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REVIEW

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

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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-

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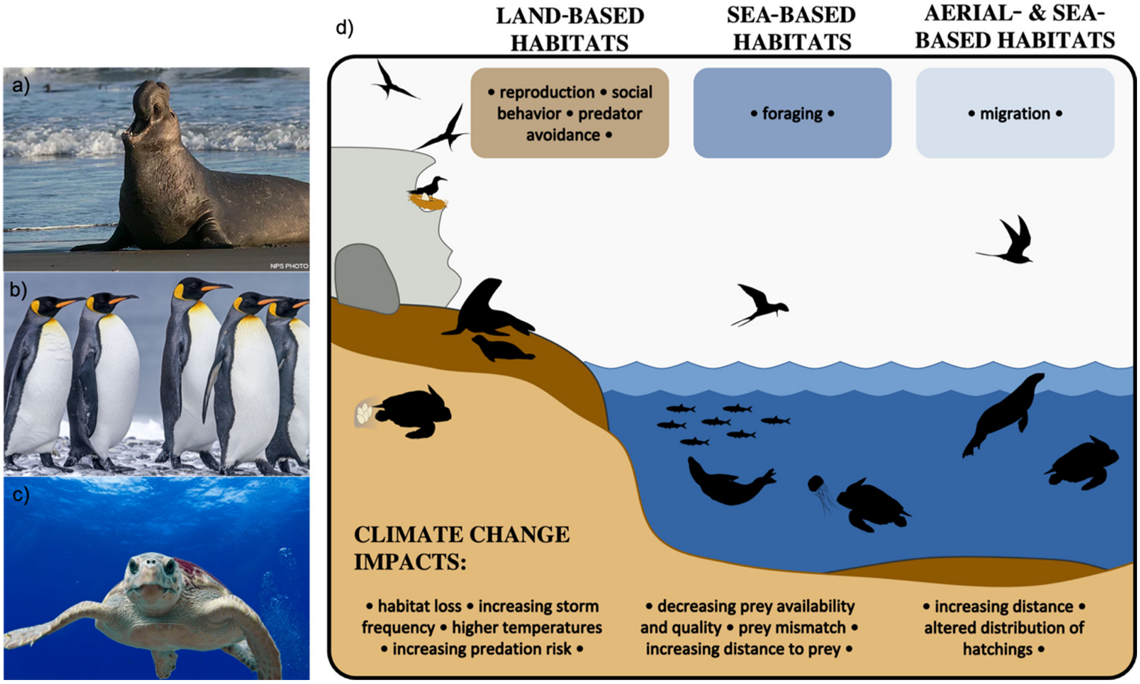

Fig. 1. Land-dependent marine megafauna species, habitat uses, and climate change impacts. Examples of land-dependent marine species include (a) pinnipeds such as the elephant seal (image credit: National Park Service), (b) seabirds such as the king penguin (image credit: Sylvain Cordier/Getty Images), and (c) sea turtles such as the loggerhead (image credit: Pixabay). (d) Land and sea-based habitats are used by these marine species for a variety of life history stages including breeding and reproduction on land and foraging and migration at 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, Lescroël et al. 2014, Traisnel & Pichegru 2019, Piatt et al. 2020). Evidence already exisits 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-taxa 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*

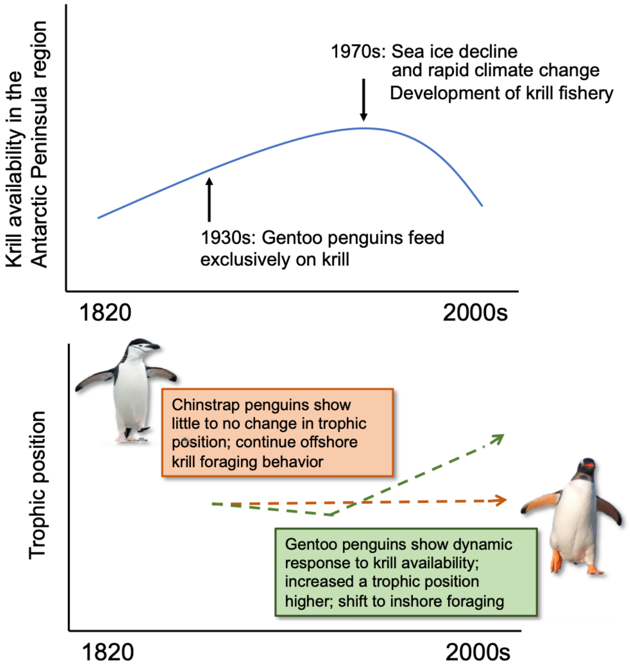

Fig. 2. Sympatric penguin species respond differently to declines in krill availability in the Antarctic Peninsula region. Conceptual summaries of (a) krill availability in the Antarctic Peninsula region and (b) concurrent trophic response of 2 sympatric penguin species, chinstrap penguins and gentoo penguins (adapted from McMahon et al. 2019). Gentoo and chinstrap penguin image credits: Wild Republic

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 been historically 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 a. 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). Mammals 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 (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.

