REVIEW

Land-dependent marine species face climate-driven impacts on land and at sea

Hannah E. Blondin1,*, Katrina C. Armstrong1, Elliott L. Hazen1,2,3, William K. Oestreich1,4, Bianca S. Santos5, Danielle E. Haulsee1, Chloe S. Mikles1, Christopher J. Knight1, Audrey E. Bennett1, Larry B. Crowder1

1Hopkins Marine Station, Department of Biology, Stanford University, Pacific Grove, CA 93950, USA
2Institute of Marine Sciences, University of California, Santa Cruz, CA 95064, USA
3Environmental Research Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Monterey, CA 93950, USA
4Monterey Bay Aquarium Research Institute, Moss Landing, CA 95039, USA
5Emmett Interdisciplinary Program in Environment and Resources, Stanford University, Stanford, CA 94305, USA

ABSTRACT: Land-dependent marine species are a unique guild of species whose life histories rely on both land and sea. This group is exposed to climate change-related stressors 2-fold, as climate change impacts likely occur at different velocities across land and sea habitat, leading to a greater probability of evolutionary traps. Thus, it is difficult to assess vulnerability and subsequently manage these populations in response to climate change. Without consideration of the factors unique to land-dependent marine species, current vulnerability assessment frameworks may fall short when evaluating climate impacts on these species. We identified commonalities in climate-related threats across taxa and geographic regions, highlighting the specific life history strategies that may be better suited to adapt to the changing climate. Accordingly, we suggest 3 considerations for assessing the vulnerability of land-dependent marine species: (1) degree of specialization, (2) intraspecies population-level differences, and (3) non-climate stressors. Where possible, we suggest how the exclusion of this information in management and conservation planning may lead to less successful outcomes. Potential compounding impacts of multiple stressors puts this group at particular risk of population collapse when losing land and/or sea habitat and functionality. Each of these considerations should be included when assessing vulnerabilities to climate change, as well as in effective and proactive management responses.

KEY WORDS: Land-dependent marine animals · Climate change · Marine megafauna · Life history · Vulnerability assessment · Seabirds · Sea turtles · Marine mammal

1. INTRODUCTION

Many marine species use and depend on multiple habitats—spatially, temporally, and ontogenetically. Often, dependence on distinct locations results from seasonal differences in abundant resources or habitats (Robinson et al. 2009). Land-dependent marine megafauna comprise a unique guild whose life histories rely on both land and sea environments (Fig. 1). Examples include seabirds and pinnipeds, which span across tropical, temperate, and polar environments, as well as sea turtles, which inhabit tropical and temperate environments (e.g. Fig. 1). These guilds often span jurisdictional boundaries from coastal areas to the high seas. Many land-dependent marine species mate and reproduce on land, such as pinnipeds and sea-
birds, which establish land-based breeding and nesting colonies (Le Boeuf 2001, Weimerskirch 2001, Dias et al. 2019, Bestley et al. 2020), or sea turtles, which mate at sea but breed on natal nesting beaches (Meylan et al. 1990, Lohmann et al. 2008, Dickson et al. 2021). Land-dependent marine species feed exclusively at sea (Musick & Limpus 1997, Le Boeuf 2001, Roper-Coudert et al. 2019, Bestley et al. 2020); however, feeding behavior can differ trophically and/or spatially across a variety of life stages (Musick & Limpus 1997, Godley et al. 2008, Riotte-Lambert & Weimerskirch 2013, Hanson et al. 2018, Orgeret et al. 2019, Ropert-Coudert et al. 2019). For example, in some species of sea birds, breeding adults are more tied to their land-based breeding grounds than juveniles and non-breeding adults, which are often less spatially restricted (Riotte-Lambert & Weimerskirch 2013, Ropert-Coudert et al. 2019).

Land and sea habitats are tightly linked for these species by both climatic and physical variables (Dickson et al. 2021). For example, reproductive success for central place foragers often depends on foraging success in waters surrounding their colonies (Thorne et al. 2015, Bestley et al. 2020, Michelot et al. 2021, Sydeman et al. 2021). As a result, marine species that depend on multiple habitats are often particularly vulnerable to anthropogenically driven climate change stressors (e.g. hypoxia at sea, sea level rise on land) due to the tight connection between climate forcing and the availability of prey resources and preferred habitats, as well as life history responses to environmental cues (Robinson et al. 2009, Silber et al. 2017, Furey et al. 2018, Abrahms et al. 2019). Within the bigger picture of global-scale climate change, many land-dependent marine species have already experienced modifications to their local environments at a rapid pace due to increasing temperatures and increases in the frequency of extreme events (Sydeman et al. 2006, Lescoët et al. 2014, Traisnel & Pichegru 2019, Piatt et al. 2020). Evidence already exists that climate change has significantly modified the life history traits and strategies in several species and taxa (e.g. polar bears Ursus maritimus: Stirling et al. 1999; albatross: Thorne et al. 2015; mammals: Isaac 2009), which inherently alters a species’ extinction risk (Isaac 2009).

Though proximity to human development may increase extinction risk (Davies et al. 2006), anthropogenic climate change has introduced a new wrinkle for species that will have widespread habitat loss. For example, in the early 2000s, the emperor penguin Aptenodytes forsteri was listed as a species of...
least concern by the iucn (forcada & trathan 2009), yet recently, scientists predicted that climate change-induced sea ice loss in antarctica would lead to the quasi-extinction of all emperor penguin colonies by 2100 (jenouvrier et al. 2021). jenouvrier et al. (2021) highlights the impacts of widespread habitat loss for animals whose life histories depend on both land and sea. emperor penguins may serve as an example for other marine land-dependent species facing a risk of extinction due to the urgent threat of climate-driven habitat loss.

land-dependent marine species are exposed to climate stressors across land and sea habitats (e.g. land: erosion, greater temperature differentials; sea: seawater deoxygenation, ocean acidification, etc.; weishampel et al. 2003, dickson et al. 2021). these species can be restricted from adapting to changes that occur in one biome (e.g. prey re-distributions at sea) due to uncoupled effects on the other (e.g. static land-based breeding habitat). land-dependent marine species are often uniquely constrained to philopatric breeding sites or regions (prince et al. 1994, miller 1997, fish et al. 2005, campbell et al. 2008, chilvers & wilkinson 2008, trathan et al. 2015). many land-dependent marine predators are highly migratory, traveling long distances between breeding and reproductive-related habitats and non-breeding/foraging-related habitats (robinson et al. 2009, block et al. 2011). recent studies have begun to explore the advantages of mobility and flexibility in deciding when and where to make life history transitions under increasing environmental variability (xu et al. 2021, beltran et al. 2022, merkle et al. 2022, oestreich et al. 2022). yet while highly mobile species may be able to shift their distribution rapidly, any potential for match–mismatch is difficult for predators already living on an energetic knife-edge (goldbogen et al. 2019). as a result, we lack an understanding of how climate change affects and will continue to affect the entire life cycle of populations for many of these land-dependent marine species (forcada & trathan 2009). in addition, land-dependent marine species often transition across jurisdictional boundaries and heavily peopled oceans, putting them through a mosaic of protection and further complicating their management (helvey & fahy 2012, harrison et al. 2018, beal et al. 2021).

while several studies have begun to document climate variability and climate change impacts on the ecology and condition of land-dependent marine species (e.g. fish et al. 2005, cimino et al. 2016, abrahms et al. 2018), others have assessed these changes within a taxon or a geographic region (e.g. hawkes et al. 2009, kovacs et al. 2011, 2012, ropert-coudert et al. 2019, bestley et al. 2020). however, we lack a cross-taxon and cross-geography synthesis on this topic. here, we seek to understand commonalities in climate-related threats both across taxa and across regions to identify factors that could make land-dependent marine species particularly vulnerable to climate change. as a result, we suggest 3 considerations for vulnerability frameworks when assessing land-dependent marine species under climate change: degree of specialization, intraspecies population-level differences, and non-climate anthropogenic stressors.

where possible, we suggest how the exclusion of these 3 considerations may lead to less successful management and conservation outcomes for land-dependent marine species. we also acknowledge the unique risk land-dependent marine species face in terms of compounding impacts of multiple stressors. case studies provide examples where climate impacts complicate conservation and management across land and sea, both in theoretical and applied contexts.

previous studies have aimed to predict responses and vulnerabilities of biological communities, species, and populations to anthropogenic change globally. for example, assessing the vulnerability of a population within a specific environment is a function of both internal and external factors, including the degree of climatic change to which a population is exposed and the degree to which a species’ traits allow it to adapt to changing conditions (chin et al. 2010, pacifici et al. 2015). additionally, several frameworks for assessing the vulnerability of populations under a changing climate have been developed—from determining the general capacity to adapt (williams et al. 2008) to evaluation under 3 dimensions (sensitivity, exposure, and adaptive capacity; foden et al. 2019, garant 2020, thurman et al. 2020). other studies have aimed to forecast how changes in habitat quality (e.g. sea surface temperature [sst], chlorophyll a) will alter and redistribute the pelagic habitat of top predators (hazen et al. 2013, hindell et al. 2020).

however, the potential (or lack thereof) for land-dependent marine species to adapt to change may differ between land and sea environments (weishampel et al. 2003, dickson et al. 2021). each habitat a species utilizes may be differentially impacted by climate change, leading to a greater probability of a compromised life history or modified annual cycle (mazaris et al. 2009a, robinson et al. 2009, cristofari et al. 2018). it is requisite to consider climate impacts on land-dependent marine species through this lens, as they often not only have complex life histories with distinct stages but are also explicitly dependent on highly distinct biomes which face varying climate-
induced threats. Climate change impacts (e.g. geographic shifts of isotherms and shifts in seasonal timing of temperatures) occur at a different pace in marine and terrestrial ecosystems (Burrows et al. 2011), yet marine species likely track climate warming better than terrestrial species (Lenoir et al. 2020). For example, Sunday et al. (2012) found that marine ectotherms shift their poleward and equatorward range boundaries predictably under climate warming due to the tight correlation between thermal tolerance and latitudinal range, whereas the range shifts of terrestrial ectotherms are inconsistent between their poleward and equatorward range limits. This suggests that while the ultimate driver of a marine species’ latitudinal range is tightly linked with temperature (or temperature-correlated parameters), the range of terrestrial animals is less predictable and may be impacted by other abiotic or biotic factors. Thus, land-dependent marine species are a challenging guild to assess under these broad generalizations and have the added challenge of not only tracking shifting climate, but doing so at different velocities within their marine and terrestrial habitats.

