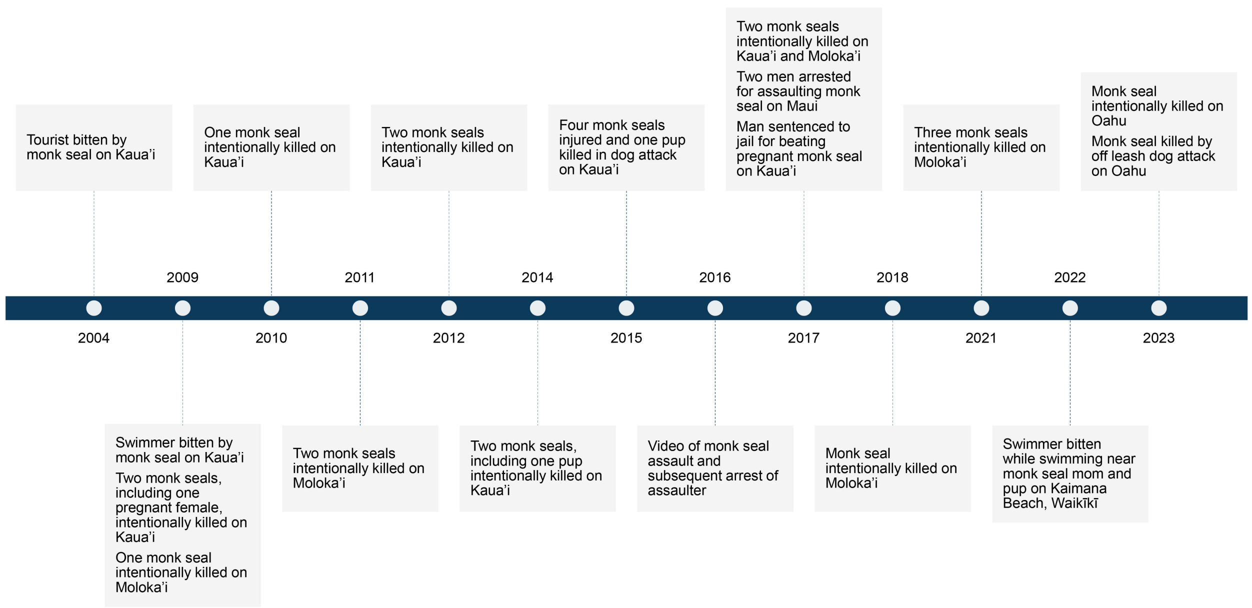

FIGURE 3
Timeline of notable events relating to interactions between humans and monk seals in the MHI that resulted in physical harm.

harming swimmers since then. Concern over these interactions grew after a number of intentional killings and assaults on seals occurred in 2009, 2011, 2012, 2016, and 2018 (Carretta et al., 2019). Many of the intentional killings occurred in areas where monk seals were in direct competition for resources with humans, especially fish, as opposed to the historical killings of monk seals in sealing expeditions that occurred prior to ESA and MMPA protections. Although these intentional monk seal killings are believed to be isolated occurrences, a single death can have a large impact on a species whose population is already critically low, especially if it involves a reproductive aged female.

Despite the recent history of negative interactions with monk seals, media coverage of monk seals tends to be largely positive (McKenzie et al., 2020). Similarly, our survey respondents reported an overall positive perception of monk seals. Of the 132 people surveyed on O'ahu, 79% of respondents expressed a very positive reaction to the monk seal's presence on the beach, and 75% expressed very positive reactions to monk seals pupping more frequently in the MHI over the past 25 years (Figure 4). No respondents stated that they had "very negative" reactions, and very few expressed "somewhat negative" or mixed positive and negative reactions to monk seals. Survey respondents included a mix of Hawai'i. residents and non-residents, with just over 61% of respondents stating they were a resident of the islands. While a higher percentage of non-residents expressed positive views toward seals than Hawai'i residents (92% positive vs. 83% positive, respectively), the difference in perception was not statistically significant (x^2 (1) = 1.66, p = 0.20).

Survey responses also indicated support for current management measures intended to limit interactions between people and monk seals that are hauled out on a beach. The majority of respondents rated all measures currently used by volunteers and managers as either very appropriate or somewhat appropriate (Figure 5). These measures include educational or cautionary signs, as well as roping or fencing off sections of the beach when seals are present. Beach closures, which are not currently used as a management approach, were the only type of management action that was seen as appropriate by less than half of survey respondents. Perceptions of Hawai'i residents and non-residents were not significantly different in terms of how they perceived seals or most management measures, with the exception that Hawai'i residents were more likely to state that beach closures were very or somewhat appropriate (48%) than non-residents residents (33%) (x^2 (2) = 6.755, p = 0.03).

The overwhelmingly positive perceptions evident from the survey data belies the evidence in Figure 3 that a prolonged conflict exists around monk seals, and the fact that some people feel strongly enough to kill monk seals. Konrad and Levine (2021), similarly found that while beachgoers in La Jolla, California were overwhelmingly positive about harbor seals pupping on a local beach, a protracted controversy over seals' use of the beach proved challenging to resolve because it had evolved into a deep-rooted, identity based conflict between small polarized groups of local residents with strong feelings in support or in opposition to seals using the local beach.

4.2 What is a monk seal?

Similarly, interviews and secondary data reviewed for this study illustrated that the conflict over monk seals in Hawai'i is not driven by the general public observing or interacting with monk seals on the beach, but by polarized groups who have strong feelings about seals and what they represent (Figure 6). On one side are people who see monk seals as vulnerable animals in need of protection and part of Hawaiian culture, with individuals willing to go to great lengths to help ensure their survival as individuals and as a species. Others view monk seals as competitors for resources or invaders that are not a part of Hawaiian culture or identity, yet receive preferential treatment from the government. Drawing on interviews and secondary source documents, we provide an overview of how these differing perceptions interact to create conflict.

4.2.1 Monk seals are vulnerable animals in need of protection

A considerable network of volunteers coordinates with NOAA to aid in monitoring and managing the presence of monk seals on

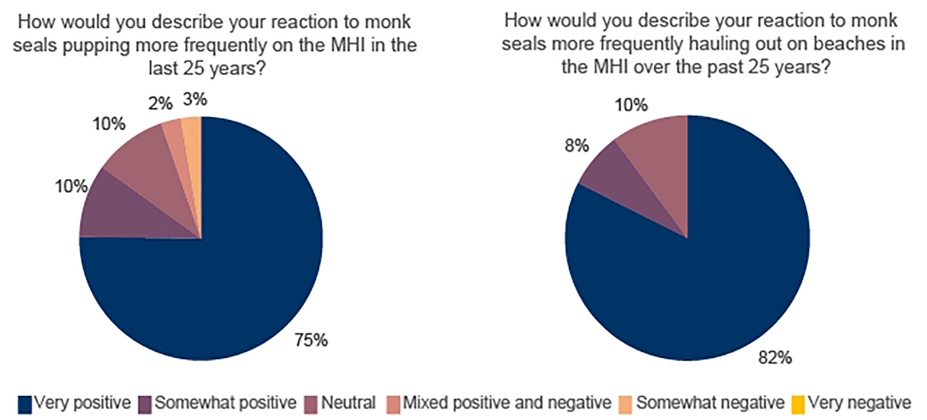

FIGURE 4
Survey respondent perceptions of monk seals hauling out and pupping on beaches in the MHI.

FIGURE 5
Survey respondent perceptions of the appropriateness of different strategies to limit human interactions with monk seals hauled out on beaches in Hawai'i.

beaches throughout the MHI. These volunteers dedicate significant amounts of their own time to supporting monk seal protection and monitoring. Although volunteer organizations have changed over time, the current organization active on Oahu is HMAR. These volunteers are part of a monk seal sightings network and visit beaches where monk seals have been reported to have hauled out. Upon reaching the beach, they determine what level of management is necessary for the situation. Seal Resting Areas (SRAs) are then

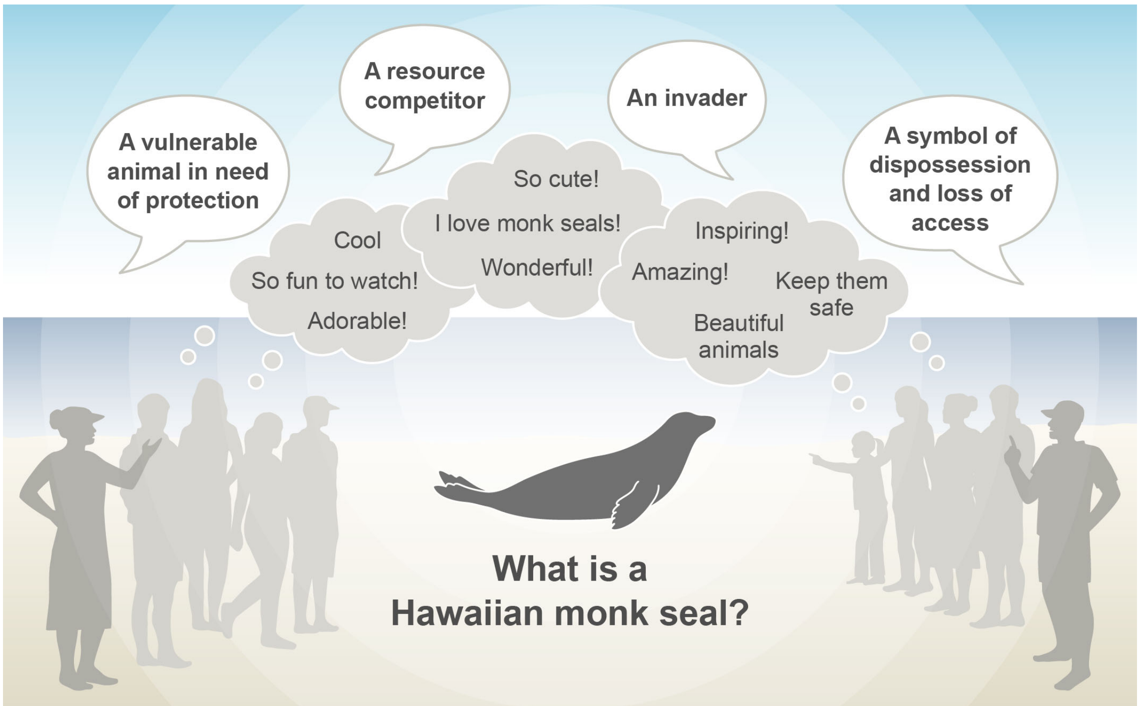

FIGURE 6
While most individuals at beaches where monk seals are present have positive perceptions of seals, conflicting social constructions of seals and what they represent drive conflict over monk seals. In this figure, text in the thought bubbles are representative of comments provided on surveys of people at beaches with monk seals. Speech bubbles represent the different narratives about monk seals and what they represent that emerged in our research and which drive conflict between people over monk seals.

established and managed by the volunteers in order to limit direct human interaction with monk seals. Actions taken at SRAs range from placing signs on the beach to using cones, ropes, and/or mesh fencing to establish a barrier around the seal. Volunteers then remain near the SRA and educate the public about monk seals and responsible wildlife viewing practices.

The volunteers interviewed expressed that they engaged in volunteer activities because of their love for monk seals, and they often expressed a strong emotional connection to the animal. One longtime volunteer stated, "[I] love them. They're an innocent victim in man's modern world, struggling to survive." These strong emotions highlight a feeling of needing to protect this endangered species that was echoed in the other sources we examined. Because of their deep emotional investment in the monk seal populations, some volunteers confront beachgoers about behavior they see as threatening to seals. For instance, in some cases where beachgoers have approached or attempted to touch or engage with resting seals, volunteers perceived these interactions to be inappropriate and as potential seal harassment and responded with strong words directed at the individual interacting with the seal. These types of negative interactions can, in some cases, cause beachgoers to associate the negative interaction with the hauled-out monk seal itself, and volunteer guidelines discourage this type of behavior for this reason. One federal monk seal manager explained the unintended impact these interactions can have:

> "They [volunteers] are the people that most of these people are going to talk to, they're not going to talk to NOAA, they're not going to talk to the state, but they're going to talk to the volunteers who, regardless of how we tried to separate and all of that sort of stuff and make sure that people understand they're a separate entity, they represent everything that is monk seals and they can create real animosity … those people may never see that volunteer again, or volunteers at all, but they might see another monk seal, right?"

Managers are aware of the emotions and concerns that volunteers have. Historically, management of human-monk seal interactions centered on preventing harm to monk seals and trying to limit negative human-seal interactions. As sentiment towards monk seals has changed, new challenges are arising. When discussing this shift, a federal monk seal manager stated, "now we actually kind of have the opposite problem, where people are overly protective of the monk seal and have a tendency to project human thoughts, emotions, and characteristics on them." This has presented management challenges, as some have interpreted federal actions designed to minimize interactions (such as relocating weaned pups away from populated beaches) as upsetting to the monk seal mother and pup, when in reality monk seals do not form long-term maternal bonds.

However, HMAR volunteers are also at the front line of conflict prevention, playing a critical role in educating the public about monk seals and safe viewing guidelines, which may help prevent interaction that could lead to potential harm, including unsafe interactions with an endangered species and potential seal aggression toward humans. The two lifeguards interviewed, who regularly observe interactions between people and seals while on duty, both emphasized the importance of volunteer actions to educate beach-goers about seals, given that the public does not necessarily know what are safe or legally appropriate ways to interact with seals. They emphasized the importance of SRAs, which are established by HMAR volunteers, and the use of ropes to prevent the types of interactions that they sometimes observe, such as throwing objects at seals, approaching them, and trying to touch or slap them, all of which are illegal and potentially dangerous.

HMAR volunteers' strong sense of connection to wildlife is common among conservation volunteers, who generally express strong feelings of connection to nature, often with a personal or spiritual connection that influences their behavior (Guiney and Oberhauser, 2009), and conservation volunteerism has been found to be strongly connected to volunteers' sense of personal identity (Fraser et al., 2009). It is common for conservation volunteers to identify with the animals they see themselves as protecting from the destructive impact of humanity on nature (Abell, 2013; Konrad and Levine, 2021). This self-identification as protectors of nature drives HMAR volunteers to spend considerable time and energy assisting in efforts to prevent unsafe interactions with monk seals in Hawai'i. However, the intense feelings that volunteers have about seals can also contribute to conflicts, particularly when volunteers see the behavior of others as violating their own deeply held conservation values (Markle, 2022).

4.2.2 Monk seals are resource competitors

The perception of threats to livelihood, culture, recreation, and identity may drive negative perceptions of monk seals among some of those who identify as fishermen throughout the MHI, as outlined in Madge (2016). From a survey done in 2011, 43% of those who answered "yes" to the question "Do you fish regularly" believed the presence of monk seals reduces fish catch (SRGII, 2011). Our study reinforces these findings. A volunteer who assists with monk seal surveys on the island of Molokai discussed the pressures of resource competition and the negative perceptions of interactions, by stating:

> "Things are very expensive on Molokai. A lot of people live sustainably, between fishing and hunting … But if you're laying a net and then a monk seal will eat the fish out of the net, they will wreck your net. I mean there are reasons why fishermen don't like them."

In the MHI, monk seal killings were first documented as early as 2009 when a man fatally shot and killed a pregnant monk seal on the North Shore of Kaua'i (D'Angelo, 2014). From 2009, there have been at least sixteen killings of monk seals on the islands of Molokai, Kaua'i, and O'ahu in which monk seals have died as a result of either a gunshot or significant trauma to the skull (D'Angelo, 2014; Carretta et al., 2022; Honore, 2023; Johanos, 2023a; 2023b, 2023c; Harting et al., 2020). Given the species' already small population, sixteen killings in 13 years threatens recovery (Harting et al., 2021).

Managers and media have stated that killings may be in part motivated by perceived fishing competition, where a focus on threats to fishing may drive this retaliatory behavior (Mooallem, 2013). It is well known that when people see wildlife as competition for resources or a threat to their livelihoods, it can result in hostile attitudes towards wildlife and, in some cases, retaliatory killings of animals (Don Carlos et al., 2009; Liu et al., 2011). This dynamic has been documented for many species in many contexts, where successful management requires attention to the social drivers of these conflicts (Herda-Rapp and Goedeke, 2005; Hill et al., 2017).

4.2.3 Monk seals are a symbol of dispossession and loss of access

Given their endangered status and protection under the ESA and MMPA, the Hawaiian monk seal is subject to strong federal protections through regulatory actions, a Recovery Plan, and Critical Habitat designations. However, the extensive government intervention in protecting this endangered species has served to heighten distrust among some Hawai'i residents. Given the colonial history of Hawai'i and dispossession of many from their Indigenous lands, some Native Hawaiians do not trust the government. Similarly, many fishermen (who may or may not also identify as Native Hawaiian), have lost access to historic fishing grounds or fishing privileges due to state or federal regulations and the establishment of marine reserves, generating similar feelings of distrust. As one federal protected species manager explained, "There is a lot of understandable distrust, animosity, and angst when it comes to federal government management." This history of disputes and distrust has served to deepen feelings of resentment for a species that is protected and regulated by a federal agency. The association of Native Hawaiian identity and identity as a fisherman as part of this conflict deepens the level of conflict, making it more challenging to resolve (Sprague and Draheim, 2015).

Fishing is deeply rooted in Hawaiian culture, and some Native Hawaiians as well as fishermen see fishing regulations established for monk seal protection to be a symbol of federal regulation and control, threatening the identity of both Hawaiians and fishermen. The regulations represent the loss of access to natural resources that Hawaiian people historically relied on. Some fishermen view the monk seal as a species that the federal government uses to control people's behavior and take away access to fishing sites; the monk seal therefore receives animosity that is actually aimed at federal government actions. As one fisherman interviewed stated:

> "It's a true perception from the fisherman here. Especially bottom fisherman who had Northwestern Hawaiian Island permits, closing it [to create a Marine National] Monument pushed fisherman out. They used the monk seal as leverage to close it down … Federal laws and the state are the ones that screw us. With the Hawaiian monk seal management plan, fishermen don't want to talk to people about it because everything we told them we wanted to protect, they took it [as protected areas that fishermen could not access]. Fishermen are burnt."

These conflicts are compounded by the perception that the state and federal government care more for the Hawaiian monk seal than the Hawaiian people. One federal manager explained how a historical management action, taken without sensitivity to local perceptions, may have reinforced mistrust:

> "I mean, initially when we had some seal killings, the idea was to put out rewards, and then we had a situation on Kaua'i where the reward money for information about a dead monk seal exceeded that which was put in place for a missing child. And that's where the whole [idea comes from, that] you care more about the monk seals than the people."

Another federal monk seal manager explained the challenges that come from the disproportionate funding dedicated to monk seal management and recovery versus social concern on the islands, stating,

> "One of the big issues is, why are millions of dollars going towards saving this animal when we still have homeless people? We still have water quality issues or whatever. So it's definitely a challenging environment."

The history of government mistrust, felt by both those identifying as fishermen and those identifying as Native Hawaiian, underlies much of the public animosity toward monk seals. This deep-rooted identity-based conflict goes beyond just human interaction with the seals themselves, making these conflicts more difficult to manage and mitigate (Madden and McQuinn, 2014). Others have described how conflicts over wildlife become a symbol or surrogate for broader issues. For example, spotted owls and Key deer hung in effigy as protests to development constraints, sparrows as a nativist symbol of human immigration, doves representing rural values, or wolves representing issues ranging from land use to tribal authority (Nie, 1999; Herda-Rapp and Marotz, 2005; Peterson et al., 2010). As such, the retaliatory killings may be less about impacts from monk seals themselves, and more about what the seals represent.

4.2.4 Monk seals are invaders

Exacerbating many multi-generational Hawai'i residents' distrust of federal monk seal management policies is the fact that older generations of Hawaiians had little to no awareness of or experience with monk seals until recently, with only 7 recorded monk seal sightings on the MHI between 1928 and 1956. Although remains dating back to 1400–1750 A.D document the presence of Hawaiian monk seals on the island of Hawai'i, misperceptions exist regarding whether monk seals are native to the MHI (Watson et al., 2011). One fisherman expressed skepticism during an interview regarding whether monk seals were historically present on the islands, stating,

> "When I first saw [a monk seal], I was twelve, 1992. I was raised at the beach. I'd see turtles but only heard about monk seals, heard people talk about them. Why didn't I see one before?"

The perception that monk seals are not native to the MHI, and that their presence there is not natural but caused by government intervention, influences how people view and value seals. Mistrust of the government compounds these misperceptions, and some individuals believe that the federal government brought monk seals from the NWHI to colonize the MHI. This perception stems, in part, from historical management actions that one NOAA manager explains:

> "So, not only did people have this misperception that they aren't from here, I don't know if you know this story but in the 90s we brought some male seals from the Northwesterns because there was a skewed sex ratio [among the monk seal population in the NWHI], and so they were injuring females severely as they were all trying to mate with the same female, [and] they were killing juveniles. So, we brought some males down here. There were already seals here and there was a lower ratio of males here, so to correct that, we brought them down. But there wasn't very good media and outreach done so people actually thought that not only were monk seals invasive, they thought we [the federal government] brought them here. So that's been an interesting one and it's been very hard to correct."

The perception that monk seals' presence on the MHI is due primarily to government intervention has been difficult for NOAA managers to overcome. Public mistrust of the federal government often supersedes efforts by NOAA to correct misperceptions about monk seal natural history. Thus, some who oppose monk seal presence in the MHI do so in part because of a perception that monk seals are an invasive species brought by the federal government that creates fishing competition and provides a justification for putting federal regulations into place to limit fishing and Hawaiian practices.

These perceptions relate to the phenomenon of shifting baselines (Soga and Gaston, 2018), where recovery goals are based on historical populations and distributions of monk seals that predate the experience of current human populations whose expectations and normative understanding of "baseline" conditions did not include monk seals in the MHI. In addition, others have demonstrated that the concept of invasiveness is not static nor agreed upon, both among scientists and between scientists and publics (Boonman-Berson et al., 2014; Crowley et al., 2017). From a risk perception perspective, the associations of monk seals as both a new and human-made risk to residents also indicate high outrage factors, which are more difficult to address than if the risk were associated only with the probability of harm (Yoe, 2019; Kasperson et al., 2022). Appropriate attention to the deep-value and identity issues associated with these perspectives will be crucial.

4.2.5 Social construction of monk seals

The diverse meanings attached to monk seals illustrate four distinct social constructs of monk seals that are also deeply tied to conflicting identities (Figure 6). Like many other enduring conflicts over wildlife, conflicts surrounding the Hawaiian monk seal have become symbolic of other meanings that are important or threatening to the values and identities of different groups involved in the conflict, where the conflict is less about the animal itself and more about what it represents (Nie, 1999; Herda-Rapp and Goedeke, 2005; Peterson et al., 2010; Madden and McQuinn, 2014; Leong et al., 2020). Some volunteers for island-based non-profit groups personally identify as protectors of this endangered species, form deep emotional attachment to the seals, and see monk seals as innocent victims of destructive human impacts on the environment. The fishermen concerned about monk seals, on the other hand, see seals as resource competitors and as symbolic of federal government restrictions on their rights and access to natural resources. Native Hawaiians who have negative views of seals often see them as invaders in their native homeland, brought by the same federal government that historically disenfranchised Hawaiians from their land, and see federal actions to protect seals as a continuation of colonial restrictions on Native Hawaiian rights and access.

Where there is the perception that protected habitats and species are seen as more valuable than the people living with those species, retaliation against the animal is often retaliation against what are viewed as conservation injustices (Western, 1994; Holmes, 2007). As multiple knowledge systems and worldviews gain wider recognition, many of the core tenets of wildlife conservation are now coming into question as stemming from the same cultural assumptions and processes that fueled colonial expansion (Domínguez and Luoma, 2020; Hessami et al., 2021). Acknowledgment of these multiple experiences and assumptions about the meanings of wildlife and their conservation is necessary to reconcile a long history of threats to people's values and identity, which for some are embodied by Hawaiian monk seal management.

4.3 Role of media and social media platforms

Compounding these issues is the emerging challenge of social media and media-driven influences on perceptions of wildlife, their management, and any surrounding conflict. Social media can spread information as well as misinformation, and the global reach of social media platforms expands the base of people engaged in wildlife management to include individuals from all over the world who pressure local resource managers to take particular actions. This spread of information has fostered both positive and negative perceptions of monk seals. The attention gained from the media coverage of Kaimana, the first monk seal pup born in Waikīkī in the summer of 2017, fostered strong positive perceptions and emotional connections amongst a broad base of the public.

Yet, this attention also increased the spotlight on management actions and the likelihood that such actions would be critiqued. An example of this can also be seen through the media coverage when Kaimana was relocated after she was weaned and Rocky (her mother) had left, to reduce her exposure to people and potential for habituation, which can be dangerous for both people and monk seals. Discussions regarding the relocation of Kaimana included projection of human emotions onto monk seals, as expressed by a federal monk seal manager:

> "When we moved Kaimana everyone was like, 'Rocky's going to be sad. Kaimana is going to be sad.' Everyone said, 'she's going to be missing her pup, you guys are messing with this mother pup bond.' It was really hard to get the point across that monk seals don't have that [enduring type of bond]."

Social media groups in support of monk seals as well as social media groups for fishermen have perpetuated different types of misinformation while reinforcing equally strong emotions. Managers described pro-monk seal social media groups where members engage in conversations about their love of monk seals, as well as the "injustices" occurring against the population. These one-sided conversations serve to reinforce strong feelings and sometimes encourage emotional behavior. This is similarly seen in fishermen's groups where one-sided emotional discourse against monk seals occurs, compounded by the opinions of significant individuals seen as "influencers."

Along with a spread of information and increase in pressure from those who felt personally connected to monk seals, these platforms can also prompt undesirable behavior and foster perceptions that can negatively impact management progress and fuel conflict. One fisherman interviewed explained,

> "I think it's a huge mistake for, especially the television media, to go and take videos of monk seals. All it does is it encourages tourists to go and take pictures and interact with them. And I cringe when I see a newscaster say how cute they are and things like that. To make them like cuddly animals. They're dangerous animals."

An HMAR volunteer also expressed concerns about how selfie culture, related to social media postings, influenced people's interactions with seals:

> "I mean selfies and cellphones are the worst thing that could ever have happened with wildlife. Whether it's a bison in Yellowstone, or whatever … there is no common sense with animals. Everybody thinks it's a pet, all warm and cuddly, and it's just not true. A mother monk seal will eat you."

The media has long played a role in shaping the public agenda, or the issues that people see as salient, a concept known as agenda-setting (Johnson, 2013). While early studies focused on broad public salience, with the proliferation of social media platforms, attention is shifting to individual level salience (Yi and Wang, 2022). Further, social media incentivizes misinformation and moral outrage rather than search for a global consensus (Kasperson et al., 2022). The degree to which conservation practitioners engage in communication in media platforms can affect conservation action and policy creation for endangered species (Soulier, 2022). The dominant support for monk seals in traditional news media aligns with manager perspectives. In social media channels, however, multiple conflicting perspectives endure. Whether and how managers engage with communication channels preferred by those who view monk seals as victims, as resource competitors, as symbols of dispossession, or as invasive species will affect the nature of how these groups engage with Hawaiian monk seal management in the future.

4.4 Management interventions to prevent and address conflict

Monk seal recovery efforts have, for the most part, taken action early and often through strategic outreach, education, and adaptive management approaches. For instance, managers have worked with volunteer groups to reduce the potential for negative interactions between overzealous volunteers and beach-goers. One federal manager discussed this adaptation in their management approach:

> "I think the approach that we've taken with seal protection zones that I was talking about; we now call them seal resting areas. You know we've issued these guidelines to the volunteers that you're not protecting the seals. That's a 500-pound animal with big teeth, it doesn't need you to protect it. You're an ambassador for it and you're bringing the attention to the public. Yeah there's a seal here let me teach you about it, not there's a seal here let me run you away from it. And I think that's been really successful and again, harder to quantify because it's not a hard data thing, but we can see that a lot of the positive sentiment is due to that."

Another example of outreach efforts is a project where cameras were placed on monk seals in the wild, which substantially improved understanding of the Hawaiian monk seal foraging landscape and behavior (Parrish and Littnan, 2007). Footage was taken to local schools and in some instances, students were able to directly participate in analyzing the footage alongside the scientific team. Students would count the amount and species of fish being eaten and not eaten by monk seals, allowing them to learn for themselves about monk seal foraging behavior and share what they learned with those in their community. Managers believed this program showed some success in addressing conflict with fishermen through correcting misperceptions about scale of competition for resources. While this type of education and outreach can address surface level disputes over monk seal diet and behavior, education in and of itself has been found to be insufficient in promoting enduring behavior change, which are also guided by social norms (Schultz, 2011). Education and outreach approaches are also limited in their ability to address identity-based drivers of beliefs about monk seals, for instance, when someone's identity as a fisherman is threatened by a new competitor for resources, regardless of the scale of the actual competition. To address these deeper levels of conflict, approaches based on improving dialogue and trust can improve outcomes (Madden and McQuinn, 2014; Draheim et al., 2015; Hill et al., 2017; Frank et al., 2019).

Monk seal managers and scientists have been working to overcome public mistrust of the government by engaging with communities transparently and providing opportunities for public involvement in research activities and in advising management policies. One federal manager described this priority by stating,

> "I absolutely am committed to just speaking the truth, right? So you will get some people that will try to say the easy thing, but even if it gets me yelled at, I'm going to tell them exactly what I think, what the science says or what is likely going to happen, so that at no point, you may not like my message, but you're never going to not trust."

Managers have also worked to increase public trust by broadening the types of people included in recovery planning conversations. The team involved in developing and conceptualizing the Main Hawaiian Islands Monk Seal Management Plan was composed of individuals not only associated with government agencies, but instead included Hawaiian cultural leaders, fishermen, scientists, and educators (NMFS, 2015).

These management efforts have aimed to help address areas of concern, particularly mistrust of government, in an attempt to bridge the gap between federal management decisions and the concerns of local stakeholders. These early efforts to intervene could help to prevent conflict escalation in the future. Continuing these efforts and adapting them to anticipate and address new issues as they arise may be instrumental in preventing deeper conflict in the future (Crowley et al., 2017).

Lessons from the field of risk communication can also help determine when to use different strategies to engage with publics that perceive different levels of hazard and outrage relating to monk seals. The main risks to people on beaches would be potential injury from interactions with monk seals. In this situation, both hazard (likelihood of harm) and outrage (differential perceptions of harm) are generally low. On the other hand, perceived risks to fishermen and other local residents appeared to activate many outrage factors, e.g. when monk seals were seen as a new, man-made risk that unfairly affected some populations more than others. Yoe (2019) outlined guidance to apply Peter Sandman's[1] framework for selecting different risk communication strategies based on hazard and outrage. In situations of low hazard and low outrage, such as with general publics on beaches, a public relations approach is appropriate. When potential for hazards is higher but outrage is still low, precaution advocacy is appropriate, such as warning people to keep their distance at beaches and pay special attention when females with pups are present. High hazard and high outrage indicates crisis or emergency communication, which is rarely needed for monk seal management. Instead, the low (but persistent) hazard and high outrage situation is prevalent for most monk seal conflicts. This is the most challenging situation, which will require different approaches based on acknowledging and engaging with the specific values and identities of the people involved.

1 https://www.psandman.com

5 Conclusion

Our case study reinforces and extends patterns seen in previous research on Hawaiian monk seal recovery efforts. Although the broader public's perceptions of monk seals in Hawai'i are largely positive, the persistence of challenging conflicts with people who view monk seals as something other than an animal in need of protection continues to impede successful recovery and coexistence. Our study illustrates the role of social construction, deep-value identity conflicts, and aspects of risk communication in driving these conflicts. These findings mirror work on invasive species conflicts by Crowley et al. (2017) that suggest that aspects of the social context, approach to management, and communication can affect conflict development. They provide principles, tools, and strategies to anticipate and respond to these drivers of conflict, which apply equally to endangered species recovery:

1. Pay explicit attention to socio-ecological considerations and contexts, including research into previous management and participatory social assessments,
2. Use deliberative or democratic approaches to community engagement and management delivery,
3. Use open and honest communication that seeks feedback and responds constructively.

These approaches are especially important when hazards are low and outrage is high, which is when destructive conflicts were seen in our study, and which in our experience forms the basis of most human-wildlife conflicts driven by deep-value differences. This is often related to conflicting meanings attached to wildlife species that are becoming more common, whether they are endangered species like the Hawaiian monk seal that have become legally protected, common species adapting to urban environments, or domestic animals adapting to live without human support (e.g., feral animals). Endangered species recovery creates this potential for conflict by intentionally seeking to increase the population of rare animals. Thus, paradoxically, success in recovering endangered species means an increased likelihood of conflict over that species, as was observed by Williams et al. (2002) for wolves. Because people's lifestyles, values, and identities have been developed in a context where the species is rare, these conflicts have a high potential of becoming protracted and deep-rooted as increased human-wildlife interactions and government interventions to protect wildlife change how people live with and think about wildlife, but there is not yet a societally uniform understanding of wildlife in that context (Leong, 2009).

Decker et al. (2011) refer to this phenomenon as subsequent impacts of management which occur *because* management objectives have been achieved. Redpath et al. (2015) go one step further, arguing that managers and conservationists often act as antagonists by promoting wildlife recovery as a priority, which may conflict with the goals and perspectives of those who view wildlife through a different lens. An understanding of this dynamic that can emerge as a result of endangered species recovery efforts is crucial to navigating out of destructive conflicts to achieve recovery and coexistence. The IUCN (2023) provides useful guidance for managers working to address human-wildlife conflict, and also urges practitioners to reflect on their own role in the conflicts, recognizing that human-wildlife conflicts are almost always underpinned by social conflicts between people. Ultimately, it is important for managers to articulate their own assumptions and values, and to work to understand the assumptions and values of those who may be affected by species recovery, to anticipate potential subsequent impacts and develop proactive mitigating actions (Decker et al., 2011). In recovering endangered species, it is critical to do this *before* conservation success is achieved, and to draw on existing guidelines to prevent potential conflict when identities are threatened and worldviews may not align.

6 Limitations and future research

Our study drew from multiple data sources and perspectives to understand the drivers of conflict over Hawaiian monk seals. We had limited perspectives drawn directly from members of the Native Hawaiian and fishing communities, and future research could engage more deeply with these populations to understand the nuanced perspectives involved, and how these perspectives may contribute to ongoing conflict or conflict mitigation. Our survey aimed to understand perspectives of people on beaches who had the potential to interact with monk seals, but the highly positive skew of perspectives amongst those on beaches with monk seals limited our ability to use the survey to understand differences between those who perceived seals in a negative vs. positive light. For this reason we relied on interviews and other sources to provide insight into the drivers of conflict over monk seals.

We chose to focus this study primarily on conflict over monk seals on the island of O‘ahu, yet there is also evidence of deep-value identity conflicts on other Hawaiian islands such as Moloka‘i and Kaua‘i. Research that collaboratively engages in dialogues about perceptions of monk seals and their recovery will be necessary to address these conflicts, with an explicit goal of helping decision-makers understand how their actions, assumptions, and priorities might contribute to conflicts. In addition, while we observed conflicts linked to perceptions of outrage factors, it is unclear whether these perceptions developed as reactions to other perceptions of harm or vice versa. Is there higher outrage because monk seals were perceived as new or human-caused invaders, or did these ideas develop because of negative emotional reactions to management? Finally, future research may examine our hypothesis that human-wildlife conflicts stem from species becoming more common. For example, how universal is this observation, and which characteristics of species or management context play more prominent roles? Without attention to these additional potential drivers, managers should anticipate future conflicts will accompany recovery of marine mammals and other protected species.

Data availability statement

The datasets presented in this article are not readily available because interviews are confidential based on IRB protocol. Anonymized survey data may be shared at author’s discretion. Requests to access the datasets should be directed to alevine@sdsu.edu.

Ethics statement

The studies involving humans were approved by San Diego State University Institutional Review Board (protocol #HS-2018-0097). The studies were conducted in accordance with the local legislation and institutional requirements. The ethics committee/institutional review board waived the requirement of written informed consent for participation from the participants or the participants’ legal guardians/next of kin because verbal informed consent was given.

Author contributions

LK: Funding acquisition, Methodology, Project administration, Writing – original draft, Writing – review & editing, Data curation, Formal analysis, Investigation, Visualization. AL: Formal analysis, Methodology, Project administration, Writing – original draft, Writing – review & editing, Conceptualization, Funding acquisition, Resources, Supervision. KL: Conceptualization, Writing – original draft, Writing – review & editing. FK: Validation, Writing – review & editing.

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Conflict of interest

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

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Seals, sharks, and social identity: ocean management preferences and priorities

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Social identity influences policy preferences and actions regarding wildlife. Using data from a survey of residents, commercial fishers, and tourists on Cape Cod, Massachusetts, this study examined the relationships between self-selected social identities (i.e., animal protection, environmental, hunter, and angler) within these stakeholder groups and ocean management priorities, support for the Marine Mammal Protection Act (MMPA), and acceptance of lethal management of seals and white sharks. Results revealed three social identity clusters: (1) identification with environmental and animal protection groups (non-consumptive), (2) identification with both non-consumptive (environmental, animal protection) and consumptive (angler, hunter) groups, and (3) identification with none of the groups. Residents were a mix of identities; tourists primarily identified with the non-consumptive and, to a lesser extent, no identification clusters; and commercial fishers identified with the mixed non-consumptive/consumptive and no identification clusters. The overlap between consumptive and non-consumptive identifications illustrates the heterogeneity of social identity. Participants in the non-consumptive cluster favored policies prioritizing wildlife, the environment, and marine mammal protections more strongly than those in other clusters. Findings contribute to research examining social identity theory to improve understanding of public wildlife management preferences, within the novel context of rebounding populations of marine predators such as pinnipeds and white sharks.

KEYWORDS
conservation, human wildlife conflict, seals, sharks, social identity

Introduction

Stakeholder groups differ in their management preferences for rebounding marine predator populations, including pinnipeds (Jackman et al., 2018; Bratton et al., 2023; Jackman et al., 2023a, Jackman et al., 2023b). For example, the return of seal and white shark populations to nearshore waters of Cape Cod, Massachusetts, USA, has been celebrated by some stakeholders and lamented by others, who call for seal and shark culls to resolve conflicts with fishing and public safety on beaches (Fraser, 2018a; Wasser, 2019). On average, residents and tourists strongly opposed lethal management, while commercial fishers held more neutral views (Bratton et al., 2023; Jackman et al., 2023b). No stakeholder group, however, is a homogenous entity (Lute and Gore, 2018; Ehrhart et al., 2022).

Stakeholder groups often include people with a range of views, experiences, activities, and demographic characteristics that can influence their policy preferences. One such characteristic is social identity, where individuals align themselves with a social group (Lute and Gore, 2018; Bruskotter, 2013). Social identity reflects deeply held, value-laden perceptions that predict behavior and views of society (Tajfel, 1978). Based on self-identity, people self-categorize into groups with shared values, which in turn shape attitudes and behavior (Turner et al., 1987; Schroeder et al., 2021). Self-affiliation with social identity groups then becomes an important part of self-concept, leading individuals to adopt behaviors in accordance with group norms and model group members (Tajfel and Turner, 1979; Hornsey, 2008). Group membership provides individuals with self-esteem and a sense of belonging, leading to an increased sense of security about one's place in the world and a feeling of separation from outsiders (Abrams and Hogg, 1988; Blount-Hill, 2021). Social identity can be a stronger predictor of attitudes toward conservation management than value orientations (Bruskotter et al., 2019).

