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A review of climate change effects on marine mammals in United States waters: Past predictions, observed impacts, current research and conservation imperatives



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ABSTRACT

We consider the current evidence of climate change effects on marine mammals that occur in U.S. waters relative to past predictions. Compelling cases of such effects have been documented, though few studies have confirmed population-level impacts on abundance or vital rates. While many of the observed effects had been predicted, some unforeseen and relatively acute consequences have also been documented. Effects often occur when climateinduced alterations are superimposed upon marine mammals' ecological (e.g., predator-prey) relationships or coincident human activities. As they were unanticipated, some of the unpredicted effects of climate change have strained the ability of existing conservation and management systems to respond effectively. The literature is replete with cases suggestive of climate change impacts on marine mammals, but which remain unconfirmed. This uncertainty is partially explained by insufficient research and monitoring designed to reveal the connections. Detecting and mitigating the impacts of climate change will require some realignment of research and monitoring priorities, coupled with rapid and flexible management that includes both conventional and novel conservation interventions.

1. Introduction

By the mid-1990s, scientists had begun to recognize the potential for climate change to induce profound impacts on marine mammals [1], and anticipated effects were reviewed by Würsig et al. [2]. The subsequent decade saw the proliferation of studies aiming to predict which species were likely to be most affected, and by which mechanisms. These studies frequently focused on how projected sea ice reductions were likely to influence marine mammals in the Arctic, where the pace of climate change was (and continues to be) most rapid and conspicuous [3]. Potential climate change effects on marine mammals globally and in regions other than the Arctic were also assessed [4–8]. Such studies can generally be described as informed speculation, wherein projections of future climate change combined with knowledge of marine mammal species' biology and ecology are used to infer, either through expert opinion or quantitative species distribution modeling, which of them are most likely to be affected by climate change. Authors acknowledged that confidence in their predictions was constrained by uncertainty in climate projections, incomplete characterization of marine mammal biology and ecology, and perhaps most importantly, uncertainty in how individuals and populations would respond when confronted with profound changes in environmental conditions (reviewed in [9]). Such studies have nevertheless been valuable for generating testable hypotheses and identifying research and conservation priorities.

By now, much of the speculation has been replaced by evidence, as numerous climate change impacts on marine mammals and their habitat have been realized (e.g., [10]). Conserving marine mammals requires understanding whether and how climate change affects them, either negatively or positively, especially at the population level. Links between climate change and demographic parameters have been reported for only relatively few species among the vastly more diverse and wellstudied terrestrial mammals [11,12]. Here, we identify observed climate

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Table 1

Publications reporting documented effects of climate change on marine mammals in United States waters.

Region	Species	Survival	Reproductive rate	Distribution/ habitat/ range/movement patterns	Prey selec- tion/distribution/ access and foraging patterns	Exposure to human activities	Predation risk	Frequency of toxicoses	Pupping/ denning habitat	Body condition
Arctic	Polar bear	[54,147]	[54,147]	[55,147–152]	[54,57]				[153,154]	[54,155]
Arctic	Walrus			[115]	[53,115]					
Arctic	Ringed seal		[116]		[116,156]					
Arctic	Bearded seal			[157]	[156]					
Arctic	Bowhead whale			[20,21]	[20]					[22]
Arctic	Beluga whale			[158,159]						
Arctic	Killer whale			[23]						
Temperate	California sea lion							[60]		
Temperate	Harp seal			[160]						
Temperate	North Atlantic right whale		[40]	[31,32,34,128]	[34,38,40]	[35,37]				[39]
Temperate	Humpback whale				[42]	[42,44,45]				
Temperate	Sei whale			[161]						
Temperate	Fin whale			[161]						
Temperate	Minke whale			[161]						
Temperate	Blue whale			[161]						
Temperate	Long-finned pilot whale			[162]						
Subtropical	Hawaiian monk seal		[50]				[50]		[4,48]	

change impacts on marine mammals that inhabit U.S. waters relative to predictions, and identify observations suggestive of climate change effects but for which the links have yet to be conclusively demonstrated. We emphasize that our intent in this paper is not to assess the severity of effects or to compare levels of vulnerability to effects between or among species. Rather, we simply evaluate whether effects are known, suspected, or just likely to have occurred. We also provide recommendations for research and conservation measures for improving detection and mitigation of impacts of climate change. The national rather than global geographical scope of our investigation is a concession to the enormity of the task and reflects the Marine Mammal Commission's mandate to inform and advise U.S. management agencies responsible for the conservation of marine mammals.

2. Methods

We carried out a non-systematic search of the peer-reviewed literature focusing on marine mammals and climate change using Web of Science [13] (cutoff date June 1, 2021) as an initial tool. Search strings consisted of keywords chosen to encompass the terminology used in marine mammal and climate change articles; keywords "cetacean", "pinniped", "polar bear", "walrus", and "sea otter" were combined with environmental keywords "climate change", "global warming", "sea level rise", "ice retreat", and "temperature increase". Common names of marine mammals found in U.S. waters were also paired to environmental keywords. The Web of Science queries returned 1,037 journal articles. We noticed that the Web of Science query results were far broader than the scope of our interest for this paper, and that fairly new, relevant publications were not returned from the queries. Consequently, we also examined the literature cited in the articles, conferred with colleagues, and searched social media, adding 67 more publications. The authors read the 1,104 publications looking for documented impacts of climate change on the demography or health of marine mammal stocks in U.S. waters. The resulting 112 publications were divided into two groups: 1) studies that documented climate change effects on marine mammal survival, reproduction, health, physiology, prey, predation risk, pupping and denning habitat, or frequency of toxicoses (Table 1); and 2) observations that *implied* climate change effects on marine mammals but which lacked compelling or conclusive evidence (Table 2). Three publications were included in both tables, having data pertinent to both groups.

3. Processes by which climate change can affect marine mammals

The cascading and interacting pathways and mechanisms by which climate change has influenced or could influence individuals and, ultimately, populations of marine mammals have been articulated by many previous authors (e.g., [2,7,14–17]). Therefore, we provide only a conceptual overview and identify some emergent themes.