Because holistic evaluations of land–sea life histories under climate change are rare, breakdowns in management are likely to occur when composing interventions and selecting spatial areas for protection or reserves (Stoms et al. 2005). For example, in Punta Tombo, Argentina, the existing terrestrial reserve protections for a breeding colony of Magellanic penguins *Spheniscus magellanicus* are insufficient to reduce chick starvation and adult mortality for this sea-dependent species (Boersma et al. 2015). Upon further investigation, researchers found that foraging trips have lengthened significantly since 1980. While the colony was protected on land, similar feeding-ground protections (e.g. via marine protected areas) did not exist as they moved further from the land-based habitat (Boersma et al. 2015). More comprehensive protection and conservation measures for land-dependent marine species can be achieved by selecting reserve sites that consider the functional climatic and physical factors and interactions that exist between land and sea ecosystems for at-risk species dependent on both (Stoms et al. 2005, Dickson et al. 2021). Yet, in order to make these decisions, we must first evaluate the vulnerabilities that exist throughout their life histories and associated habitat requirements in concert. Here, we argue that without careful consideration of specific factors unique to land-dependent marine species, current frameworks may fall short when assessing species that fall into this category.

2. CONSIDERATIONS FOR VULNERABILITY

### 2.1. Degree of specialization

Many land-dependent marine species show specialization in diet and foraging behavior, parental investment, and site fidelity. Specialization is advantageous and efficient in predictable conditions (Merkle et al. 2022, Rebstock et al. 2022), but generalization and flexibility will be critical under increasing ecosystem variability and change (Michelot et al. 2021, Merkle et al. 2022). The ability of land-dependent species to be flexible during anomalous environmental conditions will likely be an indicator of foraging efficiency and reproductive success as climate-related environmental changes continue to intensify and occur more frequently (Michelot et al. 2021, Merkle et al. 2022).

#### 2.1.1. Diet and foraging behavior

Specialization in foraging can be related to diet (i.e. prey preference, availability, or diversity), foraging behavior (e.g. diving, site fidelity, competition), or a combination of the two (Woo et al. 2008, Thiemann et al. 2011, Ceia et al. 2012, Baylis et al. 2015, Pajuelo et al. 2016, Goetsch et al. 2018, Abrahms et al. 2019, Gulka & Davoren 2019). Land-dependent populations within the same taxa or species display varying degrees of specialization and adaptability to environmental variations related to climate change (e.g. Villegas-Amtmann et al. 2011, McMahon et al. 2019). Ability to adapt foraging behavior may be an indicator of future population survival and success under increasing environmental change in some cases (e.g. herbivores: Hofman-Kamińska et al. 2019; penguins: McMahon et al. 2019; sea turtles: Albella Perez et al. 2016) but not in others (e.g. southern right whales: van den Berg et al. 2021). For example, as krill availability has varied over the last century (Fig. 2a), gentoo penguins *Pygoscelis papua* have adapted to the changing conveyor belt of food within waters of close proximity and have added other prey species such as fish and squid to their diets, shifting their trophic position higher and increasing population sizes over the last 4 decades. Concurrently, chinstrap penguins *P. antarcticus* have remained krill specialists, resulting in population declines over recent decades (Fig. 2b) (Polito et al. 2015, McMahon et al. 2019).

Differences in degree of foraging specialization have resulted in varying success across sea lion populations. California sea lions *Zalophus californianus*
are increasing across their temperate ranges and have displayed higher variation in diving behavior, foraging areas, and diet across seasons. In contrast, Galapagos sea lions *Z. wollebaeki* inhabiting equatorial regions present consistent dive and foraging behavior, and their population levels are in decline (Villegas-Amtmann et al. 2011). California sea lions, therefore, appear to have a greater capacity to adapt to environmental variability, as they have historically been exposed to predictable environmental change via seasonality (Villegas-Amtmann et al. 2011). However, at the current pace of climate change, increasing environmental variability can lead to predator–prey mismatches, where prey distributions shift differently than that of their predator spatially and/or temporally (Durant et al. 2007). Within the Gulf of California population specifically, observed declines in the California sea lion population are concurrent with warming SSTs since 1990. Multi-decadal SST anomalies have led to a reduction in highly nutritious prey for California sea lions here, causing the population to resort to lower quality prey (Adame et al. 2020). Because land-dependent marine species’ reproductive successes are often so tightly linked to local foraging successes (Croll et al. 2006, Boersma & Rebstock 2009, Lescroël et al. 2010, Vander Zanden et al. 2014, Jeanniard-du-Dot et al. 2017), population sustainability will likely depend on both the ability to adapt to changing prey fields and adjust foraging strategies, as well as how these adaptations and shifting strategies allow for continued reproductive success.

### 2.1.2. Parental investment

Many land-dependent animals are uniquely spatially constrained in their foraging behavior by the proximity of their pupping or nesting sites and therefore may sacrifice foraging suitability or reproductive success due to these spatial constraints (Thorne et al. 2015, Michelot et al. 2021). For breeding seabirds and pinnipeds, prey availability often depends on a combination of abundance, accessibility, patchiness, and distance from the colony or breeding site (Hamer et al. 2009, Carter et al. 2016, Michelot et al. 2021). For example, over a 120 d rearing period, female Antarctic fur seals *Arctocephalus gazelle* regularly alternate between the oceanic habitat in which they forage and the land-based colony where they suckle their young. Evidence from a movement model indicates that the distance to prey as well as prey aggregations are both significant factors in female breeding success. Female body length is correlated with pup survival; larger females can exploit food resources at a further distance from the haul-out site, and smaller females must make more frequent, closer, and shorter duration trips (Beauplet et al. 2004, Massardier-Galatà et al. 2017). Intermediate maternal body lengths led to optimal pup success as a result of shorter distance to intermediate levels of prey aggregation. Yet as distance to prey resources increases due to warming ocean temperatures, there could be increased pup production for large females (Massardier-Galatà et al. 2017). When parental investment is high, flexibility in foraging behavior can better buffer foraging success across poor years (Abrahms et al. 2018).

Land-based habitats are also changing quickly as a result of anthropogenic climate change. Declines in sea ice, including extent, thickness, and duration (Maslanik et al. 2007), are reducing breeding habitat available for specialized ice-associated pinnipeds (Kovacs et al. 2011). This challenge is exemplified by Pacific walrus *Odobenus rosmarus divergens* mothers and calves, which are experiencing on-shore crowding during haul-out as a result of sea ice declines, leading to high mortality rates due to trampling and predation (Fischbach et al. 2009). Mam-
mals that require stable sea ice later in the spring season and those that require long-duration ice for parental investment will be most strongly impacted by a changing climate within the polar regions (Kovacs & Lydersen 2008, Laidre et al. 2008, Kovacs et al. 2011). For example, ringed seals *Pusa hispida*, which breed and haul-out on sea ice throughout the winter months, give birth in early spring, and continue to lactate on ice for several months post-birth (Lydersen & Kovacs 1999), are critically dependent on sea ice for the entire breeding season and neonatal care (Lydersen & Kovacs 1999, Kovacs et al. 2011). Similarly, land-based habitat loss is problematic due to sea level rise and storm surge in low-lying beach breeding habitats, where pinnipeds and sea birds require land-based habitats for breeding or nesting and nursing or feeding young (Baker et al. 2006, Hatfield et al. 2012, Sydeman et al. 2012, Reynolds et al. 2015).

### 2.1.3. Site fidelity

Site fidelity has evolved across taxa as an advantage when habitat sites and resources for foraging and reproduction are predictable, leading to increased efficiency (Carroll et al. 2018, Rebstock et al. 2022, Merkle et al. 2022). Conversely, choosing a new site can be risky due to lack of information about its quality (Shimada et al. 2020). Predictable migratory routes are even heritable across generations and exist despite variability in habitat quality, prey levels, or environmental conditions (Weitkamp 2010, Almpanidou et al. 2019). However, recently, the degree to which a species, population, or individual exhibits site fidelity has been documented as an indicator of an ability to adapt to changing environmental conditions (Abrahms et al. 2019, Hazen et al. 2019, Merkle et al. 2022). As prey fields have shifted and land-based reproductive sites have become less suitable under rapidly changing environmental conditions, site fidelity specialization is becoming increasingly maladaptive in many cases (Michelot et al. 2021, Merkle et al. 2022). When conditions become more variable and habitat sites and resources are less predictable under climate change, individual flexibility or greater population-level variability may be increasingly beneficial to survival (Laidre et al. 2008, Michelot et al. 2021).