At the same time, individuals may hold multiple social identities simultaneously, which Lute and Gore (2018) have referred to as "heterogeneity in stakeholder identities." For example, hunters and fishers may also strongly identify as conservationists, environmentalists, and wildlife advocates (Siddiqi and Wolters, 2023). The recognition of multiple identities can help explain the diversity of views within segments of the population. Jackman et al. (2023b) found that a subset of commercial fishers agreed that seals have ecological benefits, which made them less likely to support lethal management. Overlapping identities among stakeholder groups can facilitate collaboration (Lute and Gore, 2018).

Social identity conflicts (and convergences) can be overlooked by wildlife managers, despite an increasing emphasis on stakeholder engagement in conservation governance (Kittinger et al., 2012; Manfredo et al., 2017; Lute and Gore, 2018, Lute and Gore, 2019). Quantifying attitudes among relevant identity groups is useful to managers addressing conservation conflicts, which are often manifestations of long-standing social conflicts between identity groups and may be impervious to short-term solutions (Madden and McQuinn, 2014; Blount-Hill, 2021). Identity groups shape large carnivore conservation, with differences between hunters, farmers, and animal rights activists exacerbating a growing urban-rural divide in policy preferences (Naughton-Treves et al., 2003; Dickman et al., 2013; Bruskotter et al., 2019).

Charismatic marine megafauna (e.g., marine mammals, white sharks) sustain high levels of public interest and support from diverse social identity groups (Kellert, 1999; Cheng, 2011). When marine mammals and white sharks conflict with fishing operations, environmental and animal protection groups align to oppose fishing groups advocating for lethal removal (Guerra, 2019; Reidy, 2019; Tixier et al., 2021). Similarly, alliances have formed between recreational boating and ocean development groups in opposition to speed limits intended to protect marine mammals from vessel strikes (Roman et al., 2013; Moore, 2023).

Environmental and animal protection groups were pivotal to the passage of the U.S. Marine Mammal Protection Act of 1972 (MMPA), which was enacted after NGO-led campaigns drew public attention to the mortality and suffering of marine mammals, pressuring government intervention (Flippen, 1997; Ray and Potter, 2011; Buck and Upton, 2012). Utilitarian interest groups such as commercial fisheries and energy interest groups have clashed with the MMPA, particularly surrounding conflicts with fishing and ocean development (Kellert, 1999). Environmentalists have advocated for ecosystem-based management with a focus on populations, while animal protectionists cite a moral obligation to protect the welfare of marine mammals as well as populations. Utilitarian groups oppose restrictions and claim marine mammal protections result in economic losses (Cheng, 2011). Conflicts involving multiple protected species also reveal unique management preferences. Under Section 120, the MMPA was amended in 1994 to allow states to apply for exemption from the MMPA to remove individually-identifiable pinnipeds preying on endangered salmonids, which are protected under the Endangered Species Act. Environmentalists and managers favored removing the pinnipeds to protect salmonids and other species dependent on the salmon run, while animal protection groups opposed the amendment, advocating for the protection of all individual pinnipeds. Utilitarian interests supported the removal of pinnipeds to protect fish stocks that have economic and cultural value to humans (Cheng, 2011; Gammon, 2018).

Although there is research on differences in stakeholder attitudes toward marine mammals such as pinnipeds (Cummings et al., 2019; Bratton et al., 2023; Jackman et al., 2023b), less attention has been paid to social identity (Jackman et al., 2023a). Members of environmental organizations were more supportive of the MMPA than non-members, who favored utilitarian interests (Kellert, 1999). A few international studies found different marine stakeholders hold unique knowledge, preferences, and behavioral intentions relating to marine resource management depending on social identity (e.g., fishing groups) (Voyer et al., 2014; Mason et al., 2015; Dyrset et al., 2022).

Interest groups also engage in shark management politics (Neff and Hueter, 2013; Friedrich et al., 2014; Koehler and Lowther, 2022). Following shark bites, groups representing conservation, tourism, recreation, and public safety interests debated the use of lethal management as an appropriate policy response (Pepin-Neff and Yang, 2012; Simmons and Mehmet, 2018). While studies have measured attitudes toward shark conservation (Drymon and

Scyphers, 2017; Pepin-Neff and Wynter, 2019; Giovos et al., 2021; Hancock et al., 2023), the influence of social group identification on management preferences remains unexamined.

This study applied social identity theory to marine predator recovery on Cape Cod, Massachusetts, USA, using data from a survey of residents, commercial fishers, and tourists to examine the complexity of views within stakeholder groups in the context of controversies over seals and white sharks (Bratton et al., 2023; Jackman et al., 2023a, Jackman et al., 2023b). We addressed the following research questions: (1) With which social identities do members of each of these three stakeholder groups (residents, commercial fishers, and tourists) on Cape Cod align? (2) To what extent is social identity associated with levels of support for the Marine Mammal Protection Act, ocean management priorities, and lethal management of seals and sharks? and (3) What is the relationship between social identity and demographic characteristics such as gender and education?

Materials and methods

Study area

Gray seal (*Halichoerus grypus*) and white shark (*Carcharodon carcharias*) populations are returning to U.S. coastal waters in the Western North Atlantic following the enactment of the MMPA of 1972 and federal protections for white sharks in 1997 (Wood et al., 2022; Winton et al., 2023). Both species suffered severe, human-caused population losses as a result of bounty hunting (seals) and commercial bycatch and recreational fishing (sharks). Shifting baseline syndrome, where depleted populations of marine predators became the norm, has resulted in human-wildlife conflict (Roman et al., 2015; Jackman et al., 2023b), with pressure mounting on managers to control populations (Garcia-Quijano, 2018; Bratton et al., 2023). Numerous local interest groups have engaged in debates over management response, including environmental conservation groups with seal/shark research and education programs (Bass et al., 2015; Chivers, 2021); organizations dedicated to animal welfare and marine mammal rescue (Fraser, 2018b); angler and commercial fisher groups (Behnke, 2021; Leggett, 2021); a community group dedicated to enhancing beach safety by using technology to coexist with sharks (Sobey, 2023); and groups formed to advocate for seal and shark culls (Williams, 2019).

Data collection

The survey was piloted on Nantucket Island, Massachusetts in 2016 among residents, tourists and recreational anglers (Jackman et al., 2018). For the Cape Cod survey, the Nantucket survey instrument was adapted to include additional questions about white sharks, experiences on Cape Cod, and commercial fishing. This questionnaire was administered to Cape Cod residents, commercial fishers, and tourists in the summer of 2021 using the Dillman et al. (2014) five contact methodology (Bratton et al., 2023; Jackman et al., 2023a, Jackman et al., 2023b). Participants were invited to complete the survey by mail or through Qualtrics, an online survey platform. Voter registration lists were used as a sampling frame for residents, with surveys mailed to a systematic random sample of 1,793 registered voters drawn from lists obtained for each of the 15 towns on Cape Cod, where voters were selected at consistent sampling intervals (99^{th}) from a random start. Contact information for commercial fishers (email and mailing addresses) was obtained from the Massachusetts Division of Marine Fisheries list of commercial fishery permit holders in Barnstable County. Surveys were distributed by mail and email to one permit holder per household and email address for the population of permit holders, with 1,456 commercial fishers invited to complete surveys. In instances where multiple permit holders resided in the same household or shared an email address, one permit holder was randomly selected to receive the survey. Individuals selected for both the voter and commercial fisher samples were removed from the voter sample. Non-resident tourists were recruited to participate in the study at the Cape Cod National Seashore using a multi-stage sampling design (Vaske, 2019; Bratton et al., 2023; Jackman et al., 2023a). Based on visitor data for 2019, a set number of sampling time blocks were allocated across the six Cape Cod National Seashore beaches to reflect visitor use distribution. Then, time blocks were randomly distributed to fill in the sampling schedule. All tourists (> 18 years old; one survey per household, n = 1074) who signed up received a survey to complete at home by email or mail, according to their preference.

Respondents

Surveys were completed by 547 residents (response rate = 32%), 564 commercial fishers (response rate = 39%), and 699 tourists (response rate = 68%). Across groups, the final sample size was 1,672 participants. In the resident subsample, non-response bias checks between respondents and non-respondents found that residents older than 65 years (χ^2 = 55.11, df = 3, P < .001) and residents in the Lower Cape Region (χ^2 = 14.69, df = 2, P < .001) were over-represented. To correct for this over-representation, resident data were weighted by voter population age and regional distribution. No significant differences in findings between weighted and unweighted data were found. For the commercial fisher sample, non-response bias checks found no differences between respondents and non-respondents in regional distribution on Cape Cod (χ^2 = 5.58, df = 2, P = .061), or between respondents and the permit holder population in distribution of fishery endorsements held. For the tourist sample, non-response bias checks determined no bias resulting from the location of beach recruitment (χ^2 = 1.49, df = 5, P = .915) (Bratton et al., 2023; Jackman et al., 2023a).

Measures

Social identity variables

Social identity was measured by asking respondents the extent to which they identified with four interest group types (animal protection, environmental, angler, and hunter). The salience of each interest group for respondents was measured on a five-point scale, ranging from not at all (1) to very strongly (5) (Lute and Gore, 2018; Bruskotter et al., 2019; Carlson et al., 2020; van Eeden et al., 2020a).

Policy and management variables

To measure priorities for ocean management, respondents indicated the extent to which they agreed management of the ocean should be in the best interests of seals, sharks, tourism, ecosystem, fisheries, and local communities, respectively (Gruber, 2014; Jackman et al., 2018). Support for the Marine Mammal Protection Act was assessed by measuring levels of respondent support for five of the law's goals: (1) preventing marine mammals from going extinct, (2) maintaining and restoring marine mammal population levels, (3) minimizing conflicts between marine mammals and commercial fishing, (4) minimizing harm and suffering of marine mammals, and (5) protecting areas of the ocean important for marine mammal feeding and breeding (Kellert, 1999; Jackman et al., 2018). Replicating measures in Jackman et al. (2018), respondents were asked whether they agreed with lethal management of seals in response to a series of situation-based scenarios: (1) "kill seals that interfere with fishing;" (2) "kill seals that lay on beaches or rocks;" (3) "kill seals if they swim in harbors;" and (4) "kill seals to reduce population levels" (Bratton et al., 2023; Jackman et al., 2023b). Acceptance of lethal management of sharks was measured with a parallel series of situation-based scenarios: (1) "kill sharks that interfere with fishing;" (2) "kill sharks that swim near beaches;" (3) "kill sharks after a bite occurs;" and (4) "kill sharks to reduce population levels" (Bratton et al., 2023). Responses to ocean management priorities, Marine Mammal Protection Act, seal lethal management scenarios, shark lethal management scenarios were all measured on seven-point scales ranging from strongly disagree (−3) to strongly agree (3).

Demographic variables

Respondents indicated their gender as female, male, or Gender X. They also provided information on the highest level of education that they completed (less than high school; high school graduate/GED; some college/no four-year degree; college graduate; some graduate school; master's degree; PhD, MD, DVM, JD or other terminal degree; and other). The education variable was recoded into three categories (less than four-year college degree, college degree/some graduate school, graduate/professional degree). Respondents also provided their age in years.

Analysis

Data from residents, commercial fishers, and tourists were pooled for analyses. All results were reported for weighted data. Five scales were created to examine differences in attitudes and management priorities related to marine mammals and sharks. Scales for MMPA support (Jackman et al., 2018), seal lethal management (Jackman et al., 2018; Bratton et al., 2023; Jackman et al., 2023b), and shark lethal management (Bratton et al, 2023) were calculated by averaging the respective set of items for each measure. The six items measuring ocean management priorities were subjected to a Principal Components Analysis (PCA), with varimax rotation (Vaske, 2019). Using eigenvalues = 1.0 and visual inspection of the scree plots, two factors were identified: marine wildlife and ecosystem priorities (managing the ocean in the best interests of – sharks, seals, ecosystem) and human-oriented priorities (managing the ocean in the best interests of – local communities, fisheries, tourism). These two factors accounted for 64% of the variance. Paired Samples *t*-tests determined significant differences in overall ratings between the two scales for ocean management priorities for each factor. The internal consistency (Cronbach's alpha) for all scales was acceptable (≥ .65) using guidelines suggested by Vaske (2019). Descriptive statistics (means, standard deviations) for rating scale data were calculated.

K-means cluster analysis was used to identify groups, or clusters, of respondents who responded similarly to the four social identification variables (Siddiqi and Wolters, 2023). Since respondents rated their level of identification with different groups separately on four, non-exclusive questions, meaning respondents could simultaneously hold multiple identities, this approach enabled the creation of groups with similar patterns of responses across identities. Ratings for each of the four social identification variables (animal protection, environmental, angler, and hunter) were collapsed into dichotomous groups representing no identification (rating = 1) to any identification (ratings = 2 through 5) for each identification variable. K-means cluster analysis then was used to determine respondents' cluster membership using the dichotomous social identification variables. Differences in demographic characteristics by cluster was determined by Likelihood-Ratio Chi-Square for categorical variables and Analysis of Variance (ANOVA) with appropriate *post-hoc* tests (LSD when equal variance could be assumed and Games-Howell when equal variance could not be assumed) for continuous variables. Due to a small sample size (n = 21, 1%), Gender X was omitted from this analysis. Analysis of Variance (ANOVA) was also utilized to detect differences in mean ratings on support for the MMPA scale, the two ocean management priorities scales (marine wildlife and ecosystem priorities, human-oriented priorities), and support for lethal management of seals and white sharks scales were identified using cluster membership as the independent variable. Effect size (Cramer's V or η) was calculated, with .10 minimal, .30 typical, and .50 indicative of a substantial relationship for Cramer's V and .10 minimal, .243 typical, and .371 indicative of a substantial relationship for η (Cohen, 2013; Vaske, 2019). A $P < .05$ was used to determine significance. SPSS v28 was used for statistical analysis.

Results

Social identity clusters

A total of 1,674 respondents (weighted; unweighted n = 1,672) were included in the cluster analysis (137 were excluded due to missing data). The K-means cluster analysis of the social identification variables revealed three clusters: (1) identification with non-consumptive environmental and animal protection groups (*n* = 783, 47%), (2) identification with both non-consumptive (environmental, animal protection) and consumptive (angler, hunter) groups (*n* = 685, 41%), and (3) identification with none of the offered groups (*n* = 205, 12%). Within stakeholder groups, residents were a mix of identities; commercial fishers identified with the mixed non-consumptive/consumptive groups and, to a lesser extent, no identification; and tourists primarily identified with non-consumptive and, to a lesser extent, no identification groups (Figure 1).

Demographic characteristics of the social identity clusters

Table 1 presents the demographic characteristics for each social identity cluster. A significant relationship was observed between cluster group and sample type. More than half of the non-consumptive cluster were tourists followed by residents. Nearly half (49%) of the mixed non-consumptive/consumptive cluster were commercial fishers with 29% residents and 22% tourists. The no identification cluster was more mixed, with 42% tourists.

There were also significant relationships between cluster type and both gender and education. The non-consumptive cluster was composed of a higher percentage of women whereas there was a higher percentage of men in the mixed non-consumptive/consumptive cluster. In terms of education, a greater proportion of participants in the non-consumptive cluster had attained higher educational degrees than participants in the mixed non-consumptive/consumptive cluster. There was no significant difference in mean age by cluster membership (non-consumptive: M = 54.5 years, SD = 16.0; mixed: M = 55.3 years, SD = 15.5; no identification: M = 54.9 years, SD = 17.0), F (2, 1664) = 0.39, P = .68.

Support for MMPA by social identity clusters

Participants in all three clusters supported the MMPA. Support for the MMPA within the non-consumptive cluster (M = 2.6) was significantly higher than participants in the mixed non-consumptive/consumptive (M = 1.8) and no identification (M = 2.0) clusters (Table 2).

Ocean management priorities by social identity clusters

Participants in the non-consumptive cluster rated their support for marine wildlife and ecosystem priorities, including seals and sharks, significantly higher than participants in the other two clusters (Table 2). Support for human-oriented priorities was significantly higher in the mixed non-consumptive/consumptive cluster than in the non-consumptive cluster. Participants in the non-consumptive cluster rated their support for marine wildlife and ecosystem priorities (M = 1.9, SD = 1.9) significantly higher than their support for human-oriented priorities (M = 0.8, SD = 1.2), t (773) = 17.8, P <.001. There were no significant differences in the mean ratings of the two ocean priorities scales within the other two clusters (mixed non-consumptive/consumptive: marine wildlife and ecosystem priorities - M = 1.0, SD = 1.3, human-oriented priorities – M = 1.0, SD = 1.1, t(673) = −0.5, P = .61; no identification: marine wildlife and ecosystem priorities - M = 1.0, SD = 1.5, human-oriented priorities – M = 0.82, SD = 1.2, t(199) = 1.4, P = .16).

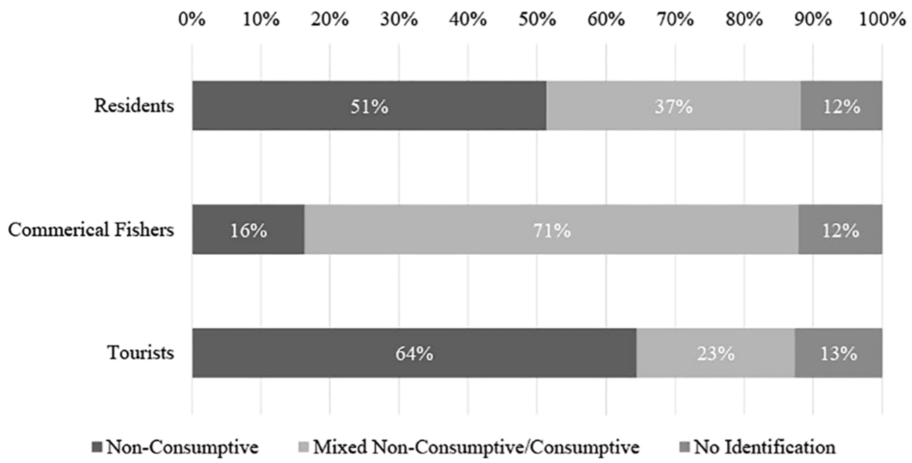

FIGURE 1
Distribution of social identity cluster membership within tourist, commercial fisher, and resident stakeholder groups (n = 1,673). Weighted results.

Support for lethal management of seals and sharks by social identity clusters

In general, there was little support for lethal management of seals or sharks, although the lack of support differed by cluster (Table 2). All three clusters significantly differed from each other in their ratings for support of lethal management of seals: participants in the non-consumptive cluster had significantly lower mean ratings than the other two clusters, demonstrating the greatest opposition to lethal management, followed by participants in the no identification cluster. Participants in the mixed non-consumptive/consumptive cluster, while showing a lack of support for lethal management, expressed the least disagreement with this management approach. In terms of lethal management of sharks, a similar pattern emerged, with participants in the non-consumptive cluster expressing the most opposition, having significantly lower mean ratings than participants in the other two clusters, whose ratings were statistically similar to each other.

Discussion

Social identity cluster composition

Findings indicated that social group identification is important for a more nuanced understanding of policy preferences related to rebounding populations of marine predators, including marine mammals. Cluster analysis did not identify strict non-consumptive and consumptive identities as might be expected. Rather, one cluster revolved around non-consumptive social identities of environmental and animal protection and another cluster identified with both non-consumptive (environmental/animal protection) and consumptive (hunter/angler) social

TABLE 1 Demographic characteristics within social identity clusters.

Characteristic	Social Identity Cluster			Likelihood Ratio Chi-Square	*P*	Cramer's V^2
	Non-Consumptive	Mixed Non-Consumptive/ Consumptive	No Identification			
	n=783	n=685	n=205			
	%	%	%			
Social Identification (rating: 2 to 5)[1]				–	–	
Environment	100	85	13			
Animal Protection	98	81	5			
Hunting	0	100	7			
Fishing	33	96	12			
Sample*				320.5	<.001	.301
Resident	35	29	31			
Fisher	10	49	28			
Tourist	55	22	41			
Gender*				201.6	<.001	.345
Men	39	75	58			
Women	61	25	42			
Education*				133.1	<.001	.200
Less than 4 year college degree	20	42	31			
College degree/ Some graduate school	35	38	39			
Graduate/ Professional degree	45	20	30			

Weighted results.
*P < .05
[1]Statistical testing not conducted since these variables were used to create cluster groups. Results reported here show the distribution of social identification asked in four separate questions within each cluster.
[2]Effect size (Cramer's V) is minimal at .10, typical at .30, and substantial at .50.

TABLE 2 Mean support ratings for MMPA, ocean management priorities, and seal and shark lethal management by social identity cluster.

Attitude/ Priority Scale[1,2]	Social Identity Cluster			F	P	η^3
	Non-Consumptive	Mixed Non-Consumptive/ Consumptive	No Identification			
	n=783	n=685	n=205			
	M (SD)	*M (SD)*	*M (SD)*			
MMPA*	2.6[a] (0.7)	1.8[b] (1.3)	2.0[b] (1.2)	121.3	<.001	.358
Ocean Management Priorities						
Marine Wildlife and Ecosystem Priorities*	1.9[a] (1.2)	1.0[b] (1.3)	1.0[b] (1.5)	102.1	<.001	.332
Human-Oriented Priorities*	0.8[a] (1.2)	1.0[b] (1.1)	0.8[a,b] (1.2)	6.4	0.002	.088
Seal Lethal Management Support*	−2.4[a] (1.1)	−0.8[b] (1.9)	−1.5[c] (1.8)	44.3	<.001	.428
Shark Lethal Management Support*	−2.1[a] (1.3)	−1.4[b] (1.6)	−1.6[b] (1.6)	44.3	<.001	.227

Weighted results.
*P <.05
[1]Scores ranged from +3 (strongly agree) to −3 (strongly disagree).
[2]Means with different superscripts are significantly different at P < .05 based on Games-Howell post-hoc tests.
[3]Effect size (η) is minimal at .10, typical at .243, and substantial at .371.

identities. The non-consumptive cluster was comprised primarily of residents and tourists, while the mixed non-consumptive/ consumptive group was comprised primarily of commercial fishers. While consumptive and non-consumptive wildlife recreationists have traditionally been regarded by managers as separate groups with distinct values (Daigle et al., 2002), findings revealed some overlap in identities. This is consistent with recent research demonstrating that hunters and fishers can hold strong pro-environmental and pro-wildlife values (Cooper et al., 2015; Bruskotter et al., 2018; Jaebker et al., 2021) and that individuals can hold multiple identities (Cooper et al., 2015; Lute and Gore, 2018; Bruskotter et al., 2019; van Eeden et al., 2019; Siddiqi and Wolters, 2023). Individuals who engage with multiple groups and identities relating to conservation likely hold unique values (Bruskotter et al., 2019), which may be misunderstood by managers or overlooked by group leaders, who tend to hold more singular views (Bruskotter et al., 2018).

Multiple social identities may help explain the diversity of viewpoints within stakeholder groups, especially commercial fishers, related to seal and shark management (Bratton et al., 2023; Jackman et al., 2023a). Studies have documented that consumptive/utilitarian stakeholder groups hold more pluralist values than the public, identifying with aspects of both domination and mutualism value orientations (Gamborg and Jensen, 2016; Liordos et al., 2023). The policy preferences of pluralists can be hard to predict, as pluralists express either mutualist or domination values depending on situational context (Teel and Manfredo, 2010; Liordos et al., 2023).

Demographic characteristics, ocean management priorities, and support for lethal management

In the context of conflicts related to marine predators, respondents in the non-consumptive cluster, made up primarily of tourists and residents, held strong pro-environmental and wildlife attitudes, prioritizing marine wildlife and ecosystem over human-oriented management concerns, supporting protections for marine mammals, and opposing lethal management of seals and white sharks more strongly than respondents in other clusters. This cluster was composed of a greater proportion of women, as well as respondents with higher educational degrees, than the mixed non-consumptive/consumptive cluster. Previous research has found women are more likely to hold values aligned with animal, wildlife and environmental protection (Chauvat et al., 2023) and less likely to support lethal wildlife management (Jackman and Rutberg, 2015; van Eeden et al., 2020b).

Support for MMPA by social identity clusters

All social identity clusters in this study demonstrated support for the MMPA. The high level of MMPA support across social identity groups, more than 50 years after its enactment, is consistent with responses to these same questions across stakeholder groups in a survey of Nantucket Island, MA residents, tourists, and recreational anglers (Jackman et al., 2018) and a national survey (Kellert, 1999). Nationwide surveys conducted in 2017 (Heimer, 2017) and 2018 (Animal Welfare Institute, 2018) found support levels for the MMPA have remained consistently high at 73% and 77%, respectively. Similarly, Bruskotter et al. (2018) found the majority of respondents in all social identity groups (i.e., animal rights advocate, environmentalist, conservationist, wildlife advocate, gun rights advocate, farmer/rancher, hunter, property rights advocate) supported the Endangered Species Act (ESA). Alignment with environmental, animal rights, conservation, and wildlife groups increased ESA support (Bruskotter et al., 2018) as was evidenced in greater support for the MMPA by the non-consumptive (animal protection/environmental) cluster in this study. Findings suggest that opponents of wildlife conservation measures, while vocal, may not be representative of public views and that public support for conservation and species protections can transcend social divisions, even in the context of conflicts with rebounding species that are perceived by some as threatening human wellbeing and livelihoods.

Leveraging shared social identities

Heterogeneity of identities within stakeholder groups can provide a foundation for collaboration in decision-making around wildlife and conservation issues (Lute and Gore, 2018; Jackman et al., 2023a). Overlapping social identities and values can transcend divisions, reduce the us v. them characterization that dominates wildlife management controversies and form a basis for managers to facilitate positive interactions between opposing groups (Lute and Gore, 2014, Lute and Gore, 2018; Jackman et al., 2023a; Siddiqi and Wolters, 2023). In the context of marine conservation, placing emphasis on ocean stewardship has been demonstrated to help divided groups recognize common values, such as belonging to a community that protects ocean ecosystems and marine wildlife (Lute and Gore, 2014; Kolandai-Matchett and Armoudian, 2020). For example, sea turtle managers have found it useful to frame conservation campaigns targeting human behavior within community norms, inviting all homeowners to “join the community” in adopting pro-turtle behaviors such as cutting unnecessary lighting, instead of singling out non-compliant individuals or groups (McDonald et al., 2014; Kolandai-Matchett and Armoudian, 2020). On Cape Cod, community members including scientists, commercial fishermen, tourists, and the public have expressed shared support for increasing research and public education on seals and sharks (Bratton et al., 2023), as well as for increasing testing of seal-safe fishing gear modifications and deterrents (Bogomolni et al., 2021) and non-lethal shark mitigation strategies (Woods Hole Group, 2019; Bratton et al., 2023).

Seal and shark conservation could be enhanced by outreach campaigns that frame pro-seal, -shark, and -environmental behaviors as community norms, appealing to overlapping identities related to animal protection and the environment. Following shark bites, managers have used this strategy to promote the adoption of shark encounter prevention behaviors among beachgoers, altering community standards and expectations for shark safety (Martin et al., 2022; Szczepaniak, 2022). Tools such as workshops can be useful for managers to convene and build trust between conflicting identity groups (NOAA Office for Coastal Management, 2015).

Limitations and future research directions

Because the study did not ask respondents to rank which of the listed social identities were most important to them (Lute and Gore, 2018), our analysis is limited in examination of the salience of various social identities. Similarly, nuance in respondents’ degree of identification with the four social identity variables was lost when the variables were dichotomized for cluster analysis. Future research should explore alternative strategies for creating multiple-identity clusters, incorporating salience and degree of identification into cluster formation. Human-wildlife conflicts contribute to the polarization of identity groups, making some identities more salient than others (Lute et al., 2014). Research has found that commercial fishers hold a strong social identity linked to heritage and role in the local community as a provider of seafood (Voyer et al., 2014; Dyrset et al., 2022). Conflicts with marine predators may threaten this identity, by impeding fishing ability and leading to more stringent restrictions on fishing operations. However, the identification of some commercial fishers with environmental and animal protection groups suggests that despite polarization, it may be possible to engage some commercial fishers in conservation efforts. The inclusion of stakeholder group names in survey titles (e.g., Cape Cod Voter Survey, Cape Cod Commercial Fisher Survey, and Cape Cod Tourist Survey) may also have made the commercial fisher identity more salient than other identities (Schroeder et al., 2021). In future research examining social identity, this limitation could be resolved by eliminating language in the survey instrument which identifies respondents as belonging to a certain stakeholder group. Instead, stakeholder categorization can be tracked through a means which is not known to respondents, such as unique survey identification numbers.

Replicating the approach of Bruskotter et al. (2019), Carlson et al. (2020) and van Eeden et al. (2020a), this analysis measures social identity through self-identification with categorical interest groups (e.g., “Environmental Groups”), rather than membership in a specific organization (Krueger and Pedraza, 2015). As only a few interest groups were listed on the survey, an expanded list of options could more fully capture the complexities of social identities (Lute and Gore, 2018). Other approaches to characterizing social identity can further inform understanding of the social dimensions of wildlife conflict, such as targeting members of specific groups to participate in interviews (Lute and Gore, 2014) or asking respondents about specific group affiliations (Jaebker et al., 2021). A more specific approach to characterizing social identity could be particularly useful in regions such as Cape Cod, where NGOs lead education, outreach, and mitigation efforts relating to seals, sharks, beach safety, and fishing, and are highly visible within the local community.

An additional factor that may limit the generalizability of this study is that surveys were administered in the summer of 2021, immediately following the COVID-19 shutdown (Jackman et al., 2023b). Visitation to the Cape Cod National Seashore was stable during the COVID-19 pandemic (Morrison, 2021) compared to past years, with NGOs conducting community outreach relating to sharks and seals remaining operational. However, studies have documented shifts in outdoor recreation participation during the COVID-19 shutdown, which likely impacted engagement with hunting, fishing, and environmental groups. The pandemic had variable impacts on hunting participation across the United States (Danks et al., 2022), while participation in recreational fishing increased (Midway et al., 2021). Interest and participation in nature-based activities, including wildlife viewing, increased during the pandemic (Morse et al., 2020; Doremus et al., 2023) with increased observation of desirable wildlife such as birds associated with wildlife-friendly values (Murray et al., 2023). Additionally, negative impacts of the COVID-19 shutdown on the commercial fishing industry (White et al., 2020), including a loss of income among commercial fishers in the Northeastern U.S (Smith et al., 2020), may have exacerbated seal-fisheries conflicts.

Recommendations and conclusions

Findings demonstrated that stakeholder groups are not homogenous entities but are composed of individuals who simultaneously hold multiple social identities. Results help explain disagreement within stakeholder groups regarding management preferences, particularly among commercial fishers and residents on Cape Cod regarding seals and white sharks (Bratton et al., 2023; Jackman et al., 2023b). Shared support for the MMPA and marine ecosystems among different identity group clusters provides a basis for community-wide appeals to advance conservation initiatives. However, differences in levels of support between clusters, particularly regarding lethal management, indicate that group-specific messaging delivered in partnership with group leaders could be an effective means to alter in-group attitudes and behaviors.

This study contributes to recent research examining social identity theory within wildlife management stakeholder groups (Bruskotter et al., 2019; Landon et al., 2019; Schroeder et al., 2021; Ehrhart et al., 2022) within the novel context of marine predator conservation. Links between social identity and attitudes toward wildlife management transcend continents (van Eeden et al., 2020b), especially as the internet and social media allow stakeholders to engage with identity groups beyond their local area (Salz and Loomis, 2005; Lute et al., 2014; Voyer et al., 2014).

Findings are increasingly relevant to managers as urbanization drives an increase in mutualism values, shifting engagement with interest groups relating to conservation nationwide (Bruskotter et al., 2019). In the United States, participation in hunting is declining, while angling and wildlife viewing are attracting a record number of participants (Cooper et al., 2015; Aiken, 2016). On Cape Cod, urbanization (Uiterwyk et al., 2019; Cape Cod Commission, 2022) has led to heightened conflicts with both terrestrial and marine species (Jackman and Rutberg, 2015; Bratton et al., 2023; Jackman et al., 2023b) and could also be impacting public engagement with environmental, animal protection, and fishing groups. Parsing social identities within stakeholder groups provides valuable insight into policy preferences in the marine environment amid human-wildlife conflict, with relevance to ocean managers navigating conflicts involving marine mammals, white sharks, and the multiple stakeholder groups present in coastal communities.

Data availability statement

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

Ethics statement

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. Written informed consent from the participants was not required to participate in this study in accordance with the national legislation and the institutional requirements.

Author contributions

RB: Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. SD-G: Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. JV: Conceptualization, Formal analysis, Methodology, Writing – review & editing. JJ: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – review & editing.

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Conflict of interest

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

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Evidence of fin whale (*Balaenoptera physalus velifera*) recovery in the Canadian Pacific

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Pacific fin whales (*Balaenoptera physalus velifera*), once the most abundant cetacean species in British Columbia (BC), were also one of the most heavily targeted by commercial whaling. Much of what we know about their phenology and ecology is from catch records, but their current status has not yet been summarized in Canadian waters. Here, we collated evidence from dedicated surveys, opportunistic sightings, and passive acoustic records that had not been reported before and reviewed them in the context of past data. This was to add new findings to what is known, and to establish if the population was showing signs of recovery. This is particularly relevant considering discussions of downlisting their population status in Canada from *endangered* to *threatened*. We then asked if this rebounding was consistent with what is known about pre-whaling presence and movement patterns, or if changes in whale distribution reflected altered oceanic regimes, prey availability, or increased anthropogenic pressures. The evidence suggested that fin whale populations in the northeast Pacific Ocean are repopulating areas along the BC coast recognized as part of their historic range. However, they are recovering in a different ocean than they were removed from, which makes them increasingly vulnerable to new anthropogenic threats. The sightings data suggested that, at least for the west coast of Vancouver Island, this repopulation has occurred over a relatively short period, with fin whales still absent from regular surveys as recent as the early 2000's. The recent acoustic recordings suggested their presence is not transitory, but that fin whales may be using locales along the BC coast for feeding and breeding activities.

KEYWORDS

fin whales, commercial whaling, population rebounding, acoustic monitoring, visual surveys, platforms of opportunity, catch records

1 Introduction

Large-scale industrial whaling ended in the Canadian northeast Pacific Ocean in 1967, but not before decimating cetacean populations. Once the most abundant species in this area, Pacific fin whales (*Balaenoptera physalus velifera*) became the most heavily hunted (Pike and MacAskie, 1969). Catch records show that more than 7,000 fin whales were killed in less than 60 years (1908–1967), more than any other species for the five whaling stations in British Columbia (BC) (Figure 1) for that period (Gregr, 2000; Nichol et al., 2002).

Here, we combine insights from previously unpublished data with the existing literature from studies and catch records from along the BC coast to consider the potential recovery of fin whales since the cessation of whaling. For context from their full geographic range, data from Alaska to California was examined. Recent visual surveys and passive acoustic monitoring (PAM) data are compared as new evidence of whale presence to whaling records and works from that period to consider if the current patterns of presence and habitat use indicate a population recovery into areas where fin whales once prevailed, or if the extent of population growth and/or dynamic environmental variables have initiated a range expansion. We question whether the consistent down-listing of fin whales under the Species at Risk Act (SARA) is warranted given the evidence. Fin whale presence along the BC coast forms the foundation of this assessment, while behavioral context will be considered where possible to ascertain spatiotemporal trends.

2 Whaling

Four whaling stations operated in BC between 1905 and 1943 during the first era of whaling. These stations were located on the west coast of Vancouver Island at Sechart and Kyuquot, and on Haida Gwaii in Rose and Naden Harbors. After World War II, during the second era of whaling, a fifth station opened in Coal Harbor on northern Vancouver Island, becoming one of the most prolific stations and one of the last operational shore-based stations in North America (Figure 1).

The industry in BC targeted five whale species: blue (*Balaenoptera musculus*), fin, humpback (*Megaptera novaeangliae*), sei (*B. borealis*) and sperm (*Physeter macrocephalus*) whales. Occasionally, north Pacific right (*Eubalaena glacialis*), Baird's beaked (*Berardius bairdii*), gray (*Eschrichtius robustus*) and minke (*Balaenoptera acutorostrata*) whales were also noted in the records (Nichol and Ford, 2018). A total of 24,427 whales were logged into catch records, of which 7,497 were fin whales (Gregr, 2000; Ford, 2014; Nichol and Ford, 2018). Despite the closure of Canadian whaling stations, between 1964 and 1974, a further 201 fin whales were taken in the Pacific by Japanese whalers, with additional removals by Soviet whalers in the offshore waters, both of which are believed to have under-reported or falsified records (Ford, 2014).

Despite overharvesting being evident in the early years of whaling, the BC industry increased production; limits on chaser boats per station were abandoned and whale processing became a 24-hour operation at the shore stations (Nichol and Ford, 2018). Initially spared from the hunt on account of their speed, strength, and use of offshore habitat, fin whales became a target species for the cull. Their predictable presence in waters close enough to shore was not great enough to warrant a stronger focus until the numbers

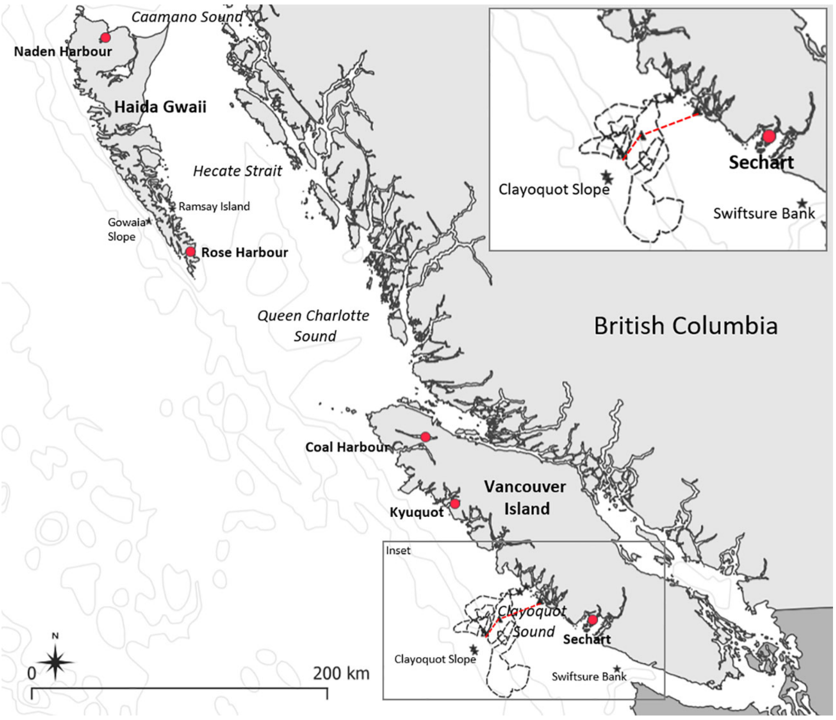

FIGURE 1
Map of the British Columbia coast. The five whaling stations are indicated with red circles (Naden, Rose and Coal Harbor, Kyuquot, and Sechart). The location of passive acoustic monitoring (PAM) systems discussed are shown with black stars (Gowgaia Slope and Ramsay Island (Frouin-Mouy et al., 2022); Clayoquot Slope, Clayoquot Sound, and Swiftsure Bank (Burnham, 2019). The track of mobile PAM systems is shown with black dashed lines and the bi-monthly pelagic survey off the west coast of Vancouver Island is shown with red dotted line, with starting, shelf crossing, and end locations marked by a black triangle. This is shown in greater detail in the inset.

of blue and right whales had dwindled (Drucker, 1951; Monks et al., 2001; Ford, 2014). Catch numbers of fin whales steadily decreased from a peak in 1911–1912, although they still formed a substantial part of the catch. The focus on fin whales was even greater in the second era of whaling (Gregr, 2000; Nichol and Ford, 2018). During this period fin whale catch peaked in 1958 with 573 animals, followed by another dramatic fall in catch (Gregr, 2000). The overall proportion of fin whales caught from BC waters was similar to that reported for Alaskan stations (Gregr, 2000), and a similar switch of target species was noted in whaling records for California (Clapham et al., 1997). Bonuses were paid based on the length of the whale, encouraging the take of more mature individuals. However, the take in this second era for fin whales was from a population that had already been exploited, which had altered the age and size structure. The minimum catch length for fin whales was set at less than the known average length at maturity and was lesser than that imposed for humpback and sei whales, typically smaller species (Flinn et al., 2002).