The fundamental driver of climate change in the global oceans is increasing atmospheric carbon, which results in increased air and ocean temperatures, ocean acidification, loss of sea ice, and increased freshwater discharge from melting ice and river outflows [18] (Fig. 1). These changes foster both abiotic (sea-level rise, altered storm activity) and biotic (food web) ecosystem responses [18]. Commercial activities, including shipping, fishing, and mineral resource extraction, vary in response to ecosystem alterations. Marine mammal responses to food web alterations (e.g., shifts in range, distribution, phenology, migration routes, diet) have physiological consequences (e.g., changes in body condition, health), as well as influencing individuals' exposure to predation, pathogens, toxins, and risks associated with human activities, and this ultimately can affect reproductive success and survival. It is important to recognize that while climate change-related ecosystem alterations may have negative effects on some species, they can benefit others [6,19] (Figs. 2 and 3).

4. Documented effects of climate change on marine mammals

The Arctic figures prominently in the literature reporting climate change effects on marine mammals, yet we identified a comparable number of cases involving temperate-region species (Table 1). Just one

Table 2

Publications suggesting effects of climate change on marine mammals in US waters, with suggestions for research or data needed to confirm that such effects are occurring. UME = Unusual Mortality Event. HAB = Harmful Algal Bloom.

Species	Predicted Effect of Climate Change	Observations	Hypothetical Mechanism(s)	Research Directions Identified in the Cited Documents
Various marine mammals	Increased infectious disease outbreaks and extent and incidence of harmful algal blooms;	Increased isolation of Vibrio parahaemolyticus in Alaska; detection of saxitoxin and domoic acid in ice seal and walrus gastrointestinal tracts;	Increased survival of pathogens with ocean warming, expansion of HAB distribution	Surveillance for infectious diseases beyond during Unusual Mortality Events to determine chronic effects on survival and reproductive effects of detected toxin levels on marine mammal health, reproduction and curvival VET
Polar bear	[75,76,163] Declines in body condition, health,	[79,80,84,85] Increased time spent on land linked to increased foraging on bowhead whale carcasses, altered gut microbiome, more	Sea ice loss, loss of access to foraging habitat, altered foraging strategy,	reproduction and survival; [79,80,84,85] Improved understanding of effects of environmental change on immunity; continued health monitoring and studies of long-term fitness
	reproduction, and survival; [54,147,164,165]	infections; increased length of summer fasting, higher energy demands, and muscle atrophy associated with remaining on sea ice; [165–169]	altered disease and contaminant exposure	subpopulation's vital rates; [123,165,166,169]
Southern sea otter	Not predicted	Increased predation of sea otters by juvenile white sharks; [98,99]	Northward range shift of white sharks	Clarification of mechanisms that cause increased presence of juvenile white sharks in the otters' range; [98,99]
California sea lion	Increased frequency of ENSO events that have well documented impacts on pinniped foraging in the California Current; [170,171]	Prey changes during ENSO causing nutritional stress, pup mortality and increased strandings; [103,172]	Ocean warming, reduced upwelling, changing prey distribution and abundance	Long term monitoring to determine whether short-term effects of ENSO are exacerbated with climate change and as a result influence population dynamics; [103,172]
Northern elephant seal	Colony range expansion towards the north, inundation of haul-out sites; [133,173]	Increasing population in CA, decreasing population in Baja California, Mexico; decreased weaning weight of pups;	Ocean warming and prey range shift; sea level rise	Collection of high-resolution topographic data near haul-out sites; tracking dispersal of seals to confirm whether reduced Baja California population is a result of emigration to CA; long-term monitoring of pup weaning weights and foraging behavior; [102,173]
Walrus	Decline in body condition due to reduced sea ice availability, increase in mortality from stampeding and overcrowding on coastal haulouts; northward shift in distribution; [51,174]	Reduced recruitment with rapid sea ice retreat; increased mortality due to stampeding; increased predation of seals and seal remains; reduced reproductive capacity; increased stress; change in prey species over time; [175–180]	Changes in foraging energetics due to loss of access to ice	Estimation of abundance, vital rates; monitoring of diet, foraging energetics in association with body condition and productivity; [51,181]
Bearded seal	Decreased consumption of benthic prey; shift to suboptimal habitat with changing ice conditions; [182,183]	Increased consumption of pelagic and/or more diverse prey species; 2019 UME; shifts in behavioral ecology; [184–186]	Extended periods of reduced ice cover; shifts in distribution of intermediate ice concentrations	Assessment of impacts of shifting habitat usage or body condition and behavior; [157]
Harbor seal	Not predicted	Decline in body condition; increased distances for foraging and time spent hauled out; reduced reproductive output; [187–189]	Ocean warming, glacial haulout availability, and prey range shifts	Further investigation into effects of marine heatwaves on prey species; Consistency in timing of surveys during molting season; [187–189]
Ribbon seal and spotted seal	Reduced reproductive success; [190] (not predicted for spotted seal)	Decline in body condition; [187]	Northeast Pacific marine heatwave; decline in sea ice extent	Improved understanding of link between ice seal UME and reductions in sea ice and resilience of ic seals to climatic perturbations; [187]
Blue whale	Altered presence in primary feeding grounds inferred from acoustic evidence; [191]	Earlier arrival and extended stays at the feeding grounds are associated with increased water temperature; [192]	Increased sea surface temperature, decline in seasonal upwelling, and change in timing of peak prey abundance	Assessment of anthropogenic threats resulting from more time spent on feeding grounds; long-term monitoring of whale behavior and ocean conditions; [192]
Bowhead whale	Not predicted	Significantly higher probability of killer whale 'rake'-like scars on bowheads in 2002-2012 than in 1990-2001; whales from Alaska and West Greenland observed together in Northwest Passage in 2010; [193,194]	Loss of sea ice	Monitoring of scarring and injuries to understand impacts of increasing vessel traffic, expanding commercial fisheries, and interactions with killer whales; [193,194]
Bryde's whale	Gradual range expansion poleward with long-term ocean warming; [7]	Increasing presence off Southern California in fall not correlated with local sea surface temperature, suggesting a seasonal poleward range expansion of the species; [195]	Ocean warming and prey range shift	Continued monitoring of movement patterns of Bryde's whales and their prey in the eastern North Pacific; [195]
Fin whale	Increased presence in the Chukchi Sea; [196]	Extended period of acoustic presence of fin whales in the southern Chukchi Sea associated with a longer ice-free period; [197]	Loss of sea ice, increased water temperature, and increased zooplankton abundance	Further research to assess the impacts of environmental changes on the distribution of fin whales; [197]
Gray whale	Not predicted	Emaciated gray whales stranding during northward migration, increased mortality of whales at 20-year intervals, 1999-2000, 2019-2021; more calves in years with longer ice-free feeding seasons; [67–70,72,73]	Altered prey availability associated with loss of sea ice	Methods to distinguish between starvation and the loss of condition due to annual fasting during migration, detailed necropsies of fresh carcasses including pathogen discovery, observations of foraging locations and prey types; assess relative contributions of environmental conditions, disease, trauma and toxins to instances of

disease, trauma and toxins to instances of malnutrition and death; [67,70]