For example, within the Northern elephant seal (*Mirounga angustirostris*) population in the Pacific Ocean, most females exhibit fidelity to foraging habitat locations during long-term post-molting migrations (Abrahms et al. 2018). Individuals that exhibit strong site fidelity within anomalous environmental conditions are more likely to have poorer body conditions compared to individuals that showed weak site fidelity (Abrahms et al. 2018). Alternatively, populations that typically show strong site fidelity may be less likely to show this behavior under increasing environmental change (e.g. guillemot seabirds: Kokko et al. 2004; elephant seals: Abrahms et al. 2018). Additionally, sites may stay the same but the timing of arrival and departure may change (e.g. loggerhead sea turtles *Caretta caretta*: Hawkes et al. 2007, Mazaris et al. 2009a, Monsinjon et al. 2019a; seabirds: Desprez et al. 2018, Merkel et al. 2019, Lameris et al. 2021).

As prey distribution and habitat availability become less predictable, the likelihood of an animal achieving the same outcome at a given location decreases, regardless of past foraging or breeding success (Carroll et al. 2018, Muhling et al. 2022). In particular, species that gain and retain information on foraging and/or breeding sites early in their life history may have less capacity to adapt to rapid environmental change (e.g. elephant seals: McIntyre et al. 2017; Cassin’s auklet *Ptychoramphus aleuticus*: Hipfner 2008; northern gannets *Morus bassanus*: Wakefield et al. 2015; sea turtles: Maurer et al. 2021). Long-term success of these populations may depend on the capacity of the individuals within the population to be flexible and exhibit exploratory behavior (Michelot et al. 2021); therefore, conservation of these species would be aided by studies that examine the degree of inter-individual variation within vulnerable populations. Additionally, studies that include multiple years of data are necessary to determine important breeding and foraging areas to protect across dynamic environmental and biological conditions (Boersma et al. 2015). Conservation and vulnerability assessments should include newly visited sites and take into account levels of individual variation within a population, calling for management that is both adaptable to change and proactive in anticipating these changes (Wege et al. 2016, Wood et al. 2021, Merkle et al. 2022).

### 2.2. Intraspecies population-level differences

Climate change is likely to act differentially on distinct populations due to variability in environmental and geographic features. Species with broader habitat preferences are more likely to display variable responses to climate change impacts compared to species with narrower habitat ranges (Thuiller et al. 2018).
Further, populations at the edges of their habitat preferences, where populations are already at their physical and environmental limits (e.g. penguins: Forcada & Trathan 2009; sea turtles: Mazaris et al. 2013) may be the most immediately vulnerable to climate-related changes.

2.2.1. Polar regions

In the polar regions, climate-related changes such as sea ice melt have proven problematic for numerous seabird and mammal species (McClintock et al. 2008, Kovacs et al. 2011, Bestley et al. 2020). For example, penguins nest on snow-free and ice-free rocky areas in the Antarctic. Increased precipitation and ice melt create considerable flooding, which destroys nesting areas and is a source of mortality for eggs and chicks (McClintock et al. 2008). However, this climate stressor is asymmetrical. While the Western Antarctic Peninsula (WAP) is warming rapidly, resulting in a contraction of Adélie penguin (Pygoscelis adeliae)-suitable habitat, other areas of the Antarctic are cooling, resulting in an expansion of Adélie penguin-suitable habitat (Fig. 3b) (Dugger et
Within the WAP region, Adélie penguins do not have the capacity to alter the timing of their breeding cycle to the quickly warming temperatures, particularly in comparison with other Adélie penguin colonies in Antarctica (Dugger et al. 2014). This complex dynamic has caused Adélie penguin colonies to decrease in size in some areas and increase in size in others (Fig. 3b) (Cimino et al. 2016). Climate-related warming will likely cause nearly 30% of the WAP Adélie penguin colonies to face population declines by 2060. Yet certain areas of Antarctica may provide refugia for the species, which could mitigate a species-wide decline (Cimino et al. 2016). Similarly, in the Arctic, static (e.g. bathymetry) and dynamic (e.g. temperature) factors are likely to contribute to regional variation in the degree of sea ice melt and resulting impacts on ice-dependent mammals (Kovacs et al. 2011).

2.2.2. Tropical regions

Land-dependent marine animals that rely on low-lying beach habitat display population-level differences that are similar to their ice-dependent counterparts. Tropical low-lying islands, which are key nesting and rearing habitat for many species of sea turtles, sea birds, and pinnipeds, face the physical impacts of sea level rise as an immediate threat (Baker et al. 2006, Fuentes et al. 2010, Reynolds et al. 2015). Endangered Hawaiian monk seals *Monachus schauinslandi*, which require sandy beaches near shallow waters for pupping, resting, and molting, are experiencing more crowding due to land loss on islands (Westlake & Gilmartin 1990, Baker et al. 2006). These pinnipeds are restricted in breeding site selection by the need to be near shallow waters, where pups can access ocean habitat without the imminent threat of large wave action and predation (Westlake & Gilmartin 1990). Crowding of pupping beaches will only worsen as islands continue to shrink. Increased crowding on Trig Island, Hawaii, has also led to secondary effects such as increased shark predation in the waters surrounding the island (Baker et al. 2006, Bertilsson-Friedman 2006). Yet differences among populations of monk seals are also present here. Despite conservation protections, the Northwest Hawaiian Island (NWHI) monk seal population continues to decline, while the less-protected Main Hawaiian Island (MHI) population continues to increase (Fig. 3a) (Gerber et al. 2011). Differences in population growth may be driven in part by local expression of climate–ocean variability combined with effects of variability and other anthropogenic impacts (Baker et al. 2012). Additionally, MHI females have longer lactation periods than those in the NWHI—likely due to more favorable foraging conditions—which could benefit pup growth and, ultimately, juvenile survival (Robinson et al. 2021). As the NWHI monk seal population faces potential extinction (Gerber et al. 2011), the longevity of the species may depend solely on the MHI population.

2.2.3. Temperate regions

In temperate regions, land-dependent marine populations may have more opportunities to survive within the context of a changing climate by shifting poleward. Northern elephant seal colonies are decreasing in Baja California (García-Aguilar et al. 2018), while the colony in the Channel Islands of California is increasing (Fig. 3c) (Lowry et al. 2014). This pattern is likely due to climate change and increased atmospheric temperatures as heat dissipation on land becomes an issue for northern elephant seals. This species cannot pant nor do they have sweat glands, instead thermoregulating via cold water edges and cool, moist sand (García-Aguilar et al. 2018). As SST and air temperatures continue to increase, the Baja California northern elephant seal colony will likely continue to shrink, while the Channel Islands population will continue to grow (Fig. 3c) (Lowry et al. 2014, García-Aguilar et al. 2018). Therefore, while sea level rise and resulting inundation is less of an immediate threat to the Channel Islands, this colony may still experience crowding similar to Hawaiian monk seals as the colony increases in size.

2.2.4. Between regions

Population-level responses are also likely to differ among geographic regions. Temperate species of Atlantic and Pacific sea turtles may have the capacity to adjust nesting sites latitudinally if beaches remain undeveloped (Pike 2014, Fuentes et al. 2020). For example, species with broader nesting ranges such as loggerheads (Fig. 3d) (e.g. Pike 2014) are more likely to find suitable nesting habitat beyond their current range relative to species with more geographic specialization in nesting habitat. Generally, temperate populations of loggerheads are predicted to maintain high levels of hatchling success, in con-
contrast to tropical populations, which are expected to decline under future scenarios of climate change. Because temperate nesting beaches exist at a lower ambient air temperature than their tropical counterparts, projected increased temperatures under climate change scenarios do not exceed the lethal levels for embryonic development, despite the estimate that temperatures in both regions are likely to increase by the same magnitude. Since the pre-climate-change ambient temperature of nesting beaches is such an important factor, it is very likely that impacts of climate change on hatching success of loggerheads will vary at both local and regional levels (Fig. 3d) (Pike 2014). For instance, while hatching success is projected to increase across the Mediterranean Sea over the next few decades, by 2050, many of these sites will reach temperature thresholds and begin to decline (Pike 2014). In many cases, warming temperatures will increase the growth rate of several sea turtle populations over the next several decades as sex ratios skew more towards females (Hays et al. 2003, Hawkes et al. 2009, Poloczanska et al. 2009, Witt et al. 2010, Laloë et al. 2014, 2016, 2017, Jensen et al. 2018, Patrício et al. 2019). However, in the longer term, temperatures are likely to reach lethal levels, which will cause growth rates to decline and populations to suffer (Hawkes et al. 2007, Pike 2014, Howard et al. 2014, Hays et al. 2017, Laloë et al. 2017, Patrício et al. 2019).