Much of what is known about fin whale ecology and habitat use has been derived from historical catch and commercial whaling records that provide details over large spatial and temporal scales. Catch dates, location, sex, length, and a variety of measures related to diet, reproductive status, and morphology were taken (Nichol and Ford, 2018). This adds to our understanding of trends on sex ratios, body lengths at maturity, pregnancy rates, and population structure. These details, along with notations of catch and whaling efforts (Pike, 1968; Gregr, 2000; Gregr et al., 2000) can be used to better understand the impacts of removals on fin whale populations.

3 Contemporary data

3.1 Visual data

Several dedicated, systematic surveys have been undertaken in BC, which aid in establishing fin whale presence, habitat use, and population abundance. However, much of the effort has been focused on the continental shelf. Vessel-based line transect surveys have estimated the fin whale population. The use of photo-identification mark-recapture methods from a dedicated research vessel helps to better estimate the number of individuals observed. However, again, much of this work to date has been limited to continental shelf waters and estimates the total population, rather than sexually mature adults. Aerial and vessel-based surveys in deeper waters have shown greater density of fin whales for the survey effort expended in areas west of Vancouver Island and Haida Gwaii, for example (Harvey et al., 2017; Figure 1), indicating there is still much to learn about fin whale presence in the offshore areas. A three-month vessel-based survey in the summer of 2018 into offshore waters extended to the limits of Canada's Exclusive Economic Zone (EEZ), including over 350,000 km^2 of survey area in offshore waters (Pacific region International Survey of Marine Megafauna (PRISMM), Wright et al., 2021) started to address the lack of data.

Additional data comes from smaller-scale vessel-based surveys. An example is from surveys undertaken between 1993 and 2007 on the west coast of Vancouver Island by a citizen science group, the Strawberry Island Marine Research and Education Society (SIMRS, Figure 1). The results of these surveys have not been previously published and were not designed to target fin whale populations specifically. The transect began at a near-shore location north of Tofino (49.1362°N, −125.9751°W) and extended to an end point 35 nm offshore (48.8450°N, −126.7192°W); 24 nm of this survey were over the continental shelf, then crossed the shelf break (48.9667°N, −126.5267°W) to continue into abyssal waters (Figure 1). This survey line crossed several bathymetric features including submarine canyons west of Clayoquot Sound. These surveys, despite noting the presence of eleven cetacean species, highlighted the absence of fin whales at that time.

Data collated from aerial or vessel-based surveys and platforms of opportunity adds to evidence of fin whale habitat use as they recover from whaling. Opportunistic data collated for the BC coast by the British Columbia Cetacean Sighting Network (BCCSN) was used to look for changes in presence in time and space, and to set the SIMRS Vancouver Island surveys in a coast-wide context. For the period of the SIMRS pelagic surveys, the total reported sightings for fin whales in the 1990's was five, three of which were before the surveys started in 1991–1992. No sightings were reported between 2000–2009, consistent with the survey results (Figure 2). Although not effort-corrected and all observations being opportunistic, the coast-wide sighting data suggests an increasing number of fin whales in BC waters and an expanding spatial range, as represented by the geographical extent the sightings were made (Figure 2).

3.2 Acoustic records

Data from passive acoustic monitoring (PAM) systems have also added to our knowledge base of fin whale habitat use in BC. Whale calls in the acoustic record indicate presence, but also give an idea of the whales' behavioral state. The most commonly described fin whale call is the 20-Hz downsweep, used while traveling and socializing (Watkins et al., 1987; McDonald et al., 1995; Edds-Walton, 1997; Sirovic et al., 2013). If 20-Hz calls appear in a regular pattern in the acoustic record, with consistent inter-call intervals, it represents 'song' and forms part of the male reproductive display (Watkins et al., 2000; Croll et al., 2002; Sirovic et al., 2013; Koot, 2015; Burnham, 2019). Also noted in the literature is the 40-Hz call, principally used during foraging (Sirovic et al., 2013; Burnham et al., 2021; Romagosa et al., 2021).

Findings from recordings from offshore Vancouver Island by Burnham et al. (2019) were furthered here by considering an extra year of data from a bottom-mounted underwater hydrophone at Clayoquot Canyon [48.6706°N, −126.8485°W; Ocean Networks Canada (ONC) node (oceannetworks.ca); Figure 1]. This analysis was undertaken from July 2018 to July 2019 and considered here as they overlap spatially with the SIMRS vessel surveys. This analysis was a manual aural-visual review of offshore recordings (July 2018–July 2019 at 48.6706°N, −126.8485°W) that systematically analyzed every 5th day. Details from similar recordings from bottom-mounted underwater hydrophones on the eastern and western coasts of Haida

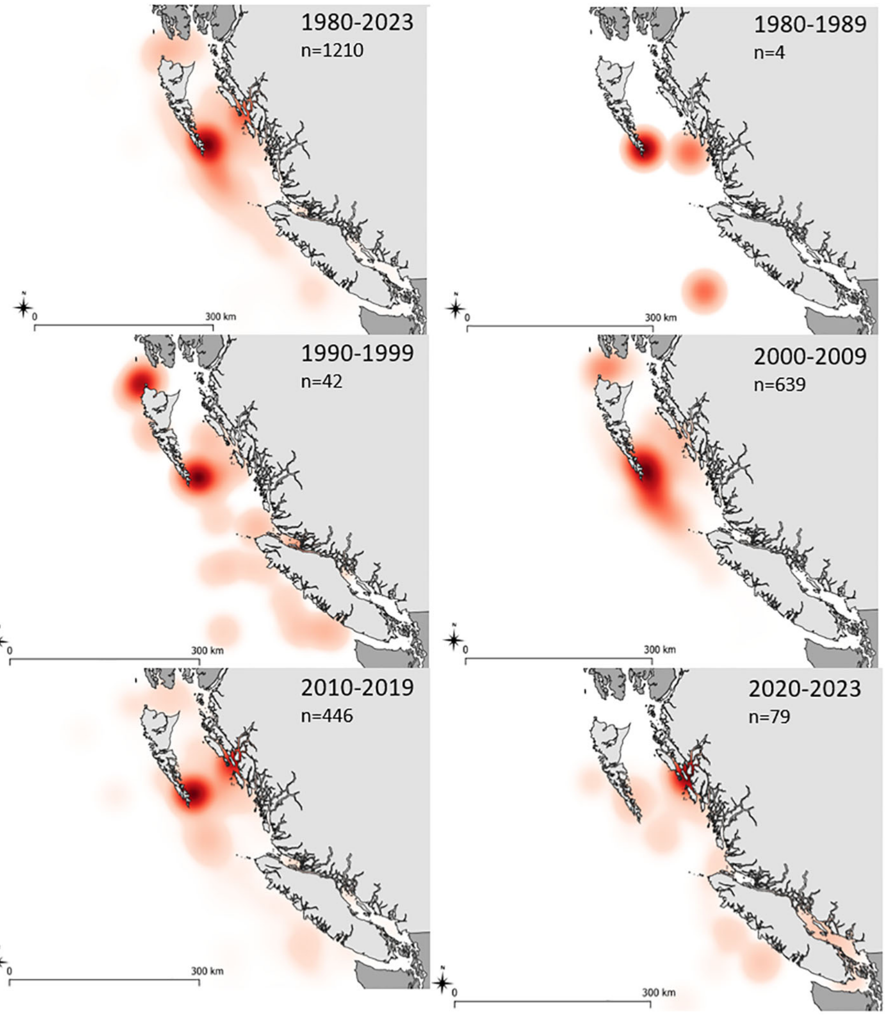

FIGURE 2
Sightings data of fin whales taken from the British Columbia Cetacean Sightings Network. These are opportunistic sightings, that have not been effort corrected. Heat-spotting allows hot-spots of whale presence through each decade and the full length of data (1980–2023) to be visualized spatially. The number of sightings per decade is also indicated.

Gwaii (Gowgaia Slope and Ramsay Island, Figure 1) were taken from analysis by Frouin-Mouy et al. (2022) to add to the coast-wide picture of whale presence using acoustic means. Using single hydrophone systems, it is not possible to discern the number of whales present or their location. Nor is there a way to absolutely determine the absence of whales when calls were not heard. Therefore, the calls in the acoustic data represents a minimum presence. However, call number, rate, and the presence of numerous coincident calls can all indicate the relative number of whales present, and suggest migration, breeding, and foraging behavior (Koot, 2015; Burnham, 2019; Burnham et al., 2019; Frouin-Mouy et al., 2022).

4 Population abundance and structure

Pre-exploitation estimates suggest that prior to the 1900's, the north Pacific fin whale population was 40,000–45,000, and was reduced to 13,620–18,680 whales by the end of commercial whaling (Ohsumi and Wada, 1974). Recognition that the northeast Pacific stock was distinct in 1973 also indicated half of the existing population of fin whales were of this stock, numbering 8,520–10,970 whales (Ohsumi and Wada, 1974).

To date, an estimate of population abundance for finwhales in Canadianwaters, especially for offshore regions is lacking where fin whales are presumed to be most numerous (COSEWIC, 2019). Dedicated, systematic surveys have estimated the population in BC to be approximately 400–500 individuals (2004–2005 survey, 496 individuals (95% CI: 202–1218) Williams and Thomas, 2007; 2004–2008 survey, 446 individuals (95% CI: 263–759) Best et al., 2015). Nichol et al. (2018) confirmed this estimate from surveys conducted between 2009 and 2014 (405 individuals (95% CI: 363–469)), complemented using photo-identification to better estimate the number of individuals. These surveys highlighted whale 'hotspots' in Hecate Strait, and Queen Charlotte and Caamano Sounds (Harvey et al., 2017; Figure 1). Sightings interpolated using density surface modelling fromthe 2018 PRISMM survey suggested a total abundance of 2,893 (95% CI: 2171 - 3855) fin whales in BC estimated from 235 sightings across two survey strata (Wright et al., 2021). This survey found over six times as many fin whale sightings in the offshore than the north coast stratum and, overall, exceeded earlier abundance estimates (see COSEWIC, 2019).

In the context of their full range along the west coast of North America, surveys conducted in northern California, Oregon, and Washington suggest a 7.5% annual increase in numbers from the mid-1990's to the mid-2000's, representing an overall five-fold increase in fin whale population size (Moore and Barlow, 2011; Nadeem et al., 2016). Central and southern California estimates were stable in population estimates during this period (Nadeem et al., 2016). In their northern range extent in Alaska, annual increases were estimated to be 4.8% between 1987 to 2003 (Nadeem et al., 2016). These kinds of population trend estimates have not been possible for fin whales in Canadian waters, given the lack of baseline data especially in offshore regions. Additionally, the logistical challenges of systematically and repeatedly surveying offshore areas exacerbates the difficulty of obtaining population estimates.

5 Habitat use

Whaling catch records provide clues about the distribution, behavior, and prey of fin whales. However, they have an inherent spatial bias; whaling efforts extended approximately 200 nautical miles (nm) offshore from whaling stations (Pike and MacAskie, 1969), but approximately 80% of the catch was within 150 nm. Fin whales were caught in both coastal shelf and offshore waters, with the distance between the coastline and the capture site of whales increasing significantly over the course of the second whaling era (Gregr, 2000). Hunting efforts on the west coast of Vancouver Island and around Haida Gwaii, in Hecate Strait and Queen Charlotte Sound (see Figure 1), were primarily in exposed waters, but occasionally in protected areas along the mainland coast and Queen Charlotte Strait (Pike and MacAskie, 1969; Gregr and Trites, 2001; Ford, 2014). The catch per station along the coast was similar, suggesting approximately equal availability and ease of capture of fin whales. In general, catches increased from spring to summer, and decreased from fall to winter (Gregr, 2000; Nichol et al., 2002, Nichol and Ford, 2018). Male and female catch numbers by search distance were approximately equal, indicating little to no spatial segregation by sex. Their increased proximity to shore and presence in Hecate Strait and Queen Charlotte Sound showed a seasonal pattern, strongest in July and August, which suggests their use of more near shore waters for summer foraging (Pike and MacAskie, 1969; Gregr, 2000). Pregnant females were noted consistently from April until September within reach of the coastal stations (Gregr, 2000). Combined, this suggests that during the whaling period BC waters were important for both reproduction and foraging.

The take of smaller bodied animals, despite the incentive toward larger whales, suggests that the fin whale population may have been segregated spatially by size, with mature animals living further offshore. Analysis of body size data also suggests the existence of a local BC foraging sub-group or sub-population, of generally smaller bodied individuals (Fujino, 1964; Pike and MacAskie, 1969; Flinn et al., 2002). This was in addition to migrating animals, with age structuring in this population movement. Larger bodied fin whales arrived in BC ahead of smaller individuals for the northward migration, and the southward migration was led by pregnant females leaving in September to give birth, resulting in a notable reduction in catch number (Gregr, 2000).

The context of fin whale presence can be enhanced from patterns of prey abundance or oceanographic regimes. Spatial modeling of the catch data shows increased whale abundance with water depth (Nichol et al., 2017) and around bathymetric features (Hui, 1985; Gregr and Trites, 2001), as well as during periods of increased chlorophyll production (Smith et al., 1986), sea surface temperature (Woodley and Gaskin, 1996), and ocean circulation (Waring et al., 1993; Woodley and Gaskin, 1996). All of these speak to the tie between whales and prey abundance (e.g., Woodley and Gaskin, 1996; Fiedler et al., 1998; Gregr, 2000; Gregr et al., 2000; Gregr and Trites, 2001). Fin whale habitat from catch data was predicted to be concentrated along the continental shelf and in a large offshore area encompassing waters up to 100 nm offshore that extended from the south end of Haida Gwaii towards Vancouver Island (Pike and MacAskie, 1969; Gregr, 2000; Gregr and Trites, 2001).

Oceanographic variables dictating prey abundance and aggregation predicts whale presence (Gregr, 2000; Gregr and Trites, 2001). Convergent currents to the north of Vancouver Island, the topography, off-shelf flow, and the formation of Haida eddies, upwell nutrients in these areas and entrain zooplankton (Thomson, 1981; Allen et al., 2001; Nichol and Ford, 2018). The higher proportion of euphausiids in stomach contents from captured fin whales also suggests whales were concentrated on the shelf break and around other bathymetric features (Mackas and Galbraith, 1992). This was distinguished from greater proportions of copepods from fin whales in sub-arctic, Alaskan, and offshore waters (Mackas, 1992).

The opportunistic sighting data must be reviewed with caveats, as results may reflect increased effort, both spatially and temporally. However, similar to the whaling data, there is a spatial bias of limiting search efforts to within reach of shore stations. Consistently, most sightings per decade were reported around Rose Harbor and the southern tip of Haida Gwaii (Figure 2). The appearance of whales in near coastal or inner waterways and fjord systems has been noted by Pilkington et al. (2018) and is also reflected in the BCCSN data showing an increase from four individuals sighted on a single occasion in 1995, to a total of 163 reports from 2010 to 2023 (Figure 2). Considering notations of foraging with the sightings, foraging activity also increased (Figure 3).

Although little effort has been dedicated to these areas, fin whales are known to use waters extending at least 200 nm offshore/ 1,000 m water depth (Nichol et al., 2017). This includes the deeper waters south and east of Haida Gwaii and in some more confined waterways (Gregr and Trites, 2001; Williams and Thomas, 2007; Ford et al., 2010; Nichol and Ford, 2018). Studies in California have

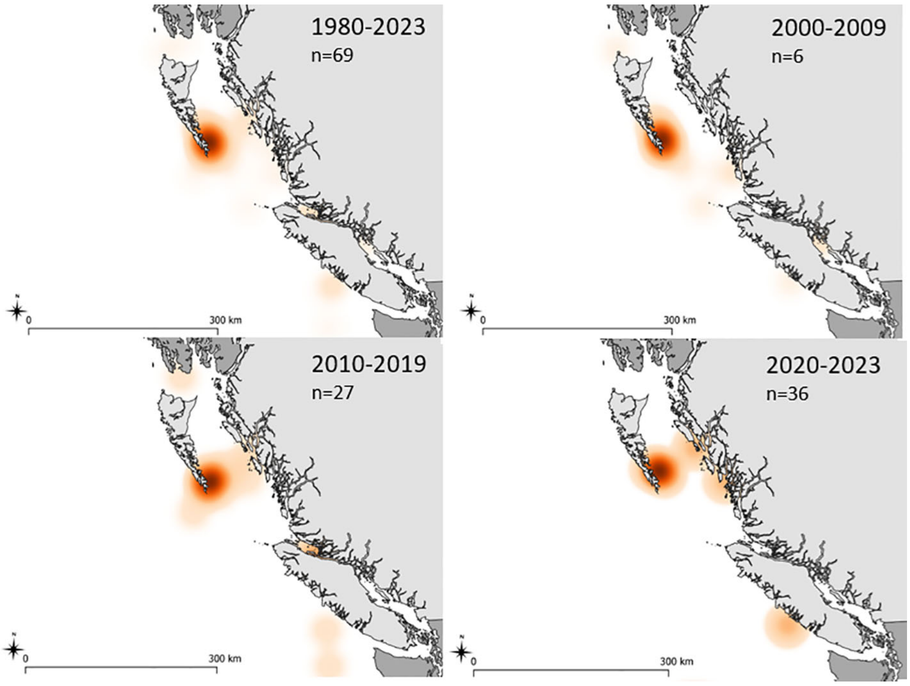

FIGURE 3
Sightings data taken from the British Columbia Cetacean Sightings Network, specifically noted as foraging fin whales. These are opportunistic sightings, that have not been effort corrected. Heat-spotting allows hot-spots of whale presence through each decade and the full length of data (1980–2023) to be visualized spatially. The number of sightings per decade is also indicated.

also shown fin whale presence to be consistent year-round and with residency times of 30 days or more (Falcone and Schorr, 2014; Scales et al., 2017), contradicting the presumed north–south migration between high-latitude feeding areas and lower latitude breeding and calving regions (Mackintosh, 1972; Sergeant, 1997). As lesser numbers were noted in the catch records in BC over the winter, it could be that the general population migrates, while some individuals or sub-groups do not. These sort of breaks from the expected whale presence in time or space may represent animals of differing age, gender, reproductive status, energetic requirements/size class, predation risk, or physiological capacities.

Review of more recent PAM data has indicated the presence of fin whales year-round in recordings. The data both from Vancouver Island and Haida Gwaii indicate the presence of both the 20-Hz and 40-Hz call, further suggesting BC is important for both feeding and breeding for fin whales. Foraging calls were most prevalent in the spring and summer, following the spring bloom and upwelling along the shelf break (Burnham, 2019; Burnham et al., 2019). The presence of 20-Hz calls in BC waters, however, substantially outnumbers the 40-Hz call type in the acoustic records. This was found in the years' worth of data analyzed from offshore Vancouver Island. As per previous studies (see Burnham, 2019), this additional PAM data showed the 20-Hz call was prevalent in January–February, when records from whaling and recent surveys or sightings are most scarce. Conception and calving are believed to occur in the winter (Mizroch et al., 1984; Folkens et al., 2002), which is when song was most frequent in the acoustic data off the west coast of Vancouver Island and further north (Frouin-Mouy et al., 2022). Births are most common between mid-October and mid-February (Lockyer, 1984; Koot, 2015), with patterning in 20-Hz calls peaking towards the latter part of this period (also see Burnham, 2019). Song patterning in the 20-Hz calls has been noted in recordings taken at Union Seamount, Nootka Sound, Barkley Sound, La Perouse Bank, and Brooks Peninsula on the west coast of Vancouver Island (Ford et al., 2010; Koot, 2015). Further, winter recordings in northern BC, the Bering Sea, and northern Gulf of Alaska to the Southern Californian Bight have also noted the presence of regularly patterned 20-Hz song (Moore et al., 2006; Stafford et al., 2007; Sirovic et al., 2013, 2015; Pilkington et al., 2018; Frouin-Mouy et al., 2022). Early notation by Burnham et al. (2019) described a doublet pattern (two tones: a backbeat and a 20-Hz note, see Burnham, 2019) that had been described in other areas of the west coast of Vancouver Island by Koot (2015), and more widely in the northeast Pacific by Sirovic et al. (2017). Song patterning is used in courtship displays but is also thought to reflect population sub-structures. The doublet structured pattern noted by Burnham (2019) and others (Ford et al., 2010; Koot, 2015) is the most prominent pattern in the north Pacific (Sirovic et al., 2017) and dominated the acoustic records from the BC offshore waters from the recorder off Vancouver Island. The presence of this song suggests a wide-ranging and highly connected population (Oleson et al., 2014; Sirovic et al., 2017). Indeed, similarity in song pattern for southern California to the southern Chukchi Sea suggests the range of this group could span the west coast of North America (Mellinger and Barlow, 2003; Sirovic et al., 2017; Burnham, 2019; Furumaki et al., 2021). The data analyzed from July 2018 to July

2019 from offshore Vancouver Island noted more than 140,000 fin whale calls in a years' worth of data, with approximately 85% of the calls 20-Hz calls and forming song patterns that peaked from January to March. However, in considering the inter-call intervals, the analysis indicated an altered or modified form of the song pattern which may suggest song evolution, similar to that seen in humpback whales (see, e.g., Allen et al., 2018) but on longer time scales, or a progressive splintering of the population into sub-groups as their numbers recover. The whaling data already suggested a sub-group specific to foraging regions in BC; something similar might become more apparent in the data for whales undertaking courtship activities. Contrary to the catch records, which suggested whale numbers decreased from September onwards, fin whale calls were found to be most numerous in the deep coast and offshore waters on the west coast of Vancouver Island and Haida Gwaii in the winter months, determined by both bottom-stationed and mobile PAM devices (see Ford et al., 2010; Koot, 2015; Burnham, 2019; Burnham et al., 2019; Frouin-Mouy et al., 2022; Figure 1).

The collated evidence suggests fin whales are present in BC waters year-round and, while predominantly found in deeper waters past the continental shelf break, they also use areas on the shelf. Contemporary research confirms a similar habitat use pattern to pre-whaling as fin whale populations in the northeast Pacific Ocean are recovering. However, they are doing so in a different ocean than they were removed from. When a population is reduced it not only faces challenges due to small population dynamics, but the removal of individuals may, to some extent, erase knowledge of quality locations for foraging, mating, and calf rearing from the collective memory of the population. This can mean the legacy of whaling persists far beyond the cessation of removal activities. Since the cessation of whaling, fin whales are starting to return to historically important habitat as the current population builds their collective memory of areas in BC waters that support their reproductive and foraging success.

6 Challenges for recovery

As fin whales reestablish patterns of foraging and breeding, they are now faced with shifts in the marine environment that were absent prior to whaling pressures. Fin whale abundance mirrors their prey, which even the whalers were aware of (Nichol et al., 2017). Fin whale sightings were most frequent along bathymetric features that aggregate prey, particularly euphausiids, which fin whales are known to target along the west coast of North America (Flinn et al., 2002). However, changing ocean regimes and anomalies of increased water temperatures in the Pacific Ocean have altered zooplankton species composition along the BC coast (Galbraith and Young, 2020), which their proclivity for offshore waters does not exclude them from (Hourston and Thomson, 2020). With warmer ocean temperatures expected due to climate change, shifts in zooplankton timing and reduced size of prey species is expected (Richardson, 2008). Although the response from fin whale populations is so far unknown, these changes will dictate the location, abundance, and quality of their prey, which may be reflected in future fin whale presence and habitat use. Climate change also has a role in sea level rise, ocean acidification, more intense marine heatwaves and storm events, and altered nutrients cycling and sequestration. The large body size, long generation time and low reproductive rates increases fin whales' vulnerability to climate change effects, either directly or through changes in habitat suitability of prey resources. Adaptations of habitat use may become apparent as whales try to exploit localized concentrations or prey hotspots (see Notarbartolo di Sciara et al., 2016). More 'opportunistic nomadism' (Jonzen et al., 2011), contractions in range, or altered or weakened migration patterns may also become apparent (Notarbartolo di Sciara et al., 2016).

The consistent signs of fin whale repopulation along the BC coast (Towers et al., 2018; Keen et al., 2021) makes them increasingly vulnerable to anthropogenic threats. Propeller driven vessels have increased remarkably in the period since whaling ceased. Marine vessel traffic in BC is concentrated around Vancouver Island, especially nearest the ports of southern BC and Washington State, but international shipping routes span much of BC waters (Erbe et al., 2014). Although all large whales are susceptible to vessel strikes, fin whales are especially vulnerable (Laist et al., 2001). As the fin whale population in the Pacific Ocean increases, and vessel traffic also increases, the number of ship strikes is expected to rise. The risk of vessel strike from increased vessel presence has been noted for fin whales in the literature (e.g., Williams and O'Hara, 2010; David et al., 2011); proposed energy projects are cited as a particular risk for whales in northern BC (see Keen et al., 2023), with similar findings reported due to the proximity of fin whale habitat to commercial shipping lanes in other regions (e.g., Castro et al., 2022). The location and effects of collisions are still poorly known, but evidence from body scars and strandings are being used to try and better estimate risk. However, unreported strikes or undocumented fatalities mean that our understanding likely underestimates the level of threat this could pose for fin whales (Williams and O'Hara, 2010). Vessel travel speed is likely the most important variable in estimating the risk of collision, and likelihood of lethality if it occurs (Laist et al., 2001; Vanderlaan and Taggart, 2007; Keeley et al., 2021).

The effects of vessel presence extend beyond collision injury and fatalities; noise levels from propeller driven vessels have changed the marine environment of BC waters considerably. The increasing reliance on commercial ocean transport routes has been the driving force behind a global doubling in ambient sound levels every decade over the last 70 years (Hildebrand, 2009; Andrew et al., 2011; Frisk, 2012). Fin whales are highly acoustic animals, especially during periods of breeding and foraging. However, increasing underwater noise additions from large vessels are concentrated in the low frequencies, where fin whale calling is focused. Acoustic disturbance can induce a stress response in whales (e.g., see Rolland et al., 2012), or disrupt key behaviors such as foraging or social or mating behaviors through the abandonment of these behaviors, avoidance of a key region where these areas are undertaken due to noise levels, and the reduced effectiveness of calling through acoustic masking. The full implications of the masking of fin whale communication signals are still largely undetermined, but increasing noise levels can change fin whale acoustic and behavioral patterns by modifying song characteristics and causing avoidance of areas with increased noise levels (Castellote et al., 2012; Southall et al., 2023). Passive acoustic monitoring will not only aid in tracking the assumed fin whale population recovery, but also allow an estimate of the potential level of threat of underwater acoustic disturbance. Soundscape analysis can detail the noise levels that whales are exposed to, and the level of exposure over time. Although masking and behavioral/calling modification is considered a sub-lethal effect it can increase the energetic load of a whale, while also decreasing the amount of information it is receiving about its surroundings, and so has the potential to impact their success or survival. In addition, if exposure is great enough (from noise amplitude and/or time of exposure) physiological effects such as temporary or permanent hearing impairment may result, with morphological damage also documented in cetacean species (see Erbe et al., 2019).

Other risks include entanglement, toxicity from plastic/micro-plastic pollution from ingestion and exposure to persistent organic and heavy metal pollutants (see Fossi et al., 2012; Espada et al., 2024) and the potential for oil spills. The assessment of each start with the consideration of the pathway of effect and risk to individuals by assessing the spatial and temporal overlap, allowing consideration of how that might escalate to risk of a group or population-level consequences more broadly. In other regions, pulmonary and neurological diseases have been described as a naturally occurring threat, whereby death occurs through individual or mass stranding.

7 Conclusions

The collation of evidence suggests that fin whales are repopulating areas along the BC coast. This is further supported by the annual population growth in areas to the north in Alaska and the south in California. However, the efforts to track the recovery of the whales in their core habitat, in deeper waters and off the shelf break, is limited. This restricts our appreciation of the current population size and dynamics, with the conclusions made so far being limited to on-the-shelf observations, which may represent more of a peripheral population recovery. Acoustics may be employed to fill the gap in our knowledge about offshore repopulation and habitat use over time and space. That said, more field observations and genetic sampling will refine our ideas of population number, site fidelity, residency times, population dynamics and composition, including potential sub-groupings or clades (Archer et al., 2013). With their long generation and gestation times, recovery to pre-whaling numbers will be slow (Best, 1993; Zerbini et al., 2010) and the legacy of whaling removals be felt for some time to come. Worldwide, fin whale populations are experiencing varying degrees of recovery, but their numbers seem to be increasing in the Southern Hemisphere (Herr et al., 2022) and North Atlantic (Vikingsson et al., 2009). A more broad, trans-boundary appreciation of population structure may be needed, especially for mitigating threats associated with commercial shipping and climate change. The consistent down-listing of fin whales by COSEWIC in Canada's Species at Risk Act (SARA) may be premature and go against the precautionary principle usually adopted when so many unknowns remain.

Author contributions

LR: Data curation, Formal analysis, Writing – original draft, Writing – review & editing. RB: Conceptualization, Data curation, Formal analysis, Supervision, Visualization, Writing – original draft, Writing – review & editing. DD: Conceptualization, Supervision, Writing – review & editing.

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Conflict of interest

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

Publisher's note

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Corrigendum: Evidence of fin whale (*Balaenoptera physalus velifera*) recovery in the Canadian Pacific

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A Corrigendum on

Evidence of fin whale (*Balaenoptera physalus velifera*) recovery in the Canadian Pacific

By Rannankari L, Burnham R and Duffus D (2024) *Front. Conserv. Sci.* 5:1392039. doi: 10.3389/fcosc.2024.1392039

In the published article, there was an error in the population abundance number for fin whales that was reported by Wright et al. (2021), as well as two other text mistakes within the same paragraph.

A correction has been made to **4 Population abundance and structure**, Paragraph 2. This previously stated:

"To date, an estimate of population abundance for fin whales in Canadian waters, especially for offshore regions is lacking where fin whales are presumed to be most numerous (COSEWIC, 2019). Dedicated, systematic surveys have estimated the population in BC to be approximately 400-500 individuals (2004-2005 survey, 496 individuals (95% CI: 202-1218) Williams and Thomas, 2007; 2004-2008 survey, 446 individuals (95% CI: 263-759) Best et al., 2015). Nichol et al. (2018) confirmed this estimate from surveys conducted between 2009 and 2014 (405 individuals (95% CI: 363-469)), complemented using photo-identification to better estimate the number of individuals. These surveys highlighted whale 'hotspots' in Hecate Strait, and Queen Charlotte and Caamano Sounds (Harvey et al., 2017; Figure 1). Sightings interpolated using density surface modeling from the 2018 PRISM survey suggested a total count of 23,692 (95% CI: 19,121-29,356) fin whales for British Columbia from 29 sightings (Wright et al., 2021), far exceeding earlier estimates (see COSEWIC, 2019). Much more of these efforts were given to offshore survey. For the north-coast region, in an area comparable to the earlier work of Best et al. (2015) but ten years later, the model predicted 2,893 fin whales (95% CI: 2,171-3,855, Wright et al., 2021). Each of these dedicated surveys highlighted similar areas of increased whale density in BC."

The corrected sentence appears below:

"To date, an estimate of population abundance for fin whales in Canadian waters, especially for offshore regions is lacking where fin whales are presumed to be most numerous (COSEWIC, 2019). Dedicated, systematic surveys have estimated the population in BC to be approximately 400-500 individuals (2004-2005 survey, 496 individuals (95% CI: 202-1218) Williams and

Thomas, 2007; 2004-2008 survey, 446 individuals (95% CI: 263-759) Best et al., 2015). Nichol et al. (2018) confirmed this estimate from surveys conducted between 2009 and 2014 (405 individuals (95% CI: 363-469)), complemented using photo-identification to better estimate the number of individuals. These surveys highlighted whale 'hotspots' in Hecate Strait, and Queen Charlotte and Caamano Sounds (Harvey et al., 2017; Figure 1). Sightings interpolated using density surface modelling from the 2018 PRISMM survey suggested a total abundance of 2,893 (95% CI: 2171 - 3855) fin whales in BC estimated from 235 sightings across two survey strata (Wright et al., 2021). This survey found over six times as many fin whale sightings in the offshore than the north coast stratum and, overall, exceeded earlier abundance estimates (see The Committee on the Status of Endangered Wildlife in Canada (COSEWIC), 2019)".

The authors apologize for this error and state that this does not change the scientific conclusions of the article in any way. The original article has been updated.

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Successful citizen science tools to monitor animal populations require innovation and communication: SealSpotter as a case study

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In rapidly changing ocean systems, there is a dual need to engage and educate community members and carry out rapid data acquisition. There is a body of evidence to support community or citizen science projects as successful vehicles for achieving these goals, with a particular need to increase global ocean literacy. The online SealSpotter program is a citizen science initiative aimed at monitoring trends in Australian fur seal (*Arctocephalus pusillus doriferus*) populations and connecting people to the marine environment. Here we present the findings of five years of monitoring of fur seals using drone surveys counted by citizen scientists via SealSpotter. Over five years, global participants from 23 countries were engaged in counting seals with a focus on the annual breeding season and pup abundance, with an average of 13,479 images and 171,137 seals counted per year. SealSpotter participants presented more conservative (lower) counts than expert counts, however both groups detected similar trends in abundance, emphasizing success of the project aims that included obtaining a precise index of pup abundance; ultimately a more achievable goal than accuracy due to the difficulties in measuring absolute abundance. We reflect on SealSpotter's accomplishments and highlight the potential for marine citizen science programs as important tools for addressing global ocean literacy needs. The SealSpotter program contributes to our understanding of marine ecosystems through a simple but effective citizen science program.

KEYWORDS
Arctocephalus pusillus doriferus, citizen science, drones, marine mammal, monitoring, ocean literacy, population trends, remote piloted aircraft

1 Introduction

Anthropogenic stressors to the marine environment are leading to great uncertainty for marine environments. Climate change impacts include shifts in species abundance, phenology, physiology, and distribution (Hoegh-Guldberg and Bruno, 2010). In the marine environment, climate-driven species redistribution is a pronounced impact of global warming (Pecl et al., 2017), with broad global estimates of between 25–85% of marine species having already shifted in range (Melbourne-Thomas et al., 2021). Linking changes or declines in animal populations with environmental change requires frequently collected and reliable data. Given the number of species and regions that are undergoing change and ideally require monitoring, efficient methods to observe changes and forecast future scenarios are needed (Chapin et al., 2010).

In order to respond to changing ocean systems, scientists, policy makers, and decision makers require rapid acquisition of reliable information. People also need to be connected to the ocean to support the policies and decisions being made such as adaptation policies for planned coastal retreat of developed areas (e.g., The State of Victoria Department of Environment, Land, Water and Planning, 2020). Conservation scientists are therefore faced with two concurrent pressures; the need to gain real-time data, and the need to connect people to the ocean (Kelly et al., 2021; Nash et al., 2022). 'Ocean literacy' is broadly used to describe a sense of connectedness and understanding between the community and the ocean (Schoedinger et al., 2010), and while the term has evolved since its inception a decade ago, ocean literacy broadly conceptualizes increased knowledge, awareness, and attitudes to the marine environment (McKinley et al., 2023). Ocean literacy is currently endorsed by the United Nations Ocean Decade, with 'an Inspiring Ocean' named as one of the key ocean decade actions currently targeted by the decade initiative (McKinley et al., 2023; Ryabinin et al., 2019). Within the current decade (2021 – 2030) and beyond, an increase in global ocean literacy is being promoted as a means to combat changing marine environments and better protect the ocean (Ellwood et al., 2017; Kelly et al., 2021).

Community or citizen science provides an opportunity to both increase data collection (Brown and Williams, 2019) and foster ocean literacy and connection to the environment (Worm et al., 2021; Kelly et al., 2022b). Ocean education initiatives and citizen science tools can empower people with new skills that may be important towards changing individual and community awareness, behaviors, and activism around ocean issues (Kelly et al., 2023). Many have praised citizen science projects for providing access and experience in the scientific process to the public and for fostering emotional connections to local environments and the ocean (Ellwood et al., 2017; Kelly et al., 2020). Democratizing science through citizen science is an important aspiration; however, research of over 14 million participants in major online citizen science programs identified that 80% of participants were trained in science, therefore it is important to test this goal rather than assume success (Strasser et al., 2019).

The Zooniverse[1] is a well-known online citizen science platform that currently supports 90 projects from different disciplines including climate, biology, medicine, astronomy, social science and the humanities. Participants are asked to perform tasks for research projects and many participate in multiple projects, contributing to many noteworthy discoveries including the discovery of new galaxies (Spiers et al., 2019). The sustainability of citizen science relies on maintaining engagement while optimizing projects for scientific outputs, but the high number of citizen science projects available also causes competition for participants and forces developers to consider design flexibility and life expectancy. Understanding the target audience from the community and the tension between engagement and data outputs is critical.

To be successful, citizen science methods must balance functionality to maximize participation, promotion for engagement, and be purpose built to fulfill the research questions by obtaining data of suitable quality; good design, training and researcher engagement are critical (Cox et al., 2015; Brown and Williams, 2019; Spiers et al., 2019; Weiser et al., 2020). Participation may be uneven where a small number of individuals perform a majority of the work; also, retention of experienced individuals is valuable because they are often long-term participants and their increasing skills can improve data quality providing another tension in the sustainability, participant diversity and democratization of citizen science projects (Spiers et al., 2019; Strasser et al., 2023). Citizen science platforms must remain flexible to manage such conflicts and/or be designed with purpose to accurately communicate expectations and limitations for potential participants to ensure transparency.

The combination of emerging technologies such as aerial imaging has been widely adapted to wildlife monitoring programs that use citizen scientists to aid in counting species. Remote sensing technologies, such as the use of Remote Piloted Aircraft (RPA) platforms (or drones) and associated cameras or sensors, are a powerful tool that allow for rapid data acquisition and consistent monitoring. In marine and coastal settings, the use of drones is helping to overcome a number of data collection challenges, such as identifying and sampling marine species (Apprill et al., 2017; Hodgson et al., 2020; Wiley et al., 2023), mapping coastal environments (Ierodiaconou et al., 2022; Pucino et al., 2021), and understanding environmental changes (Yaney-Keller et al., 2019). Drones have seen great success in collecting population data on species that are typically challenging to access, such as marine mammals and wetland and marine birds (Hodgson et al., 2020; Howell et al., 2023). Despite concerns around the disturbance of wildlife from drone flights, best practice guidelines have been identified (Hodgson and Koh, 2016) and drone surveys can still present a less-invasive method than hands-on approaches to population monitoring. Such best practice guidelines include testing localized wildlife sensitivities to drones because they can be species and site specific (Sorrell et al., 2023; Weimerskirch et al., 2018).