Table 2 (continued)

Species	Predicted Effect of Climate Change	Observations	Hypothetical Mechanism(s)	Research Directions Identified in the Cited Documents
Humpback whale	Not predicted	Declining mother-calf encounter rate between 2013 and 2018 was associated with multiple changes in ocean conditions; earlier arrival at feeding grounds in warmer years is associated with higher risk of entanglement; [198]	Nutritional stress due to increased freshwater run-off and slowing of coastal upwelling in Alaska affecting prey; increased sea surface temperature and decreased productivity	Expanded surveys to assess potentially large-scale relocation of mother-calf pairs; long-term monitoring of reproductive rate on feeding grounds; health assessment and improved understanding of relationship between reproductive rate, regional prey availability, and marine regime shifts; long-term monitoring of whale behavior and ocean conditions; [198]
Beluga	Range reduction due to sea-ice loss; [7]	Increases in competitor species, water temperature change affecting fish health and distribution; Cook Inlet belugas stay in northern upper inlet longer during warmer years; significant relationship between Pacific Decadal Oscillation and mercury concentration in beluga tissues; [199.200]	Ocean warming, competition for prey and decreased prey health, increased presence of killer whales, increased siltation blocking access to feeding areas	Assess changes in prey availability and predation risk; study winter foraging patterns to understand links between climate variables, diet, and mercury concentrations; [199,200]
Killer whale	Not predicted	Significantly higher probability of killer whale 'rake'-like scars on BCB bowheads in 2002-2012 than in 1990-2001; [194]	Range expansion, longer open-water periods	Additional effort to assess potential influence of reporting and sampling bias on estimates of killer whale abundance; [194]
Harbor porpoise	Not predicted	Northward range expansion by bottlenose dolphins and increased overlap with harbor porpoise habitat, observations of interspecies aggression in California, increased harbor porpoise strandings due to trauma; [104–108]	Ocean warming, bottlenose dolphin range shift	Determine influence of short-term coastal conditions versus climate change on bottlenose dolphin distribution; assess factors triggering dolphin aggression toward harbor porpoises; [105,107,109]
Florida manatee	Increased mortality and strandings;	Carcasses with cold-stress lesions; periodic UMEs; emaciated animals; occasional extralimital observations north of current range; reduced adult survival in years with intense storms; [86,92–95,97]	Sea level rise; ocean acidification; reduction in warm-water habitat; increased storm frequency	Understanding of current impacts of climate change on Florida sea grass and HABs; importance of distribution shifts and/or increase in population size driving extralimital observations; monitor manatee response to loss of warm-water habitat; [93,95–97]

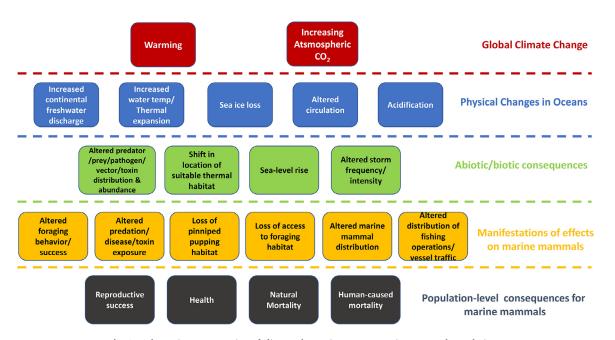


Fig. 1. Schematic representation of climate change impacts on marine mammal populations.

species, the Hawaiian monk seal (*Neomonachus schauinslandi*), had experienced documented climate change impacts in subtropical U.S. waters. The most commonly documented manifestation of climate change on marine mammals in U.S. waters was altered distribution or movement patterns, whereas prey-related effects were somewhat less common. As marine mammals often alter their distribution and movements in response to changes in prey, we recognize that these two consequences of climate change are not independent. Accordingly, we identified some studies that report both changes in distribution of marine mammals and prey-related effects (Table 1). Impacts on vital rates (survival or reproduction) were observed in only four species, and other climate-induced alterations (including loss of pinniped pupping habitat and increased mortality associated with harmful algal blooms) were reported even less frequently.

In most cases, marine mammals have suffered impacts such as increased mortality as a result of human activities, poorer body condition, reduced reproductive success, and more predation. Yet, in several cases, particular species or populations appear to have benefited from the en-



Fig. 2. Examples of marine mammal species in U.S. waters for which effects of climate change have been documented, see Table 2. a. Humpback whale off Jeffreys Ledge, Gulf of Maine; b. male polar bear; c. North Atlantic right whale, Florida; d. Hawaiian monk seals, Northwestern Hawaiian Islands. Photo credits: a. Lauri Leach; b. Ian Stirling; c. Florida Fish and Wildlife Conservation Commission, taken under NOAA research permit #15488; d. Shawn Farry Permit # 16632.



Fig. 3. Examples of species in U.S. waters potentially impacted by climate change. a. emaciated California sea lion pup on the rookery at b. San Miguel Island, California; c. northern elephant seal at d. Point Reyes National Seashore, California; e. emaciated stranded gray whale, San Francisco Bay, California; f. Florida manatee at g. Blue Spring State Park, Orange City, Florida. Photo credits: a., b., c., d., e., Frances M.D. Gulland NOAA permit # 18786; f. Lauri Leach; g. Debbie Ridgely.

hanced feeding opportunities or seasonal range expansions enabled by climate change (e.g., bowhead whales *Balaena mysticetus* [20–22], Arctic killer whales *Orcinus orca* [23]).

Observations of consequences to marine mammals resulting from climate change have accelerated concomitant with rates of sea ice loss and ocean warming that exceeded predictions [10]. The examples listed in Table 1, which all have compelling evidence linking climate change to effects on marine mammals, likely represent the proverbial tip of the iceberg. Many of these consequences were predicted, but unforeseen effects have also been documented. As they were unanticipated, some of these unpredicted effects have strained the ability of existing conservation and management systems to respond. Some notable examples are described below.