Across polar, temperate, and tropical regions, anticipated impacts of climate change on land-dependent marine species are a function of both life history strategies and specific regional nuances. Therefore, there is not a ‘one-size fits all’ approach to managing at the species level when population-level response may vary due to individual variability or habitat conditions. Many land-dependent marine species are relatively long-lived and have low fecundity, meaning the ability to adapt to new conditions caused by climate change at the current rate is likely quite low (Dunham & Overall 1994). It is more probable that these populations will respond to new conditions via behavioral plasticity (e.g. changes in timing of nesting season) (Mazaris et al. 2009a, Hamann et al. 2010) and range shifts, and that local extinctions or dispersal will occur (Fuentes et al. 2010, Bernhardt & Leslie 2013, Cristofari et al. 2018). It is, therefore, critical to account for these behavioral changes when considering new conservation initiatives (Muñoz et al. 2015, Beever et al. 2017). Importantly, although land-dependent marine species inhabiting temperate regions may increase their chance of survival by shifting their range, they are not without other significant climate-related impacts to their life histories. For example, the reduction of land-based habitat will likely lead to an increasing number of density-dependent issues within remaining suitable habitat (Baker et al. 2006, Fischbach et al. 2009, Reynolds et al. 2015).

### 2.3. Anthropogenic stressors beyond human-induced climate change

For most land-dependent marine species, the ability to adapt to naturally occurring and anthropogenically induced climate-related stressors is further limited by additional human-caused threats. Numerous examples of this phenomenon have been documented across taxa, geographic regions, and within both land-based and sea-based habitats (Halpern et al. 2008, 2015). Within marine taxa which rely upon terrestrial habitats for reproduction, many species are impacted by anthropogenic activities within their land-based habitats. In particular, those species that nest or breed on tropical and temperate beaches affected by sea level rise and storm surge or inundation are further limited by human development, colonization, and other changes to their environment (Mazaris et al. 2009b, Reece et al. 2013, Von Holle et al. 2019). Within the US Marine National Monuments of the Pacific, seabird colonies, whose nesting habitats are being destroyed by sea level rise and flooding, are unable to move inland due to development. Many populations were also largely eradicated from these islands during human settlement, which left many of these species particularly vulnerable to extinction (Reynolds et al. 2015). Similarly, human development has further exacerbated climate-related threats to sea turtle nesting sites (Fish et al. 2005, Mazaris et al. 2009b). The vulnerability of Caribbean sea turtle nesting beaches varies within a spectrum of anthropogenic land use adjacent to the beach, and many of the most vulnerable beaches are those with adjacent hotels (Fish et al. 2005).

Additionally, changes in human uses of the ocean can put animals with high degrees of specialization at even greater risk. In the subtropical zone, African penguins *Spheniscus demersus* are impacted by consistently higher SSTs and lower productivity near nesting sites. These climate change impacts have reduced local levels of forage fish, forcing these penguins to migrate to areas of lower SST and higher chlorophyll (Sherley et al. 2017). These conditions have created an ecological trap for African penguins, resulting in low juvenile penguin survival and an
80% population decline in the Western Cape colony. This circumstance is intensified by overfishing, which has depleted remaining cooler water sources of prey. As a result, juvenile penguin mortality is high and breeding numbers are low (Sherley et al. 2017).

While evidence previously suggested that proximity to high levels of human impact is a significant predictor of extinction risk (Davies et al. 2006), climate change has now also allowed rapid anthropogenic development in previously inaccessible marine ecosystems (e.g. McCarthy et al. 2022). Within the polar regions, industrial shipping was once limited by heavy ice conditions. Today, due to thinning sea ice conditions and advances in technology, shipping traffic and human presence have increased rapidly since 1990 (Fig. 4) (Liggett et al. 2011, Bender et al. 2016, Dawson et al. 2018, Bestley et al. 2020). Collision risk with pups is now a serious threat that has increased pup mortality in recent years for Caspian seals *Phoca caspica* and White Sea harp seals *P. groenlandica* (Härkönen et al. 2008, Wilson et al. 2017, 2020). Several other species of seals (e.g. ringed seal, bearded seal) and populations of walruses have also been identified as at-risk from ice-breaking ships throughout other areas of the Arctic and sub-Arctic seas (Wilson et al. 2020). Increased vessel traffic has led to a number of threats, including ship strike, displacement from breeding sites due to noise, breeding site destruction, and separation of mothers and pups (Wilson et al. 2017, 2020, McCarthy et al. 2022).

Conditions within the polar regions are already rapidly changing due to anthropogenic climate change (Box et al. 2019, Meredith et al. 2019, Overland et al. 2019, Rogers et al. 2020). Yet because anthropogenic uses have previously been relatively minimal in this region and have quickly expanded over the last 2 decades (Fig. 4), researchers and managers lack information on the impacts of human-induced stressors, such as the introduction of organisms and disease (Cowan et al. 2011, Van Hemert et al. 2014, Grimaldi et al. 2015, VanWormer et al. 2019), pollution (Tin et al. 2009, Bengtson Nash 2011), and habitat alteration (Bestley et al. 2020) on local populations. As a result, several studies have called for identification of and management action on current and future risks related to increased human presence in the polar regions (Post et al. 2009, Tin et al. 2009, Bestley et al. 2020).

### 3. COMPOUNDING IMPACTS OF MULTIPLE STRESSORS

Importantly, the considerations described here do not act independently, and given simultaneous losses of land- and sea-based habitats or functionality, land-dependent marine species are at particular risk of compounding impacts related to climate change. Sea turtles face threats on land (loss of nesting beaches, increasing air temperatures) and at sea (changes in productivity, interactions with fishing gear) (Hawkes et al. 2009, Hamann et al. 2010, Rees et al. 2016). Warming at nesting beaches in the Great Barrier Reef is greatly altering the sex-ratios of green sea turtle (*Chelonia mydas*) hatchlings, while nearby nesting beaches remain unsuitable for adaptation due to development (Jensen et al. 2018). Additionally, several studies have acknowledged the potential for mobile prey resources to decouple from land-based reproductive areas within a changing climate (Fig. 5).
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For example, island-nesting albatross may have increased distance to travel to foraging grounds (Thorne et al. 2015, 2016) and will also lose breeding habitat (Baker et al. 2006). As alluded to above, climate change-induced habitat losses will result in a variety of secondary effects such as increased competition (Kovacs et al. 2011, 2012, Fink 2017), increased predation risk (Baker 2008), increased juvenile mortality rates (e.g. as a result of trampling: Fischbach et al. 2009), disease (Kovacs et al. 2011), and other density-dependent issues. Facing multiple threats makes holistic management approaches even more important for species that rely on multiple habitats.

Multiple impacts can also result from a single environmental change. For example, as an ectotherm, increases in temperature have widespread direct and indirect impacts across sea turtle phenology and all phases of life history (Hawkes et al. 2009, Poloczanska et al. 2009, Witt et al. 2010, Fisher et al. 2014, Pike 2014, Laloë et al. 2014, 2016, 2017, Booth 2017, Hays et al. 2017). Indirectly, increasing temperatures cause sea ice melt, leading to sea level rise, which threatens nesting habitat (Fish et al. 2005, Hawkes et al. 2009, Fuentes et al. 2010, Katselidis et al. 2014). Increases in SST can also impact migratory routes, neonatal dispersal, food availability, and biological parameters that influence prey and predator distribution (Hawkes et al. 2009, Thomson et al. 2015, Crear et al. 2016, Esteban et al. 2020). Directly, increasing nest temperatures threaten hatchling fitness and survival, timing of reproduction, incubation conditions, and sex ratios (Hawkes et al. 2009, Howard et al. 2014, Laloë et al. 2014, 2016, 2017, Hays et al. 2017, Monsinjon et al. 2019b). Yet the pace and magnitude at which temperature increases are different on land and at sea (Burrows et al. 2011) and across geographic regions, making it exceptionally difficult to predict how the multiple stressors linked to increasing temperature will ultimately impact sea turtle populations globally. As an ectotherm, sea turtles may extend their ranges of tolerable latitudes poleward and contract equatorward in the marine environment, but terrestrially, this contraction in equatorward habitat may lag in comparison (Sunday et al. 2012). Survival issues may arise for species if marine and terrestrial ranges are pulled in conflicting directions, and connectivity between the 2 environments is strained, potentially leading to ecological traps (e.g. Sherley et al. 2017). When connectivity between essential habitats is not considered in conservation and management efforts, management is less likely to be successful (Dunn et al. 2019).

Managers still lack evidence for how multiple stressors will interact and affect populations (e.g. synergistic, additive, antagonistic). Even when multiple stressors are considered, cumulative effects are often documented inconsistently across countries, environments, and industries (Hague et al. 2022). For the king penguin Aptenodytes patagonicus, natural habitat fragmentation prevents populations located north of the Antarctic Polar Front (APF) from finding new land-based refugia in concurrence with southward-shifting foraging grounds. As foraging grounds become increasingly distant and chick-rearing habitat becomes less suitable, these populations will face declines in breeding success (Fig. 5) (Chen et al. 2011, Bost et al. 2015, Cristofari et al. 2018). The interactions between climate change and other factors (e.g. habitat loss, fragmentation) will likely cause extinction thresholds for populations, like King penguins north of the APF (Fig. 5), to be reached even sooner (Travis 2003). In marine and coastal systems, cumulative effects of multiple stressors are often synergistic, meaning the combined effects of multiple stressors is more significant for populations than the sum of their individual effects (Crain et al. 2008). Land-dependent marine species face the reality of synergistic effects at sea in addition to simultaneous losses of land- and sea-based habitats and/or functionality.