In the context of pinniped research, drone surveys have many benefits in addition to more frequent population counts and the provision of precise and reliable abundance data for trends analyses (Hodgson et al., 2018; Wood et al., 2021). They provide a rapid and less invasive method to collect data and reduce occupational health and safety risk to researchers working along rocky coastlines. Drones allow researchers to conduct more frequent surveys of pup numbers over the breeding season, thus overcoming many

1 https://www.zooniverse.org/projects [Accessed 22/05/2024].

10.3389/fcosc.2024.1412510

challenges of studying seals at this time. During the height of pup births, disturbance to the seals could interfere with breeding behaviors and cause young pup mortality through stampedes and it can be difficult to access the site because of aggressive guarding by breeding bull seals (McIntosh et al., 2018). However, drone surveys generate large amounts of imagery data, which presents numerous challenges including accessing sufficient digital storage space and developing efficient data processing workflows. Additionally, when counting thousands of colonially grouped seals, the time commitment required for experts to process the images may be unsustainable, leading to the development of citizen science and artificial intelligence to improve efficiency (McIntosh et al., 2018; Gonzalez et al., 2016; Dujon et al., 2021; Christin et al., 2019). The Australian fur seal (*Arctocephalus pusillus doriferus*) has seen large fluxes in population and recent declines of over 20% in pup numbers have been reported (McIntosh et al., 2018). Similar to seal populations around the globe, Australian fur seals are under threat from marine-based industry activities (Cummings et al., 2019), climate impacts (McLean et al., 2018), and marine pollution (McIntosh et al., 2015; Taylor et al., 2021). Australian fur seals typically breed on rocky offshore islands, where the numbers of individual animals may fluctuate based on foraging needs and prey availability, or time of year (e.g., breeding season).

Typically, to estimate population size, estimates of pup production are used because they are the only age class all available at one time and one pup represents one breeding female (Berkson and DeMaster, 1985). The methods of estimating pup production are via direct ground counts, capture mark resight (CMR) and aerial surveys by small, piloted aircraft; recently, drones have also been used (McIntosh et al. 2018);. In 2017, on-ground survey methods were compared with counts performed from drone images (Sorrell et al., 2019). This study demonstrated that drone image counts were lower than a CMR because the CMR method is more accurate, being able to estimate all seal pups present at the time of the survey including those under the water or rocks. In comparison, ground counts were less accurate than the drone surveys because they only included pups that were able to be seen at the time of the survey. The drone image counts were higher than ground counts, but lower than CMR because, similar to ground counts, only the pups that could be seen in the images could be counted. Importantly, repeated image counts taken by the drone, performed by different users, resulted in similar estimates of abundance, showing that the method provides precise and reliable results (Sorrell et al., 2019). Precision and accuracy are often used interchangeably, but their distinction is important. An accurate estimate is one that is close to the true population number, yet the true size of open wildlife populations is rarely known (Sutherland et al., 2004). By contrast, precision is a measure of the consistency of replicated estimates irrespective of true population size (Sutherland et al., 2004). Regular, precise counts assist the detection of small-scale population fluctuations and improve confidence in the resulting trends. For population monitoring, a focus on techniques that prioritize precision over accuracy is therefore accepted practice (Sorrell et al., 2019; Sutherland et al., 2004; Hodgson et al., 2016; Wood et al., 2021).

Given the logistic benefits of using drones, the reliable scientific results, and the benefits towards ocean literacy and education, we decided to utilize drone surveys and citizen science for monitoring the fur seals. In 2018, we tested the portal (Sorrell et al., 2019), launching the global online citizen science program called 'SealSpotter'[2] in 2019. Our next goal was to determine whether long-term trends could be measured and how participants engaged with the program in order to remain flexible and sustain engagement. Additionally, to be an authentic citizen science program, SealSpotter needed to succeed independent of expert or researcher counts. This would have the added benefit of providing efficiencies for the scientists so they could focus on analyses and communication of results.

The current SealSpotter project has five main goals: 1) to count abundances of four categories of fur seals: adults-juveniles, live pups, dead pups and individuals entangled in marine plastic debris; 2) to provide annual pup abundance indices to better understand the declines observed for Australian fur seals and capture any change in trends over time; 3) provide an online citizen science collaboration for community benefit and education opportunities; 4) provide labelled images for the development of machine learning and automation processes; and 5) retain a digital library of image surveys that can be revisited for future research projects. Here we provide results that highlight the success of the SealSpotter program in addressing these aims. We report on five years of the program since 2018 and reflect on the success of SealSpotter as a whole, discussing our lessons learned and recommendations for other similar citizen science programs.

2 Methods

2.1 Image collection and processing

Fur seals were counted from photographs taken from an RPA, flown over the area potentially occupied by pups (McIntosh et al., 2018; Sorrell et al., 2019). Image acquisition took place over the breeding season that occurs during the Austral-summer from late October when the first pups were born to early January when the breeding season was finished; with most pups born by mid-December. In this study, survey results were compared by date of survey and may therefore span across years (e.g. December 2017-January 2018).

We used a quadcopter-type RPA equipped with a downward facing camera to count the number of pups, juveniles, and adults in the breeding areas of fur seals at two breeding sites (Figure 1): Seal Rocks (38°30'S, 145°10'E) and The Skerries (37°45'S, 149°31'E). These sites were selected as long-term monitoring sites for the SealSpotter program being two of the largest breeding sites for the species, spanning different oceanographic areas of north-central Bass Strait and the East Australian Current respectively, and being

2 https://www.penguins.org.au/conservation/research/seal-research/ [Accessed March 12, 2024].

10.3389/fcosc.2024.1412510

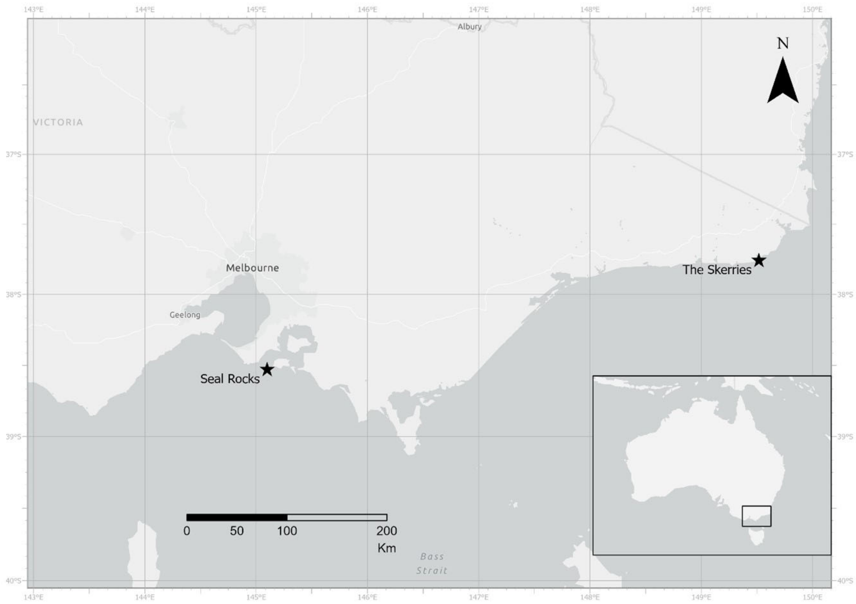

FIGURE 1
Map of the two Australian fur seal (*Arctocephalus pusillus doriferus*) breeding sites monitored using aerial imaging taken from drones.

amenable to the method (McIntosh et al., 2018; Sorrell et al., 2019). The Skerries is a very remote location and is visited once per breeding season (between mid-December and early January), whereas Seal Rocks is 1.8 km from Phillip Island and is surveyed approximately every 7 - 10 days during the breeding season (late October to early January) resulting in more data for the Seal Rocks site.

The RPA was flown over the sites at altitudes tested to avoid disturbance while providing sufficient image resolution for pup identification (30-70 m above the seals depending on the topography of the site and the drone size: DJI Phantom 4-Pro (<2kg system) or DJI Matrice 210 equipped with a Zenmuse X7 35mm camera (<7kg system). Surveys were flown by licensed pilots under Ethics and Research permits and the Nature Parks' Remote Pilot Operators Certificate (ReOC) from the Australian Civil Aviation Safety Authority (CASA).

To increase the distance range for the method when flying visual line of sight, ratifying the CASA regulations for drones in Australia, we adapted the DJI Phantom 4-Pro survey settings (McIntosh et al., 2018; Sorrell et al., 2019) for a DJI Matrice 210 with a Zenmuse X7 camera and 35mm lens for high resolution image quality. The camera faced directly down and the focus was set to infinity for all surveys. For variable light conditions (eg patchy cloud), automatic camera settings were used for adjustment of ISO, white balance, shutter speed, and aperture; where light conditions were more stable (eg even cloud cover or clear sky) manual settings were used to ensure consistent exposure throughout each survey. Side-lap and front-lap were set nominally at 70% to enhance stitching of images, allowing for the complexity of the topography at both sites. A 2-s delay was set between image captures, resulting in air speed during capture of ~7 m/s depending on altitude.

Flights maximized battery time and survey coverage, but also varied slightly depending on the site profile and system in use (lower flight altitudes for smaller Phantom 4-Pro and higher for larger Matrice 210). For Seal Rocks, there are 10 m high plateau areas that have fur seals and seabirds on them, and so the drone is flown at 40-70 m above sea level to avoid collisions and minimize disturbance. At The Skerries, the site is lower, allowing flights of 30-60 m above sea level without observed disturbance to the seals and seabirds breeding and roosting on the sites.

The images were processed using Agisoft Metashape Professional (Version 1.8.4) and a photomosaic image model of the survey area created. The photomosaic was then exported as smaller tiles (1200 x 1000 pixels typically) and loaded into the SealSpotter portal for counting without image overlap. Tile size was selected to maximize zoom and image resolution for ease of counting within the SealSpotter portal.

2.2 Citizen science

The first use of SealSpotter was by Sorrell et al. (2019) who recruited 644 participants in February 2018, mostly within Australia, and opened the portal for one month to count the seals. The online community of the Penguin Foundation[3], an initial financial sponsor of the program, helped trial the prototype in May 2018, providing critical feedback to improve the portal that was officially launched 8-23 June, 2019 (more detail in section 2.4).

Citizen scientists counted the fur seals online for 18 separate surveys and outputs were shared via online newsletters twice per year. The citizen scientists were able to email the expert researchers for discussion and to suggest improvements to the portal, as well as present ideas for research topics, making this a true collaboration.

3 https://penguinfoundation.org.au [Accessed 29 March 2024].

Community engagement targets were to capture sufficient participation for reliable results, provide learning opportunities particularly for youth, and achieve global participation.

SealSpotter was promoted without specific budget, through tourism marketing campaigns, social media, radio and print media and through supportive scientific agencies and schools. Participants accessed the SealSpotter website[4] online, were asked to register (more detail in section 2.5) and invited to watch a short tutorial video explaining a brief overview of fur seal biology, the purpose of the research and a demonstration of the task they were being asked to complete. They then clicked an acceptance box to agree that the data they provided would be used for research purposes, that their name and contact information if provided would not be shared with third parties and that if they were under 15 years old they needed adult supervision to participate. Once in the main portal, participants would see an image of fur seals on land and would begin counting using the four designated categories, namely Adults and juveniles, Live pups, Dead pups, and Entangled fur seals (Figure 2). Pups were recognized by their lanugo coat (soft dark brown or black birth pelage) and small size; juveniles were recognized as having the same foraging coat as adults but being typically smaller and non-reproductive; these were in the same category as adults because it can be difficult to discern juvenile males from adult females (Figure 2). Originally, we did not separate live and dead pups because the total number of pups represents an equal number of breeding females since they do not have twins; also, we did not want to burden participants with too many categories. However, the citizen scientists requested this change, and we enacted that change. Participants preferred to count live and dead pups separately because some found it emotionally disturbing to pool them; for other participants the preference was driven by gaining more information, specifically to compare the live and dead pup counts over time and identify potential occurrences of disease or unusual mortality events. The two categories were added during processing to provide the total number of pups, a priority metric. Entangled fur seals were those caught in marine plastic debris; typically netting, rope or fishing line.

After registration on the SealSpotter portal, each new participant received the same 10 training images which demonstrated the variety of categories and images expected to be counted. These images were not provided in subsequent counting sessions. This also allowed us to recognize whether a computer bot or malware algorithm was attempting to affect the system because nonsense counts could be detected during the analyses workflow and deleted. Once the participants completed the first 10 training images, they progressively received randomly assigned images until they exited the SealSpotter portal or completed the full set. Within the four categories, participants would select the seals they could see and the corresponding colored shape would be placed on the seal (Figure 2). Each unique identification of a seal was assigned an x and y coordinate and a unique time-stamp, providing labelled images for future machine learning development and allowing the data to be mapped (McIntosh et al., 2018; Sorrell et al., 2019).

The lead scientists were able to set the preferred number of replicate image counts for the project, this was set at 10 to maximize participant counts of each image and ensure all images were counted, while balancing the participation of inexperienced and young participants with more skilled participants. This way we balanced inclusion with scientific priorities. Once an image was counted at least 10 times, it was placed at the end of the image library to allow images with fewer counts to be prioritized. If a survey was completed, an uncounted survey was uploaded to maintain participation. Outlier counts of images, classified as greater than 1.5× the standard deviation from the median count (Sorrell et al., 2019), were considered likely unreliable and removed. Remaining counts from each image (3-7 counts per image) were averaged to provide the final count per image, then all images summed to determine the total result per survey and site.

To minimize double counting of seals that partially appear in two images (i.e., on the edges), participants were asked to count the seal when over half of the body was in the image. We considered the common cell biology approach used to avoid double counts of cells when counting through a microscope. In this approach, a hemocytometer overlays the field of view with a lined grid and cell counts are taken separately for each box of the grid (similar to the tiled mosaic of SealSpotter images). To avoid double counting cells that sit on the shared edges of the box, only the cells that touch the upper and left edge of each box are counted. Over the whole grid, all cells are counted without overlap (Chen and Chiang, 2024). However, our goals were to keep the instructions simple as well as limit double counting, which was expected to be minimal particularly given few participants were expected to complete full sets of randomly assigned images, therefore we simply requested participants to count seals if over half the body was in the image.

Cheat sheets were accessible through the portal to help participants perform the tasks and identify the different seal categories accurately. In these images there was a slide bar that moved across the image revealing and hiding labels for seals as determined by an expert (author Rebecca McIntosh - RM). In the main screen, a shading bar was available to lighten or darken images to suit viewer's preferences for each image and a comment box was provided before the image was submitted to allow people to comment on the image or ask a question. Any questions submitted were answered within two weeks by the lead scientists (RM and Ross Holmberg - RH).

2.3 Expert validation

Expert counts were needed to compare the performance of citizen science counts, and an expert was expected to have an established skill level of high standard. To ensure the expert counts were 'gold standard', the counting precision and accuracy of expected expert, RM, was tested. RM participated in all SealSpotter Challenges counting 30,641 image tiles alongside the citizen scientists from 13 complete survey image sets; these counts were identified as 'regular image counts'. The variability of

4 https://www.penguins.org.au/conservation/research/seal-research/ [Accessed 12 March 2024].

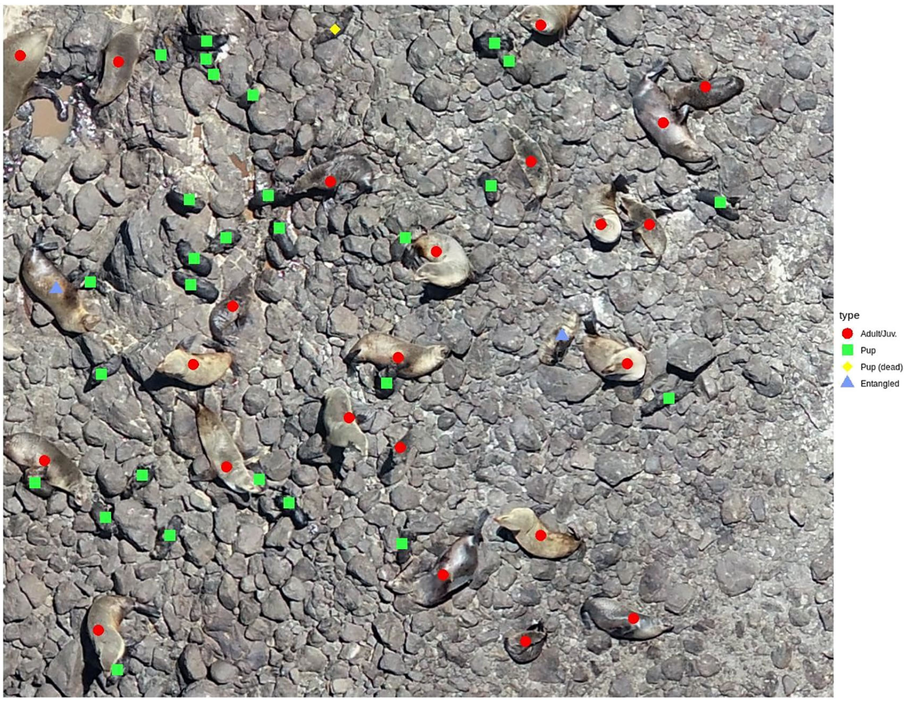

FIGURE 2
Labelled tiled image from SealSpotter showing the four categories of Australian fur seals counted at Seal Rocks, Victoria by Citizen Scientists around the globe. Color and shapes are used to label the categories of fur seals to include participants with color vison deficiency.

the 'expert's' image counts was determined from a subset of 105 image tiles, randomly selected from the pool of images that had been counted via the regular method and provided to RM for a second count; identified as 'randomized image counts'. The randomly selected images were independently assessed by RH for variability in complexity and fur seal density to ensure a representative comparison with typical SealSpotter image tiles. Re-counting a large sub-sample of randomly selected images was considered a better method than counting fewer images more times because it reduced the effect of image recognition, where unique images may be remembered by the counter, which could improve repeat counts.

A linear model was used to plot the randomized image counts against the regular image counts and the prediction intervals were calculated at the 95% confidence level (not the 95% confidence interval of the expected value because it would be too narrow) based on the count comparison to reflect the random effect of the data. Since the line of perfect match (slope = 1 and intercept = 0) sits in the middle of the interval, the expert status was justified if the counting was consistent at each comparison subject to a residual standard error of less than five pups per image.

Finally, counts performed by an expert (RM) were regressed against the average final citizen scientist count (excluding the expert count) for the total pup category (live pups + dead pups) per survey date and site. We then performed a one-way, unpaired t-test of the means of both counts. All statistics were performed using the 'R' programming language (version 4.2.3) (R Core Team, 2018). Supplementary Materials are identified by an 'S' in front of the figure number.

2.4 The SealSpotter Challenge

To improve engagement in the SealSpotter portal (which can be accessed at any time), and ensure prioritized breeding season surveys were successfully counted, the Annual SealSpotter Challenge was developed. This maximized success by satisfying different preferences of participants via two available experiences – one short term and the other continuous. A SealSpotter Challenge lasts two to three weeks, and typically involves counting seals from three to four surveys taken during the breeding season: one from The Skerries and up to three from Seal Rocks.

We tested the best approach in May 2018 when working with the Penguin Foundation and found that most participants preferred an end date for participation; they didn't like an indefinite end date because it caused a feeling of burden for participation. In contrast, a short time-window provided a feeling of achievable participation with the positive benefits of contributing to conservation, and the forward focus of having an event to look forward to in the following year. This method was also loosely based upon the Aussie Bird Count by Birdlife Australia[5]. But the preference for the challenge was primarily driven by the citizen scientists themselves. Citizen science projects in Zooniverse have also identified that a scarcity of data and the release of data subsets has been associated with sustained volunteer engagement (Spiers et al., 2019). Such an approach is suited to SealSpotter because the scientific purpose is to monitor annual breeding events. For the participants who

5 https://aussiebirdcount.org.au/ [accessed 4 April 2024].

engaged regularly, the portal is open all year and additional surveys are uploaded by the scientists when notified by participants that they have finished an image set. Annual Seal Spotter Challenges occurred in June 2019, April 2020, May 2021 and June 2022, and an additional Challenge was promoted specifically for Melbourne, Australia, in response to the Covid-19 lockdown in Aug 2020.

2.5 Participant summary

When registering to participate, people could volunteer broad personal information including age class (<25, 25-50, >50), location (country, state or city), their wildlife monitoring experience (none, some, lots) and an email address if they wanted to receive annual newsletters reporting the results and project progress. Broad age categories were used to protect young people online and followed best practice guidelines for cyber security based upon social media requirements. This included an agreement for Phillip Island Nature Parks to use the data provided in the portal for scientific purposes, not share personal information with a third party and an agreement to maintain user anonymity unless permission was provided otherwise, in which case the person would be contacted directly to ask for permission.

People may register out of curiosity but not actively participate in the counting (Strasser et al., 2023), therefore registration and active participation at a given time were reported from December 2017 to May 2023. The different registered age classes, self-designated skill level, and country or continent were also collated. De-identified participant image counts and active number of participants were determined per month to explore patterns in participation, and the cumulative unique image count determined. The number of image counts were grouped in bins by year to examine annual effort by participants and a Lorenz curve calculated of cumulative images counted and cumulative unique participants to gauge proportional effort (Strasser et al., 2023). A stratified plot of the number of users that contributed at least one image count was created to visualize the effort over time and multi-year participants.

Counting ability or accuracy, compared to the expert (RM), was tested for the adult and juvenile age-class, total pup counts (live + dead), dead pup count and entanglement count. Because of the difficulties in identifying marine debris entanglements and distinguishing live from dead pups, we expected the dead pup and entanglement counts to be low per image and less reliable as raw data, requiring further quality checks and analyses separate to this research. Using the expert image counts as the reference or "true" count and removing zero counts, a single data point for a reference count (slope = 1 and intercept = 0) was derived from all images with the same reference seal count. Using adult-juvenile data as an example, an initial list was created of all images counted by the expert and the number of adult-juvenile seals in each of them. Then, all images that were inside the list and counted by participants were selected. Lastly, we grouped the images by the reference count; for example, if three images had expert counts of 27 adult-juvenile seals in them, the corresponding participant counts from those three images were used to identify the mean and standard deviation values for the participants as comparisons and a smooth line was plotted through the means using the default "geom_smooth()" function that uses a local polynomial regression with a degree of 2 ($y = ax + bx^2 + c$) to fit the data.

The effect of individual participant experience, measured by effort over time and age group, was then explored using box plots of their R-squared values. These values were derived by treating the expert seal count in all images as the dependent variable, and participant counts as predictions or a set of random observations (the "model"). In this method we evaluated how well a participant (or "model") can predict observations using the R-squared value. If a participant makes a perfect prediction, i.e. all counts matched the expert counts, the value is 1. If a user makes random guesses based on the count distribution, the value is 0. If a user makes a random guess based on some arbitrary distributions, the value is negative. We expected that more experience and higher age classes would result in counts more similar to the expert reference.

The SealSpotter Challenge participant that counted the most images was offered an "Adopt a Seal" package from the Penguin Foundation[6] as a prize for their effort. In 2018 the lead participant declined physical prizes such as merchandise or soft-toys due to sustainability practices and a lack of interest in consumerism, leading to the symbolic and educational opportunity to adopt a seal.

At the end of each challenge, we provided newsletters to all participants, detailing the results of each challenge in context with previous years, information on the participation and any open-source publications resulting from the project at that time. Participants that counted over 1,000 images each year were highlighted in the newsletter for their achievements if they agreed to be acknowledged.

Finally, emailed feedback from SealSpotter participants was encouraged via the newsletters to capture motivations and experiences of taking part in SealSpotter. Such information was used to help improve the experience and the portal. We collated common terms and words sent in emails received from participants. Using the R programming language with the packages "tm", "wordcloud" and "worldcloud 2" to remove numbers, punctuation, irrelevant and filler terms. We then counted the frequency of terms and visualized frequent words (appearing more than twice in responses) as a word cloud.

3 Results

3.1 Participant summary

We saw global participation in the annual SealSpotter Challenge, with participants from 15 to 93 countries from every continent. Only Australia was targeted in 2018, then participants from 25, 37, 93 and finally 15 countries were engaged between 2019 and 2021. Over 10 school, university and youth programs were engaged to participate in SealSpotter Challenges or used data from SealSpotter to teach ecology, mathematics or geography.

6 https://penguinfoundation.org.au/donate/adopt/australian-fur-seal [accessed 28 May 2024].

A total of 3,879 people registered from 2018 – 2022, which included 2,833 individual active participants counting a total of 381,827 images including replicates and 55,614 unique images (Supplementary Figure S1). For each SealSpotter Challenge, participants counted an average total of 13,479 images and 171,137 seals per annual event. Of the registrations that disclosed their experience level, for all years (2018 – 2022), the majority were new to SealSpotter and/or new to counting animals from drone images, having had no previous experience. We observed a spike in registration during 2020, likely caused by multiple SealSpotter Challenges during Covid-19 lockdowns. Registrations assigned 855 people to the under 25 age class, 841 people to 25-50 years and finally 455 people to over 50 years (Figure 3).

Assessing individual participant effort, 232 participants counted seals in sequential years and 139 participants rejoined after taking a break for a year or more. Most participants (1,262) counted under 10 images, which indicates that their effort did not provide an authentic contribution to the research and 84% contributed to ~25% of the image counts (Supplementary Figure S2). There was a total of 78 participants who counted more than 1,000 images and four who counted 10,000 images (Supplementary Figure S2). SealSpotter demonstrated a good return rate with 263, 76, 22 and 7 unique participants counting seals in two, three, four, and five years respectively (Figure 4).

Feedback regarding the SealSpotter portal was collated from 16 participants, or ~5% of participants in a single year and revealed frequently recorded words that could be contributed to seal biology, health, and environments (e.g., 'adults', 'seabirds', 'sickness', 'dead', 'populations'); positive feedback (e.g., 'fascinating', 'awesome'); the challenge itself (e.g. 'challenge', 'images'); as well as difficulties experienced using the SealSpotter portal (e.g., 'hard', 'missed') (Figure 5). Participants included self-care, recreation, and relaxation as part of the benefits obtained from taking part in the SealSpotter program. The SealSpotter program was also recognized as a positive experience for people that are less mobile or prefer to work on a conservation project from the comfort of their own home.

3.2 Validation of citizen and expert counts

The nominated expert (RM) counted 30,641 images and was proven an expert because the randomized image counts (n=105) closely matched the regular image counts (Figure 6). The line of perfect match (slope = 1 and intercept = 0) and position of the points close to the line and within the 95% confidence levels justified that the nominated expert counting was consistent at different times subject to a small random error (residual standard error = 2.35 seals per image). Note that the area within the two dashed lines represents the prediction interval at 95% confidence level that reflects the random effect of the data, not the 95% confidence interval that reflects the uncertainty of the average value, which would have been too narrow. Despite appearing constant, the interval grows slightly wider when seal counts are larger, which is consistent with the data – there are less data points of large counts, and they are less concentrated around the fitted line.

To date, there has been no mass mortality of pups detected at Seal Rocks or The Skerries. For images that contained dead pups, the expert would count a maximum of 15 dead pups. Participants tended to overcount dead pups in images with one expert count (mean 2.3 ± 8.5, n=1,485 participants) and undercount when more pups were present; for example when the expert counted 15 dead pups, 23 participants counted 6.8 ± 4.2 dead pups (Supplementary Figure S3). Using the expert counts as the reference or "true" count, participant classification of dead pups was inconsistent. This supported the decision to combine these categories for a total pup count when comparing abundance and trends.

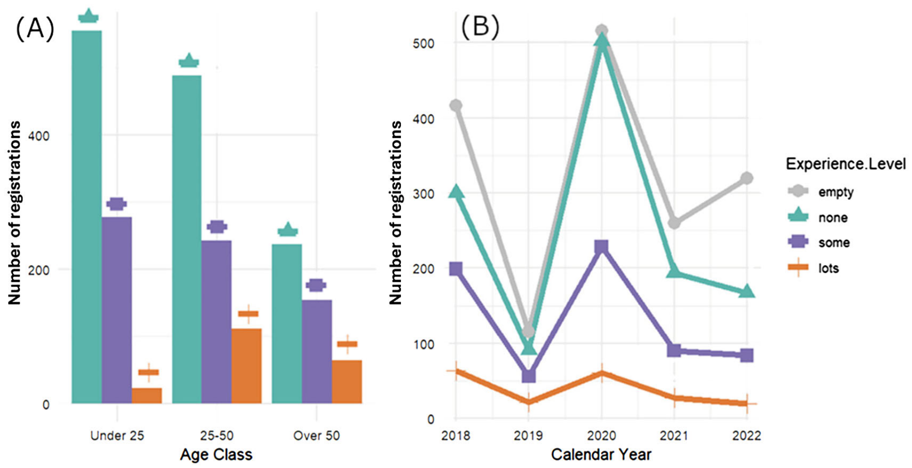

FIGURE 3
The number of SealSpotter registrations by age group and self-identified level of experience **(A)**, and over time **(B)**. The categories of experience level were: empty or did not disclose (grey + circle), none or no experience (green + triangle), some experience (purple + square), and lots of experience (orange + no symbol). We observed spikes in registrations at the program's initial inception in 2018 and again during the COVID-19 pandemic lockdown in 2020. Registrations under 50 with no experience were the dominant users of the SealSpotter portal, whereas experienced users show less fluctuation in registration over time.

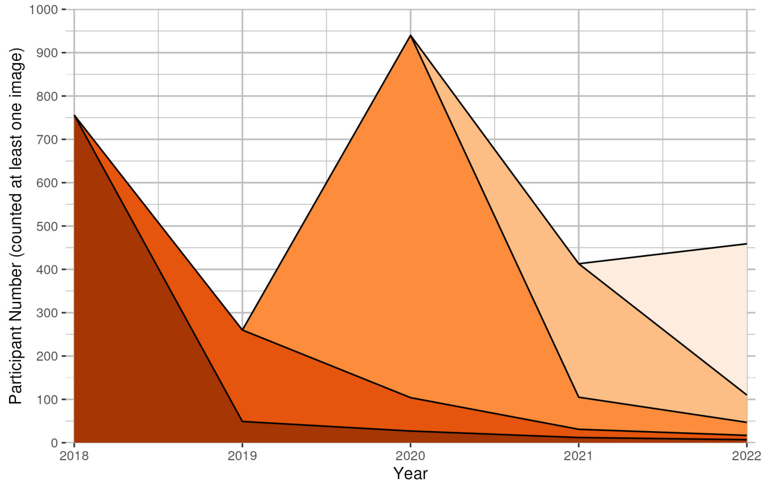

FIGURE 4
Stratified plot of participant retention from 2018-2022 where included participants counted at least one image in the SealSpotter portal.

A maximum of four entangled seals were counted by the expert in a single image, but participants overestimated entangled seals when none were present and underestimated them when they were present (Supplementary Figure S3). Therefore, an expert counter or other method would be required for reliable outputs for this category.

Participant counts of images for the adult-juvenile category were more similar to expert counts than the total pup image counts; however, as the count number increased, so did the variability in the participant counts for both categories (Figure 7). Age-class of participants and the degree of experience (as measured by time engaged rather than self-identified skill level) influenced the similarity between participant and expert counts with older age classes and more years of experience resulting in higher similarity of counts (Figure 8).

3.3 Seal population trends

Generally, participants and expert counts were highly correlated (95% significance level, y = 664 + 1.02 x, R^2_{adj} = 0.86, $F_{1,12}$ = 78.1, P < 0.001, n = 14, Supplementary Figure S4). Results of a Welch Two Sample T-test suggests the expert (RM) consistently counted higher numbers of pups when compared to SealSpotter participants (t = -2.117, df = 24.92, P = 0.044) (Table 1; Supplementary Figure S5). The difference between the citizen science count and the expert count averaged 763 pups ± 230 SD.

Citizen and expert counts documented similar trends in fur seal pup abundance at both sites, Seal Rocks and The Skerries (Figure 9). Lower pup numbers at Seal Rocks was observed by both citizen scientist and expert counts on 30/11/2018. This survey was restricted to Seal Rock (i.e., excluding Black Rock and East Reef),

FIGURE 5
Frequent (appearing two or more times) words or terms that arose from 16 feedback emails shared with scientists. From a total of 207 unique words, the term "Seal" was the most popular word, arising 11 different times. Words in pink arose five times each, purple were mentioned three times each and orange words arose three times each.

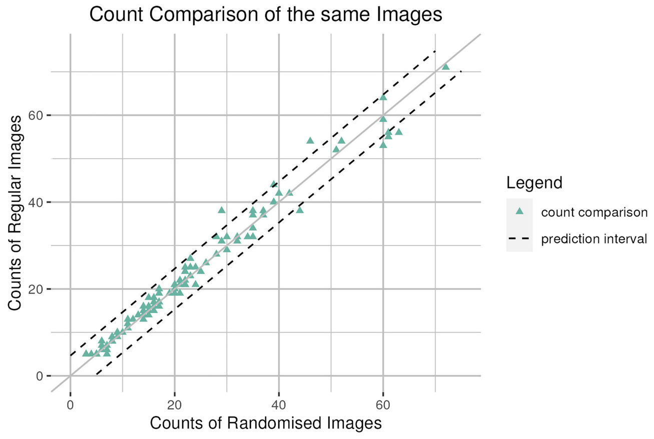

FIGURE 6
Count comparison of the same images (n=105) to determine expert status of an experienced seal researcher. The solid line provides the perfect match, the triangles the counts and the area within the two dashed lines the prediction interval at 95% confidence level based on the count comparison.

due to changed flight conditions (Table 1). Overall, outputs from a regression-based linear model suggest that the populations of Australian fur seal remain stable at both sites (Expert counts: Seal Rocks at 95% significance level, $y = 1.01\ x10 +^{4} - 0.378\ x$, $R^2_{adj} < 0.01$, $F_{1,7} = 0.777$, $P = 0.407$, n = 9; The Skerries, $y = 1.35\ x10 +^{3} + 0.177\ x$, R^2_{adj} 0.42, $F_{1,2} = 3.13$, $P = 0.219$, n = 4. Citizen Counts: Seal Rocks, $y = 4.88\ x10 +^{3} - 0.124\ x$, $R^2_{adj} < 0.01$, $F_{1,11} = 0.165$, $P = 0.692$, n = 13; The Skerries, $y = 378 + 0.0538\ x$, $R^2_{adj} < 0.01$, $F_{1,3} = 0.0594$, $P = 0.823$, n = 5).

4 Discussion

4.1 Seal Spotter as a tool for monitoring seal populations

In this study we encouraged citizen scientists to generate data on Australian fur seal abundances, greatly reducing the time required by a few research scientists to count images. Although citizen science counts were consistently lower than expert counts across all years and sites and for all categories (adults-juveniles, total pups, dead pups and entangled seals) (Figure 7; Supplementary Figure S3), the citizen scientist counts of total pups provided a reliable index of population, detecting similar trends as expert counts. Adult and juvenile counts will also provide valuable insights for population trends, but were not as reliable as pup counts because they are not all ashore at one time, unlike young pups that have not yet learned to swim.

Typically, population monitoring relies on precision rather than accuracy, as evidenced by a number of similar citizen science projects, because it is more important to have a reliable index over time than to count every individual, which can be impractical especially for high densities of colonial animals (Hodgson et al., 2016; Sorrell et al., 2019; Wood et al., 2021). Thus, when using these counts in the monitoring of Australian fur seal populations, it is important to understand that SealSpotter pup abundance counts will provide a conservative index of pup abundance compared to what is actually present at the site, but that this index is a reliable measure of change over time.

The disparity between expert and non-expert counts aligns with other research that utilizes citizen scientist counts of pinnipeds (Wood et al., 2021). Therefore, similar to other successful citizen science programs, SealSpotter can be used to detect general population trends such as stable, increasing or decreasing abundances. Other useful applications of SealSpotter will be to assess trends in entangled individuals and monitor adults and juveniles. The dead pup count would also allow for the detection

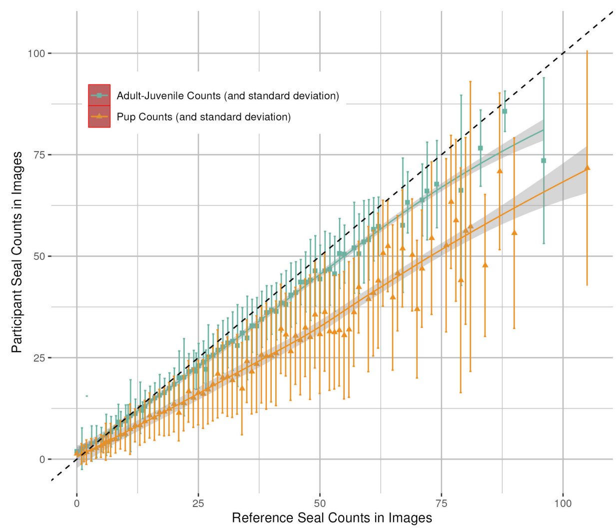

FIGURE 7
The similarity of unique image counts of fur seals by participants and the reference, as counted by the expert (black dashed line), for the adult-juvenile and total pup (live + dead) categories in SealSpotter. The data points are the mean participant count and the error bars represent the standard deviation of the multiple participant image counts.

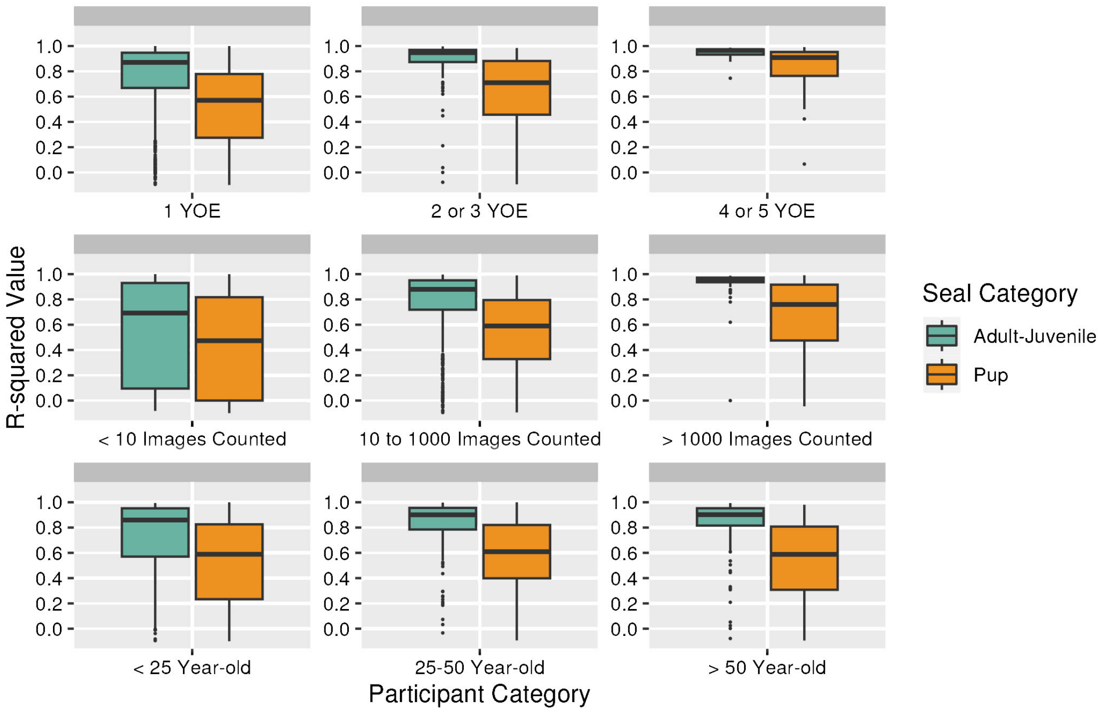

FIGURE 8
The influence of years of experience (YOE), number of images counted and self-designated age category on the similarity between participant (User) counts and the expert count of unique images in SealSpotter.

of mass mortality events that could be caused by disease or heat waves. Such information is valuable for rapid responses to population changes and improved conservation outcomes. While it would be ideal to improve the similarity between expert and participant counts, it is important to highlight that lower numbers of seals have greater similarity. Therefore, trends will become more reliable under conditions of population decline when action becomes more critical.