4.1. North Atlantic right whale deaths and health decline

The population of the critically endangered North Atlantic right whale (*Eubalaena glacialis*) now numbers less than 400 individuals [24]. After several decades of a slow increase from near extinction due to whaling, the population has been declining since 2011 at an alarming rate [24,25]. While there are two clear and immediate causes of the decline, this unfortunate reversal in the population trajectory has also been linked to climate change.

The primary causes of death of North Atlantic right whales in recent decades have been entanglement in fishing gear and vessel strikes [26,27]. Efforts to mitigate the threat of vessel strikes initially appeared to be effective [28], but measures to reduce entanglement have not [28,29]. The population was able to grow during the 1990s and early 2000s despite continuation of ship strikes and entanglements, but its rate of increase then was still far below those of some right whale populations (*E. australis*) in the Southern Hemisphere [30].

Major changes in the seasonal movements and distribution patterns of North Atlantic right whales (summarized in [31,32]) were coincident with the renewed population decline that began approximately a decade ago and also linked to changes in the abundance and distribution of their main prey, late-stage copepods Calanus finmarchicus, driven by rapid warming in the Gulf of Maine [33-38]. Relatively large numbers of right whales began to appear in eastern Canadian waters, unexpectedly, making them vulnerable to ship strike and entanglement in snow crab gear. A sharp increase in documented deaths occurred in 2017, when 12 of the 17 reported right whale carcasses were found in Canada. Over the previous five years, 1-4 dead right whales per year had been reported along the entire North American coast, with a total of six found in Canada (one in 2012, 2014 and 2016, three in 2015) [27]. Nine of the 10 dead whales found in 2019 were also located in Canada. This marked change in both number and distribution of right whale carcasses led NOAA to declare an Unusual Mortality Event (UME) in 2017¹.

While the proximate causes of mortality were not new (entanglement and ship strike), climate change appears to have driven the change in foraging distribution, leading to both the spike in numbers and the unanticipated locations of right whale carcasses in 2017 and 2019 [35]. Besides making the right whales more vulnerable to entanglements and ship strikes in recent years due to changes in foraging areas, climate change has also apparently diminished their foraging opportunities, in terms of the availability and quality of prey, in turn impacting health and reproduction. Rolland et al. [39] documented declining health of right whales, and Meyer-Gutbrod et al. [40]. linked the whales' calving rates to *C. finmarchicus* abundance. Pace et al. [25] found that calving rates were unusually low following 2010, coincident with the climatedriven distribution shifts in both the whales and their prey.

4.2. West coast humpback whale entanglements

An unprecedented marine heatwave in the California Current ecosystem during 2014-2016 led to a compression of coastal upwelling and consequent inshore shift of forage fish [41,42]. Large whales, particularly humpback whales (*Megaptera novaeangliae*), moved closer to the coast than usual, following their prey [43]. Meanwhile, a Harmful Algal Bloom (HAB) of *Pseudo-nitzschia* diatoms, also associated with warmer waters [44], resulted in high levels of the biotoxin domoic acid in filterfeeding prey. The high toxin levels prompted a delay in the opening of the Dungeness crab (*Metacarcinus magister*) fishery to prevent exposure of humans to contaminated crabs. This delay, combined with the shift in whale distribution, led to unusually high spatio-temporal overlap of whales and crab gear, ultimately resulting in a dramatic spike in humpback whale entanglements [42,43,45].

4.3. Loss of terrestrial habitat for the Hawaiian monk seal

The Hawaiian monk seal, an endangered species, requires terrestrial habitat for parturition, nursing, molting, and resting that is both safe from shark attack and within commuting distance to marine foraging habitat [46,47]. Baker et al. [4] first raised concern about the threat that climate change posed to the small, low-lying Northwestern Hawaiian Islands (NWHI) due to global sea-level rise. Simple passive flooding scenarios predicted considerable loss of habitat by 2100 based upon contemporary Intergovernmental Panel on Climate Change predictions of sea-level rise. Reynolds et al. [48] obtained high-resolution elevation data and refined the assessment of potential habitat loss in the NWHI. Loss of terrestrial habitat has been most conspicuous at the largest Hawaiian atoll, French Frigate Shoals. Islets have been gradually shrinking there for decades, and by 2000 Whaleskate Island, where the largest percentage of French Frigate Shoals monk seal pups had been born, had disappeared and monk seals subsequently began to give birth most commonly at nearby Trig Island. Then, in an abrupt departure from further gradual erosion, the next two most important pupping islets at French Frigate Shoals virtually disappeared in the span of two months in 2018. Trig Island finally succumbed to inundation, and East Island was obliterated by Hurricane Walaka. The latter was most surprising, as East Island was expected to be the most resilient in the atoll due to its relatively high elevation [4,48]. These unanticipated events illustrate that sea-level rise in combination with storms, tides, and perhaps other factors can lead to rapid changes in shoreline morphology.

The loss of shoreline habitat has apparently made pups vulnerable to a novel source of predation. Galápagos sharks are ubiquitous in the NWHI, but only prey on monk seal pups at French Frigate Shoals, and this has been documented only since Whaleskate Island was greatly diminished [49]. These sharks are able to approach the shoreline on islands within French Frigate Shoals more closely than is the case at more typical pupping sites and this enables them to attack pups. Drowning associated with storms or high tides has also become much more common. Consequently, only 57% of French Frigate Shoals pups survived to weaning in 2018 compared to an average 95% throughout the rest of the NWHI [50].

4.4. Coastal haulouts of Pacific walruses

Since 2007, summer sea ice in the Chukchi Sea has retreated offshore to areas too deep for walruses (*Odobenus rosmarus*) to feed, and as a result many of them now move to coastal areas where they rest on land between feeding excursions [51]. In the absence of summer sea ice, thousands of animals have been observed to congregate on U.S. and Russia coastal haulouts in the late summer [51]. Some of these haulouts are near communities where there is risk that human activities such as gunfire or aircraft over-flights, or the presence of animals such as polar bears (*Ursus maritimus*) and feral dogs drawn to the haul-out sites, will trigger stampedes and result in trampling and death of walruses [51].