Fig. 5. Fragmented nature of king penguin habitat compounds climate change impacts on land and sea habitats: as the Antarctic Polar Front (APF) shifts southward over the next century, populations north (orange) and south (green) of the APF will be impacted differently. Downward arrows: decreasing; upward arrows: increasing
4. CONCLUSIONS

While degree of specialization, intraspecies population-level differences, and additional anthropogenic stressors affect all marine species' ability to cope with a changing climate, they may have an oversized effect on land-dependent marine predators. We argue that in light of these considerations, 'one-size-fits-all' approaches may not be equally successful across populations (e.g. sea turtles: Fuentes et al. 2011). Additionally, considering the full life cycle of a species and how the land and sea phases are linked to one another can help us to better identify management pitfalls. Therefore, population and site-specific analyses of vulnerable populations across life history stages are critical to understand how climate change and its related impacts affect an entire species. Protected areas have been championed as a key solution for conserving vulnerable species; however, in many cases, these areas are insufficient to protect across land and sea, across life history stages, and across changing environmental and biological conditions (Boersma & Parrish 1999, Dryden et al. 2008, Yorio 2009, Agardy et al. 2011, Nel et al. 2013, Boersma et al. 2015, Ropert-Coudert et al. 2019, Abalo-Morla et al. 2022). While protecting land-based life history phases within clear jurisdictional boundaries is important, protecting dynamic seabased habitats may be equally necessary, as these phases may be critical to population survival (Dryden et al. 2008, Agardy et al. 2011, Maxwell et al. 2020). Further, without consideration of the compounding impacts of climate and other stressors across biomes, the life history strategies we have reviewed may indicate which conservation measures are most likely to fall short.

Holistic management measures across both land and sea habitats can also be complicated by governance structures and shared jurisdiction required for the recovery and conservation of these species. For example, in the USA, sea turtle management remains under the jurisdiction of the National Oceanic and Atmospheric Administration while they are in marine habitats, but becomes the responsibility of the Fish and Wildlife Service during their time on nesting beaches. Many of these same species also migrate across countries' exclusive economic zones and open-ocean habitats, which could change with climate-driven redistribution (Harrison et al. 2018). Given the unique habitat needs of land-dependent marine species, collaborative efforts across multiple agencies and multiple countries are needed for unified and comprehensive management strategies. As land-dependent marine populations respond to environmental variability and changes, they may be forced to occupy new areas, which can result in new human–wildlife conflicts. Proactive management that anticipates these responses and conflicts can be less resource-intensive and better suited to achieve conservation outcomes. However, for these management efforts to be successful, identification of ‘hope spots’—when and where populations may show behavioral plasticity—must consider land–sea connectivity requirements for this group.

Acknowledgements. We thank Megan Cimino from NOAA Southwest Fisheries Science Center and Matthew Oliver from University of Delaware for providing data on Adélie penguin colonies in Antarctica. We also thank Samantha Andrzejaczek from Stanford University for providing feedback during study conception and Natalie Arnoldi from Stanford University for providing feedback on Fig. 1. The research presented here did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

LITERATURE CITED

- Abalo-Morla S, Belda EJ, March D, Revuelta O and others (2022) Assessing the use of marine protected areas by loggerhead sea turtles (Caretta caretta) tracked from the western Mediterranean. Glob Ecol Conserv 38:e02196
- Abella Perez E, Marco A, Martins S, Hawkes LA (2016) Is this what a climate change-resilient population of marine turtles looks like? Biol Conserv 193:124–132
- Abrahms B, Hazen EL, Bograd SJ, Brashares JS and others (2018) Climate mediates the success of migration strategies in a marine predator. Ecol Lett 21:63–71
- Abrahms B, Welch H, Brodie S, Jacob MG and others (2019) Dynamic ensemble models to predict distributions and anthropogenic risk exposure for highly mobile species. Divers Distrib 25:1182–1193
- Adame K, Elorriaga-Verplancken FR, Beier E, Acevedo-Whitehouse K, Pardo MA (2020) The demographic decline of a sea lion population followed multi-decadal sea surface warming. Sci Rep 10:10499
- Agardy T, di Sciarra GN, Christie P (2011) Mind the gap: addressing the shortcomings of marine protected areas through large scale marine spatial planning. Mar Policy 35:226–232
- Almpanidou V, Markantonatou V, Mazaris AD (2019) Thermal heterogeneity along the migration corridors of sea turtles: implications for climate change ecology. J Exp Mar Bio Ecol 520:151223
- Baker JD (2008) Variation in the relationship between offspring size and survival provides insight into causes of mortality in Hawaiian monk seals. Endang Species Res 5:55–64
- Baker JD, Littnan CL, Johnston DW (2006) Potential effects of sea level rise on the terrestrial habitats of endangered and endemic megafauna in the Northwestern Hawaiian Islands. Endang Species Res 2:21–30
- Baker JD, Howell EA, Polovina JJ (2012) Relative influence of climate variability and direct anthropogenic impact on
a sub-tropical Pacific top predator, the Hawaiian monk seal. Mar Ecol Prog Ser 469:175–189

Baylis AMM, Orben RA, Arnould JPY, Peters K, Knox T, Costa DP, Staniland LJ (2015) Diving deeper into individual foraging specializations of a large marine predator, the southern sea lion. Oecologia 179:1053–1065

Beal M, Dias MP, Phillips RA, Oppel S and others (2021) Global political responsibility for the conservation of albatrosses and large petrels. Sci Adv 7:eabd7225

Beauplet G, Dubroca L, Guinet C, Cherel Y, Dabin W, Gagne C, Hindell M (2004) Foraging ecology of sub-antarctic fur seals Arctocephalus tropicalis breeding on Amsterdam Island: seasonal changes in relation to maternal characteristics and pup growth. Mar Ecol Prog Ser 273:211–225

Beeever EA, Hall LE, Varner J, Loosen AE and others (2017) Behavioral flexibility as a mechanism for coping with climate change. Front Ecol Environ 15:299–309

Beltran RS, Yuen AL, Condit R, Robinson PW, Czapanskiy MF, Crocker DE, Costa DP (2022) Elephant seals time their long-distance migrations using a map sense. Curr Biol 32:R156–R157

Bender NA, Crosbie K, Lynch HJ (2016) Patterns of tourism in the Antarctic Peninsula region: a 20-year analysis. Antarct Sci 28:194–203

Bengtson Nash S (2011) Persistent organic pollutants in Chelonia mydas. Wildl Res 38:463–470

Bernhardt JR, Leslie HM (2013) Resilience to climate change in coastal marine ecosystems. Annu Rev Mar Sci 5:371–392

Bertilsson-Friedman P (2006) Distribution and frequencies of shark-inflicted injuries to the endangered Hawaiian monk seal (Monachus schauinslandi). J Zool (Lond) 268:361–368

Bestley S, Roupert-Coudert Y, Bengtson Nash S, Brooks CM and others (2020) Marine ecosystem assessment for the Southern Ocean: birds and marine mammals in a changing climate. Front Ecol Evol 8:566936

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ and others (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90

Boersma PD, Parrish JK (1999) Limiting abuse: marine protected areas, a limited solution. Ecol Econ 31:287–304

Boersma PD, Rebstock GA (2009) Foraging distance affects reproductive success in Magellanic penguins. Mar Ecol Prog Ser 375:263–275

Boersma PD, Rebstock GA, García-Borborough P (2015) Marine protection is needed for Magellanic penguins in Argentina based on long-term data. Biol Conserv 182:197–204

Booth DT (2017) Influence of incubation temperature on sea turtle hatching quality. Integr Zool 12:352–360

Bost CA, Cotté C, Terray P, Barbraud C and others (2015) Large-scale climatic anomalies affect marine predator foraging behaviour and demography. Nat Commun 6:8220

Box JE, Colgan WT, Christensen TR, Schmidt NM and others (2019) Key indicators of Arctic climate change: 1971–2017. Environ Res Lett 14:045010

Burrows MT, Schoeman DS, Buckley LB, Moore P and others (2011) The pace of shifting climate in marine and terrestrial ecosystems. Science 334:652–656

Campbell RA, Gales NJ, Lento GM, Baker CS (2008) Islands in the sea: extreme female natal site fidelity in the Australian sea lion, Neophoca cinerea. Biol Lett 4:139–142

Carroll G, Harcourt R, Pitcher BJ, Slip D, Jonsen I (2018) Recent prey capture experience and dynamic habitat quality mediate short-term foraging site fidelity in a seabird. Proc R Soc B 285:20180788

Carter MD, Bennett KA, Embling CB, Hosegood PJ, Russell DJF (2016) Navigating uncertain waters: a critical review of inferring foraging behaviour from location and dive data in pinnipeds. Mov Ecol 4:25

Ceia FR, Phillips RA, Ramos JA, Cherel Y, Vieira RP, Richard P, Xavier JC (2012) Short- and long-term consistency in the foraging niche of wandering albatrosses. Mar Biol 159:1581–1591

Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026

Chilvers BL, Wilkinson IS (2008) Philopatry and site fidelity of New Zealand sea lions (Phocarctos hookeri). Wildl Res 35:463–470

Chin A, Kyne PM, Walker TI, McCauley RB (2010) An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia’s Great Barrier Reef. Glob Change Biol 16:1936–1953

Cimino MA, Lynch HJ, Saba VS, Oliver MJ (2016) Projected asymmetric response of Adélie penguins to Antarctic climate change. Sci Rep 6:28785