From every 10 image counts, 3-7 replicates were useable. When considering authentic engagement in science and contribution, this outcome is the balance of the tension between reliable results and open inclusion. Including younger age classes allows for school programs, teaching opportunities of ecology, statistics and ocean literacy and communication opportunities for species-on-the-move and climate change discussions (Nursey-Bray et al., 2018; Pecl et al., 2023). SealSpotter is predominantly accessed by non-experts, allowing opportunity for engagement, skill development and education. One way we can improve this balance is by finding a different method of training rather than the 10 training images. This is especially important given the large number of participants that count fewer than 10 images after registering.

The difference between expert and citizen scientist pup counts can be explained by experience and level of difficulty. The pups are camouflaged on the rocks in their lanugo coat. The expert has over 20 years of experience counting fur seals and sea lions and has a heightened ability to observe the pups in the images. More experienced and older participants of SealSpotter provided image counts more similar to the expert than less experienced and younger participants. This highlights the value of encouraging loyalty to the SealSpotter program to increase capability and improve data. However, this will not be prioritized over inclusivity and democratization because a balance must be met with participants providing an authentic contribution to science. This gap between participant and expert counts will also improve as new sensors become available and image resolution increases providing clearer images for counting.

A decline in total pup abundance has been detected using 5-year population censuses via capture-mark-resight for the Australian fur seal population after the peak was reached in 2007 (McIntosh et al., 2022). Pup abundance at Seal Rocks declined by -28% between 2007 and 2013 and a further -6% to the 2017 census; at The Skerries the percent change between censuses was -19% between 2007 and 2013 and -28% between 2013 and 2017 censuses (McIntosh et al., 2022). However, these declining trends are based on one data point every 5-years, which reduces the reliability and resolution of the result. The annual drone surveys presented here begin with the 2017 breeding season and suggest that the decline may have stabilized at both Seal Rocks and The Skerries (Figure 9). Seal Rocks is the largest breeding site of Australian fur seal and displays high variability in pup abundance between breeding seasons compared to The Skerries, the fourth largest breeding site for the species that provides more stable pup estimates. The Skerries is situated next to the remote Croajingalong National Park in the southern East Australian current, a global hotspot for ocean warming (Ramírez et al., 2017), while Seal Rocks is in north-central Bass Strait further from productive foraging areas and close to popular tourist locations and the urban city of Melbourne potentially exposing it to higher levels of pollutants and disturbance (McIntosh et al.,

TABLE 1 Mean pup counts from drone surveys performed by citizen scientists and an expert seal scientist using the SealSpotter portal at two Australian fur seal breeding sites; Seal Rocks and The Skerries.

Survey date	SealSpotter count	Expert count
Seal Rocks		
07/12/2017	3143	3694
15/12/2017	3259	3905
26/12/2017	2584	3091
28/12/2017	3223	3837
30/11/2018	1781	2506
27/12/2018	1865	3005
13/12/2019	3070	3791
27/12/2019	1906	3099
30/11/2020	2356	3130
14/12/2020	2545	NA
28/12/2020	2693	NA
14/12/2021	3448	NA
11/01/2022	2220	NA
The Skerries		
16/01/2018	1401	1815
24/01/2019	1484	1690
19/12/2019	1082	1920
8/01/2021	1205	NA
21/12/2021	1631	2010

The overall average count and standard deviation (SD) is provided for comparison (Average ± SD), 2272 ± 763.2 (citizen counts) 2884 ± 816.4 (expert counts).

2022). Therefore, annual surveys are vital for continued monitoring of the trends at these sites to understand the species' response to climate change and other anthropogenic pressures (McIntosh et al., 2022; Wall et al., 2023). As high order marine predators, Australian fur seals are sentinel species for change in the marine environment. Obtaining reliable indices of the population allows informed predictions and management decisions to be made.

4.2 Seal Spotter as a tool to increase ocean literacy

The global participation in the SealSpotter program, of 3,879 registrations and 2,558 active participants, demonstrated the large-scale uptake of the program and therefore its outreach success. Principally, ocean literacy initiatives should encourage engagement with the marine environment in ways that shape people's understanding of and appreciation for the ocean (Worm et al., 2021). Of all SealSpotter participants engaged in the last five years, 855 were under the age of 25 (Figure 3), largely through local schools and university programs that were interested in and education Science, Technology, Engineering and Mathematics (STEM) programs. Successful engagement of youth in ocean literacy programs has the capacity to increase engagement of the broader community and empower the next generation of ocean leaders through shared learning and conversations in the community (Kelly et al., 2022a).

A focal point of the United Nations Ocean Decade is to increase ocean literacy and ocean equity, by ensuring less prominent groups are included in ocean-focused decision making and ocean sciences (Shellock et al., 2022). It is important to recognize when discussing the benefits of citizen science that geography and language are major factors for

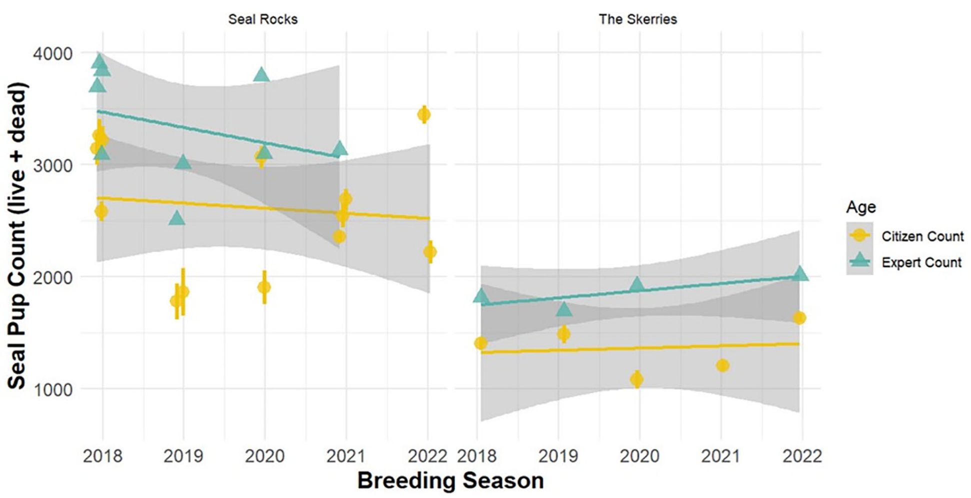

FIGURE 9
Australian fur seal counts (for live + dead pups) over the last 5 years (2018 - 2022) at Seal Rocks and The Skerries with the linear trend and 95% confidence intervals shown by the grey shaded area. Both expert (green + triangle) and citizen counts (yellow + circle) show similar population trends for Seal Rocks and The Skerries. The expert count is almost always higher suggesting seal spotter participants provide a conservative estimate of true pup numbers. Surveys graphed by date with year provided on the x-axis, therefore 2019 refers to the surveys flown for the December 2018 to January2019 breeding season. For tabulated results see Table 1.

participation in a wide variety of citizen science projects. In a study of over 14 million online citizen science participants, most were from English speaking OECD countries, The Organization for Economic Cooperation and Development (Strasser et al., 2023). Importantly, access for First Nations peoples may not be prioritized. SealSpotter did reach every continent of the globe, but the English language used for training and presentation of the portal likely targets participants with skills in English language, as demonstrated by the English language email communications examined in the word-cloud results (Figure 5). While conveying both biological learnings and positive recreational benefits of SealSpotter participation, the word-cloud analysis was designed *post-hoc* and unfortunately not all email correspondence had been saved resulting in the small sample size. Also, most email correspondence was provided by highly engaged participants and may not be representative of all participants.

In 2018 the SealSpotter program partnered with two national educational programs focused on increasing STEM opportunities and engagements for women and girls. Of particular success was the capacity to partner with STEM Sisters[7] and the CSIRO Indigenous STEM Education Project[8] with 10 and over 20 online participants respectively. In both instances, the organizations partnered with the SealSpotter program to deliver a short course exploring the scientific method through SealSpotter, including a guest lecture from the SealSpotter program leader (RM). Additionally, numerous universities and schools have used subsets of SealSpotter data to build learning programs. These teaching and training partnerships are an excellent way to apply real data from an ongoing conservation research program that can develop participants' learnings of statistics, conservation, wildlife monitoring and technology. Nature-based opportunities compared to computing, medical or astronomy opportunities, can show higher participation of young people and be less gender biased towards males particularly if designed to include school students (Spiers et al., 2019; Strasser et al., 2023), providing useful demographic information for developing such projects. Nature-based platforms such as SealSpotter may be able to engage pre-existing communities such as bird watchers and wildlife enthusiasts that have been organized for more than a century (Strasser et al., 2023). Understanding that programs such as SealSpotter may be a digitization of existing participation could assist marketing approaches, but certainly democratizes participation for people with diverse abilities and/or limited access to places of interest or like-minded communities.

It is important to also consider what narrative will be communicated with or learned by participants of citizen science projects. The "species-on-the-move" framing (Pecl et al., 2023) encourages citizen scientists to document changes in species distributions caused by ocean warming. Here, species-on-the-move are framed as adapting or shifting due to environmental pressures, thus not always perceived as a negative impact. This adaptive framing approach presents a more positive narrative that could be applied to Australian fur seal trends, should they experience a population decline or shifts in range under climate change scenarios.

4.3 Considerations for building successful community science tools

SealSpotter has been a successful community science program, which has achieved its project goals and community engagement targets that included enough participation for reliable results, learning opportunities, particularly for youth, and global participation. This has been a long-term project and one that will continue to grow and evolve. Already, this application has been extended as 'Sea lion Spotter' for the Endangered Australian sea lion (*Neophoca cinerea*) in South Australia[4]. We acknowledge that marine citizen science is broad and comprises many different approaches, styles, and project scopes (Ellwood et al., 2017; Kelly et al., 2020). Here we reflect on the many lessons learned throughout SealSpotter's five-year project life and provide three key recommendations to guide other scientists seeking to develop successful community science tools.

4.3.1 Know your study site and species and choose your platform and audience

Seal Rocks hosts one species of seal, the Australian fur seal. The Skerries also hosts a small population of breeding long-nosed fur seals (*Arctocephalus forsteri*) that birth approximately one month later than the Australian fur seals. Given how similar the two species look for inexperienced participants, participants cannot be expected to distinguish them. Therefore, the timing of the surveys is important to understand the species contribution of your pup counts. If species differentiation is important for your results; you must perform surveys at the best time of year and/or only use experts for counting. However, this should not deter scientists from developing citizen science projects in complex environments, as passionate community members can often be experts of local wildlife and ecosystems or develop the skills. For example, community bird watchers are celebrated for their rapid and reliable identification of similar seabird species (Viola et al., 2022). In these cases, expert amateurs can collect accurate data with little intervention from scientific partners. Alternatively, the benefits of engaging novices or young people can include education and awareness raising, which may be a priority of the project and worth sacrificing some degree of data integrity that can be managed in the processing stage. An understanding of the audience or users of community science tools is necessary during project inception for success (Ellwood et al., 2017). Indeed, an understanding of organisms at the species level may not matter from a scientific perspective and is dependent on what variables are being monitored and why. For example, if scientists require an index of population change at a given location as an index of general ecosystem health,

7 https://sgbcllen.org.au/students-engage-in-seal-research/ [Accessed May 20, 2024].

8 https://www.csiro.au/en/education/programs/indigenous-stem-education-project [Accessed May 20, 2024].

4 https://www.www.sealionspotter.com/ [Accessed May 20, 2024].

it might be acceptable to monitor the total number of fur seal pups regardless of species.

The SealSpotter platform was built from the ground up to maintain flexibility and responsiveness with the program (SealSpotter source code provided at https://github.com/Research-coder/sealSpotter). Categories for counting can be easily changed by the research team and portals can be individualized for different projects, taxa and/or participants. This has allowed the provision of targeted portals for specific student requirements such as counting new births or counting females suckling pups compared to the number sucking juveniles, which is another metric of breeding failure or pup mortality.

Data scarcity or competition to interact with a limited dataset can encourage participation, similar to approaches used to create games (Spiers et al., 2019). The two- to three-week SealSpotter Challenge utilizes this behavioral preference of participants. Citizen science games, also known as Games With Purpose are popular for increasing engagement, but require more resources and introduce additional ethical considerations, as well as a need to understand the trade-offs (if any) for data quality and/or biases (Miller et al., 2023). For example, the drive of the player to earn more points may undermine the scientists need for accurate data collection. SealSpotter is a simple platform built by scientists on a budget to be flexible and transferrable to other uses, therefore the added complexity of gamification has not been introduced.

It is important to note that a number of free-to-use platforms exist specifically for citizen science programs including: RedMap[9], the Range Extension Database and Mapping Project, an Australia-wide tool for marine users to document new and vagrant marine organisms; eBird[10] a tool for birders to log avian sightings; iNaturalist[11] that includes a broader range of taxa where specific challenges can be set (Smith and Davis, 2019); DotDotGoose a free open source tool to assist with counting objects defined from within images (Ersts, 2024), and Zooniverse[12] that provides a wide scope of citizen science projects beyond recording wildlife sightings. The choice of platform and approach presents a number of trade-offs. One sacrifice of SealSpotter is the loss of access to thousands of highly engaged participants on pre-existing platforms such as Zooniverse and the need to recruit others to promote the portal. However, some projects have higher interactions than others on Zooniverse therefore using such a platform for a citizen science project does not guarantee success or high engagement (Spiers et al., 2019). Crucially, SealSpotter has 371 loyal participants that have been with the program over multiple years. Since the success of SealSpotter relies on identifying highly camouflaged fur seals on complex terrain, experienced and long-term participants are valuable for reliable scientific outputs. While SealSpotter requires minimal resources other than time to develop and maintain it, resources are needed if scientists prefer to engage a web designer and to regularly test the platform to maintain developments in cybersecurity requirements. Scientists seeking to develop successful community science tools must assess the pros and cons of available approaches to reach their target audience and project goals.

4.3.2 Listen to feedback and refine your methods

The SealSpotter program attracted an engaged community of citizen scientists from around the world. We posit that the success of this community engagement may be due to the multiple channels for scientist-participant communication. We recommend citizen scientist programs provide accessible ways for participants to leave feedback and build trust, with the option to remain anonymous. For example, the SealSpotter portal allows multiple channels to submit feedback through the website or by contacting the scientists directly through an organizational email. Such an approach has also proven successful for the Redmap project (Nursey-Bray et al., 2018).

Programs that are adaptive to community needs have been highlighted as a key to building trust and success in community science programs (Chiaravallti et al., 2022). From the feedback provided on the SealSpotter portal, the SealSpotter team adapted the original portal and project structure in response to participant feedback. Comments relating to dead seals arose numerous times in comments and email communication with participants (Figure 5). Though, it is important to note that words in Figure 5 have been listed without context, “dead” can refer to the counting of dead pups and how people found this challenging and sometimes upsetting. In other contexts “dead” could also refer to someone commenting on how many dead pups they have seen compared to other challenges. Because of the high volume of requests, we provided a new category to allow participants to count dead pups separately from live pups. Although these data are combined for a total pup count, the data may be useful in the future to detect large scale mortality in the event of a disease outbreak or anomalous heat wave. One major change resulting from participant feedback was the development of the two to three week-long SealSpotter challenges, an initiative to encourage use of the SealSpotter portal during a brief period of time where users who counted the most seals would be recognized in an annual newsletter (with permission). Participants who requested this believed that a time limit and sense of competition may better motivate them and their peers. Additionally, based on participant requests to have resources more readily available, we designed and included ‘cheat sheets’ within the portal where participants could click on a link to bring up several example images and use a slide bar to move between a counted image and the uncounted image to see how an expert (RM) would perform the count. This provided accessible guides on classifying the fur seals and helped participants improve. These brief examples of participant feedback demonstrate how programs such as SealSpotter can evolve to fit both citizen needs and those of the scientist. Citizen scientist programs work well when communication feedback loops are established and suggested changes are taken onboard. We recommend allowing multiple pathways for communication between scientists and citizen scientists to enable good communication and trust between all parties.

9 https://www.redmap.org.au [Accessed May 20, 2024].

10 https://ebird.org [Accessed May 20, 2024].

11 https://www.inaturalist.org [Accessed May 20, 2024].

12 https://www.zooniverse.org [Accessed May 20, 2024].

Interestingly, we saw spikes in participation during the 2020 Coronavirus (COVID-19) Pandemic particularly of new participants (those that identified as having no experience in using the seal spotter portal; Figure 3). During 2020, many people remained at home and under lockdown restrictions. As such we promoted the use of the SealSpotter portal through social media campaigns to engage people with the natural world and for education and entertainment. Virtual engagement in citizen science initiatives can lead to tangible effects for conservation (Yammine et al., 2018), and so we recommend the use of social media to promote citizen science projects.

4.3.3 Assess project accessibility and participant effort

SealSpotter is designed to be easy to access and use. There are no intensive tutorials, sign-ups, or hurdles to access the portal. The SealSpotter team adapted the program over its lifetime based on user feedback to increase accessibility. These changes included altering the shape and color of symbols used for the four categories of seal (adult/juvenile, live pup, dead pup, and entangled seal) so that people with color or other vision challenges could more easily participate. We were also requested to include closed caption text for the introductory video to benefit hearing impaired participants. There was a high number of new participants each year, many loyal participants, and some that rejoined the program after a break, therefore we have been working with an engaged citizen scientist community (Figure 4). We also demonstrated that the loyal participants and older age classes provided image counts more similar to the expert. We deliberately made the decision to preference inclusion of participants over reliability of counts by increasing the number of replicate image counts to 10 per image, which typically resulted in three to seven useable image counts for averaging. The SealSpotter program considers both elements to be important; however, individual projects must find a balance between obtaining reliable data and including young, less serious, or inexperienced participants. Such a nuanced approach to social inclusivity and scientific efficiency is common for citizen science programs and therefore ensuring authentic contributions is critical to ensure motivation (Spiers et al., 2019). SealSpotter included 10 compulsory training images after registering. That 1,262 participants counted fewer than 10 images demonstrates that we need to change how we train people so that their contribution is authentic and transparent.

Translating social media views of the promotional material to registration and extended engagement is a challenge for the SealSpotter program, as evidenced through the large proportion of new and inexperienced participants each year compared to the low numbers of regular and experienced participants. The use of partners and collaborations with external organizations improved the attraction and engagement of participants. SealSpotter, in its current form, was projected to have a life span of 10 years, based on expected participant enthusiasm for the project. We are currently halfway through that timeline and beginning to develop an improved portal with a more flexible and interactive platform for easy manipulation and an improved professional and attractive design. We expect this tool to become invaluable for monitoring various wildlife populations and for identifying the health of an ecosystem, therefore we hope that we can evolve SealSpotter to maintain authentic collaboration with citizen scientists and keep the program interesting and relevant. An important lesson from SealSpotter is to set realistic timelines and goals to assess value and success of the program regularly (from scientific and participant perspectives) and adapt as necessary.

4.4 Next steps

Following the success of the SealSpotter program in creating reliable data and limiting the workload of expert scientists, a future goal of the SealSpotter program is to access machine learning and artificial intelligence for more rapid seal counts and estimates of individual animal size (Hodgson et al., 2020; Dujon et al., 2021), but on a population rather than individual scale. These technological advances may allow for rapid basic counts and regular health indices because the fatter the seals, the more food they have accessed in the ecosystem, while the citizen scientists progress to more complex tasks that require human participation. Future questions may include the number of females suckling pups versus juveniles to explore survival and recruitment, or how adult male bull seals position themselves in harems and in response to other bull males, or whether fatter and healthier pups are more likely to congregate and skinnier pups be excluded. We will continue to support the citizen science outputs from SealSpotter and its value for education and ocean literacy and we will trial a language translation process to increase accessibility with non-English speaking countries and participants. We will create an opportunity to access the 10 training images prior to starting the survey image counts. This provides transparency in the activity, self-determination of the participant, and may maximize the number of image counts performed per survey. Drone technologies are continuing to advance (Wiley et al., 2023) and testing the use of thermal imaging is one such application being developed for coastal and marine settings that may enhance our understanding of seal populations, behavior and survival (Hinke et al., 2022) and improve validation of dead pups and entangled seals to reduce the gap between expert and participant counts.

Using AI and deep learning techniques for counting the seals is under development across the globe (Chen et al., 2023; Christin et al., 2019). Images of fur seals are complex for AI processes because seals present multiple shapes and sizes, at times wet and/or dry or a combination, and resting on often complex rocky terrain that camouflages them with rockpools that can appear as seal-like shapes. Despite this, success is anticipated and thermal sensors could prove more capable of providing computer derived counts. However, simultaneous color (RGB) and thermal imagery may be required to identify both dead and live pups. If AI is able to provide simple population counts from images, the role of citizen scientists may shift to answering more complex and specific questions beyond the capabilities of current AI.

We will also examine the role of human research ethics in evaluating citizen science participation and incentives (Groot and Abma, 2022). This may be overlooked in many programs including SealSpotter that have addressed this by de-identifying the participant data. However, participants may prefer greater scrutiny of the use of their data by scientists through the approval of human ethics committees.

5 Conclusion

Conservation efforts for marine species require a global increase in ocean literacy and engagement in the marine sciences. The SealSpotter program is an example of a highly successful citizen science program. Our results show that citizen science programs can be effective and reliable tools for monitoring wildlife populations, when they are designed appropriately and engage in active assessments of their own goals and targets, as well as incorporate feedback from participants as active collaborators. SealSpotter has attracted an engaged global community of all ages and is one of many international citizen science programs working to connect people to the marine environment.

Data availability statement

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

Ethics statement

The animal study was approved by Phillip Island Nature Parks Ethics Committee. The study was conducted in accordance with the local legislation and institutional requirements. Research was performed under Australian Civil Aviation Safety Authority legislation, Phillip Island Nature Parks Ethics approvals and Wildlife Research Permits 10007974, 10009034 and 10010309.

Author contributions

PP: Writing – original draft, Writing – review & editing. RH: Writing – original draft, Writing – review & editing. RM: Writing – original draft, Writing – review & editing.

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Conflict of interest

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

Publisher's note

Supplementary material

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Climate change stands as the new challenge for whale watching and North Pacific gray whales (*Eschrichtius robustus*) in Bahia Magdalena, Mexico, after their recovery from overexploitation

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Introduction: Social-ecological systems (SES) recognize the intricate relationship between human activities and the environment and advocate for comprehensive approaches to address complex environmental issues. This study investigates the factors influencing whale watching, particularly the gray whale (*Eschrichtius robustus*) in northern Mexico, after significant recovery following overexploitation. Despite reaching a peak in 2015, the eastern North Pacific gray whales experienced unusual mortality events (UME), the most recent from 2019 to 2023, leading to a population decline and historically low calf production in 2022. This decline is evident in the reduced presence of whales and calves in winter breeding lagoons. Concurrently, whale watching has become a significant tourist attraction in these areas.

Methods: Our objective was to develop a mental model of the SES of gray whale watching, integrating ecological and socioeconomic data to identify key variables and interactions that support system resilience. From an ecological perspective, we analyzed the long-term temporal trends of eight years of gray whale counts in the southernmost breeding and nursing lagoons within the Bahía Magdalena–Bahía Almejas Complex, Mexico. Additionally, we incorporated the current discussion in the literature about the potential impact of global climate change on gray whale populations. In the socioeconomic subsystem, we used participatory methods, including interviews, surveys, and workshops with government officials, tourism operators, and visitors. We also added on-site assessments of compliance with welfare regulations to understand tourism dynamics.

Results: Our findings identified as main external stressors the changes in ice levels in feeding areas and sea warming in breeding areas, and as internal stressors the compliance with official regulations and the number of vessels observing whales at the same time. The key socioeconomic factor of the system was tourist satisfaction, influenced by factors such as the quality of the information provided by operators.

Discussion: Ultimately, our mental model provides a framework for further exploration of relevant interactions and trajectories, offering insights for developing effective management strategies.

KEYWORDS

gray whale, social-ecological system, whale watching, climate change, resilience

1 Introduction

Social-ecological systems (SES), often referred to as social-ecosystems, emphasize the intricate interplay between social and ecological elements, recognizing the inherent connection between human activities and the natural environment (Mehring et al., 2017). This interconnectedness demands an integrated research and management approach to effectively address complex environmental challenges (Hummel et al., 2017; Mehring et al., 2017). Analyzing environmental issues within an SES framework offers insights into how ecosystem benefits support society amidst changing conditions, facilitating adaptive management strategies against climate change, biodiversity loss, and other environmental challenges (Hummel et al., 2011).

Nature-based tourism systems involve direct and non-linear hidden interactions between socioeconomic and ecological components (Biggs et al., 2012). Understanding these complex relationships and involving humans as an integral part of the ecosystem is crucial for promoting environmental conservation, identifying systemic alterations, and guiding sustainable practices (Schlüter et al., 2012). Studying the interactions between recreational activities and wildlife as social-ecological systems has helped delineate the positive, negative, and neutral effects to achieve a balance between human needs and the protection of natural ecosystems (Miller et al., 2022). Nature tourism, such as whale watching (WW), serves as a prime example of an SES where communities are intricately linked to whales and their habitats, forming cohesive and integrated systems (Reyers et al., 2018; Rodríguez-Izquierdo et al., 2019; Sousa et al., 2023).

SES are characterized by operating across diverse spatial, temporal, and social scales, requiring transdisciplinary approaches for understanding and intervention (Levin, 1998; Levin et al., 2013; Liehr et al., 2017). SES are complex adaptive systems that, when faced with stressors, can undergo regime shifts (Levin et al., 2013). It is, therefore, important to understand the system's capacity to absorb disturbances and continue functioning (Walker et al., 2004). This type of analysis is possible through the study of specific resilience in SES, which involves identifying the specific boundaries of a system that, if exceeded, could lead to a change in its functioning, thereby affecting its overall dynamics (Carpenter and Gunderson, 2001). When the goal is adaptive capacity, the study of specific resilience helps to understand the behavior of the system under certain stressors and also allows for the development of specific actions to guide that part of the system toward a desirable state (Li et al., 2020). In particular, 'resilience thinking' describes the important qualities a system must maintain or enhance to progress towards a more desirable state, typically aiming for a more sustainable social-ecological system while enduring a series of changes to withstand the impacts of stressors (Folke et al., 2010; Walker and Salt, 2006).

Recently, some studies have demonstrated that one of the primary stressors threatening whales and their observation is global climate change (GCC) (Lambert et al., 2010; Schumann et al., 2013; Salvadeo et al., 2015; Sousa et al., 2023). Certain whale populations, which are tourist attractions during their migration or in their breeding and nurturing areas, are directly impacted by global climate change (Lambert et al., 2010; Sousa et al., 2023). These impacts range from distribution and migration patterns shifts to effects on nutritional status, reproductive success, abundance, and population structure (Moore and Huntington, 2008; Schumann et al., 2013). Of particular concern is the population of the eastern North Pacific gray whale (*Eschrichtius robustus*), known for one of the world's longest migrations, covering approximately 11,000 kilometers across more than 40 degrees of latitude (Swartz, 1986). This migration exposes the whales to extensive climatic gradients influenced by various environmental phenomena. Gray whales migrate to Baja California Sur, in Mexico, to mate, calve, and rear their young in warmer waters during the winter months, particularly in lagoons such as Laguna Ojo de Liebre (the northernmost breeding area), Laguna San Ignacio, and the Bahía Magdalena–Bahía Almejas Complex (BMAC; the southernmost breeding area) (Swartz, 1986). These areas are crucial for their survival and reproductive success but are vulnerable to the impacts of climate variability and change, such as alterations in sea surface temperature (SST) during warm and cold periods of the El Niño-Southern Oscillation (ENSO) and changes in ice levels in the Arctic (Gardner and Chavez-Rosales, 2000; Urbán et al., 2003a; Salvadeo et al., 2015).

This population has recovered from historical overexploitation and reached its maximum environmental carrying capacity (maximum population size that can be sustained under the area's climatic conditions for feeding) by the late 1990s, and population levels peaked in 2015 (Eguchi et al., 2023a; Moore et al., 2001). However, due to a significant increase in the number of stranded dead whales, at least two Unusual Mortality Events (UME) were declared for this population, one from 1999 to 2001 attributed to exceeding the carrying capacity of the feeding areas and a second one from 2019 to 2023 (Eguchi et al., 2023a). Population size estimates conducted by NOAA NMFS-SWFSC during the recent Unusual Mortality Event (UME) reveal that the number of eastern North Pacific gray whales had reached a minimum level comparable to that of the 1970s, when whaling effects were more recent and estimates were below 15,000 gray whales. A notable difference in whale population estimates between 2016 (27,000 gray whales, 95% CI: 24,420–29,830) and the 2022-2023 season (14,526 whales, 95% CI: 13,194–15,858) indicates a 46% decline over the past seven years (Eguchi et al., 2023a). The production of calves reflects a more dramatic state; the historically lowest estimate of calf production was in 2022, with 216 calves (SE = 33.4, 95% CI = 1,236.5-1,753.5), whereas in 2016 the estimate was 1,458.3 calves (SE = 132.4, 95% CI = 159-290) (Eguchi et al., 2023b). In seeking an explanation for these changes, a recent study finds a clear relationship between the estimated abundance of the last 50 years of eastern North Pacific gray whales with a historical decline in the biomass of food (crustaceans) and access to feeding areas attributed to oceanographic changes in the Arctic region (Stewart et al., 2023).

Whale watching has experienced a rapid growth worldwide in the last decade, surpassing overall tourism growth (Higham et al., 2014; Hoyt and Parsons, 2014; Orams, 2002). In 2009, the International Fund for Animal Welfare (IFAW) estimated that whale watching income exceeded $2.1 billion USD annually, welcomed 13 million tourists, and generated 13,000 jobs worldwide (O'Connor et al., 2009). This extraordinary growth relies extensively on promoting whale watching as an inherently sustainable activity (Neves, 2010). However, concerns persist regarding the sustainability of whale watching (Markwell, 2015), prompting efforts to minimize negative interactions with whales and vessels while ensuring economic stability (Higham et al., 2009; Hoyt, 2005; Lambert et al., 2010; Orams, 2000). Studies have highlighted that cetaceans react to human presence similarly to natural predators, exhibiting stress responses in the presence of vessels, altering their behavior, and compromising their well-being (Frid and Dill, 2002; Bejder et al., 2006; Nowacek et al., 2001). Vessel collisions with whales pose risks to both whale and human safety, contributing to concerns regarding the sustainability of whale-watching activities, particularly in developing regions like Mexico and other Latin American and Asian countries (Cisneros-Montemayor et al., 2010; Mustika et al., 2013; Rodger et al., 2011).

Understanding the stressors and components that determine the resilience of a Social-Ecological System (SES), such as whale watching, is crucial for effective and sustainable management (Chontasi-Morales et al., 2021; Márquez-González and Sánchez-Crispín, 2007). Direct collaboration with stakeholders, from conceptualization to validation, is essential to ensure the accuracy and acceptance of intervention measures within the SES. However, obtaining direct information from stakeholders can be challenging, necessitating a holistic exploratory perspective that integrates empirical data and mental models to capture relevant causal relationships and enhance understanding of emerging phenomena in SES (Groesser and Schaffernicht, 2012; Radosavljevic et al., 2023; Schlüter et al., 2019). In particular, Lambert et al. (2010) have emphasized the need to study the resilience of whale watching in the context of climate change. Recently, collaborative studies have emerged to describe some components of the SES of whale watching in this context (Meynecke et al., 2017; Richards et al., 2021; Sousa et al., 2023). However, there is an urgent need for research that more balancedly assesses whale watching from both environmental and social viewpoints (Suárez-Rojas et al., 2022).

This work is the first to include *in situ* data on long-term trends in whale numbers in the region, the behavior of tourist vessels, and transdisciplinary collaborative work not only with the most interested stakeholders, namely the tour operators, but also including tourists, their expectations, and satisfaction. A clear way to represent the elements that determine the resilience of SES is by highlighting their interconnections and qualitative feedback through conceptual models of the system (Meynecke et al., 2017; Richards et al., 2021). This conceptualization is often known as a "dynamic hypothesis" because it is a theory about how the system's structure and observed temporal behavior appear in key variables (Maani and Cavana, 2007). Recently, the conceptual model has been used to describe the effects of climate change on whale watching (Meynecke et al., 2017; Richards et al., 2021). This work aims to develop a mental model that identifies the elements determining the resilience of the social-ecological system of gray whale watching in the face of climate change. Based on a transdisciplinary approach and the collection of *in situ* data, we explore possible adaptation strategies to promote the sustainability of whale watching.

2 Materials and methods

This study was conducted within the Bahía Magdalena–Bahía Almejas Complex (BMAC), located in Baja California Sur (BCS), Mexico, designated as an approved site for whale-watching activities in the Official Gazette of the Federation (DOF, 2011).

Spanning between 24° 20' to -25° 44' N and -111° 27' to -112° 15' W, the BMAC is the largest inlet on the west coast of the Baja California peninsula, covering a total area of 1409 km² (Bizzarro, 2008). Whale-watching activities in the area primarily take place in three key locations: 1) Puerto Adolfo López Mateos (PALM); located in the northernmost area, conducts whale-watching activities in the Santo Domingo Channel (SDC), a system of channels covering approximately 300 km² (Bizzarro, 2008); 2) Puerto San Carlos (PSC), dedicated to whale-watching in Bahía Magdalena (BM), is another significant site for these activities (Álvarez-Borrego et al., 1975); and 3) Puerto Chale (PCH), situated in the southernmost region, conducts whale-watching activities within the 414 km² of Bahía Almejas (BA) (Figure 1). The main whale-watching areas in the three lagoons are the ocean entrance points. Hereafter, when referring to the whales from any of these sites, we mention the bays, and when referring to the localities in socioeconomic aspects, we refer to the names of the communities. To identify the elements that describe the resilience of the SES of whale watching and thus shape the mental model of the system, we divided the SES into two major blocks: the ecological and socioeconomic subsystems.

2.1 Elements of the ecological subsystem

To construct the SES, a group of researchers first conducted biological monitoring of gray whales and analyzed trends over time. Between 2016 and 2023, a group of researchers and volunteers conducted vessel censuses in the study area, supervised by the Marine Mammal Research Program (PRIMMA) of the Autonomous University of Baja California Sur (UABCS) (sanignaciograywhales.org). During these annual censuses, whose reports have been published in the International Whaling Commission (Urbán et al., 2016, 2017, 2018, 2019, 2020, 2021, 2022, 2023), we performed systematic counts along predetermined routes for each lagoon. For each lagoon, we conducted at least three annual censuses, at least one per month from the second week of January to the second week of March, culminating in a total of 29 censuses per lagoon, except for Bahía Magdalena, which had 30 censuses (88 censuses in total) (Figure 2). These censuses estimate the minimum number of gray whales within the main winter breeding and nursing lagoons along the Pacific coast of the Baja California peninsula. In each census, we used a portable Global

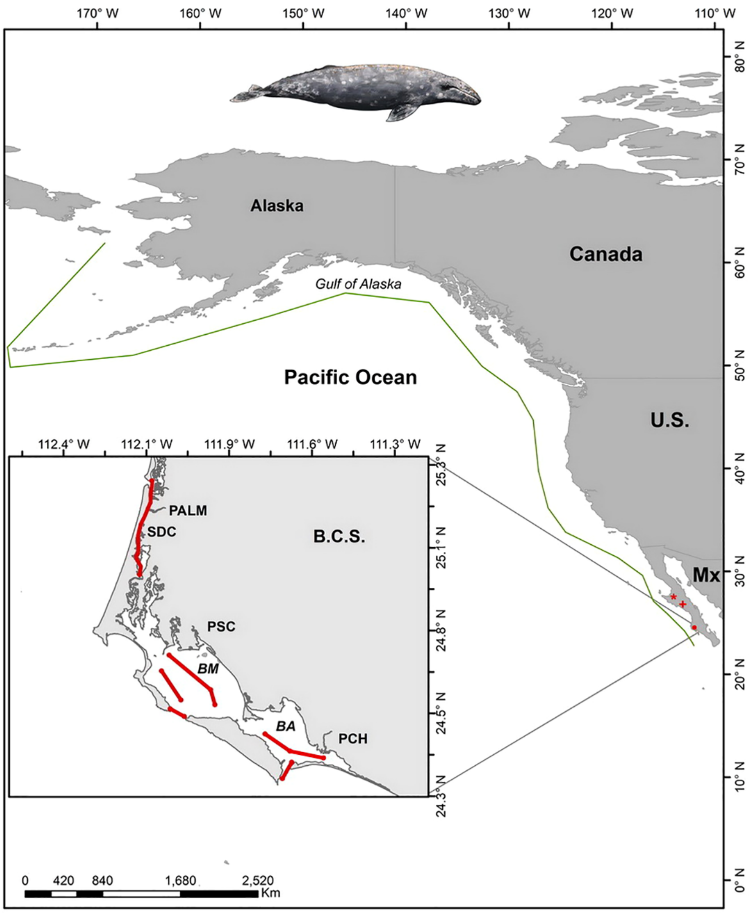

FIGURE 1
Migration route and calving and breeding bays of the gray whale (*Eschrichtius robustus*). Green line: example of migration route. Laguna Ojo de Liebre (✱), Laguna San Ignacio (+), Bahía Magdalena – Bahía Almejas Lagoon Complex (BMAC) (●). In the small box, locations and lagoons of BMAC; Locations: PALM (Puerto Adolfo López Mateos), PSC (Puerto San Carlos), PCH (Puerto Chale). Lagoons: Santo Domingo Channel (SDC), BM (Magdalena Bay), BA (Almejas Bay). The red lines indicate the navigation routes followed during the whale census counts conducted by PRIMMA-UABCS.