¹ https://www.fisheries.noaa.gov/national/marine-life-distress/2017-2021north-atlantic-right-whale-unusual-mortality-event

Concerted efforts by management agencies and local communities seek to avoid such disturbances [52]. Those animals that stay with the ice as it moves over deep water north of the continental shelf face the risk of starvation [51]. The reduction in seasonal areal extent of sea ice may also have significant cascading effects on walrus prey. Measurements of markers of sea ice organic carbon (iPOC) in walrus livers collected between 2012 and 2016 suggest adult females and juveniles in the northern Bering Sea are particularly dependent upon prey that relies upon iPOC [53].

4.5. Declining sea ice and land use by polar bears

Nineteen largely discrete sub-populations of polar bears are distributed throughout the Arctic. Status reviews by the IUCN Species Survival Commission's Polar Bear Specialist Group show that over the long term (approx. three generations) the size of two sub-populations has been stable, one has increased, and four have declined, while data are inadequate to assess long-term trends for the other 12. Over the short term (approx. the most recent generation) five sub-populations have been stable, two have increased, and four have declined². Of the two shared U.S. sub-populations, the Southern Beaufort Sea sub-population (shared with Canada) decreased over the long and short terms with declines in body condition, size, and reproduction linked to declining sea ice [54]. The extent of ice retreat is correlated with Southern Beaufort Sea bears' increased reliance on land in the summer which brings them into more frequent contact and conflict with human communities and industrial activities and may also increase their risk of exposure to terrestrial pathogens [55]. Data are insufficient to assess long-term trends of the Chukchi Sea sub-population (shared with Russia), but in the short term (2008-2016) it is thought to be stable [56]. There are indications that in this sub-population bears are also spending more time on land given the longer ice-free periods. While recruitment and body condition remain good [57], there are suggestions of declining cub survival [58].

4.6. Domoic acid toxicosis in California sea lions and sea otters

Blooms of the diatom *Pseudo-nizschia* which produces domoic acid have been increasing in duration and extent along the west coast of North America over the past 20 years, at least partially due to climate change effects [59]. The largest and most extensive bloom on record occurred in 2015, when toxin-producing algae extended along the entire west coast of the U.S. in association with a warm-water anomaly, and domoic acid was detected in marine mammal samples [60]. Domoic acid poisoning of marine mammals was first reported in 1998 when several hundred California sea lions (*Zalophus californianus*) died acutely in association with a bloom in Monterey Bay [61]. Since that first report, domoic acid toxicosis has been increasingly recognized in other species of marine mammals along the California coast such as harbor seals (*Phoca vitulina*) [62] and northern fur seals (*Callorhinus ursinus*) [63]. It was reported as the cause of death of 20% of necropsied sea otters (*Enhydra lutris*) between 1998 and 2012 [64,65].

5. Predicted and suspected climate change effects

Some climate change effects on marine mammals are likely occurring but have yet to be documented (Table 2). A variety of issues conspire to thwart confirmation of the role of climate change as causal to observed changes in health or vital rates. Most marine mammal populations, particularly cetaceans living far from shore, are not closely monitored, and therefore even substantial changes in abundance, range, phenology, reproductive success, or health are unlikely to be detected [66]. Even when coastal species experience increased mortality, logistical challenges associated with access to carcasses and tissues for diagnosis can frustrate determination of causes of death. Moreover, distributions of marine toxins, pathogens, and the latter's intermediate hosts and vectors that could alter disease exposure are even less well studied. In some cases, climate change is but one of several confounding natural and anthropogenic factors that influence marine mammal populations. Finally, there is considerable uncertainty related to time scale, in that populations may respond differently to observed relatively short-term or episodic anomalous conditions versus the long-term directional alterations associated with climate change.

5.1. Eastern North Pacific gray whale unusual mortality events

Hundreds of gray whales (Eschrichtius robustus) have died across their range extending from coastal waters along western North America to the Alaskan Arctic since 2019, leading to the declaration of a UME [67]. A similar UME occurred twenty years earlier, with the gray whale population declining by approximately 20% over the course of the UME, but the cause or causes were never determined [68-71]. Annual changes in calf production have been correlated with annual variability in duration of ice cover of the feeding grounds, but relationships between Arctic or subarctic ice cover and adult mortality of gray whales have not been established [72,73]. Given the extent of environmental changes in high northern latitudes in recent years, it is likely that changes in ice cover or prey variability are associated with the current gray whale die-off. However, the causes of most of the deaths in 2019 and 2020 remain unclear. Some were due to entanglements or ship strikes [67], while others may have been influenced by nutritional stress related to changes in prey [74] or the frequency of occurrence and distribution of harmful algal blooms [75]. Thus, the relationships between climate change and gray whale demography remain unclear, as do the mechanisms by which effects could be occurring.

5.2. Prevalence of infectious diseases and toxicoses

Increases in infectious disease outbreaks in marine mammals associated with climate change have been predicted [76]. To date, however, no increases in disease epidemics driven by climate change have been detected in marine mammals in U.S. waters. Although some bacteria and antibodies to viruses have been reported in marine mammals from northern sites where monitoring programs had not previously detected them, their impacts are unknown due to the lack of clinical data for potentially affected marine mammals. For example, a common cause of seafood poisoning in humans is the bacterium Vibrio parahaemolyticus, which proliferates at temperatures above 15°C and salinities less than 25 ppt, and production of its toxin is enhanced in warmer waters [77,78]. The first human cases of poisoning due to ingestion of Vibriocontaminated oysters from Prince William Sound, Alaska, were documented in 2004. Since then, seafood in Alaska has been tested routinely, and marine mammals, when handled, have been tested opportunistically for infection with Vibrio spp. In 2013, Goertz et al. [79] documented Vibrio in fecal samples from belugas (Delphinapterus leucas), sea otters and a harbor porpoise (Phocoena phocoena), expanding the known distribution of these bacteria in Alaska to Seward, Cook Inlet, Kachemak Bay, Kodiak, and Dillingham. The bacteria were not, however, associated with disease and were detected only in animals being handled for tagging or after stranding. Whether Vibrio is now causing disease in Alaskan marine mammals is unknown.