Cowan DA, Chown SL, Convey P, Tufin M, Hughes K, Pointing S, Vincent WF (2011) Non-indigenous microorganisms in the Antarctic: assessing the risks. Trends Microbiol 19:540–548

Crain CM, Kroeker K, Halpern BS (2008) Interactive and cumulative effects of multiple human stressors in marine systems. Ecol Lett 11:1304–1315

Crear DP, Lawson DD, Seminoff JA, Eguchi T, LeRoux RA, Lowe CG (2016) Seasonal shifts in the movement and distribution of green sea turtles Chelonia mydas in response to anthropogenically altered water temperatures. Mar Ecol Prog Ser 548:219–232

Cristofari R, Liu X, Bonadonna F, Cherel Y and others (2018) Climate-driven range shifts of the king penguin in a fragmented ecosystem. Nat Clim Chang 8:245–251

Croll DA, Demer DA, Hewitt RP, Janssen JK, Goebel ME, Tershy BR (2006) Effects of variability in prey abundance on reproduction and foraging in chinstrap penguins (Pygoscelis antarctica). J Zool (Lond) 269:506–513

Davies RG, Orme CDL, Olson V, Thomas GH and others (2006) Human impacts and the global distribution of extinction risk. Proc R Soc B 273:2127–2133

Dawson J, Pizzolato L, Howell SE, Copland L, Johnston ME (2018) Temporal and spatial patterns of ship traffic in the Canadian Arctic from 1990 to 2015. Arctic 71:15–26

Desprez M, Jenouvrier S, Barbraud C, Delord K, Weimerskirch H (2018) Linking oceanographic conditions, migratory schedules and foraging behaviour during the non-breeding season to reproductive performance in a long-lived seabird. Funct Ecol 32:2040–2053

Dias MP, Martin R, Pearmain EJ, Burfield LJ and others (2019) Threats to seabirds: a global assessment. Bio Cons 237:525–537

Dickson LC, Katselidis KA, Eizaguirre C, Schofield G (2021) Incorporating geographical scale and multiple environmental factors to delineate the breeding distribution of sea turtles. Drones (Basel) 5:142
Dryden J, Grech A, Moloney J, Hamann M (2008) Rezoning of the Great Barrier Reef World Heritage Area: Does it afford greater protection for marine turtles? Wildl Res 35: 477–485

Dugger KM, Ballard G, Ainley DG, Lyver POB, Schine C (2014) Adélie penguins coping with environmental change: results from a natural experiment at the edge of their breeding range. Front Ecol Evol 2:68

Dunham AE, Overall KL (1994) Population responses to environmental change: life history variation, individual-based models, and the population dynamics of short-lived organisms. Integr Comp Biol 34:382–396

Dunn DC, Harrison A-L, Curtice C, DeLand S and others (2019) The importance of migratory connectivity for global ocean policy. Proc R Soc B 286:20191472

Durant JM, Hjermann D, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33: 271–283

Esteban N, Mortimer JA, Stokes HJ, Laløé JO, Unsworth ARK, Hays GC (2020) A global review of green turtle diet: sea surface temperature as a potential driver of omnivory levels. Mar Biol 167:183

Fink S (2017) Loss of habitat: impacts on pinnipeds and their welfare. In: Butterworth A (ed) Marine mammal welfare. Springer, Cham, p 241–252

Fischbach AS, Monson DH, Jay CV (2009) Enumeration of Pacific walrus carcasses on beaches of the Chukchi Sea in Alaska following a mortality event, September 2009. Open file report 2009–1292. US Geological Survey, Reston, VA

Fisher LR, Godfrey MH, Owens DW (2014) Incubation temperature effects on hatching performance in the loggerhead sea turtle (Caretta caretta). PLOS ONE 9:e114880

Foden WB, Young BE, Akçakaya HR, Garcia RA and others (2019) Climate change vulnerability assessment of species. Wiley Interdiscip Rev Clim Change 10:e551

Forcada J, Thranan PN (2009) Penguin responses to climate change in the Southern Ocean. Glob Change Biol 15: 482–491

Fusseis MMPB, Limpus CJ, Hamann M, Dawson J (2010) Potential impacts of projected sea-level rise on sea turtle rookeries. Aquat Conserv 20:132–139

Fusseis MMPB, Limpus CJ, Hamann M (2011) Vulnerability of sea turtle nesting grounds to climate change. Glob Change Biol 17:140–153

Gerber LR, Estes J, Crawford TG, Peavey LE, Read AJ (2011) Managing for extinction? Conflicting conservation objectives in a large marine reserve. Conserv Lett 4: 417–422

Godley BJ, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, Witt MJ (2008) Satellite tracking of sea turtles: Where have we been and where do we go next? Endang Species Res 4:3–22

Goetsch C, Conners MG, Budge SM, Mitani Y and others (2018) Energy-rich mesopelagic fishes revealed as a critical prey resource for a deep-diving predator using quantitative fatty acid signature analysis. Front Mar Sci 5:430

Goldbogen JA, Cade DE, Wisniewska DM, Potvin J and others (2019) Why whales are big but not bigger: physiological drivers and ecological limits in the age of ocean giants. Science 366:1367–1372

Grimaldi WW, Seddon PJ, Lyver POB, Nakagawa S, Tompkins DM (2015) Infectious diseases of Antarctic penguins: current status and future threats. Polar Biol 38: 591–606

Gulka J, Davoren GK (2019) High individual flexibility in the foraging behavior of a marine predator, the common murre. Mar Biol 166:83

Hague EL, Sparling CE, Morris C, Vaughan D and others (2022) Same space, different standards: a review of cumulative effects assessment practice for marine mammals. Front Mar Sci 9:822467

Halpern BS, Walbridge S, Selkoe KA, Kappel CV and others (2008) A global map of human impact on marine ecosystems. Science 319:948–952

Halpern BS, Frazier M, Potapenko J, Casey KS and others (2009) Fine-scale foraging behaviour of a large, medium-ranging marine predator. J Anim Ecol 78: 880–889

Hamann M, Godfrey MH, Seminoff JA, Arthur K and others (2010) Global research priorities for sea turtles: informing management and conservation in the 21st century. Endang Species Res 11:245–269

Hamer KC, Humphreys EM, Magalhães MC, Garthe S and others (2009) Fine-scale foraging behaviour of a large, medium-ranging marine predator. J Anim Ecol 78: 880–889

Hanson N, Jones EL, Harris RN (2018) Multi-decadal and ontogenetic trophic shifts inferred from stable isotope ratios of pinniped teeth. Oikos 127:134–146

Härkönen T, Jüssi M, Baimukanov M, Bignert A and others (2008) Pup production and breeding distribution of the Caspian seal (Phoca caspica) in relation to human impacts. Ambio 37:356–361

Harrison AL, Costa DP, Winship AJ, Benson SR and others (2018) The political biogeography of migratory marine predators. Nat Ecol Evol 2:1571–1578

Hattfield JS, Reynolds MH, Seavy NE, Krause CM (2012) Population dynamics of Hawaiian seabird colonies vulnerable to sea-level rise. Conserv Biol 26:667–678

Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2007) Investigating the potential impacts of climate change on a marine turtle population. Glob Change Biol 13:923–932

Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2009) Climate change and marine turtles. Endang Species Res 7:137–154

Hays GC, Broderick AC, Glen F, Godley BJ (2003) Climate change and sea turtles: a 150-year reconstruction of
incubation temperatures at a major marine turtle rookery. Glob Change Biol 9:642–646
Hays GC, Mazaris AD, Schofield G, Laloë JO (2017) Population viability at extreme sex-ratio skews produced by temperature-dependent sex determination. Proc R Soc B 284:20162576
Hazen EL, Jørgensen S, Rykaczewski RR, Bograd SJ and others (2020) Tracking of marine predators to protect Southern Ocean ecosystems. Nature 580:87–92
Häder DM, Reisinger RR, Ropert-Coudert Y, Hückstädt LA and others (2014) Thermal tolerances of sea turtle embryos: current understanding and future directions. Endang Species Res 26:75–86
Hof AR, Jansson R, Nilsson C (2012) Future climate change will favour non-specialist mammals in the (sub)Arctic. PLOS ONE 7:e52574
Holman-Kamińska E, Bocherens H, Drucker DG, Fyfe RM, Hofman AR, Jansson R, Nilsson C (2012) Future climate change: a modeling approach. PLOS ONE 12:e0173797
Howard R, Bell I, Pike DA (2014) Thermal tolerances of sea turtle embryos: current understanding and future directions. Endang Species Res 26:75–86
IPCC (2007) Climate change 2007: synthesis report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva
Isaac JL (2009) Effects of climate change on life history: implications for extinction risk in mammals. Endang Species Res 7:115–123
Jeanniard-du-Dot T, Trites AW, Arnould JPY, Guinet C (2017) Reproductive success is energetically linked to foraging efficiency in Antarctic fur seals. PLOS ONE 12:e0174001
Jenouvrier S, Che-Castaldo J, Wolf S, Holland M and others (2021) The call of the emperor penguin: legal responses to species threatened by climate change. Glob Change Biol 27:5008–5029
Jensen MP, Allen CD, Eguchi T, Bell IP and others (2018) Environmental warming and feminization of one of the largest sea turtle populations in the world. Curr Biol 28: 154–159.e4
Katselidis KA, Schofield G, Stamou G, Dimopoulos P, Pantis JD (2014) Employing sea-level rise scenarios to strategically select sea turtle nesting habitat important for long-term management at a temperate breeding area. J Exp Mar Biol Ecol 450:47–54
Kokko H, Harris MP, Wanless S (2004) Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot Uria aalge. J Anim Ecol 73:367–376
Kovacs KM, Lydersen C (2008) Climate change impacts on seals and whales in the North Atlantic Arctic and adjacent shelf seas. Sci Prog 91:117–150