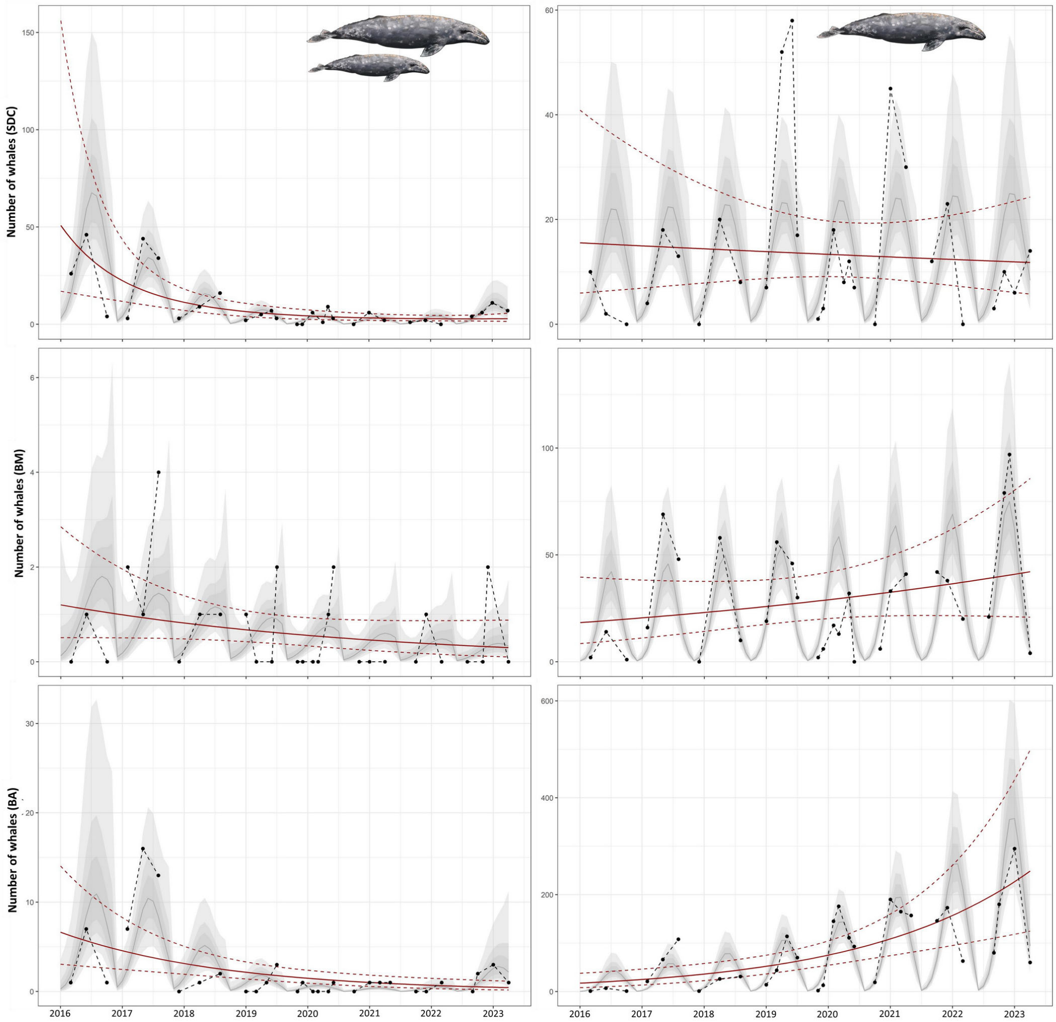

FIGURE 2
Trends in the number of mother-calf pairs (left) and single whales (right) counted per year in each lagoon of the Bahía Magdalena-Bahía Almejas complex from 2016 to 2023: Santo Domingo Canal (SDC), Bahía Magdalena (BM), and Bahía Almejas (BA). The points connected by dotted lines represent the original counts. The 95%, 75%, and 50% credible intervals (CI) of the estimated number of whales from the full model with long-term and seasonal scales are shown as shaded areas in grayscale. The solid red line represents the median of the long-term trend, and the dotted gold lines are its 95% credible intervals (CI).

Positioning System (GPS) device to follow a predetermined transect in each lagoon. For the lagoons of the BMAC, we followed the pre-designed routes by authors such as Fleischer et al. (1995), Gardner and Chavez-Rosales (2000), and Perez-Cortez et al. (2004) (Figure 1). This duplication of census effort allows us to compare whale counts within the year along the same census transect of each lagoon, and to compare with historical counts from previous years (Jones and Swartz, 1984; Urbán et al., 2003b).

For these censuses, we used the methodology proposed by Jones and Swartz (1984), which consists of navigating small outboard motorboats of 7 to 8 meters in length, following pre-designed routes at a speed of 11 km/h during the whale count. This speed is used to minimize the probability of whales outpacing the vessel, giving observers enough time to detect whales surfacing along the tracking route. Whales were recorded by two pairs of observers, one on the port side and another on the starboard side. Whales were counted only when they were at a right angle to the observers, and a fifth person recorded the sighting in a logbook, noting the time of the sighting, the number of whales, their swimming direction, and whether a calf accompanied them or if they were single whales. Additionally, we recorded some environmental conditions such as the Beaufort Sea state, wind direction, cloud cover, sea surface temperature, and depth. Censuses were not conducted or were aborted if in progress wind and sea state conditions exceeded Beaufort Sea state 3 (winds over 18 km/h with consistent whitecaps). By convention, “mother-calf pairs” (i.e., female whales with calves of the year) are counted as a single unit. “Single whales” refer to females without calves, adult males, and immature or juvenile animals.

Using the annual census data, we created temporal models for each lagoon and whale group (number of mother-calf pairs and single whales). We implemented Bayesian mixed-effects temporal models with an integrated nested Laplace approximation (INLA) approach (Rue et al., 2009), which has proven to be a great alternative for modeling time series, providing results in terms of posterior probability distributions instead of fixed values, and incorporating various types of random effects of temporal nature (Blangiardo et al., 2013; Zuur and Leno, 2018). We used years 2016 to 2023 as covariates to show long-term trends and the weekly scale from week 1 to week 16 of the year to cover the weeks of the first three months of each year, covering the census period to show temporal trends. We tested various model structures with combinations of the covariates. We used the best model results to show the long-term and seasonal temporal trends of the estimated number of gray whales over the eight years of systematic censuses.

2.2 Elements of the socioeconomic subsystem

During the biological monitoring, researchers identified some practices during whale watching that could affect the whales' well-being. As a result, we designed and evaluated compliance with the guidelines of the official Mexican regulations, specifically the Mexican Official Standard NOM-131-SEMARNAT-2010 (DOF, 2011). We assessed compliance with guidelines such as the maximum observation time (30 minutes), the maximum allowed navigation speed (9 km/h in the observation area, decreasing to 4 km/h when starting the observation activity), the observation distance between the vessel and the whales (60 meters), the trajectory of the vessel's approach to the whale (in a diagonal line from the rear side of the whale), and the maximum number of vessels observing the same whale or group of whales (four vessels). For the *in situ* evaluation of violations of the official regulations, we used a survey and registration method adapted from Quintana-Martín Montalvo et al. (2021) (the modified survey is available in Supplementary Table 1). This involved data collection by a group of researchers from a smaller vessel (45 feet or 13.7 meters long), positioned approximately 300 meters from a group of whales being observed by tourists. Sampling was conducted for a minimum of 6 minutes (2 scans to check for compliance or violation) and a maximum of 45 minutes (15 scans) as soon as visual contact with the group was lost or the whale-watching activity ended by a vessel or group of vessels. The size and composition of the group (adults and calves) were estimated visually. We then conducted a Principal Component Analysis (PCA) to identify the main violations of the official standard in each community and group of whales (mother-calf pairs, single whales, and groups of more than three whales) (Greenacre et al., 2023) to reduce the dimensionality of the multiple violations assessed and observe only the primary relationships between communities and violations (Chan and Shi, 1997; Greenacre et al., 2023). We used the scores of the projection of each locality in the principal components space to represent the position of the original observations in the principal components space, which helped to understand the influence of each principal component on the observations. We also performed a Pearson correlation analysis between the principal components and the violations to analyze and visualize how each community is associated with the principal components and the violations (Greenacre et al., 2023). To understand the dynamics of whale-watching tourism and its economic impact in the study area, we analyzed available data from the Mexican government's Secretariat of Environment and Natural Resources (SEMARNAT). SEMARNAT collects information reported annually by tourism operators regarding the number of permits, trips, income, and jobs generated by whale-watching in Mexico (SEMARNAT, 2024).

Analyzing the trends of the last eight years of whale counts, the lack of compliance with official regulations by tourism operators, and the economic importance of whale watching in the localities, we approached the communities to begin participatory work involving key stakeholders according to the nature of the activity, including tour operators conducting gray whale watching, tourists, and government representatives. In early winter 2022, we conducted 18 interviews with representatives of service operators. These interviews aimed to delve deeply into their experiences in tourism, tourists' perceptions, their understanding and views on official regulations, as well as their knowledge and perceptions of climate change and its impact on gray whales and whale-watching activities (the interview questions for tour operators are available in the Supplementary Table 2). We conducted the interviews in the three communities of the BMAC (Figure 1) and one additional interview with a representative of the Director of the Biosphere Reserve of the Pacific Islands in the Baja California Peninsula of the National Commission of Natural Protected Areas (CONANP).

Our research was a collaborative effort, with a wealth of information obtained from interviews. At the end of the winters of 2022 and 2023, we conducted 12 participatory workshops using mixed methodologies in focus groups. These workshops were aimed at people from communities near the observation area, with a primary focus on tour operators. The workshops, distributed among the three localities, were a platform for sharing and gathering insights. The first round of workshops in each locality focused on understanding the community's perception of climate change, its effects on gray whales and tourism, and sharing the results of the whale count censuses. The second part involved providing updated information on the status of the gray whale population, the observed effects of climate change on migration routes and breeding lagoons, and their interest in regulations and whale welfare. The third part provided detailed information on current regulations and their importance for whale conservation and tourist safety.

Between the third and fourth rounds of workshops, we conducted semi-structured surveys among 235 tourists to gather information on their level of interest in gray whale watching, overall satisfaction with the activity, satisfaction with the information provided during the tour, compliance with regulations, and the number of vessels encountered during the tour. For each of these sections, we asked participants to indicate their level of agreement on a Likert scale (1 - strongly disagree to 5 - strongly agree) (Pett, 2015). Additionally, we collected data on socio-demographic aspects, travel expenditures, and asked about scenarios in which they would be willing to return about the amount of information received during the WW trip, the number of vessels watching whales at the same time (crowding), and the number of whales (especially mother-calf pairs) (the survey questions for tourists are available in the Supplementary Table 3). The intention to return has been widely addressed in the theory of planned behavior, which states that tourists' intention to return depends on attitudes, subjective norms, and perceived behavioral control (Ajzen, 1991). Perceived crowding reveals a subjective perception of the number of vessels encountered affecting tourist satisfaction (Vaske and Donnelly, 2002).

We performed descriptive statistical analyses to understand the factors related to tourist satisfaction and to assess whether communities exhibited tendencies to commit specific types of normative violations. Through a correlation tree, we identified the segmentation of tourists based on their overall satisfaction with gray whale watching. Correlation trees reveal complex and non-linear relationships between predictive variables and the response variable (satisfaction level) (Breiman et al., 2017).

Finally, we conducted the fourth round of workshops where researchers shared our interpretation of the interviews, the results of the tourist surveys, the evaluation of compliance with regulations, and the relationship with the results of the whale censuses. In this final round, we conducted a feedback process where, through brainstorming sessions, we identified the essential variables of the SES and their interactions, discussed important adaptation actions for the system to be resilient to the effects of climate change, emphasizing that these actions are crucial for the future of gray whale watching and tourism. We validated the mental model of the SES via focal groups. To qualitatively understand the behavior of the system elements and the flows indicating how the variables interact, we represented the polarities of the links connecting these variables to show cause-effect relationships (Loucks and Van Beek, 2017). We represented these polarities with a plus (+) or minus (−) sign to show the direction of the relationship between the two interconnected variables (Maani and Cavana, 2007).

3 Results

We grouped the elements describing the resilience of the SES of gray whale watching in the BMAC into large blocks of the natural and socioeconomic subsystems, subsequently describing their interactions graphically in a mental model of the system.

3.1 Ecological subsystem

We obtained six models, selecting one for each locality with a different grouping of whales (mother-calf pairs and single whales). For all competing models, the negative binomial probability better represented the response variable than the Poisson distribution. Model selection was carried out using the Watanabe-Akaike Information Criterion (WAIC) (Table 1).

In the case of single whales, the best model was the same for each locality, including the number of continuous weeks (CW) from January 2016 to March 2023 (long-term scale), and the week of the year (WY) from January to March (seasonal scale) with second-order polynomials. Mother-calf pairs had different models for each locality; the most complex model was for BA with CW with third-order polynomials and WY with second-order polynomials, followed by SDC with second-order polynomials in both covariates. The simplest model for mother-calf pairs was for BM with CW plus WY with second-order polynomials (Table 1). There is a differentiated segregation of whales in the bays. The northernmost region (SDC) hosts the highest number of mother-calf pairs, while BM and BA have more single whales. On the other hand, the number of single whales has been higher in BA, with the annual average number of whales in this area being between three and seven times higher than in BM and between five and fourteen times higher than in SDC over the past four years (Figure 2).

TABLE 1 Best models of gray whale counts (μy) for each lagoon: SDC (Santo Domingo Channel), BM (Bahía Magdalena), and BA (Bahía Almejas) based on long-term and seasonal weekly scales selected by the Watanabe-Akaike Information Criterion (WAIC).

	Model structure	WAIC
Mother-calf pairs		
SDC	$\mu_{yi} \sim CW_i + (CW_i^2) + WY + (WY_i^2)$	186.4
BM	$\mu_{yi} \sim CW_i + WY_i + I(WY_i^2)$	68.7
BA	$\mu_{yi} \sim CW_i + (CW_i^2) + I(CW_i^3) + WY_i + (WY_i^2)$	106.7
Solitary whales		
SDC	$\mu_{yi} \sim CW_i + WY_i + (WY_i^2)$	235.1
BM	$\mu_{yi} \sim CW_i + WY_i + (WY_i^2)$	244.2
BA	$\mu_y i \sim CW_i + WY_i + (WY_i^2)$	305.9

The covariate used for the long-term scale is the number of continuous weeks (CW) from January 2016 to March 2023, and for the seasonal scale, it is the number of weeks of the year (WY) from January to March.

The data reveals a trend of decreasing mother-calf pairs over the years. The highest counts were observed in 2016 and 2017 in SDC, with maximum counts of 46 and 44 pairs, respectively. However, the following year (2018), only about one-third of that number was counted. This trend is consistent across all lagoons, with the most drastic changes observed in SDC, followed by BA. Between 2017 and 2022, there was a 95% decrease in the maximum number of mother-calf pairs counted in SDC, a 94% decrease in BA, and a 75% decrease in PSC. While 2023 saw a slightly higher increase than the average trend estimated in the long-term model, the overall trend is a cause for concern (Figure 2).

The trend in the number of single whales has been increasing in BM and BA, although it is more pronounced in the southernmost area. Following the lowest counts of single whales in 2016 in BM, there was a drop in 2020, with slightly higher maximum counts in 2021 and 2022, but even in these years, the maximum whale count was 41% less than in 2017. However, by 2023, there was a historic increase with a maximum count of 97 single whales, 131% more than in 2022 and 40% more than in 2017. In the case of BA, the maximum count of single whales increased consistently until 2021, with three times more whales in 2019 than the previous year. Between 2020 and 2022, there were no clear differences, but there was a 10% decrease between 2021 and 2022. However, in 2023, there was a considerable increase with a maximum count of 295 single whales (70% more whales than in 2022). SDC is the only lagoon showing a long-term decreasing trend in single whales. In 2022, SDC had a maximum count of single whales almost 50% lower than in 2021 and 60% lower than in 2019, and in 2023 was the only lagoon with fewer single whales than the previous year, with a 64% decrease (Figure 2).

The number of whales in the breeding lagoons, mainly the mother-calf pairs, and their declining trend over time are the primary state factors of the SES, as without whales, the system simply would not exist. Going from a maximum of 44 mother-calf pairs to two implies a change in the main factor of the SES, raising other questions related to how the system can remain resilient to these changes: Will the number of whales observed be important to tourists? Have tour operators noticed these changes in the whales? Is tourism conducted in the same way? Are there implications if tourism remains the same or grows?, among others.

3.2 Socioeconomic subsystem

After examining the temporal trend of gray whales visiting the Bahía Magdalena area over time, we compared the three localities within the BMAC. We evaluated how this tourist activity aligned with the official Mexican regulations. By assessing compliance with the Mexican Official Standard NOM-131-SEMARNAT-2010 using principal component analysis, we observed that violations of exceeded observation time (Time), improper approach trajectory to the whales (Trajectory), and high navigation speed (Speed) are distributed differently in the principal components (Figure 3). Trajectory and Speed are strongly correlated with the first principal component (Comp.1), with correlations of $r = 0.90$ and $r = 0.77$, respectively (Table 2). This suggests that Comp.1 represents a variability axis where long trajectories and high-speed violations predominate. On the other hand, Time shows a high correlation with the second principal component (Comp.2, $r = 0.92$), while Speed has a negative correlation with Comp.2 ($r = -0.53$) (Table 2). This indicates that Comp.2 represents a variability axis where long violation times oppose high-speed violations. By examining the scores of the communities in these components, we observed that when operators from the community of PSC observe single whales (PSC.single), they have high scores in both components (Table 2), suggesting that this community has improper approaches to the whales and prolonged violation times (Figure 3). Operators from PCH have a high score in Comp.1 and a negative score in Comp.2 when observing single whales, indicating that this community tends to have improper approach trajectories to the whales, navigate at high speeds, but usually respect the maximum observation time. In contrast, in the presence of mother-calf pairs, all localities have low scores in both components, indicating better approach trajectories, slow navigation, and no exceeding the maximum observation times (Figure 3).

Currently, we do not have evaluations from different years with varying numbers of whales, but we have the experience of being constantly present during the winter season, conducting whale monitoring, and evaluating compliance with regulations on different days of the week and at various times, some with higher tourism intensity than others. Therefore, we observed an increase in poor practices during times of higher influx of tourist vessels in the observation areas, mainly the mouths of the lagoons to the open sea.

Subsequently, our objective was to understand the importance of whale watching as an economic activity. By examining the available data in the SEMARNAT database (SEMARNAT, 2024),

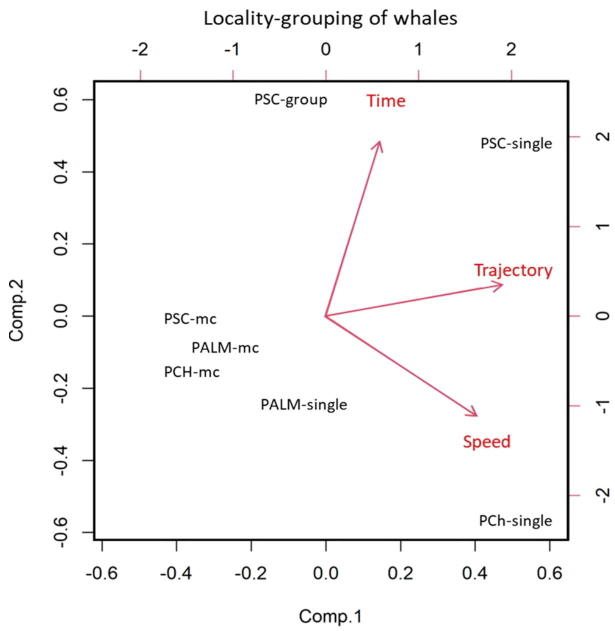

FIGURE 3
Principal Component Analysis. Representative infractions of non-compliance with regulations in different groupings of gray whales in the communities of BMAC. PSC: Puerto San Carlos, PALM: Puerto Adolfo López Mateos, PCh: Puerto Chale. Chale. Group: groups of three or more whales, mc: mothers with calves, single: solitary whales.

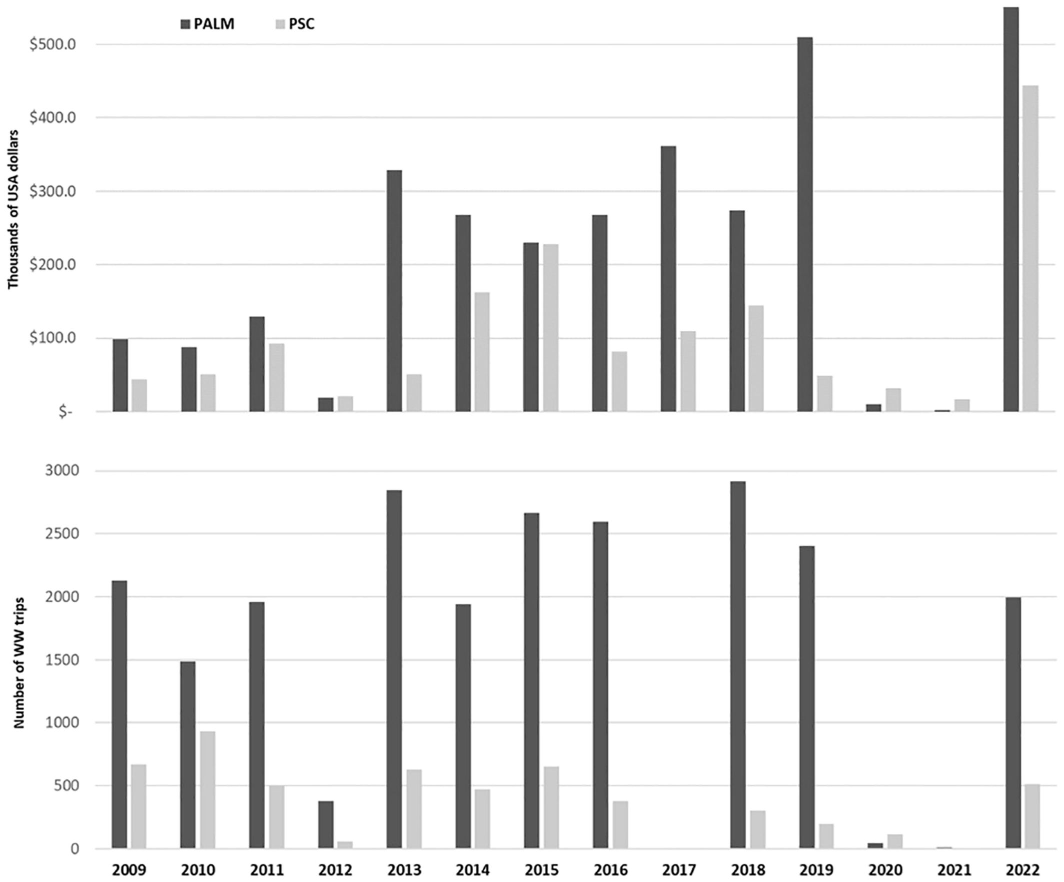

FIGURE 4
Top: Economic income in thousands of U.S. dollars from whale watching in Puerto Adolfo López Mateos (PALM) and Puerto San Carlos (PSC). Bottom: Number of reported whale-watching trips in Puerto Adolfo López Mateos (PALM) and Puerto San Carlos (PSC). Data from (SEMARNAT, 2024).

we observed that despite the geographical proximity of the localities within the same lagoon complex, there are significant variations in the number of tourists visiting these areas and their economic contributions. Interestingly, we observed a notable increase in economic income in PALM, where there has been a clearer decrease in gray whales, particularly mother-calf pairs (Figure 4). The differences in income between PALM and PSC are evident, with the former consistently being a higher income generator and conducting a greater number of trips since 2009 (Figure 4). However, there are cases where PSC's earnings could be proportionally higher, such as in 2015, when it generated $228,280 dollars in 655 trips, just $1,780 dollars less than PALM, despite conducting only one-third of the trips. However, there are no available records in the SEMARNAT databases for the southernmost site (PCH) despite its official inclusion as a whale watching area in 2013 (DOF, 2012).

Specifically for PALM, starting in 2013, there was a significant increase in income, exceeding $200,000, much higher than in previous years (Figure 4). Since 2013, revenues in this community have ranged from $230,000 to $940,000 in 2022, followed by a notable decrease in 2020 and 2021, marking the lowest historical incomes from whale watching in PALM ($10,300 and $1,930, respectively). The difference between the second-highest income

TABLE 2 Correlations indicating the relationship between violations of NOM-131-SEMARNAT-2010 (Time, Trajectory, Speed) and the principal components (Comp.1, Comp.2).

	Infraction	Comp.1	Comp.2
Correlations *r*	Time	0.27	0.92
	Trajectory	0.90	0.17
	Speed	0.77	-0.53
	locality-whale group		
Scores	PCH.single	1.77	-1.63
	PCH.mc	-1.14	-0.37
	PSC.single	1.94	1.36
	PSC.mc	-1.07	-0.10
	PSC.group	-0.41	1.69
	PALM.single	-0.23	-0.65
	PALM.mc	-0.85	-0.31

The scores represent the projected values of the groupings formed by each locality-whale group located in the space of the principal components. PSC: Puerto San Carlos, PALM: Puerto Adolfo López Mateos, PCh: Puerto Chale. Group: groups of three or more whales, mc: mother-calf pairs, single: single whales.

year and the highest is notable; in 2022, revenues were 85% higher than in 2019. Similar to PALM, PSC experienced its highest income year in 2022 ($444,300), followed by 2015 ($228,930), and then 2014 ($162,000). In 2020, revenues slightly exceeded those of 2012, which was the worst year, and in 2022, revenues were 94% higher than in 2015, the second-highest income year (Figure 4).

The number of trips appears to have remained relatively stable in PALM, fluctuating between 2,400 and 2,900 trips per year since 2013. A similar pattern is observed in PSC from 2009 to 2015, but a steady decline in the number of trips has been recorded until 2020. In 2020, the historical minimum of trips was recorded, with only 112, only surpassed by 2010 when only 55 trips were reported (Figure 4). The growth pattern in the number of trips is less noticeable compared to the economic income, particularly for PALM, where a historical record of earnings was achieved in 2019, before the onset of the SARS-CoV-2 Coronavirus pandemic, which was then greatly surpassed in 2022 (Figure 4). Despite some years with declines in tourist activity, the increase in recent years is clear, especially the upturn in 2022, which underscores the importance of a growing activity, contrary to the decline in gray whales. The low values in 2012 for both economic income and the number of trips should be taken with caution, as we did not find an explanation for these values, and even service operators mentioned that they do not reflect the tourist dynamics of that year. It also appears that the record of travel information for 2017 by SEMARNAT is missing.

The next step was to understand in depth the perceptions, knowledge, and needs identified by whale-watching operators. We conducted a total of 18 interviews with whale-watching operators from the three communities in the BMAC. In PALM, eight whale-watching operators were interviewed, including the leaders of the two cooperatives and two individuals registered for whale watching. Unlike the other two communities, whale-watching operators in PALM stand out for their high level of organization, maintaining constant communication and making decisions related to whale watching through democratic processes. They also associate with foreign companies arriving on yachts or cruises, facilitating information exchange, and raising awareness about recent events, such as the unusual mortality of gray whales. Additionally, alternative nature tourism activities were identified in PALM due to its diverse environments, including dunes, mangroves, and wildlife. The operators expressed their understanding of the need for training and close communication with whale researchers in the area.

In PSC, six whale-watching operators were interviewed, perceiving high competition among operators who often adjust prices to attract tourists. There is discontent with fishing activities during the whale-watching season, with limited knowledge of the recent UME among the operators. Some operators wanted local guides to be trained to join boat operators and share information to improve onboard safety.

In the southernmost community, PCH, three whale-watching operators were interviewed. They demonstrated great interest in learning about gray whale ecology and sharing information with tourists. Despite being relatively new to tourism, PCH is optimistic due to its proximity to the state capital city and perceived competitive advantages over other communities. The operators expressed interest in the presence of surveillance authorities to ensure compliance with regulations and prevent unauthorized tourist activities.

To gain a more comprehensive view of the current situation of whale watching, we also interviewed the current representative of the Biosphere Reserve of the Pacific Islands of the Baja California Peninsula, belonging to the federal government agency called the National Commission of Natural Protected Areas (CONANP). During the interview, differences were highlighted between fishing and tourism groups in the level of organization among the communities and disparities and complaints among certain communities. There is a perception that the number of permits for whale-watching activities is excessive, underscoring the need to regulate tourism to ensure its sustainability. Additionally, there is a call for developing alternative nature-based tourism activities to alleviate pressure on whale watching. Furthermore, there is an emphasis on the need for closer engagement from researchers and government authorities with the communities, particularly with whale-watching operators, due to growing dissatisfaction related to the decline in whales in recent seasons.

Through in-depth interviews, we identified that in all three localities there is a recognition of the decline in whales, especially mother-calf pairs. Although there are varying levels of knowledge related to the effects of climate change, everyone expressed a strong interest in learning more. We began to identify input variables to the SES related to its resilience, such as interest in diversifying tourist activities, training to learn more about the biology and ecology of whales, and we found that not everyone was fully aware of the official regulations and their importance.

In order to directly share the requested information, such as general aspects of the biology and ecology of the gray whale, the results of the biological monitoring conducted by PRIMMA, and to learn more about the recent UME of gray whales, we organized 12 participatory workshops (4 per site). In the first three rounds of workshops, we shared this information and discussed sustainable and resilient tourism, the importance and benefits of applying NOM-131-SEMARNAT-2010, and discussed some improvement and adaptation strategies to climate change, which were later taken up and established in the fourth round of workshops. Additionally, we identified an interest in understanding tourists' perceptions and satisfaction with the activity. Tourists often came with the idea of touching whales, generated by social media, which was reflected in an insistence by tourists to get too close to increase their chance of touching a whale, which could lead to several operators harassing the whales.

To understand the tourist typology and the factors associated with their satisfaction, we administered 235 semi-structured surveys to tourists immediately after their gray whale watching trips between 2022 and 2023. Sixty-four percent of these surveys were collected in PALM, 22% in PCH, and 14% in PSC. The age range of the surveyed tourists varied between 13 to 80 years old, with most being between 27 and 51 years old in all sites. Tourists mentioned their main motivations for visiting the area and watching whales, where 62% of the tourists stated that their primary motivation was simply to see the whales, with a particular interest in seeing calves.

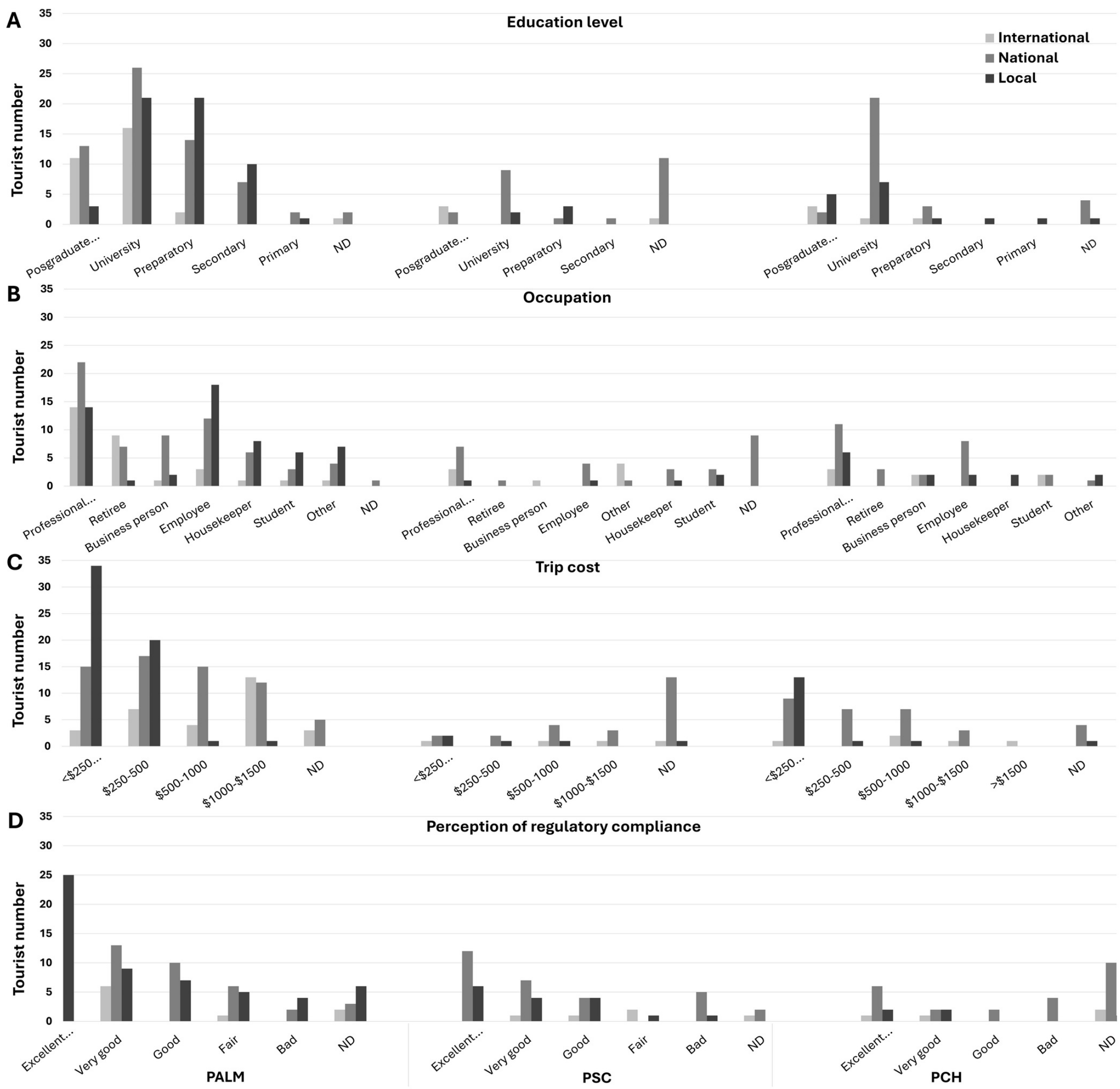

FIGURE 5
Tourist Typology: Some descriptive characteristics of tourists who visited different whale-watching locations, such as **(A)** Education level, **(B)** Occupation, **(C)** Trip cost. Tourist origin: Travelers from another country (International), tourists from Mexico traveling from a different state to Baja California Sur (National), and tourists from BCS (Local). PSC: Puerto San Carlos, PCH: Puerto Chale, PALM: Puerto Adolfo López Mateos. ND: Tourists who chose not to answer this question. **(D)** Tourists' perception of compliance with NOM-131-SEMARNAT-2010.

Only 25% reported having an interest in seeing the entire natural environment. Thirteen percent said they were visiting the area only because it was part of a tour package. In all localities, most tourists reported having completed university studies, followed by high school and postgraduate education. The most frequent occupation in all localities was professional work (34% of the total), followed by employee (20%). Of the total tourists, 34% spent less than $250 dollars, 23.8% spent between $250 - $500 dollars, and 15.3%, a similar percentage of tourists, spent between $500-1000 and $1000-1500 dollars. In PAL and PCH, the majority spent less than $250 dollars (34.4% and 45.1%, respectively); however, in PSC a high percentage of tourists preferred not to mention how much they had spent (45.5%) (Figure 5).

Half of the respondents were national tourists, one-third were locals, and 17% were foreigners. PSC had the highest proportion of national tourists (55%), followed by PCH (25%) and PALM (20%) (Figure 5). When analyzing the proportion of tourists according to their origin (international, national, or local), we observed that international tourists (tourists from another country) had the highest proportion of university (41%) and postgraduate (28%) studies. The majority of national tourists (Mexicans who do not live in B.C.S.) had university studies (22%), followed by high school (12%) and postgraduate (11%) studies. Among local tourists (residents of B.C.S.), university and pre-university (high school) studies predominated (27% each), followed by secondary education (13%) (Figure 5A). Fifty-one percent of international tourists mentioned having a professional job, followed by retired tourists (23%). Most national tourists had professional jobs (34%), followed by employees (20%), and only 10% were retired tourists (Figure 5B).

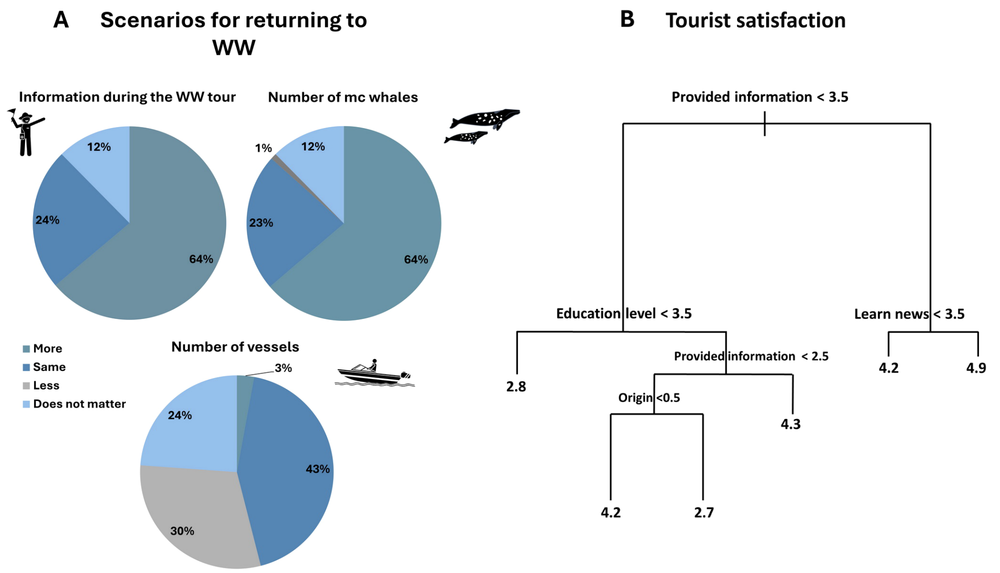

FIGURE 6
(A) (left) Percentage of total tourists who would return for whale watching under different scenarios, considering the amount of information provided during the tour, the number of whales in the lagoon, and the number of boats in the observation area. **(B)** (right) Relationship between tourist satisfaction and activities during the whale-watching event.

After providing a general overview of the guidelines for proper whale watching according to NOM-131-SEMARNAT-2010, we sought to measure tourists' perceptions of compliance with these guidelines. Among tourists visiting PALM, 51% rated compliance as excellent, 8% considered it moderate, and only 4% rated it as poor. In comparison, a smaller proportion of visitors to PCH and PSC rated compliance as excellent, with 35% and 39%, respectively. However, 12% of respondents rated compliance as deficient in both PCH and PSC. Additionally, 11% of all tourists refused to rate the compliance of their tour (Figure 5D). Interestingly, there were no clear differences in the compliance rating according to the tourists' origin. Among international tourists, 56% rated compliance as excellent, followed by 43% of locals and 42% of nationals. Conversely, no foreigners rated compliance as deficient, while only 6% of locals and 9% of nationals perceived compliance as deficient. These findings suggest a generally positive perception of compliance with whale-watching guidelines among tourists, regardless of their origin (Figure 5D).

Tourists were willing to return for whale watching under certain circumstances, with no clear differences observed between communities or tourist origins. Sixty-four percent mentioned that they would consider returning if provided with more information during the whale-watching tour. In comparison, 23% said they would do so with the same information (Figure 6A). Interestingly, none of the respondents mentioned returning with less information than they received. Similarly, when asked about their willingness to return if they saw the same number of mother whales with calves, only 12% responded that the number of whales does not affect their decision to return. However, most tourists expressed that they would be more likely to return if the number of whale-watching vessels in the observation area was lower (30%) or at least the same as they observed during their tour (43%). Another 24% mentioned that a change in the number of vessels does not affect their decision (Figure 6A). Additionally, 40% of respondents expressed interest in engaging in more tourist activities in the area besides whale watching, even if it meant incurring higher expenses. About 33% said they neither agreed nor disagreed with this idea, while 21% chose not to answer. These responses indicate a potential to diversify tourist activities to enhance visitor experiences and support local economies.