Similarly, antibodies to phocine distemper virus (PDV) and RNA sequences of PDV, a virus that has caused severe epidemics in harbor seals in the North Atlantic, have been detected in samples from pinnipeds in the Arctic collected between 2000 and 2016 [80]. Whether this virus causes disease in these animals, and whether its prevalence has changed with climate change, is unknown. Rare data on disease exposure over multiple decades come from one of the polar bear subpopulations outside U.S. waters in western Hudson Bay [81]. Prevalence of antibodies to viruses in these bears did not change between 1986-1989

² https://pbsg.npolar.no/web/en/status/index.html

and 2015-2017, whereas antibodies to the parasites *Toxoplasma gondii* and *Trichinella* spp. did, and prevalence of antibodies to *Trichinella* was highest in bears sampled after periods on land in contact with human settlements. The population in western Hudson Bay, where spring sea ice has been declining steadily for the past half-century causing bears to spend increasing time on land, has become an archetype for climate change impacts on polar bears [82].

A climate change-driven increase in the extent of harmful algal blooms in the Arctic resulting in marine mammal toxicosis was predicted [76]. The increase in blooms has occurred [75,83], and testing of marine mammal samples that were archived over the last 20 years has revealed domoic acid and saxitoxin in the gastrointestinal contents of several species sampled in Alaska between 2005 and 2013 (walruses, ice seals, belugas, humpback whales and bowhead whales). The effects of these biotoxins on health and reproduction are unknown, due to lack of clinical data on the sampled animals [84,85] and limited opportunities to examine sick stranded marine mammals in Alaska.

5.3. Causes of death of Florida manatees

The Florida manatee (Trichechus manatus latirostris) is a subspecies of the West Indian manatee for which impacts of climate change have been predicted and suspected, but are not documented with certainty [86-88]. Die-offs caused by harmful algal blooms, cold stress, and starvation occur regularly, yet how these are linked to climate change remains unclear [89]. Manatee habitat in the temperate-tropical transition zone of the southeastern U.S. is subject to warming, increasing intensity of storms and frequency of hurricanes, rising sea levels, and decreased duration of winter freeze periods [90,91]. As sub-tropical animals situated in the northernmost parts of the species' range, manatees in U.S. waters are seasonally exposed to water temperatures below 20°C, putting them at risk of cold-induced disease and mortality [92,93]. Their over-winter survival in Florida has been dependent upon access to warm-water refugia offered by natural artesian springs, artificial warm-water discharges from power plants, and canals, boat basins, and drainage ditches with limited mixing of surface and bottom waters [94]. The northward movement of manatees in recent years associated with warmer summers increases the distance between some warm-water refugia and the animals' foraging areas [95]. Furthermore, natural springs are decreasing due to sea level rise and ground-water loss, and the desire to close coal-fired power plants for political, social, environmental, and economic reasons will further decrease availability of artificial warm-water refugia [96]. Thus, despite general warming trends, and however counterintuitive it may seem, manatees that move northward during warmer, longer summers are likely to become more susceptible to winter cold snaps as their access to warm-water refugia decreases [97].

5.4. White shark predation on southern sea otters

The difficulty of attributing marine mammal disease or mortality to changing environmental conditions with certainty, even when data are relatively rich, is illustrated by the increased mortality of southern sea otters due to predation by great white sharks (*Carcharodon carcharias*) in recent years [98]. It is unclear whether this is due to (i) an increase in ability of juvenile sharks to find sea otters in areas of low kelp coverage at the margins of the sea otters' range, (ii) increased numbers of white sharks in coastal waters after gill nets were banned, or (iii) a broadened seasonal thermal window enabling sharks to be present in the sea otters' range for longer periods [98,99].

5.6. El Niño-Southern Oscillation and other oceanographic anomalies

The impacts of El Niño-Southern Oscillation (ENSO) and other episodic ocean anomalies on pinniped populations have been well documented [100–103]. Reduced upwelling alters prey abundance, distri-

bution, and fat content, resulting in changes to pinniped foraging behavior and success, affecting the body condition and survival of various age classes, ultimately manifesting in declines in pinniped abundance. These patterns may well portend impacts on pinniped populations driven by climate change, however it is not clear that short-term responses to episodic climate variability can be extrapolated to predict responses to long-term directional climate change.

In the 1980s, the distribution of the California coastal stock of bottlenose dolphins (Tursiops truncatus) expanded 600 km northward from the Southern California Bight to Monterey Bay, associated with warmwater intrusion during El Niño conditions [104]. This range expansion persisted, and then was further extended northward over the following decade [105]. As bottlenose dolphins expanded their distribution into Monterey Bay and further north, their habitat use began to directly overlap with that of harbor porpoises [106] and coincided with the first observations of aggression by bottlenose dolphins towards harbor porpoises in California. From 2000, harbor porpoises in central California were observed being attacked and killed by bottlenose dolphins [107]. The increase in strandings of harbor porpoises that had died from trauma in 2008 and 2009 resulted in the declaration of a UME, initially assumed to be due to fishery bycatch as this had been common in previous decades [108]. Post-mortem evidence of fractures and hemorrhages in stranded porpoises, presumably caused by bottlenose dolphins, were documented between San Luis Obispo County in the south to Sonoma County in the north. Such interspecies interactions are indirect, and sometimes unexpected, consequences of climate change that can complicate ecological predictions and interpretations of stranding data [109].

6. Research and conservation

6.1. Monitoring

Since the addition of Section 117 of the Marine Mammal Protection Act (MMPA) in 1994, the primary focus of the U.S. government's investment in marine mammal science has been to obtain information needed for stock assessment reports. The MMPA prescribes that these reports contain information on each stock's range, abundance, population trend, and levels of direct human-caused injury and mortality. At the core of the U.S. marine mammal stock assessments is the Potential Biological Removal (PBR) level, which is a biological reference point for determining allowable levels of direct anthropogenic mortality [110]. The PBR framework has proven to be an extremely valuable tool for conserving marine mammal populations while allowing various human activities that have the potential to harm them, such as commercial fishing, to occur.

Because the U.S. stock assessment process was designed to address *direct* human-caused mortality of marine mammals, it does not explicitly take account of *indirect* threats such as climate change. Fortunately, surveillance conducted to inform stock assessments, such as surveys of abundance and distribution, makes it possible to infer some climate-induced changes in these parameters. Furthermore, many marine mammal species in the U.S. are listed under the Endangered Species Act (ESA), which is designed to identify and mitigate all threats that increase extinction risk. Consequently, research to inform the recovery of ESA-listed species implicitly encompasses the consequences of climate change.