Kovacs KM, Lydersen C, Overland JE, Moore SE (2011) Impacts of changing sea-ice conditions on Arctic marine mammals. Mar Biodivers 41:181–194
Kovacs KM, Aguilar A, Aurioles D, Burkanov V and others (2012) Global threats to pinnipeds. Mar Mamm Sci 28: 414–436
Laidre KL, Stirling I, Lowry LF, Wiig Ø, Heide-Jørgensen MP, Ferguson SH (2008) Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. Ecol Appl 18:S97–S125
Laloë JO, Cozens J, Renom B, Taxonera A, Hays GC (2014) Effects of rising temperature on the viability of an important sea turtle rookery. Nat Clim Chang 4:513–518
Laloë JO, Esteban N, Berkel J, Hays GC (2016) Sand temperatures for nesting sea turtles in the Caribbean: implications for hatching sex ratios in the face of climate change. J Exp Mar Biol Ecol 474:92–99
Laloë JO, Cozens J, Renom B, Taxonera A, Hays GC (2017) Climate change and temperature-linked hatching mortality at a globally important sea turtle nesting site. Glob Change Biol 23:4922–4931
Lamers TK, Hoekendijk J, Aarts G, Aarts A and others (2021) Migratory vertebrates shift migration timing and distributions in a warming Arctic. Anim Migr 8: 110–131
Le Boeuf BJ (1991) Pinniped mating systems on land, ice and in the water: emphasis on the Phocidae. In: Renouf D (ed) The behaviour of pinnipeds. Springer, Dordrecht, p 45–65
Lenoir J, Bertrand R, Comte L, Bourgeaud L, Hattab T, Muri- enne J, Grenouillet G (2020) Species better track climate warming in the oceans than on land. Nat Ecol Evol 4: 1044–1059
Lescroël A, Ballard G, Tonjolo V, Barton KJ, Wilson PR, Lyver POB, Ainley DG (2010) Working less to gain more: when breeding quality relates to foraging efficiency. Ecology 91:2044–2055
Lescroël A, Ballard G, Grémil del D, Authier M, Ainley DG (2014) Antarctic climate change: extreme events disrupt plastic phenotypic response in Adélie penguins. PLOS ONE 9:e85291
Liggett D, McIntosh A, Thompson A, Gilbert N, Storey B (2011) From frozen continent to tourism hotspot? Five decades of Antarctic tourism development and management, and a glimpse into the future. Tour Manage 32: 357–366
Lohmann KJ, Putman NF, Lohmann CMF (2008) Geomagnetic imprinting: a unifying hypothesis of long-distance natal homing in salmon and sea turtles. Proc Natl Acad Sci USA 105:19096–19101
Lowry MS, Condit R, Hatfield B, Allen SG and others (2014) Abundance, distribution, and population growth of the northern elephant seal (Mirounga angustirostris) in the United States from 1991 to 2010. Aquat Mamm 40:20–31
Lydersen C, Kovacs KM (1999) Behaviour and energetics of ice-breeding, North Atlantic phocid seals during the lacc- tation period. Mar Ecol Prog Ser 187:265–281
Maslanik JA, Fowler C, Stroeve J, Drobot S, Zwally J, Yi D, Emery W (2007) A younger, thinner Arctic ice cover: increased potential for rapid, extensive sea-ice loss. Geophys Res Lett 34:2004–2008
Massardier-Galatà L, Morinay J, Bailleul F, Wajnberg E, Guinet C, Coquillard P (2017) Breeding success of a marine central place forager in the context of climate change: a modeling approach. PLOS ONE 12:e0173797
Maurer AS, Seminoff JA, Layman CA, Stapleton SP, Godfrey MH, Reiskind MOB (2021) Population viability of sea turtles in the context of global warming. Bioscience 71:790–804

Maxwell SM, Gjerde KM, Conners MG, Crowder LB (2020) Mobile protected areas for biodiversity on the high seas. Science 367:252–254

Mazaris AD, Kallimanis AS, Tzanopoulos J, Sgardelis SP, Pantis JD (2009a) Sea surface temperature variations in core foraging grounds drive nesting trends and phenology of loggerhead turtles in the Mediterranean Sea. J Exp Mar Biol Ecol 379:23–27

Mazaris AD, Matsinos G, Pantis JD (2009b) Evaluating the impacts of coastal squeeze on sea turtle nesting. Ocean Coast Manage 52:139–145

Mazaris AD, Kallimanis AS, Pantis JD, Hays GC (2013) Phenological response of sea turtles to environmental variation across a species’ northern range. Proc R Soc B 280: 20122397

McCarthy AH, Peck LS, Aldridge DC (2022) Ship traffic connects Antarctica’s fragile coasts to worldwide ecosystems. Proc Natl Acad Sci USA 119:e2110303118

McClintock J, Ducklow H, Fraser W (2008) Ecological responses to climate change on the Antarctic Peninsula. Am Sci 96:302–310

Mclntyre T, Bester MN, Bornemann H, Tosh CA, de Bruyn PJN (2017) Slow to change? Individual fidelity to three-dimensional foraging habitats in southern elephant seals, Mirounga leonina. Anim Behav 127:91–99

McMahon KW, Michelson CI, Hart T, McCarthy MD, Patterson WP, Polito MJ (2019) Divergent trophic responses of sympatric penguin species to historic anthropogenic exploitation and recent climate change. Proc Natl Acad Sci USA 116:25721–25727

Meredith M, Sommerkorn M, Cassotta S, Derksen C and others (2019) Polar regions. In: Pörtner HO, Roberts DC, Masson-Delmotte V, Zhai P and others (eds) IPCC special report on the ocean and cryosphere in a changing climate. Cambridge University Press, Cambridge, p 203–320

Merkel B, Descamps S, Yoccoz NG, Danielsen J and others (2019) Earlier colony arrival but no trend in hatching timing in two congeneric seabirds (Uria spp.) across the North Atlantic. Biol Lett 15:20190634

Merkle JA, Abrahms B, Armstrong JB, Sawyer H, Costa DP, Chaloup AD (2022) Site fidelity as a maladaptive behavior in theAnthropocene. Front Ecol Environ 5:2359–2373

Muir JA, Limpus CJ (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz P, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 137–163

Muhling BA, Snyder S, Hazen EL, Whitlock RE and others (2022) Risk and reward in foraging migrations of North Pacific alcabores determined from estimates of energy intake and movement costs. Front Mar Sci 9:730428

Muir JA, Márquez AL, Real R (2015) An approach to consider behavioral plasticity as a source of uncertainty when forecasting species’ response to climate change. Ecol Evol 5:2359–2373

Musick JA, Limpus CJ (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz P, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 137–163

Nakicenovic N, Alcamo J, Davis G, Vries BD and others (2000) IPCC special report: emissions scenarios. A special report of IPCC Working Group III. IPCC, Geneva

NEL R, PUNT AE, HUGHES GR (2013) Are coastal protected areas always effective in achieving population recovery for nesting sea turtles? PLOS ONE 8:e63525

Oestreich WK, Abrahms B, McKenna MF, Goldbogen JA, Crowder LB, Ryan JP (2022) Acoustic signature reveals blue whales tune life-history transitions to oceanographic conditions. Funct Ecol 36:882–895

O’ergeret F, Cox SL, Weimerskirch H, Guinet C (2019) Body condition influences ontogeny of foraging behavior in juvenile southern elephant seals. Ecol Evol 9:223–236

Overland J, Dunlea E, Box JE, Corell R and others (2019) The urgency of Arctic change. Polar Sci 21:6–13

Pacifici M, Foden WB, Visconti P, Watson JEM and others (2015) Assessing species vulnerability to climate change. Nat Clim Chang 5:215–224

Pajuelo M, Björndal KA, Arendt MD, Foley AM, Schroeder BA, Witherington BE, Boltan AB (2016) Long-term resource use and foraging specialization in male loggerhead turtles. Mar Biol 163:235

Patricio AR, Varela MR, Barbosa C, Broderick AC and others (2019) Climate change resilience of a globally important sea turtle nesting population. Glob Change Biol 25: 522–535

Piatt JF, Parrish JK, Renner HM, Schoen SK and others (2020) Extreme mortality and reproductive failure of common murres resulting from the northeast Pacific marine heatwave of 2014–2016. PLOS ONE 15:e0226087

Pike DA (2014) Forecasting the viability of sea turtle eggs in a warming world. Glob Change Biol 20:7–15

Polito MJ, Trivelpiece WZ, Patterson WP, Karnovsky NJ, Reiss CS, Emslie SD (2015) Contrasting specialist and generalist patterns facilitate foraging niche partitioning in sympatric populations of Pygoscelis penguins. Mar Ecol Prog Ser 519:221–237

Poloczanska ES, Limpus CJ, Hays GC (2009) Vulnerability of marine turtles to climate change. Adv Mar Biol 56: 151–211