According to the correlation tree analysis, tourist satisfaction was primarily associated with the level of satisfaction with the information provided during the tour (Figure 6B). This factor served as the main determinant of satisfaction, indicating that tourists who felt adequately informed during the whale-watching tour were more likely to report higher levels of satisfaction. According to the conditions shown by the correlation tree, the highest degree of tourist satisfaction (4.9 out of a scale of 5) was obtained when there was medium to high satisfaction with the information received (>= 3.5, right branch of the tree) and subsequently, if tourists considered themselves moderately to highly in agreement with having learned new information during the tour (>= 3.5 out of a scale of 5). This suggests that tourists who felt they gained new insights or knowledge during the experience had higher satisfaction (Figure 6B). The next level of satisfaction was related to the tourists' educational level. Tourists with university or postgraduate education who had satisfaction with the information received equal to or greater than the average (>= 2.5 out of 5) reported being moderately to highly satisfied with the activity (4.3 out of 5). Another important factor is whether the respondents were local or foreign tourists (national or international). Interestingly, it was found that Mexicans from outside Baja California Sur (BCS) were less satisfied with the information received than local tourists. This distinction

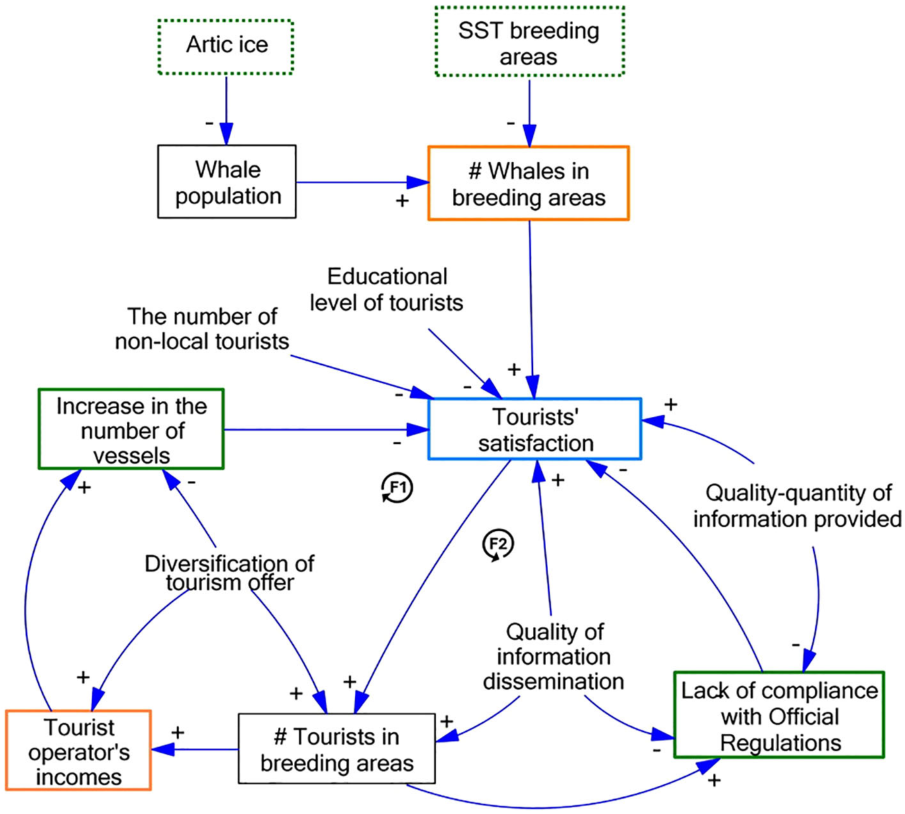

FIGURE 7
The mental model of the SES for gray whale watching in the BMAC. The main variables determining the system's desired state are enclosed in a box. Variables determining the system's resilience are enclosed in orange. The main internal stressor variables of the system are enclosed in a green box, and external stressors are indicated with a dashed green line. The variable encompassing the system's responses to both resilience and internal stressors is in blue. Arrows in the model and the signs indicate the direction of influence (one factor increases, and the other increases or decreases). F1 and F2 are the feedback loops.

highlights the importance of considering cultural or regional differences in tourists' expectations and experiences during whale-watching tours. It is worth noting that factors related to information and learning something new are found in three of the five nodes of the tree, including the main node, highlighting the importance of these factors in tourists' overall satisfaction with the WW activity.

Once the data from the ecological and socioeconomic subsystems were analyzed, the results were presented in the fourth participatory workshop, following feedback from each section, through brainstorming sessions and focus groups. Among the participants, whom tour operators mostly represented, some civil associations, and representatives of CONANP, we consolidated the mental model of the social-ecological system of whale watching on a medium or meso scale that includes the three localities of the Bahía Magdalena–Bahía Almejas Complex, integrating various ecological and socioeconomic components to understand their interactions and responses to changes over time (Figure 7).

We found that resilience in this SES is defined by the system's ability to sustain economic activity over time while facing its main stressor: the effect of climate change on gray whales. Climatic variables such as ice levels in the feeding area and sea surface temperature in the breeding areas influence the number and condition of whales visiting the bays, serving as input variables and identified as external stressors to the system over which we have no control. The state of the biological component, represented by the number of whales, is related to actions that can make the SES resilient.

Tourist satisfaction emerges as a central variable within the SES, influencing and being influenced by most of the other variables. Satisfaction is a variable that balances the two indicators of the resilience of the activity: the number of whales and the economic income of tour operators. Satisfaction is strongly linked to the information provided by tour operators, with increased quantity and quality of information increasing satisfaction and potentially fostering greater environmental awareness among tourists. Additionally, improving the information used in marketing campaigns to promote the activity can lead to better compliance with regulations and reduce the pressure on tour operators to get closer to the whales. We did not lose sight of the fact that satisfaction is also influenced by the educational level of tourists; the higher the education, the greater their demand, and it is also higher among non-local tourists (non-residents of B.C.S.) (Figure 7).

Tourist preferences support efforts to control the increase in the number of vessels in the whale-watching area, which could improve satisfaction. Additionally, diversifying tourist activities in each locality could reduce the number of vessels dedicated exclusively to whale watching, allowing for better organization and compliance with regulations even with fewer whales (Figure 7).

Two main causal relationships were identified between elements, defined as feedback loops in the SES mental model. These elements are connected in such a way that if we follow the causality starting from any element in the loop, we can eventually return to the first element. The first feedback loop (F1) is defined by the relationship between the increase in tourists and economic income and whether this generates a higher number of vessels watching whales simultaneously, which would negatively affect tourist satisfaction. The second feedback loop (F2) is defined by the effect on satisfaction from poor practices that lead to non-compliance with official regulations due to increased tourism (Figure 7). Overall, the mental model provides information on the complex interactions within the SES of whale watching in a simple and easily understandable way, and helps to emphasize the importance of adaptive management strategies to ensure the resilience of both the economic activity and the whale populations in the area.

4 Discussion

This study contributes significantly to understanding the social-ecological system (SES) of gray whale watching in Mexico. It involved developing a mental model of the system that incorporates ecological variables, such as the temporal trend of whale counts in breeding and calving lagoons, population estimates, and the intricate relationship between gray whales and environmental changes. Additionally, it integrates social variables such as the temporal behavior of tourism and compliance with official regulations. It also analyzes variables associated with tourist satisfaction, aiming for a more resilient and sustainable system. Research focused on SES, which integrally incorporates ecological and socioeconomic aspects in marine environments, is limited but crucial (Refulio-Coronado et al., 2021). Since economic activities are closely linked to the environment, strategies must strengthen vulnerable components against regime shifts or persistent pressures (Hummel et al., 2011).

In our study, we analyzed ecological and socioeconomic factors at the local level; however, we identified key system factors that influence a medium or meso scale similarly across the three breeding lagoons of the BMAC and their corresponding localities that conduct WW. Components of the ecological subsystem, such as the decline of whales in WW areas, and those of the socioeconomic subsystem, such as tourist satisfaction, non-compliance with regulations, economic income, and the increase in vessels observing whales, are represented through a mental model that illustrates the interactions and feedback within the SES of gray whale watching in the BMAC (Groesser and Schaffernicht, 2012). This holistic and participatory approach, involving various sources of information and stakeholders, enhances the resilience of the SES (Berkes, 2012; Refulio-Coronado et al., 2021).

The study reveals an eight-year long-term trend of gray whale counts in the breeding and nursing lagoons of the BMAC, reflecting a clear trend of declining mother-calf pairs in all lagoons and an apparent increase in single whales in the two southernmost lagoons. In recent years, a historically low drop in the maximum count of mother-calf pairs and a stagnation in the counts of single whales correspond with the years of the recent UME (2019-2022) of gray whales (Eguchi et al., 2023a). The recent UME has been associated with changes in climatic conditions in the feeding areas (Stewart et al., 2023). These changes in the gray whale feeding area have been associated with the extent of Arctic ice, which influences the physical accessibility of gray whales to feeding areas. Although a negative relationship has been observed between high ice densities (more than 45 to 55%) and gray whale counts (Stewart et al., 2023), especially calf production, recent lower estimates do not align with this pattern (Perryman et al., 2020). These discrepancies suggest that the recent mortality event and changes in calf production may be differently linked to ice conditions and other factors (Perryman et al., 2020; Stewart et al., 2023). Recent studies have estimated the carrying capacity of the feeding area and calf production in relation to ice cover and access to feeding areas, incorporating benthic crustacean biomass as an explanatory variable indicative of food availability. While ice accessibility remains crucial, a clearer trend emerges when comparing the carrying capacity of gray whales and calf production with food biomass (Stewart et al., 2023). Latitudinal shifts have also been observed, with ice moving northward, leading to decreased productivity in the Bering Strait and increased productivity further north (Frey et al., 2022; Grebmeier et al., 2018). These changes in the Arctic could be related to a decrease in per capita biomass of gray whale prey, which could affect the whale population (Stewart et al., 2023) and their migration.

On the other hand, Baja California peninsula serves as vital habitat for winter aggregations of gray whales in breeding lagoons. These lagoons provide refuge in their protected waters of the Pacific Ocean for specific mating and lactation events. Whales favor them due to their latitudinal gradient of warmer temperatures, allowing calves to maintain their body temperature while accumulating fat from maternal milk (Sumich, 1986; Swartz, 1986). The lagoons are separated by approximately one degree of latitude for the nearest and northernmost (Laguna Ojo de Liebre and Laguna San Ignacio) and three degrees for the furthest (L. Ojo de Liebre and BMAC). Historically, the northernmost lagoon closest to the feeding areas tends to host the highest number of whales, followed by the middle zone (L. San Ignacio), and finally, the area with the lowest proportion of whales is BMAC. However, these proportions show certain variations over the years (Salvadeo et al., 2015; Urbán et al., 2003b).

In general, global sea surface temperature is increasing and is expected to continue rising due to global climate change, with projections ranging from 0.6 to around 3°C, depending on the scenario (IPCC, 2019). Consequently, current tropical zones are expected to expand to higher latitudes, temperate zones will shift toward the poles, and polar zones will contract. Many species, including whales, are expected to move toward the poles in search of optimal temperature conditions, potentially altering their migration patterns; in the case of gray whales, potentially shortening the migratory route (García-Molinos et al., 2015; van Weelden et al., 2021). In particular, the North Pacific Ocean has been identified as one of the three oceans that harbor marine mammal species most vulnerable to global warming, with the gray whale being the second most vulnerable species, even under a low greenhouse gas emissions scenario (RCP 2.6) (Albouy et al., 2020).

The declining trends in gray whales shown in this study, especially mother-calf pairs, may be due to physiological stress from food reduction (Christiansen et al., 2021) and changes in the temperature of breeding and nursing areas. Studies suggest that during colder years associated with La Niña conditions, whales tend to migrate further south, reaching areas like Los Cabos in the Gulf of California and even Bahía de Banderas in Nayarit, Mexico. Conversely, during warmer years related to ENSO conditions, fewer mother-calf pairs have been observed in the Santo Domingo Channel in the BMAC region (Salvadeo et al., 2013). It is likely that with warmer anomalies in the sea surface temperature, mother-calf pairs do not migrate as far south. These latitudinal changes in the presence of gray whale mother-calf pairs in relation to sea surface temperature are especially evident in the southernmost breeding and nursing area, which corresponds to the study area of this research (Salvadeo et al., 2013). Therefore, alternative management strategies are needed to increase specific resilience and adapt to these fluctuations in whale numbers and a potentially significant historical decline (Lambert et al., 2010; Sousa et al., 2023). The strategies must ensure that the activity does not negatively impact gray whales and that economic revenues are maintained at least at the current levels.

Regarding the social subsystem, tourist satisfaction emerges as a central variable in the SES mental model, linking various aspects of whale watching and balancing the two indicators of system resilience, the number of whales and the income of tour operators. The external stressors of the system are composed of climatic conditions that affect the number of whales, and therefore there are no variables that can influence them. However, we identified two internal stressors: the lack of compliance with official whale-watching regulations and the simultaneous increase in boats watching whales.

Among the variables that influence tourist satisfaction, the number of whales sighted has been identified as one of the most significant (Lee et al., 2019; Suárez-Rojas et al., 2022). However, during interactions with tourists, most indicated that they would understand the situation if the current status of the whales was explained during the tour. It has been previously noted that tourists value interpretive services in whale watching (Lee et al., 2019). Satisfaction was also directly influenced by the quality of information received during the WW trip. Information is an important element for tourist satisfaction and serves as an indicator of sustainability (Tavares et al., 2018; Naidoo et al., 2011). Educational information for tourists enhances their concern for animal welfare and responsible behavior, which can help improve whale-watching practices (Suárez-Rojas et al., 2022). It is common around the world to use tour guides as communicators of the country, its offerings, laws, norms, regulations, expected behavior patterns, and the quality of guide services is usually important for the final satisfaction of tourists (Sandaruwani and Gnanapala, 2016). However, in none of the three communities studied here is a tour guide service, so we recommend training local guides to reinforce tourists' pro-environmental perceptions by facilitating awareness, reflection, and appreciation by local people working as guides (Walker and Weiler, 2017).

Ensuring accurate marketing information before the trip and managing tourists' expectations is essential. It is also important to consider that tourists' pressure to interact closely with whales is influenced by disseminated images on internet government pages (Cho et al., 2014; Sheungting Lo and McKercher, 2016). In this study, tour operators mentioned feeling pressure from tourists who insisted on getting too close to the whales to increase their chances of touching them. We believe that the quality of disseminated information is a factor influencing tourists' expectations and satisfaction (Sheungting Lo and McKercher, 2016).

This study also observed a lack of compliance with regulations, especially regarding certain infractions such as the approach trajectory to the whales, the maximum observation time, and the navigation speed. Although there is generally no high appreciation of non-compliance with these guidelines by tourists, this may be due to their lack of awareness of the regulations due to the lack of information shared by operators. In other parts of the world, tourists have indicated they are willing to pay more for WW tours that ensure the safety of the observed animals, especially respecting navigation speed (Suárez-Rojas et al., 2022). Sharing information is important for compliance with guidelines and tourists might even accept an increase in observation distance if they were informed about the potential impacts on whale welfare (Kessler et al., 2014). In other regions, tour operators have considered regulatory compliance as an important factor within the conceptualization of the SES of whale watching in the face of climate change, as this could reduce pressure on the whales (Meynecke et al., 2017).

Tourists mentioned being willing to return under the scenario of maintaining or reducing the number of vessels watching whales simultaneously. Previous studies conducted in Bahía de Banderas, Mexico, found that perceived crowding by tourists negatively affects the likelihood of tourists returning for a whale-watching trip (Avila-Foucat et al., 2013). Crowding impacts satisfaction in other recreational activities (Needham et al., 2011), so it is important to consider satisfaction with vessel crowding when designing coastal management policies. Despite the official standard indicating that only four vessels can watch whales at the same time, two is the optimal number of vessels for tourist satisfaction (Avila-Foucat et al., 2013). Since tourism continues to grow, regulating the number of vessels in the water has been very complicated for service providers, as it would require many tourists to wait a long time in the water. Different management recommendations have been issued, such as codes of conduct, zoning, closure areas, seasonal timing, vessel permits, and performance and education programs (Avila-Foucat et al., 2013; Casis-García, 2010).

Collaboration between tour operators, authorities, and researchers is vital for adaptive management (Dimmock et al., 2014; Garrod and Fennell, 2004; Lusseau, 2014). Maintaining communication channels, providing updated information, ensuring that operators' economic income remains unchanged regardless of the number of whales, and implementing collaborative actions can improve operators' satisfaction and facilitate adaptive management based on the current state of the whales (Meynecke et al., 2017; Richards et al., 2021; Sousa et al., 2023). In Mexico, the number of whale-watching permits does not have a specific directive. The number of permits has been previously used to measure adaptive management, considering specific population aspects (Organ et al., 2012; Runge et al., 2013). Achieving an equitable distribution of economic benefits among community stakeholders and implementing monitoring and surveillance mechanisms is essential. Also, the impact of the COVID-19 pandemic on whale-watching tourism remains uncertain, but a resurgence is expected due to pent-up demand and remote work trends (Adelman, 2022; Feng and Xia, 2022; Mckercher, 2021; Vogler, 2021). This study shows a significant resurgence in WW tourism activity in 2023.

Adapting best practices to local conditions can minimize negative impacts on organisms and ensure the sustainability of whale-watching tourism (Gómez-Gallardo Unzueta et al., 2023). There are some examples of integrated management strategies that work in whale watching. Tour operators in Laguna San Ignacio, Baja California Sur, Mexico (the northernmost breeding lagoon of the gray whale), have established since the beginning of the activity in the 1990s a Rural Association of Collective Interest (ARIC) (Gómez-Gallardo Unzueta et al., 2023). This organization, comprised by the tour operators themselves, has allowed them to organize and establish internal guidelines, such as the maximum number of vessels that can navigate simultaneously; only 16 vessels can practice whale watching at the same time in the entire authorized area, regardless of the number of permits, which tends to increase annually. Additionally, each vessel can remain in the water for a maximum of 90 minutes, and they have an operator who acts as an onboard observer dedicated solely to ensuring compliance with the guidelines; otherwise, they communicate via radio with the violating vessel (Amerson and Parsons, 2018; Gómez-Gallardo Unzueta et al., 2023). Similarly, blue whale (*Balaenoptera musculus*) watching in Loreto, Baja California Sur, Mexico, has specifications generated in collaboration between tour operators and researchers, established in the "Management Program of the Bahía de Loreto National Park" (DOF, 2019).

Studies analyzing tourism activities as SES, combining environmental and social sciences interdisciplinarily, are few and recent (Miller et al., 2022; Richards et al., 2021; Sumanapala and Wolf, 2019). For over a decade, the importance of analyzing the resilience of whale watching to climate change has been discussed (Lambert et al., 2010). However, few studies have analyzed it (Meynecke et al., 2017; Richards et al., 2021; Sousa et al., 2023). These studies have been conducted through participatory workshops and bibliographic data, primarily in Meynecke et al. (2017) and Richards et al. (2021). However, they have not used *in situ* data on tourist characteristics and satisfaction, nor how the activity's compliance with regulations and adequate information can influence the resilience of WW to climate change. Therefore, we recommend making efforts to indicate tourists' preferences to analyze their intersection with other factors that will help ensure the resilience of this activity. It is also important to consider actions directed to animal welfare, such as compliance with regulations, especially in cases like the gray whale, which is already suffering the effects of climate change. Additionally, analyzing different migratory destinations of the same whale population helps understand similarities and differences between localities, which can, in turn, conceptualize an SES that encompasses medium-scale interactions of common factors as described here.

While our study sheds light on the SES of gray whale watching, it is not exhaustive. Knowing some additional factors could help better understand the SES, such as the fixed and variable costs for operators to carry out the activity (Sousa et al., 2023), and possible changes in the whales' migration timing (Richards et al., 2021). Continuous feedback and stakeholder collaboration can refine understanding and contribute to adaptive management agreements. Our mental model and all the gathered information can serve as a basis for future mathematical models, such as dynamic systems modeling (Richards et al., 2021), which has even been used to evaluate the effect of management decisions in gray whale watching in Ojo de Liebre, Mexico (Rodríguez-Izquierdo et al., 2019). This would allow quantitative explorations of the adaptive responses of the SES to different scenarios, understanding its thresholds and feedback loops, particularly in policy applications (Kwakkel and Pruyt, 2013).

5 Conclusion

The present mental model provides an analytical framework for understanding the dynamics of whale watching, particularly in unique locations such as the communities of the Bahía Magdalena–Bahía Almejas Lagoon Complex, and its correlation with changes in the population dynamics of gray whales attributed to recent climatic changes. This knowledge has the potential to guide adaptive management decisions, prioritizing benefits for the entire community and long-term economic stability while mitigating adverse impacts on whale populations. This study lays the foundation for developing joint strategies to improve resilience and sustainability within the tourism sector by initiating discussions and fostering collaboration among stakeholders. Additionally, it serves as a cornerstone for implementing mathematical methodologies to evaluate scenarios and determine critical system thresholds.

Data availability statement

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

Ethics statement

Ethical approval was not required for the studies involving humans because the people involved participated voluntarily and their identity and responses to the interviews are kept confidential. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study. Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because this study was fully observational following the "Guidelines for the treatment of marine mammals in field research," supported by the Society for Marine Mammalogy (Gales et al., 2009). Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

Author contributions

OG: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. LV: Conceptualization, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. VA: Formal analysis, Methodology, Writing – review & editing. EV: Data curation, Formal analysis, Methodology, Writing – review & editing. MA: Data curation, Formal analysis, Methodology, Supervision, Visualization, Writing – review & editing. GQ: Methodology, Writing – review & editing. JR: Funding acquisition, Project administration, Writing – review & editing. SS: Funding acquisition, Project administration, Writing – review & editing. EM: Conceptualization, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

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

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1397204/full#supplementary-material

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Pinniped response to diadromous fish restoration in the Penobscot River Estuary

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Successful conservation of pinnipeds in the northwest Atlantic has led to increasing populations of harbor seals (*Phoca vitulina*) and gray seals (*Halichoerus grypus*) in the Gulf of Maine. Within this region, habitat restoration and diadromous fish conservation in the Penobscot River have also been top priorities for the past decade. To understand the overlap between the regional recovery of pinnipeds and the aggregative response of pinnipeds to increasing forage fish, we assessed how counts, distribution, and behavior of seals in the Penobscot River Estuary have changed over time from 2012 to 2020 and determined whether those changes were related to changes in fish biomass that are occurring as the result of diadromous fish restoration. We did not see increased counts of hauled-out seals, but consistent with regional harbor seal phenology, hauled out seal counts were highest in late spring and declined throughout the summer and into the fall. The number of swimming harbor and gray seals, analyzed as a proxy for changes in behavior, showed a stronger annual trend with an increase throughout the study period. Fish biomass was negatively associated with total number of hauled out seals and swimming gray seals but positively associated with swimming harbor seals. We also documented the potential displacement of harbor seals when gray seals are present. Together, these results begin to provide insights into how regional conservation and local restoration efforts interact to affect multiple trophic levels in an ecosystem. Continued monitoring of predator-prey interactions, along with diet and movement studies, will further elucidate seal aggregative response to increasing prey species in this system and the potential impact of recovering predator populations on restored prey populations. Knowledge gained regarding pinniped response to increasing fish biomass has important implications for other systems with ongoing conservation measures that aim to improve habitat, decrease exploitation, or recover protected species. Studies like these can be critical for finding paths forward to reconcile the potentially competing objectives of marine mammal protection and fish restoration.

KEYWORDS

fish biomass, gray seal, harbor seal, predator-prey interactions, protected species, recovery, river restoration

1 Introduction

Habitat restoration and conservation efforts have led to many successful recovery stories worldwide. These success stories often result in unintended consequences, such as increasing interaction between protected species and humans, or negative impacts to vulnerable, protected prey populations following protected predator recovery (Yodzis, 2001; Marshall et al., 2016). Ecosystem-based management has been proposed as one solution to these challenges (Okey and Wright, 2004; Wells et al., 2020), and progress towards its implementation has been made through the development of ecosystem models that account for predator-prey interactions (Townsend et al., 2019). Yet, balancing the competing needs of multiple protected species with human use is complicated by persistent gaps in knowledge surrounding food web structure (Pringle and Hutchinson, 2020), particularly in recovering systems (Vander Zanden et al., 2006). Gaining a better understanding of how predators and prey both respond to habitat restoration efforts could ultimately increase our ability to successfully and adaptively manage natural resources while promoting overall ecosystem health.

In the Northeast United States (U.S.), seals occupy the role of top or near-top predators in many coastal ecosystems that are the focus of contemporary restoration and conservation efforts (Hayes et al., 2022). Seals, which were historically hunted to near or complete local extirpation, have been generally increasing in the region since federal legislation mandating protection of all marine mammals in U.S. waters was passed in 1972 (Roman et al., 2013; Hayes et al., 2022). Harbor seals (*Phoca vitulina*) were the first to experience population growth (Gilbert et al., 2005), followed by immigration and rapid population growth of gray seals (*Halichoerus grypus*) (Wood et al., 2022). More recently, as gray seal numbers continue to grow, the harbor seal population has appeared to be steady or in decline (Sigourney et al., 2021; Hayes et al., 2022). While gray and harbor seals are often found hauled out together and exhibit site fidelity to the same locations, gray seals have also displaced harbor seals at some sites (Murray, 2008; Pace et al., 2019), which could be a factor in the recent decline of harbor seal population growth rates (Waring et al., 2015).

The growth of seal populations in the Northeast U.S. has occurred alongside numerous other conservation efforts in the region, including many focused on recovering depleted fish populations. Although the recovery of healthy prey populations can support the growth and recovery of predator populations, these efforts may at times be perceived as in conflict, with predator population growth inhibiting prey recovery. For example, gray seals are often blamed for the failed recovery of cod (*Gadus morhua*) in Canada (Chouinard et al., 2005). In the Pacific Northwest, pinniped consumption may negatively impact or prevent the recovery of populations of salmonids, steelhead trout (*Oncorhynchus mykiss irideus*), and Pacific herring (*Clupea pallasii*), even if these species comprise a small percentage of pinniped diet (Berejikian et al., 2016; Nelson et al., 2023; Moore et al., 2024). These interactions and their impacts are complex; the scale of impact can be dependent on the periodicity of migration for diadromous species (Falkegård et al., 2023), and the direction of impact can vary from negative to positive depending on interacting bottom-up and indirect effects of predation (Conwell et al., 2024; Trzcinski et al., 2024). It is therefore challenging to predict how recovering populations of prey will impact predators and vice versa.

The Penobscot River Estuary, the largest watershed in the state of Maine in the Northeast U.S., provides an opportunity to examine how protected predators respond to major habitat restoration and fish conservation efforts. In addition to harbor and gray seals, the Penobscot River is also home to 12 species of diadromous fish, all of which have experienced significant population declines due to dam construction, pollution, and overfishing (Saunders et al., 2006; Bernier, 2017). Along with the declines in diadromous fish populations, loss or reduction of ecological services, such as regulating and provisioning estuary and marine food webs, have also occurred (Ouellet et al., 2022). With the goal of restoring diadromous fish runs and their ecological services while balancing the need for hydropower production, major restoration efforts have included the removal of two dams in 2012 and 2013, the installation of the river's first fish lift in 2014, and the construction of a nature-like fish bypass at a second dam in 2016 (NRCM, 2019).

Restoration and conservation efforts in the Penobscot River have resulted in increasing diadromous fish use of the river and estuary each year (Gardner et al., 2013; Scherelis et al., 2019; Stevens et al., 2023). Fish counts at the river's southernmost dam reveal significant increases in blueback herring (*Alosa aestivalis)* and alewives (*Alosa pseudoharengus*), collectively known as river herring, since dam removal began in 2012 (MDMR, 2018, 2019). Similarly, fish biomass in the estuary, as estimated by hydroacoustic surveys, has been increasing since 2012 during a period of diadromous fish restoration, with more areas of high fish density appearing in later years (Stevens et al., 2023). The estuary biomass is a complex composed of mainly Clupeidae species which are known forage fish for seals in the Northwest Atlantic (Bowen and Harrison, 1996; Hammill et al., 2014; Sette et al., 2020). Accordingly, anecdotal reports of seals have increased as fish populations have recovered, along with concern regarding the impacts of these predators on fish species of conservation concern in the river. Some studies have reported increased observations of seal predation on diadromous fish, primarily Atlantic salmon (Kusnierz et al., 2014), while others suggest that increasing forage fish may provide protection to adult salmon against seal predation (Leach et al., 2022).

While habitat restoration and conservation efforts in rivers and estuaries have often focused on diadromous fish, the bottom-up effects of ecological restoration on fish predators in these systems remains understudied. This study therefore aims to investigate the overlap between the regional recovery of pinnipeds and the aggregative response of pinnipeds to increasing forage fish populations. Our objectives were to: 1) assess how counts, distribution, and behavior of seals in the Penobscot River Estuary have changed over time, seasonally and annually, from 2012 to 2020; and 2) determine if these changes are related to changes in fish biomass. Because the response of predators to increasing prey could include an increase in presence or a shift in behavior, we evaluated counts of hauled out seals to assess changes in relative abundance over time and evaluated the number of animals that were swimming as a proxy for behavior. Considering the divergent recovery trajectories of gray seals and harbor seals in the region, we used two years of species-specific data to evaluate species-specific interactions and relationships with fish biomass over time. Knowledge gained regarding pinniped response to increasing fish biomass could improve our understanding of current and potential future impacts of prey-focused ecological restoration on predators. Lessons learned also could be applicable to other systems with ongoing conservation measures that aim to improve habitat, decrease exploitation, or recover protected species. This insight could inform future management decisions on how to best reconcile the potentially competing objectives of marine mammal protection and fish restoration.

2 Materials and methods

2.1 Data collection

Boat-based transect surveys of the Penobscot River Estuary were conducted by the National Oceanic and Atmospheric Administration (NOAA) from 2012 through 2020 to assess fish and seal abundance and distribution. As described in Lipsky et al. (2019), hydroacoustic surveys of the Penobscot River Estuary were conducted from April through October, as weather allowed, each year (Supplementary Table S1). Surveys were scheduled weekly through mid-June, during the peaks of several diadromous fish runs, and biweekly throughout the remainder of the season. Beginning on a flood tide, surveys followed pre-determined transect lines from south to north (Figure 1). This section of the river is approximately 50 kilometers long (Lipsky et al., 2019).

Along the transect, fish abundance and distribution were characterized via hydroacoustic data gathered using mobile split beam echosounders at 38kHz and 120kHz frequencies (O'Malley et al., 2017). Concurrently, both sides of the river, as well as the area in front of the boat, were continuously scanned for marine mammal sightings using 10x50 magnification binoculars, and the time, species, number of animals, and behavioral data for all sightings were recorded. In addition, the number of hauled out seals were recorded at three major seal haul-outs along the survey route: Odom Ledge, Fort Point Ledge, and Eastern Shore (Figure 1). Odom Ledge (44° 30' 57"N 68° 48' 03"W) and Fort Point Ledge (44° 27' 38"N 68° 48' 35"W) are emergent ledges at most tide heights and marked on NOAA navigational chart **US5ME26M** as navigational hazards. Eastern Shore (44° 28' 11"N 68° 47' 13"W) is an area characterized as emergent rocky habitat near low tide (also described as a navigational hazard on NOAA charts). We acknowledge that since these surveys were designed to assess relative seal abundance, these counts represent a minimum number present, not absolute abundance.

Prior to 2019, the incidental take of marine mammals during this work was authorized by Letter of Authorization #2016-22582 issued by the National Marine Fisheries Service (NMFS) and haul-outs were not directly approached closer than 500 meters for targeted assessment of seals. During 2019 and 2020, haul-outs were approached to within 100 meters and photographs were taken using a Canon 7D Mark I camera with a 100-400 millimeter lens so that counts and species identification could be verified after the survey. This pinniped-focused research was authorized by NMFS permit #21719-01.

2.2 Data filtering

Site-specific factors including time from low tide, time of day, and wind have been shown to affect the number of seals hauled out at a given time (Schneider and Payne, 1983; Yochem et al., 1987; Watts, 1996; Raposa and Dapp, 2009). Our surveys typically occurred in the morning, began at Fort Point at low tide, and could only be conducted in relatively good weather, so these potentially confounding factors were partially controlled for in the survey design. The data were filtered to further limit variation in environmental effects so that we could conservatively assess trends in counts over time.

Typically, seal surveys in our region are conducted within two hours on either side of low tide (Gilbert et al., 2005; Waring et al., 2015; Sigourney et al., 2021), as this is when the greatest number of animals tend to be hauled out on land (Watts, 1996). We therefore excluded any surveys that did not begin within two hours of low tide from the analysis. Approximate time from low tide was calculated for each survey using the "rtide" package (v0.0.5; Thorley et al., 2018) and R version 4.4.1 in RStudio (v2024.04.2 + 764) and historic tide data from a station near Fort Point.

Environmental variables, such as fog, sea state, and wind, were not recorded during the surveys, so our ability to directly account for the effects of these environmental factors is limited. The hydroacoustic survey, however, has informal requirements for sea state because high winds and rough seas are not conducive to quality acoustic data collection due to the generation of acoustic noise (Simmonds and MacLennan, 2008). Therefore, we assumed that all surveys were conducted in relatively similar weather conditions in the absence of high winds and rough seas. To verify this assumption, approximate wind speed data for each sighting were pulled from NOAA's National Climatic Data Center's (NCDC) recordings from a sensor at Bangor International Airport (approximately 38 kilometers from the start of the survey). An average wind speed was calculated for the time we surveyed the southern section of the estuary during each survey using the NCDC data. Most surveys occurred at wind speeds less than 5 kilometers per hour, and the highest estimated wind speed was 8.06 kilometers per hour. A negative binomial generalized linear model, which was used to account for overdispersion of the data, showed that there was not a significant relationship between wind speed and seal counts ($p = 0.611$) and no outliers were detected (MASS package v.7.3-61; Venables and Ripley, 2002). Therefore, we did not exclude any surveys due to wind speed.

Finally, incomplete surveys missing data from any of the three primary seal haul-outs or a biomass estimate were excluded. In total, this conservative filtering approach retained 93 out of 134 surveys for the analyses across the full time series (Supplementary Tables S2, S3). Similar filtering of the 2019 and 2020 photo-count data, which included species-level information on hauled out seals, retained 20 out of 24 surveys (Supplementary Table S4).

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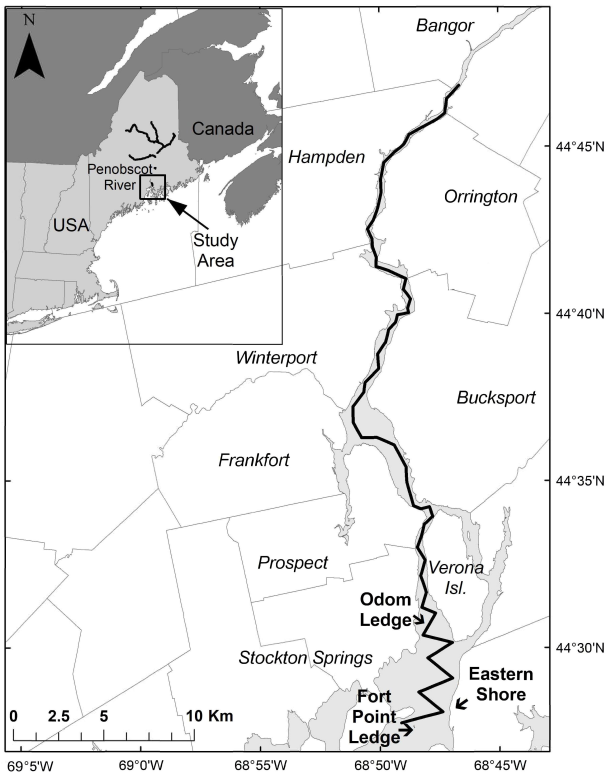

FIGURE 1
Map of transect survey route with major seal haul-out locations labeled in relation to the Northeast U.S.

2.3 Data analysis

2.3.1 Temporal analysis of hauled out and swimming seals

To assess change in seal abundance and behavior in the Penobscot River Estuary over time, as well as whether those changes were related to changes in fish biomass, we analyzed the total number of hauled out seals and number of swimming gray and harbor seals per survey. Seal assessment methods typically estimate abundance using hauled out seal counts with a correction factor to account for the number of seals at sea (Gilbert et al., 2005; Waring et al., 2015; Sigourney et al., 2021), and use in-water counts to characterize distribution (Herr et al., 2009; Vincent et al., 2017) or behavior (e.g., in response to underwater sound; Ampela et al., 2021) at sea. Accordingly, we analyzed our counts of hauled out and swimming animals separately, using hauled out seal counts to represent relative abundance (without a correction factor) and counts of swimming seals to explore changes in behavior. Our surveys took place near low tide, when most seals are expected to be hauled out on the tidally emergent ledges in this system. As such, changes in the number of swimming seals during the survey could reflect changes in behaviors including foraging, socializing, and transiting. Because species-level identification can be difficult at a distance and the survey originally did not approach haul-outs for targeted assessments of seals, all analyses that include data from 2012 to 2018 focus on the total number of hauled out seals (i.e., counts of both gray and harbor seals) instead of specifying species. Swimming animals, however, were often documented closer to the survey vessel where they could be easily identified, so swimming counts for each species were analyzed separately. Each survey date was associated with a standard week and an estimated value of fish biomass present in the estuary, calculated by Stevens et al. (2023) using the hydroacoustic data collected along the survey transect line.

We used generalized linear models (GLMs) to assess the effect of year, standard week, and fish biomass on seal counts. We also evaluated the interaction between biomass and the two temporal variables, to assess if the effect of biomass on seals varied throughout the survey season or between years. The swimming seal models further assessed whether the total number of hauled out seals was related to the number of animals swimming. All covariates were centered (by subtracting the mean) and scaled (by dividing by the standard deviation) for modeling analysis, so that regression coefficients could be directly compared between covariates measured on different scales (Schielzeth, 2010). We assessed biomass to be skewed so we transformed this covariate to $\log_{10}$ biomass (logBiomass). We assessed our models for covariate collinearity using variance inflation factors (VIF) and used simulation-based tests for overdispersion, zero-inflation, and temporal autocorrelation (DHARMa package v.0.4.6; Hartig, 2022). When data were not overdispersed, we ran GLMs using a Poisson distribution appropriate for positive integer count data. When overdispersion was detected, GLMs were run using a negative binomial distribution (MASS package v. 7.3-61; Venables and Ripley, 2002). When zero-inflation was detected, we ran a zero-inflation GLM with a negative binomial distribution (pscl package v. 1.5.9; Jackman, 2024). From the global model for each dataset, we conducted all-subsets model selection (MuMIn package v.1.48.4; Bartoń, 2024) and ranked models based on the corrected Akaike's Information Criterion (AICc). We report model fit as Nagelkerke's pseudo-R^2 for Poisson and negative binomial models and as R^2 based on the residual variance divided by the total variance for zero-inflated models (performance package, v. 0.12.2; Lüdecke et al., 2021). The goal of our model selection process was to identify informative covariates and evaluate their effect on seal counts. Covariate importance was evaluated based on standardized effect sizes and Akaike weights (Schielzeth, 2010).

2.3.2 Species-specific analysis of hauled out seals

Using similar methods, the 2019 and 2020 photo-count data were used to explore species-specific relationships between the number of hauled out seals, week, and biomass. Counts of gray seals were also included as a covariate in the harbor seal model, and vice versa, to explore whether interspecific interactions affect counts of hauled out seals.