Title IV of the MMPA, added in 1994, mandates the collection of marine mammal health data and correlating them with data on physical, chemical, and biological environmental parameters. This provides another avenue for investigating the impacts of climate change on marine mammals, but the resources to address Title IV have been insufficient to date. The predominant focus has been on responding to the welfare needs of sick or injured marine mammals that strand, rather than on correlating health data with ecosystem changes, or, specifically, climate change. Long-term, systematic collection of health data coupled with

routine integration of information from multidisciplinary research programs and local observations supported by governmental structures are needed, rather than one-off investigations into relatively small disease outbreaks [111]. Health monitoring programs could also be developed to target specific marine mammal populations and health metrics that are feasible to monitor, as has been done for North Atlantic right whales [39]. Data on individual animal health need to be collected explicitly and integrated with long-term national disease surveillance programs. For example, expansion of the Marine Mammal Health and Stranding Response Program of the National Marine Fisheries Service could enhance the collection of health data from cetaceans and pinnipeds, and integration of this program with state and federal programs at the National Wildlife Health Center for manatee, walrus, polar bear, sea otter, and terrestrial wildlife disease surveillance could greatly improve understanding of long-term marine disease trends. Uploading these data to the U.S. Integrated Ocean Observing System (IOOS) would facilitate their availability for integrated analyses [112]. Harmful algal bloom monitoring data should be entered into the IOOS program nation-wide, with special focus on increased Arctic surveillance [113].

Current research and monitoring associated with MMPA and ESA mandates provides some information regarding climate change impacts on marine mammals in U.S. waters, but this is more fortuitous than by design. Because of the impacts that climate change is already having on marine mammals, the predictions that those impacts will increase in the future, and the uncertainty about their nature and severity, the task of detecting and measuring responses to climate change ought to be a central focus of U.S. government marine mammal research. This need not entail a wholesale departure from ongoing stock assessment research and monitoring. Some mere adjustments to study designs could yield great benefits. For example, survey areas could be adjusted to increase the likelihood of detecting range shifts. Estimating total (or at least minimum) abundance is a prerequisite for determining PBR, and this can be challenging and expensive to achieve. However, alternative metrics such as occupancy or abundance indices tend to be cheaper and easier to obtain, and these could in some instances serve as means to detect marine mammal responses to climate change. Oleson et al. [114] is a fine example in which adjustments to established surveillance methods for North Atlantic right whales were recommended in order to continue estimating abundance but with improved tracking of changes in distribution, phenology, health, and threats to the whales that could be at least partially driven by climate change.

6.2. Ecosystem research

Marine mammals can be affected by changes in biological communities across all trophic levels in response to variable ocean conditions. As described above for the North Atlantic right whale, recent changes in the distribution, health, and reproductive rate of the animals have been linked to climate-driven shifts in the quality and distribution of their zooplankton prey. In the Arctic, however, it is less clear whether the shifting diets of ice seals and the foraging patterns of walruses associated with periods of reduced ice cover [115,116] (see Table 2) are ultimately a result of climate change and will have population-level consequences. Such knowledge gaps may be informed by regional studies that integrate research across a suite of species at various temporal and spatial scales. Such an approach will require greater collaboration among marine mammal specialists and other marine scientists with taxon-specific expertise, oceanographers, climate scientists and modelers, and marine ecologists to collect, combine, and analyze long-term data sets. In some cases, existing data products produced by regional associations of the IOOS can provide key information on environmental variability. For example, the Alaska Ocean Observing System data portal hosts information on sea ice loss, ocean acidification, and harmful algal blooms, while the Gulf of Mexico Coastal OOS tracks freshwater discharge that can negatively affect bottlenose dolphins near the Mississippi delta after extreme storm events. Thompson et al. [117] California cooperative oceanic fisheries investigations. Data report 59 provide a prime example of a detailed cross-disciplinary product concerning the aftermath of the 2014-2016 marine heatwave relative to the ocean conditions and marine organisms of the California Current System. Studies of similar scope and design would contribute to understanding of other recent climate anomalies as well as ongoing directional changes.

6.3. Process research

Past and ongoing efforts to assess and quantify the relative vulnerability of marine mammals to climate change are important for generating testable hypotheses [118]. However, it is important to subsequently test these hypotheses in order to advance understanding of how marine mammals actually respond to climate change, relative to predictions. More emphasis on process studies is required to determine how climate change affects individual animals, and how stage-specific vital rates are mediated by factors such as sea ice extent and volume, snow cover, thermal tolerance, prey and pathogen distribution and abundance, and harmful algal blooms. Studies of marine mammal health need to move away from single-case observations and focus on improving understanding of disease pathogenesis and epidemiology (e.g., how detected pathogens cause disease and affect populations, how they are spread), linking health changes to environmental variables and population parameters. Such studies will be critical for making reliable predictions of future impacts and designing mitigation methods (such as treatment, vaccination, or control of vectors). Small, local, "resident" populations, Arctic pinnipeds, and some polar bear populations may prove to be far more threatened by climate change than by the direct anthropogenic threats that assessment and management efforts tend to focus on. In such cases, research priorities need to change.

6.4. Timely and flexible management and conservation measures

Achieving marine mammal conservation objectives, already a challenging endeavor, is certain to become even more so in the context of climate change. A general strategy proposed for conservation of wildlife populations and ecosystems (e.g., coral reefs) threatened by climate change has been to reduce non-climate-related stressors in order to increase species resilience to climate change impacts, which themselves may not be amenable to mitigation [119–123]. While this approach is probably necessary, in most cases it will likely prove insufficient, as climate change impacts per se remain unaddressed. The UN Environment Program draft "Post-2020 Global Biodiversity Framework"³ calls for protection of 30% of global land and ocean areas by the year 2030, and the United States government⁴ has committed to this goal domestically. Designing protected areas in a manner that enhances the resilience of wild species (including marine mammals) to climate change will be challenging [124].

The imperative to replace slow and static management with dynamic approaches has been recognized in the broader context of marine conservation in a rapidly changing climate [125–127]. Experience to date has demonstrated that climate change is accelerating and its effects on marine mammals can be unpredictable and evinced through complex interactions. No one predicted, or reasonably could have predicted, some of the convoluted scenarios described above that ultimately resulted in impacts on marine mammals. Consequently, management structures must become more agile so that effective actions can be implemented rapidly and adjusted as needed.

The Canadian government response to the 2017 spike in North Atlantic right whale deaths illustrates the advantage of agile management. During 2017, when unusual numbers of whales were dying in Canadian

³ https://www.unep.org/resources/publication/1st-draft-post-2020-globalbiodiversity-framework. Publication date: 12 July 2021.