Post E, Forchhammer MC, Bret-Harte MS, Callaghan TV and others (2009) Ecological dynamics across the Arctic associated with recent climate change. Science 325: 1355–1358

Prince PA, Rothery P, Croxall JP, Wood AG (1994) Population dynamics of black-browed and grey-headed albatrosses Diomedea melanophris and D. chrysostoma at Bird Island, South Georgia. Ibis 136:50–71

Rebstock GA, Abrahms B, Boersma PD (2022) Site fidelity increases reproductive success by increasing foraging efficiency in a marine predator. Behav Ecol 33:868–875

Reece JS, Passeri D, Ehrhart L, Haugen SC and others (2013) Sea level rise, land use, and climate change influence the
distribution of loggerhead turtle nests at the largest USA rookery (Melbourne Beach, Florida). Mar Ecol Prog Ser 493:259–274

Rees AF, Allaro-Shiguelo J, Barata PCR, Bjorndal KA and others (2016) Are we working towards global research priorities for management and conservation of sea turtles? Endang Species Res 31:337–382

Reynolds MH, Courtot KN, Berkowitz P, Storlazzi CD, Moore J, Flint E (2015) Will the effects of sea-level rise create ecological traps for Pacific island seabirds? PLOS ONE 10:e0136773

Riottte-Lambert L, Weimerskirch H (2013) Do naïve juvenile seabirds forage differently from adults? Proc R Soc B 280:20131434

Robinson RA, Crick HQP, Learmonth JA, Maclean IMD and others (2009) Travelling through a warming world: climate change and migratory species. Endang Species Res 7:87–99

Robinson SJ, Harting AL, Mercer T, Johanos TC, Baker JD, Littnan CL (2021) Sighting patterns reveal unobserved pupping events to revise reproductive rate estimates for Hawaiian monk seals in the main Hawaiian Islands. Mar Mamm Sci 37:420–432

Rogers AD, Frinault BAV, Barnes DKA, Bindoff NL and others (2020) Antarctic futures: an assessment of climate-driven changes in ecosystem structure, function, and service provisioning in the Southern Ocean. Annu Rev Mar Sci 12:87–120

Ropert-Coudert Y, Chiaradia A, Ainley D, Barbosa A and others (2019) Happy feet in a hostile world? The future of penguins depends on proactive management of current and expected threats. Front Mar Sci 6:248

Schwartz MW, Iverson LR, Prasad AM, Matthews SN, O’Connor RJ (2006) Predicting extinctions as a result of climate change. Ecology 87:1611–1615

Sherley RB, Ludnya K, Dyer BM, Lamont T and others (2017) Metapopulation tracking juvenile penguins reveals an ecosystem-wide ecological trap. Curr Biol 27:563–568

Shimada T, Limbus CJ, Hamann M, Bell I, Esteban N, Groom R, Hays GC (2020) Fidelity to foraging sites after long migrations. J Anim Ecol 89:1008–1016

Silber GK, Leitchir MD, Thomas PO, Baker JD and others (2017) Projecting marine mammal distribution in a changing climate. Front Mar Sci 4:413

Stirling I, Lunn NJ, Iacozza J (1999) Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. Arctic 52:294–306

Stoms DM, Davis FW, Andelman SJ, Carr MH and others (2005) Integrated coastal reserve planning: making the land–sea connection. Front Ecol Environ 3:429

Sunday JM, Bates AE, Dulvy NK (2012) Thermal tolerance and the global redistribution of animals. Nat Clim Chang 2:686–690

Sydeman WJ, Bradley RW, Warzybok P, Abraham CL and others (2006) Planktivorous auklet Ptychoramphus aleuticus responses to ocean climate, 2005: Unusual atmospheric blocking? Geophys Res Lett 33:L22509

Sydeman WJ, Thompson SA, Kitaysky A (2012) Seabirds and climate change: roadmap for the future. Mar Ecol Prog Ser 454:107–117

Sydeman WJ, Hunt GL, Pikitch EK, Parrish JK and others (2021) South Africa’s experimental fisheries closures and recovery of the endangered African penguin. ICES J Mar Sci 78:3538–3543

Thiemann GW, Iverson SJ, Stirling I, Obbard ME (2011) Individual patterns of prey selection and dietary specialization in an Arctic marine carnivore. Oikos 120:1469–1478

Thomson JA, BurkhOLDER DA, Heithaus MR, Fourqurean JW, Fraser MW, Statton J, Kendrick GA (2015) Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. Glob Change Biol 21:1463–1474

Thorne LH, Hazen EL, Bograd SJ, Foley DG and others (2015) Foraging behavior links climate variability and reproduction in North Pacific albatrosses. Mov Ecol 3:27

Thorne LH, Conners MG, Hazen EL, Bograd SJ, Antolos M, Costa DP, Shafer SA (2016) Effects of El Niño-driven changes in wind patterns on North Pacific albatrosses. J R Soc Interface 13:20160196

Thullier W, Lavorel S, Araujo MB (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. Glob Ecol Biogeogr 14:347–357

Thurman LL, Stein BA, Beever EA, Poden W and others (2020) Persist in place or shift in space? Evaluating the adaptive capacity of species to climate change. Front Ecol Environ 18:520–528

Tin T, Fleming ZL, Hughes KA, Ainley DG and others (2009) Impacts of local human activities on the Antarctic environment. Antarct Sci 21:3–33

Traisnel G, Pichegru L (2019) Success comes with consistency in hard times: foraging repeatability relates to sex and breeding output in African penguins. Mar Ecol Prog Ser 608:279–289

Trathan PN, García-Borboroglu P, Boersma D, Bost CA and others (2015) Pollution, habitat loss, fishing, and climate change as critical threats to penguins. Conserv Biol 29:31–41

Travis JMJ (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. Proc R Soc B 270:467–473

van den Berg GL, Vermeulen E, Valenzuela LO, Bérubé M and others (2021) Decadal shift in foraging strategy of a migratory Southern Ocean predator. Glob Change Biol 27:1052–1067

Van Hemert C, Pearce JM, Handel CM (2014) Wildlife health in a rapidly changing North: focus on avian disease. Front Ecol Environ 12:548–556

Vander Zanden HB, Pfaller JB, Reich KJ, Pajuelo M and others (2014) Foraging areas differentially affect reproductive output and interpretation of trends in abundance of loggerhead turtles. Mar Biol 161:585–598

Vander Zanden HB, Pfaller JB, Reich KJ, Pajuelo M and others (2014) Foraging areas differentially affect reproductive output and interpretation of trends in abundance of loggerhead turtles. Mar Biol 161:585–598

VanWormer E, Mazet JAK, Hall A, Gill VA and others (2019) Viral emergence in marine mammals in the North Pacific may be linked to Arctic sea ice reduction. Sci Rep 9:15569

Vellegras-Amtmann S, Simmons SE, Kuhn CE, Huckstadt LA, Costa DP (2011) Latitudinal range as predictors of species sensitivity to climate change: an example from an iconic seagrass ecosystem. Antarct Sci 23:875–885

Wege M, Tosh CA, de Bruyn PJN, Bester MN (2016) Cross-seasonal foraging site fidelity of subantarctic fur seals: implications for marine conservation areas. Mar Ecol Prog Ser 554:225–239
Weimerskirch H (2001) Seabird demography and its relationship with the marine environment. In: Schreiber EA, Burger J (eds) Biology of marine birds. CRC Press, Boca Raton, FL, p 115–136

Weishampel JF, Bagley DA, Ehrhart LM, Rodenbeck BL (2003) Spatiotemporal patterns of annual sea turtle nesting behaviors along an East Central Florida beach. Biol Conserv 110:295–303

Weitkamp LA (2010) Marine distributions of Chinook salmon from the west coast of North America determined by coded wire tag recoveries. Trans Am Fish Soc 139:147–170

Westlake RL, Gilmartin WG (1990) Hawaiian monk seal pupping locations in the northwestern Hawaiian Islands. Pac Sci 44:366–383

Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. PLOS Biol 6:2621–2626

Wilson SC, Trukhanova I, Dmitrieva L, Goodman SJ (2020) Estimating risk to ice-breeding pinnipeds from shipping in Arctic and sub-Arctic seas. Mar Policy 111:103694

Witt MJ, Hawkes LA, Godfrey MH, Godley BJ, Broderick AC (2010) Predicting the impacts of climate change on a globally distributed species: the case of the loggerhead turtle. J Exp Biol 213:901–911

Woo KJ, Elliott KH, Davidson M, Gaston AJ, Davoren GK (2008) Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. J Anim Ecol 77:1082–1091

Wood MJ, Canonne C, Besnard A, Lachish S and others (2021) Demographic profiles and environmental drivers of variation relate to individual breeding state in a long-lived trans-oceanic migratory seabird, the Manx shearwater. PLOS ONE 16: e0260812

Xu W, Barker K, Shawler A, Van Scoyoc A and others (2021) The plasticity of ungulate migration in a changing world. Ecology 102:e03293

Yorio P (2009) Marine protected areas, spatial scales, and governance: implications for the conservation of breeding seabirds. Conserv Lett 2:171–178

Editorial responsibility: Graeme Hays, Burwood, Victoria, Australia
Reviewed by: S. Fossette and 2 anonymous referees

Submitted: March 31, 2022
Accepted: September 5, 2022
Proofs received from author(s): October 14, 2022