3 Results

Hauled out and swimming seals were observed during 96.77% and 78.49% of surveys (n = 93), respectively. Across all surveys from 2012 to 2020, on average, 31.83 (sd: 23.73; range: 0-97) seals were observed per survey on haul-outs and 4.51 (sd: 4.87; range: 0-19) seals were observed per survey swimming. Among the swimming seals, which could be identified to species, 78.28% were harbor seals and 21.72% were gray seals across the full dataset. Similarly, when hauled out seals were identified to species through photo-analysis, an average of 80.39% (sd: 21.41; range: 45.45-100%) and 81.96% (sd: 15.39; range: 50.67-100%) of the hauled out seals counted per survey in 2019 and 2020, respectively, were harbor seals.

There was large interannual variation in seal counts across the time series, but on average, the greatest number of hauled out seals was observed at Odom Ledge (average: 17.27, sd: 16.61, range: 0-60) and Fort Point (average: 12.19, sd: 13.23, range: 0-60), with fewer seals observed at Eastern Shore (average: 2.20, sd: 4.74, range: 0-23) and other sites. Hauled out seals were observed at lesser-used rocky sites, primarily in the lower estuary, on seven days across the study period, four of which occurred in 2019 and 2020. The number of seals at Odom Ledge tended to decrease from 2012 to 2020; while the minimum number of animals appeared constant across low years, the maximum number of animals observed in years with many seals consistently decreased from 2012 to 2013 and again from 2015 to 2018 (Figure 2B). In contrast, the number of seals counted at Eastern Shore tended to increase throughout the time series, particularly after 2015, with the highest mean and median values observed in 2018 and 2020 (Figure 2C).

3.1 Temporal analysis of hauled out and swimming seals

To determine whether the number of seals in the Penobscot River Estuary changed over time and whether those changes were related to increasing fish biomass, within the context of known seasonal dynamics (e.g., breeding and molting periods), generalized linear models were used to explore the effects of year, fish biomass, and week on the total number of hauled out seals and the number of swimming gray and harbor seals counted during each survey. The number of hauled out seals was modeled using a zero-inflated negative binomial model to account for overdispersion detected in the initial Poisson model (ratio observed:expected variance = 9.91, $p < 1x10^{-15}$) and evidence of zero-inflation detected after applying a negative binomial family (ratio observed:predicted zeros = 5.56, p = 0.03). There was no evidence of temporal autocorrelation within years in the negative binomial GLM that would warrant addition of an autoregressive term (Durbin-Watson test, all $p > 0.05$). Furthermore, there no evidence of an influence of covariate collinearity in the final global model (all VIF < 3.75). The interaction terms between logBiomass and the temporal covariates were not significant in the global model, so they were removed prior to nested model selection. Subsequent model ranking revealed

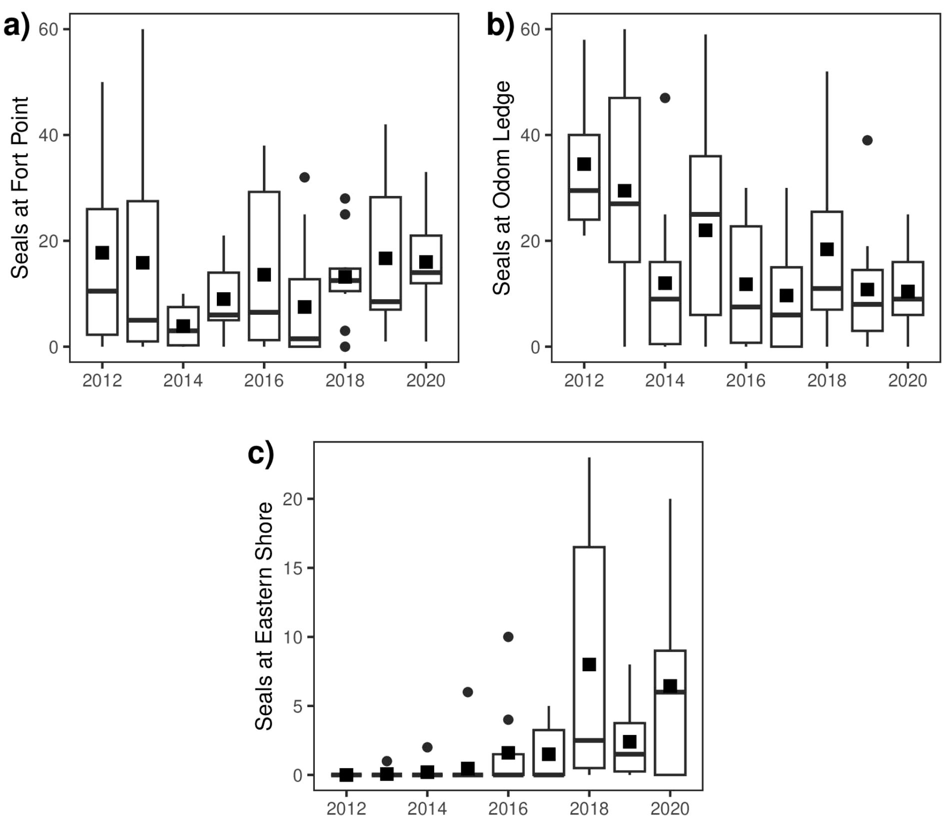

FIGURE 2
Number of seals (gray and harbor) per survey counted at three haul-out sites [**(A)** Fort Point, **(B)** Odom Ledge, and **(C)** Eastern Shore] in the Penobscot River Estuary from 2012-2020. Box plots show the median and lower and upper quartiles; black squares indicate the mean; whiskers extend to 1.5x the interquartile range; and individual dots show values falling beyond this range.

two top models with strong evidence based on Akaike weights (Tables 1, 2). The top model included only standard week, while the second top model included both standard week and logBiomass. Standard week had a negative effect, reflecting that the number of hauled out seals was highest earlier in the year and decreased throughout the surveys each year (Figure 3A). LogBiomass also had a negative effect, reflecting that fewer seals were hauled out when fish biomass was greater, but this effect was smaller and there was more variation around the relationship (Figure 3A).

The number of swimming harbor seals was also modeled using a zero-inflated negative binomial model to account for overdispersion detected in the initial Poisson model (ratio observed:expected variance = 3.53, $p < 1x10^{-15}$) and evidence of possible zero-inflation detected after applying a negative binomial family (ratio observed:predicted zeros = 1.16, p=0.35). There was no evidence of temporal autocorrelation within years after a Bonferroni correction (Durbin-Watson test: 2017 p=0.03, 2019 p=0.03, all other years $p > 0.05$). Furthermore, there was no evidence of an influence of covariate collinearity in the final global model (all VIF < 2.2). The interaction terms between logBiomass and the temporal covariates were not significant, so they were removed prior to nested model selection. Subsequent model ranking again revealed two top models with very similar support based on Akaike weights (Tables 1, 3). The top model included only year, while the second top model included both year and logBiomass. Year had a positive effect, reflecting that the number of swimming harbor seals increased over time throughout our study (Figure 3B). LogBiomass also had a positive effect, reflecting that there were more swimming harbor seals when fish biomass was greater (Figure 3B).

The number of swimming gray seals was modeled using a Poisson GLM as the initial model showed no evidence of overdispersion (ratio observed:expected variance = 1.21, p = 0.36), zero-inflation (ratio observed:predicted zeros = 0.98, p = 0.85), or temporal autocorrelation within years (Durbin-Watson test, all p >0.05). Furthermore, there was no evidence of an influence of covariate collinearity (all VIF < 2.0). The interaction term between logBiomass and year was not significant, so it was excluded prior to nested model selection. Subsequent model ranking revealed that the top model contained logBiomass, standard week, year, and the interaction term between logBiomass and week. Upon inspection of the effect plots, however, it appeared that the relationship of swimming gray seal counts with standard week and logBiomass might be nonlinear. Following a reviewer recommendation, we therefore added quadratic terms for both covariates and re-ran the model selection process, which revealed two models within 2 ΔAICc (Tables 1, 3). The top model contained the linear and quadratic terms for standard week, year, biomass, and the interaction between biomass and week. The second top model also included the quadratic term for logBiomass, but based on its effect size and Akaike weight, this quadratic term was considered less likely to be informative. The number of swimming gray seals increased across years and appeared to peak between weeks 30 and 35 (Figure 3C). The observed relationship between counts of swimming gray seals and logBiomass appeared to be negative (Figure 3C).

3.2 Species-specific analysis of hauled out seals

To determine whether the changes in relative abundance were driven by species-specific patterns, GLMs were used to explore the effects of week, biomass, and presence of the other seal species on counts of hauled out harbor and gray seals during 2019 and 2020, when photographs of haul-outs enabled species identification. The harbor seal data were modeled using a negative binomial GLM to account for overdispersion detected in an initial Poisson model (ratio observed:expected variance = 6.86, $p < 1x10^{-15}$). There were no zero-counts, evidence of temporal autocorrelation in the dataset (Durbin-Watson test, all p>0.05), or evidence of an influence of covariate collinearity (all VIF < 1.4). Model ranking revealed two top models within 2 ΔAICc with strong evidence based on Akaike weights (Tables 1, 4). Both of the top models included a negative effect of standard week, reflecting that harbor seal counts decreased throughout the survey season. One of the top models also included a slightly positive effect of the number of gray seals present, though this trend appeared driven by a few surveys with a large number of gray seals (Figure 4A).

The gray seal data were also modeled using a negative binomial GLM to account for overdispersion detected in an initial Poisson model (ratio observed:expected variance = 6.40, $p < 1x10^{-15}$). The model showed no evidence of zero-inflation (ratio observed: predicted zeros = 1.01, p = 1), temporal autocorrelation (Durbin-Watson test, all p>0.05), or influence of covariate collinearity (all VIF < 2.7). Because our swimming gray seal model provided evidence for a nonlinear relationship with standard week, we included a quadratic term for standard week in this model as well. The only top model within 2 ΔAICc included the linear and quadratic terms for standard week (Tables 1, 4). Gray seal counts appeared to increase throughout the survey season starting around week 20, peaking between weeks 30 and 35, and declining for the rest of the season (Figure 4B).

To further explore the relationship between the numbers of gray seals and harbor seals, we considered the spatial distribution of the two species when hauled out in the estuary in 2019 and 2020 (Figure 5). Both gray and harbor seals utilized Fort Point and Odom Ledge, but only harbor seals were observed at Eastern Shore. Harbor seals were observed at Eastern Shore in the late summer and early fall, with the greatest increases in numbers typically observed during times when gray seal counts increased at the other haulouts.

4 Discussion

The Penobscot River Estuary survey has provided a unique opportunity to study long-term trends in rebounding seal populations in a system that is recovering a forage base of diadromous fish. Separate conservation efforts targeted at predators and prey in this region have both reported individual success (Hayes et al., 2022; Stevens et al., 2023), but the interaction of the two programs had not previously been studied. By considering these putative predator-prey relationships, as well as potential interactions between the two seal species that are recovering in this system,

TABLE 1 Model coefficients for the top models exploring drivers of the number of hauled out seals, swimming harbor seals, and swimming gray seals during surveys of the Penobscot River Estuary from 2012-2020, and the numbers of hauled out harbor and gray seals in 2019-2020.

	Count Model				Zero-Inflation Model				
	Estimate	Standard Error	Z value	Pr(>|Z|)	Estimate	Standard Error	Z value	Pr(>|Z|)	R^2
Total Hauled Out Seals, 2012-2020, Model 1									0.99
(Intercept)	3.349	0.070	48.168	$<2x10^{-16}$	-4.589	1.308	-3.507	0.001	
Week	-0.527	0.072	-7.295	$2.98x10^{-13}$	1.621	0.953	1.701	0.089	
Total Hauled Out Seals, 2012-2020, Model 2									0.99
(Intercept)	3.344	0.069	48.183	$<2x10^{-16}$	-7.075	4.199	-1.685	0.092	
Week	-0.528	0.073	-7.252	$4.09x10^{-13}$	3.622	2.861	1.266	0.206	
Log(Biomass)	-0.086	0.068	-1.249	0.212	1.883	1.717	1.097	0.273	
Swimming Harbor Seals, 2012-2020, Model 1									0.78
(Intercept)	1.340	0.127	10.538	$<2x10^{-16}$	-1.415	0.441	-3.212	0.001	
Year	0.508	0.121	4.194	$2.74x10^{-5}$	-0.269	0.360	-0.748	0.455	
Swimming Harbor Seals, 2012-2020, Model 2									0.78
(Intercept)	1.330	0.123	10.768	$<2x10^{-16}$	-1.413	0.475	-2.974	0.003	
Year	0.379	0.125	3.035	0.002	-0.475	0.464	-1.022	0.307	
Log(Biomass)	0.274	0.131	2.086	0.037	0.250	0.422	0.593	0.553	
Swimming Gray Seals, 2012-2020, Model 1									0.83
(Intercept)	-0.923	0.207	-4.453	$8.46x10^{-6}$	–	–	–	–	
Year	0.836	0.128	6.542	$6.07x10^{-11}$	–	–	–	–	
Week	7.178	1.592	4.509	$6.52x10^{-6}$	–	–	–	–	
$Week^2$	-6.182	1.487	-4.156	$3.24x10^{-5}$	–	–	–	–	
log(Biomass)	-0.305	0.153	-1.996	0.046	–	–	–	–	
log(Biomass):Week	0.511	0.195	2.619	0.009	–	–	–	–	
Hauled Out Harbor Seals, 2019-2020, Model 1									0.95
(Intercept)	3.664	0.081	45.159	$<2x10^{-16}$	–	–	–	–	
Week	-0.672	0.091	-7.415	$1.22x10^{-13}$	–	–	–	–	
Gray Seals	0.160	0.085	1.895	0.058	–	–	–	–	
Hauled Out Harbor Seals, 2019-2020, Model 2									0.91
(Intercept)	3.679	0.088	41.63	$<2x10^{-16}$	–	–	–	–	
Week	-0.623	0.093	-6.71	$1.94x10^{-11}$	–	–	–	–	
Hauled Out Gray Seals, 2019-2020, Model 1									0.65
(Intercept)	1.788	0.226	7.906	$2.66x10^{-15}$	–	–	–	–	
Week	9.198	2.463	3.735	$1.88x10^{-4}$	–	–	–	–	
$Week^2$	-8.676	2.417	-3.590	$3.31x10^{-4}$	–	–	–	–	

Tested covariates across most models included week, year, log_{10}(biomass), and the interaction between biomass and the two temporal covariates. The total number of hauled out seals was also included as a covariate in the models of swimming seals, quadratic terms for week and biomass were evaluated in only the model of swimming gray seals and a quadratic term for week was evaluated in the 2019-2020 gray seal model. Counts of harbor seals were included as a covariate in the 2019-2020 gray seal model, and vice versa; year and interaction terms were not included in these two model sets. R^2 is reported as the residual variance divided by the total variance for zero-inflated models (performance package, v. 0.12.2; Lüdecke et al., 2021) and as Nagelkerke's pseudo-R^2 for Poisson and negative binomial models. Model coefficients for the other models within 2 ΔAICc of the top model are reported in Supplementary Table S8.

TABLE 2 Model ranking of generalized linear models evaluating the effects of log_{10}(biomass), standard week, and year on the number of hauled out seals per survey in the Penobscot River Estuary, 2012-2020.

							Log-Likelihood	AICc	ΔAICc	Akaike weight
1.	Seals~			Week			-390.8	792.3	0.00	0.44
2.	Seals~	Biomass	+	Week			-388.8	792.9	0.57	0.33
3.	Seals~	Biomass	+	Week	+	Year	-387.1	794.3	1.98	0.16

Models are ranked by the corrected Akaike's Information Criterion (AICc). Models within 2 ΔAICc of the top model are shown here; see Supplementary Table S5 for data on the full set of tested models.

we contribute to the ongoing conversation about complex, sometimes unintended consequences, of marine mammal recovery (Cammen et al., 2019).

In our analysis, we utilized complementary data collection of predators using visual counts and putative prey through hydroacoustic measurements. While neither effort is meant to estimate absolute population size, our ability to track the relative abundance change is powerful due to the repeatability of the survey that follows the same route, at relatively the same point in the tide cycle, in similar weather conditions, allowing observations of changes over time that provide ecological insights.

Throughout our study, hauled out seal counts, assessed both as total counts of seals for the full time series and at the species-level for harbor and gray seals during the two most recent years, did not demonstrate increases over the time period but were most closely related to seasonal phenology. Appropriately since the majority of hauled out seals were harbor seals, we found total seal counts generally followed patterns consistent with harbor seal biological and life-cycle milestones. Seal counts peaked early in our survey season, which corresponds with harbor seal pupping season in May and June, when harbor seals move into the Gulf of Maine and tend to spend more time on the rocks (Brown and Mate, 1983). Seal counts were lowest in fall, consistent with dispersal to southern New England and mid-Atlantic waters (Hayes et al., 2022). For gray seals in 2019 and 2020, counts appeared to increase starting in mid-May (around week 20), peaked in late July and August (between weeks 30 and 35), and then declined. Gray seals in the U.S. and Canada experience a spring molting season between mid-April and June (Lesage and Hammill, 2001; Pace et al., 2019). Gray seals appear to move into our study area after dispersing at the end of their molting season and before they congregate at pupping colonies for their winter pupping season (Lesage and Hammill, 2001). Year was not included in any of our top models, however, it should be noted that in 2012, only 4 surveys were retained for this analysis, most of which occurred early in the season. Similarly, 9 of the 16 surveys conducted in 2013 occurred early in the season. It is possible that the wide variation and high means seen from those years in Figure 2 are contributing to the lack of detectable trend across years.

The periodicity of migration for diadromous species to and from the ocean creates a critical overlap in space and time for predators and their prey, which may limit the recovery of depressed populations despite restoration measures (Falkegård et al., 2023). In the Penobscot River Estuary, the peak in seal counts overlaps with the timing of the diadromous fish migrations. Adult Atlantic salmon migrating from the ocean into the river typically peak between mid-May and early July (weeks 20-27), adult river herring migration peaks between mid-May and mid-June (weeks 20-25), and American shad migration peaks between late May through late June (weeks 22-26) (Bruchs et al., 2018). Downstream migration of juvenile Atlantic salmon smolts also occurs in spring (McCormick et al., 1998; Saunders et al., 2006; Stich et al., 2015). This overlap in presence occurs at a time of high energetic demand for female harbor seals that must alter their behavior, including foraging, to support lactation and their own metabolism (Boness et al., 1994; Bowen et al., 2001; Schwarz et al., 2018).

To indirectly explore changes in seal behavioral trends in the Penobscot River Estuary throughout and following restoration, we analyzed counts of swimming harbor and gray seals across the time series. For both species, we observed increasing numbers of swimming seals from 2012 to 2020. For gray seals, we found that counts of swimming animals peaked in late July and August (between weeks 30 to 35), similar to the counts of hauled out gray seals in 2019 and 2020. For this species, it is possible that the increasing number of swimming seals reflects the increasing size of the population in the northwest Atlantic (Hayes et al., 2022). The fact that standard week and the total number of hauled out seals, which is consistent with regional harbor seal trends, were not strongly related to counts of swimming harbor seals is a promising indication that these counts represent ecologically-relevant behavior, not just population size in the river. The increase in swimming harbor seals, however, is difficult to interpret using our data because a swimming seal may be engaging in a variety of behaviors, including foraging, transiting, or socializing. To complicate matters, we would expect seals to spend varying amounts of time hauled out or in the water throughout the season. For example, we might expect more seals to be hauled out during the pupping and molting seasons (Stobo and Fowler, 1994), more males to spend time in the water during the mating season (Hayes et al., 2006), and the presence of gray seals could alter harbor seal haul-out patterns and increase their susceptibility to flushing from haul-out sites when disturbed (Murray, 2008; Russell et al., 2015). Additionally, because our study system is not closed, it is also possible that the increase in swimming harbor seals is the result of seals coming into the survey area from nearby regions. There are several other harbor seal haul-outs in the upper part of Penobscot Bay within 10 to 25 kilometers of our study site, a distance easily traveled by harbor seals during

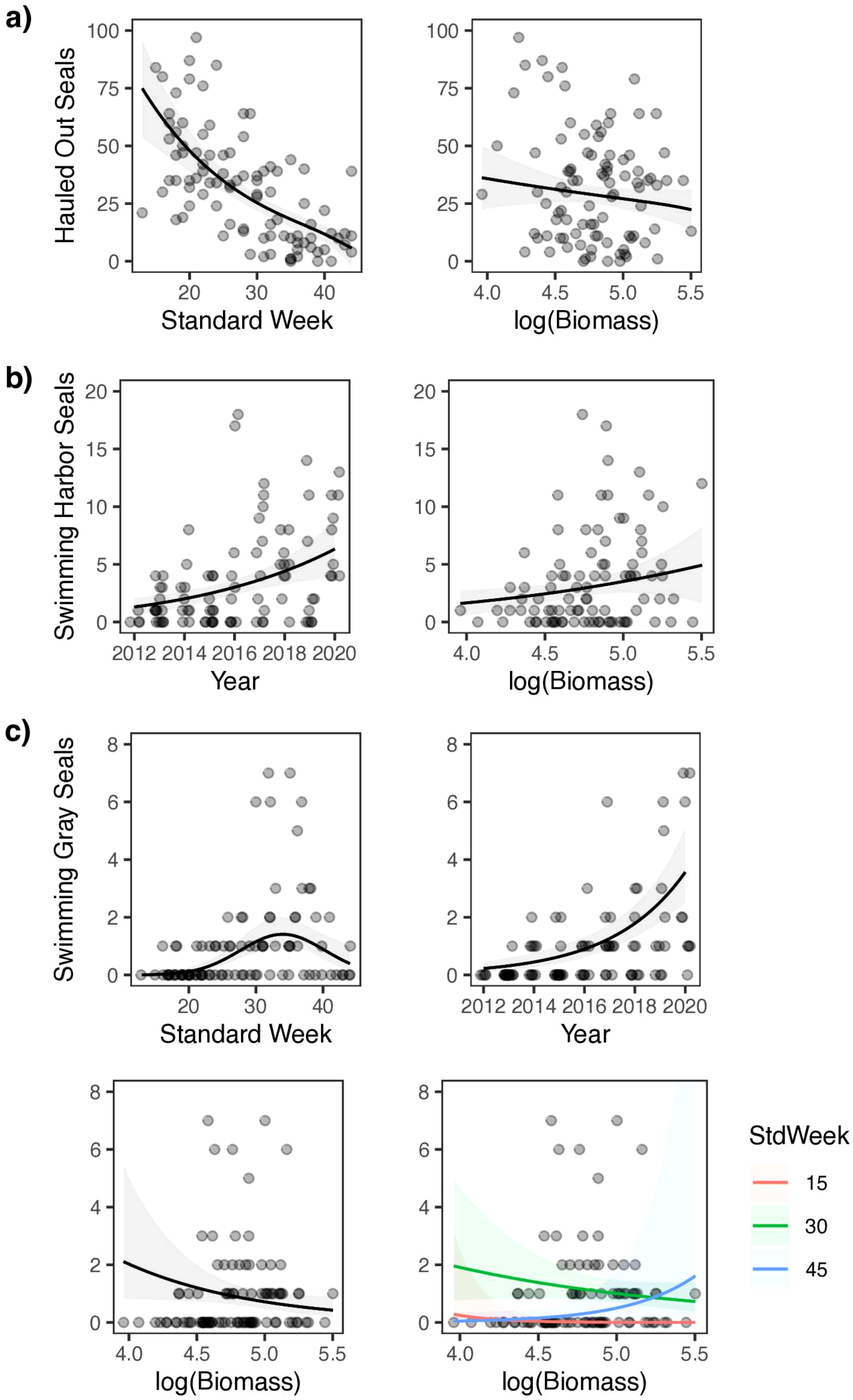

FIGURE 3
Partial effect plots showing the effects of year, log_{10}(biomass), standard week, and the interaction of log_{10}(biomass) with the temporal covariates on the **(A)** total number of hauled out seals, **(B)** number of swimming harbor seals and **(C)** number of swimming gray seals, counted during surveys of the Penobscot River Estuary, 2012 to 2020. Biomass refers to fish biomass in the estuary, as estimated by hydroacoustic surveys by Stevens et al. (2023). Only covariates found in the top two models are plotted. Trend lines with 95% confidence intervals depict the predicted relationships from models 2 for the total number of hauled out seals and the number of swimming harbor seals, and from model 1 for the number of swimming gray seals (see Tables 1–3 for additional model information). Standard weeks correspond to seasons as follows: spring (March-June) includes weeks 17-26; summer (July-August) includes weeks 27-35; and fall (September-October) includes weeks 36-44.

TABLE 3 Model ranking of generalized linear models evaluating the effects of the number of hauled out seals, log_{10}(biomass), standard week, and year on the numbers of swimming harbor and gray seals per survey in the Penobscot River Estuary, 2012-2020.

											Log-Likelihood	AICc	ΔAICc	Akaike Weight
1.	Harbor Seals~							Year			-209.8	430.2	0.00	0.29
2.	Harbor Seals~			Biomass	+			Year			-207.5	430.3	0.11	0.28
3.	Harbor Seals~			Biomass	+	Week	+	Year			-205.7	431.6	1.33	0.15
4.	Harbor Seals~	All Seals	+	Biomass	+			Year			-205.9	431.9	1.67	0.13
1.	Gray Seals~			Biomass	+	Week+ $Week^2$	+	Year	+	Bio: Wk	-88.8	190.5	0.00	0.36
2.	Gray Seals~			Biomass+ $Biomass^2$	+	Week+ $Week^2$	+	Year	+	Bio: Wk	-88.3	191.9	1.38	0.18

Models are ranked by the corrected Akaike's Information Criterion (AICc). Models within 2 ΔAICc of the top model are shown here; see Supplementary Table S6 for data on the full set of tested models.

foraging trips (Lowry et al., 2001; Cunningham et al., 2008; Sharples et al., 2012). Expanding the geographic scope of this study in the future, for example, by placing tags on seals from nearby haul-outs, could help reveal whether the estuary has become a more desirable foraging location for seals located elsewhere in this part of the Gulf of Maine. Furthermore, diet studies will also be important to confirm the predator-prey interactions that we are assuming in our interpretation of the data and to more clearly understand the potential impact of seal predation on continued fish recovery efforts.

In addition to describing how seals in the Penobscot River have changed over time, our study set out to test if these changes are related to changes in fish biomass that have occurred as a result of river restoration. LogBiomass was found among the top models for total hauled out seals and swimming seals of both species; however, its effect size was typically smaller than that reported for the temporal covariates, reflecting more noise around the predicted relationships. In the models that included logBiomass, its effect was slightly negative for total hauled out seals and swimming gray seals but slightly positive for harbor seals. Here and elsewhere, the complex relationships between seals and their prey complicate efforts to understand the impacts of fish abundance on pinniped populations (Li et al., 2010). Studies in the Pacific Northwest have shown that the response of seals to prey aggregations, for example, during herring spawning, can vary depending on the size of the aggregation, prey energy density, and the availability of alternative prey (Thomas et al., 2011; Lance et al., 2012). Other studies have not found a strong relationship between forage fish abundance and predator productivity, especially for highly mobile, generalist predators, such as seals (Hilborn et al., 2017; Free et al., 2021). However, seals also are central place foragers, and increases in local prey abundance near breeding sites could lead to benefits through reduced foraging effort (Free et al., 2021). For example, declines in pup production of Northern fur seals (*Callorhinus ursinus*) in Alaska have been attributed in part to fisheries-depletion of important prey (Short et al., 2021). As a result of the depletion of local prey resources, lactating females must expend increased foraging effort during longer foraging trips, likely contributing to reduced pup growth and survival at St. Paul Island (Short et al., 2021; McHuron et al., 2023). In the Penobscot River Estuary, where fish trends are reversed as a result of river restoration efforts, it is thus possible that increasing local prey abundance could lead to reduced foraging effort and subsequent increasing pinniped productivity and pup survival. Our data do not allow us to test this hypothesis and instead reflect a weak relationship between relative abundance and fish biomass. This may be due to the mismatch between the spring peak in seal counts and summer peak in biomass, so it is possible that seal counts could begin to increase more significantly over time.

In addition to predator-prey interactions, we considered the impact of ecological restoration on interactions between predator

TABLE 4 Model ranking of generalized linear models evaluating the effects of log_{10}(biomass), standard week, and the number of gray and harbor seals on the numbers of hauled out harbor and gray seals per survey in the Penobscot River Estuary, 2019-2020.

					Log-Likelihood	AICc	ΔAICc	Akaike Weight
1.	Harbor Seals~	Week	+	Gray Seals	-80.7	172.1	0.00	0.44
2.	Harbor Seals~	Week			-82.5	172.5	0.39	0.36
1.	Gray Seals~	Week+ $Week^2$			-58.0	126.8	0.00	0.64

Models are ranked by the corrected Akaike's Information Criterion (AICc). Models within 2 ΔAICc of the top model are shown here; see Supplementary Table S7 for data on the full set of tested models.

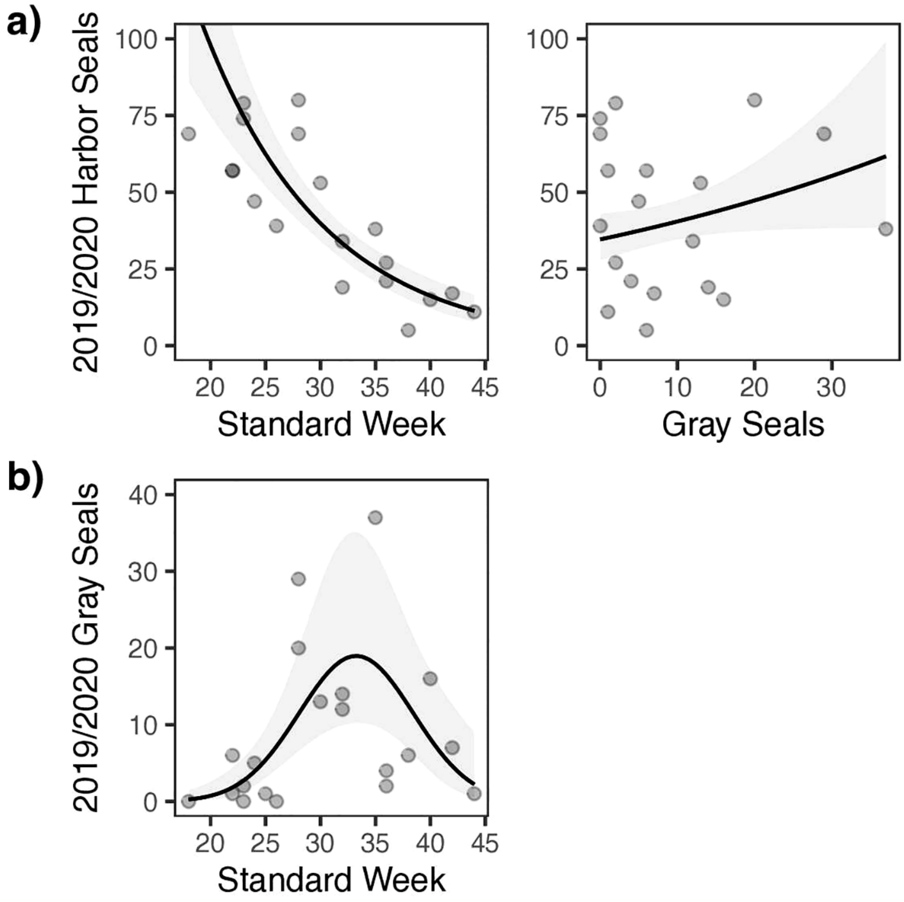

FIGURE 4
Partial effect plots showing the effects of standard week and the other seal species on the number of hauled out **(A)** harbor seals and **(B)** gray seals counted using photographs of haul-outs during surveys of the Penobscot River Estuary, 2019 to 2020. Only covariates found in the top model are plotted. Trend lines with 95% confidence intervals depict the predicted relationships from model 1 for both species (see Tables 1, 4 for additional model information). Standard weeks correspond to seasons as follows: spring (March-June) includes weeks 17-26; summer (July-August) includes weeks 27-35; and fall (September-October) includes weeks 36-44.

species. Though there have been a limited number of reported instances of direct antagonistic interactions between gray and harbor seals (van Neer et al., 2015; Westphal et al., 2023), we assume most ecological interactions between the two species occur as a result of indirect competition for food and/or haul-out space. During our surveys in 2019 and 2020, the first sighting of gray seals at Fort Point and Odom Ledge coincided with a decline in harbor seals at Fort Point Ledge, which reversed when gray seals left near the end of the season. Coincident with the first sighting of gray seals on Fort Point Ledge, we also observed the first sightings of harbor seals at Eastern Shore, located across the river from Fort Point Ledge, suggesting harbor seals may move to this haul-out when gray seals are present. The potential displacement of harbor seals by gray seals when they first arrive at haul-out sites in the estuary is consistent with inter-specific interactions observed between gray and harbor seals elsewhere (Murray, 2008; Pace et al., 2019; Sette et al., 2020). There are also some indications in our dataset that this displacement began earlier than we documented it in 2019; the number of seals observed at Eastern Shore began to increase around 2016 (Figure 2C), suggesting that gray seals may have started increasing in the estuary around that time.

During this study, individual gray seals were documented on haul-outs only four times from 2012 to 2018, though as we have mentioned, species level identification in those years may not have been accurate as haul-outs were not specifically approached as in 2019 and 2020. The presence of multiple gray seals at the haul-out sites was first documented on our July 8, 2019 survey. Throughout the rest of the 2019 season, we observed gray seals hauled out on three major haul-outs in the survey area, with as many as 26 gray seals seen at one haul-out site in one day. While this influx of gray seals appears to be new for the Penobscot River Estuary, it reflects similar changes that have been documented throughout the Gulf of Maine (Gilbert et al., 2005; Pace et al., 2019).

We recognize that hauled out and swimming pinnipeds can be difficult to detect and count from a distance and expect that imperfect detection due to availability bias and perception bias during our surveys may have led to some of the observed variation in seal counts during our study. For example, variation in seal behavior, dive duration, environmental conditions, and observer experience can affect the probability that a seal will be detected during a survey, meaning that seal presence may not have been accurately and consistently captured. Additionally, the number of

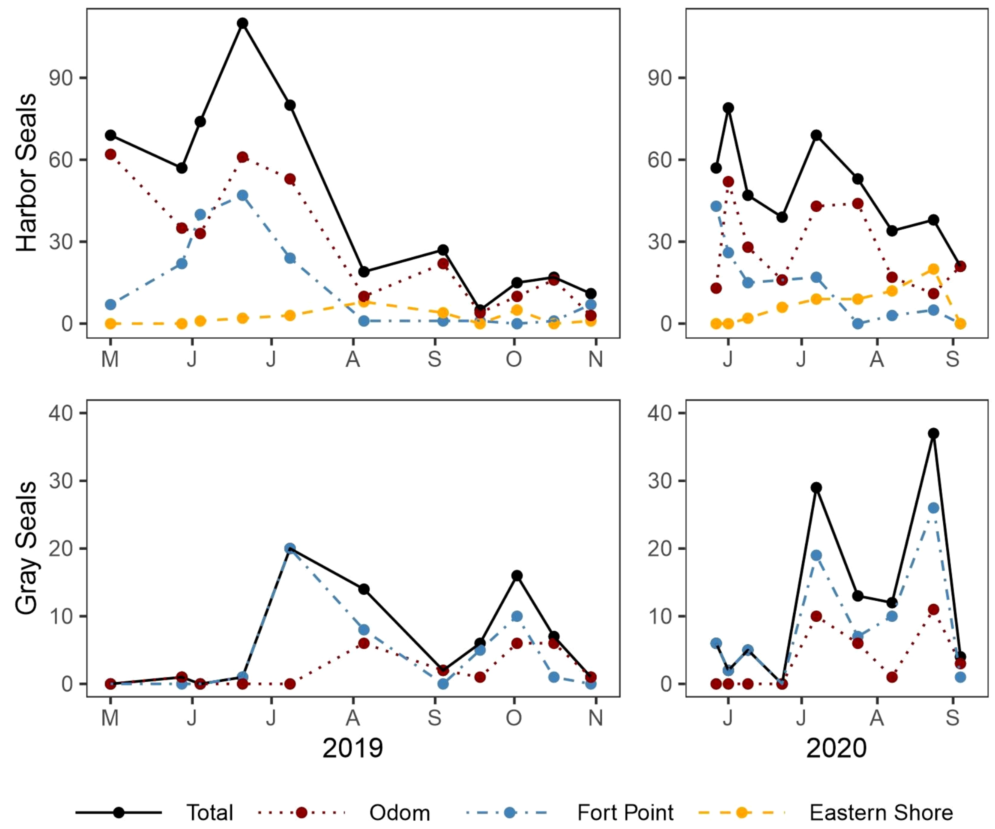

FIGURE 5
Number of harbor and gray seals counted via photographs taken at three haul-out sites (Fort Point, Odom Ledge, and Eastern Shore) in the Penobscot River Estuary from May to November, 2019 and June to September, 2020.

seals present in an area, as well as the proportion hauled out at a certain time are highly variable (Pace et al., 2019), which could also affect our results. It is also possible that disturbance of seals affected our counts and the potential observed patterns over time. Odom Ledge is adjacent to the main boating channel, so seals on that ledge are regularly exposed to vessel traffic in the estuary. Based on our observations during the survey, the seals appeared more likely to flush earlier in the season before presumably habituating to vessel presence as the season went on. Seals were also more likely to be disturbed by the closer vessel approaches during the survey in 2019 and 2020 compared to the previous years. Finally, distribution patterns may have also influenced counts in the post-dam removal period (2014-2020) due to the expanded access that pinnipeds had outside the survey area to an additional 14 kilometers of free-flowing river. Despite those caveats, we report expected seasonal patterns and local abundance trends that mirror regional trends for hauled out gray and harbor seals. Within that context, changes in fish biomass that have occurred during the study period appear to have little effect on the relative abundance of seals in the Penobscot River Estuary. Several ecological models of predator-prey dynamics predict that the predator population will lag slightly behind that of the prey (Gause, 1935). It is therefore possible that more time is needed before pinnipeds exhibit a stronger response to the growth in fish populations in the Penobscot River, especially considering the different life histories and reproductive strategies of seals compared to river herring. Continued assessment of pinnipeds in this system therefore remains important, and we recommend a particular focus on targeted assessments of seal behavior, which this study suggested have significantly changed over time during this period of shifting prey base.

Continued work to understand seal diet and response to fish restoration efforts in the Penobscot River Estuary, and ultimately the subsequent impact seals have on those fish populations, is not only important for understanding predator-prey dynamics in systems focusing on habitat restoration, fish conservation, or recovery from human exploitation, but could also inform future efforts to conserve or recover other predator species. For example, pinniped aggregative response to increasing forage fish has major implications regarding if and when increasing prey provides population-level benefits to seals and should be considered when developing recovery plans for prey species of conservation concern (Hill et al., 2020). Although seals in the Penobscot are not threatened or endangered, efforts to recover other opportunistic predators could also use this work to evaluate the potential for habitat restoration and increasing forage fish to help achieve their recovery goals.

Data availability statement

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

Ethics statement

Ethical review and approval was not required for the study on animals in accordance with the local legislation and institutional requirements.

Author contributions

LL: Data curation, Formal analysis, Funding acquisition, Investigation, Writing – original draft, Writing - review & editing. JS: Data curation, Investigation, Methodology, Project administration, Writing – review & editing. KC: Conceptualization, Formal analysis, Funding acquisition, Methodology, Visualization, Writing – review & editing.

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Conflict of interest

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

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1408982/full#supplementary-material

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