⁴ https://www.whitehouse.gov/briefing-room/presidential-

actions/2021/01/27/executive-order-on-tackling-the-climate-crisis-at-home-and-abroad/

waters, the federal government developed and quickly implemented fishery closures and vessel speed and routing rules [128]. The measures taken were too late to prevent further losses in 2017. However, an unprecedented management scheme involving intensive surveillance coupled with speed rules and both static and dynamic fishery closures was implemented in 2018, during which year no right whales were documented as dead, entangled, or struck by vessels in Canada [128]. Unfortunately, with adjustments to the management scheme and apparent changes in whale distribution in 2019, eight more right whale carcasses were found in the Gulf of St. Lawrence that year [129]. Expansion of existing measures and implementation of new ones resulted in no documented whale deaths in 2020. Additional modifications were put in place in 2021⁵.

Another example at a local level comes from Alaska. To reduce walrus stampedes and mortality from crushing, some Alaska communities have developed management programs to reduce disturbance [52]. These include the establishment of "quiet zones" on beaches when walruses are present, tying up stray dogs, and keeping vehicles off the beach. Some communities have appointed an elder as a haulout steward to oversee hunting and visitor programs. The community of Point Lay has worked with air carriers to change flight routes and ensured that visitors keep a respectful distance from the haul-out site. The U.S. Fish and Wildlife Service has published outreach materials, developed flight advisories and guidelines for local air carriers and pilots, and established temporary flight restrictions over large haul-out areas.

6.5. Direct intervention

In addition to rapid and flexible management, direct intervention to mitigate climate change impacts on marine mammals is required. Clearly, the global scale of climate change and resulting alteration of large marine ecosystems can make any management measures other than reducing global greenhouse gas emissions seem insignificant. However, there are situations where impacts occur on a small spatial scale or affect a sufficiently small population of marine mammals that novel interventions are both feasible and effective.

Direct interventions to enhance ringed seal reproduction have not been made in the United States, but efforts to conserve Saimaa ringed seals (Pusa hispida saimensis) in Finland illustrate the potential for mitigating the impact of climate change on ringed seals, albeit only on a relatively small and local scale. Saimaa ringed seals inhabit a freshwater lake in southeastern Finland, and the total subspecies population numbers only approximately 400 [130]. Like all ringed seals, they give birth and nurse their pups in subnivean lairs, which provide offspring with protection from both harsh weather and predators [131]. In years with too little snow for lair construction, pup mortality significantly increases due to exposure and predation [132]. In response, a coalition of government, university, and public volunteers builds snowdrifts manually in areas where females give birth. When natural snow conditions are unfavorable, more than 90% of observed pups have been born in these man-made snowdrifts, and early pup survival has improved [132]. Looking forward to a time when Lake Saimaa has insufficient ice formation to support snow lairs, conservationists are successfully experimenting with artificial floating lairs [130]. These conservation measures taken on behalf of Saimaa ringed seals should embolden others to likewise conceive, design, experiment with, and evaluate the feasibility and efficacy of novel interventions for other species. Restoring and improving the resilience of the islets upon which the persistence of monk seals in the Northwestern Hawaiian Islands depends is one example [50]. Modification of landscapes adjoining pinniped breeding sites has also been recommended to mitigate the flooding of rookeries by sea-level rise. For example, at Point Reyes National Seashore in California, removal of a parking lot adjacent to an elephant seal (*Mirounga angustirostris*) rookery would allow inland expansion of the rookery, thus reducing the vulnerability of pups to drowning [133].

Assisted colonization refers to the introduction of a species beyond its natural range to protect the animals from human-induced threats, including climate change [134]. This much-debated concept has been circulating in the field of conservation science for more than a decade, but is still rarely applied [135–137], especially in marine systems [138]. Marine mammals typically have fewer barriers to movement than terrestrial species, such that range shifts in response to climate change tend to occur naturally. Nevertheless, scenarios may arise in which assisted colonization will be warranted. Successful translocations of pinnipeds and reintroductions of sea otters have been achieved [139-142]. While translocating cetaceans is more challenging, Yangtze finless porpoises (Neophocaena asiaeorientalis asiaeorientalis) have been captured and moved into ex situ "semi-natural" reserves where they have survived well and reproduced successfully [143]. Establishing a population of sea otters in Oregon may require human assistance, and such an action would amount to reintroduction rather than assisted recolonization [144]. While enhancing resilience to climate change is not the primary motivation for reintroducing southern sea otters to more northerly habitat in Oregon, the action, if undertaken, might achieve that nevertheless. Although opportunities for assisted colonization and reintroduction of marine mammals to mitigate climate change impacts may be few, these tools should be considered.

Finally, mitigating the effects of climate change may not always involve actions to improve or restore habitat or to manage individuals and populations directly. As previously noted, right whale deaths due to entanglement increased dramatically following a climate-induced shift in their distribution. In addition to implementing further time-area closures and modifications to traditional gear, so-called "rope-less" fishing gear technology is an active area of research and development [145]. Broad adoption of such technology would mean that whales would be safe from one of their principal threats – entanglement in the vertical lines associated with lobster and crab fishing – regardless of where they range in response to a changing climate.

7. Conclusions

Despite many predictions about the impacts of climate change on marine mammals, there are few conclusive studies linking climate change to marine mammal demography and health. Two endangered species in U.S. waters (the Hawaiian monk seal and the North Atlantic right whale) have experienced increased mortality in recent years as an indirect consequence of climate-associated changes in their ecology and behavior, and at low population sizes, such an increase in mortality is a serious threat to species survival. Increased mortality of more abundant marine mammals such as walruses, humpback whales, sea otters, and California sea lions has also been associated indirectly with climate change, but the impacts on populations are less clear. In contrast, the sizes of most bowhead whale populations have remained stable or improved during recent years of sea-ice loss in the Arctic [146]. As demographic effects of climate change on most marine mammal species in U.S. waters remain unclear, more targeted research is required to understand these effects and develop appropriate mitigation. More rapid and dynamic implementation of marine mammal management measures is required to address unexpected climate change-induced impacts in a timely fashion. Finally, novel evidence-based conservation interventions should be deployed to complement more traditional marine mammal management and recovery measures.

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⁵ https://www.canada.ca/en/transport-canada/news/2021/02/governmentof-canada-outlines-its-2021-measures-to-protect-north-atlantic-rightwhales.html

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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