2005, Schwartz et al. 2006, Isaac 2009, Hof et al. 2012). 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

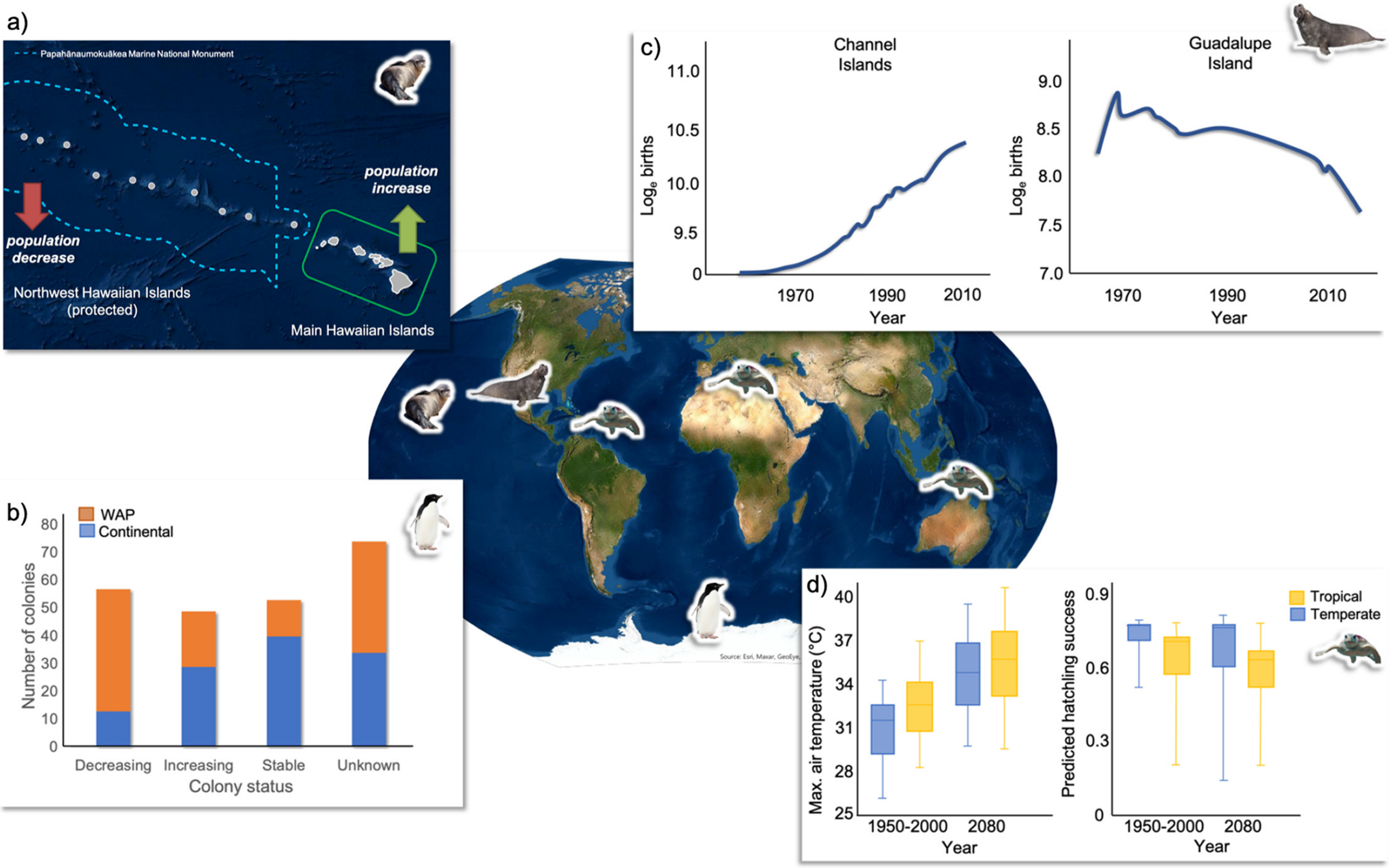

Fig. 3. Complex responses to climate change for populations within the same species. Uncoupled and divergent effects of climate change coupled with geographically distinct baselines and specific regional nuances leads to complex responses for populations within the same species. (a) The range of Hawaiian monk seals spans the Hawaiian Islands. The protected subpopulation in the Northwestern Hawaiian Islands is declining, whereas the subpopulation in the main Hawaiian Islands is increasing (adapted from Gerber et al. 2011; image credit: M Swiet Productions/Getty Images). (b) Adélie penguin colony status by spatial area in Antarctica showing variation in response to climate change (adapted from Cimino et al. 2016; image credit: Christopher Michel). (c) Log total births of northern elephant seal populations over time in the Channel Islands, California, USA (left) and Guadalupe Island, Baja California, Mexico (right) (image credit: NOAA Fisheries). (d) Changes in the predicted maximum air temperature during summer months under climate change scenario a1 (an intermediate emissions scenario; IPCC 2007, Nakicenovic et al. 2000) (left) and corresponding hatchling success (right) of loggerhead sea turtle populations across tropical and temperate locations. Boxplots show median and interquartile range. Predicted hatchling success is largely dependent on baseline temperatures of nesting sites (adapted from Pike 2014; image credit: Pixabay)

al. 2014, Cimino et al. 2016). 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 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

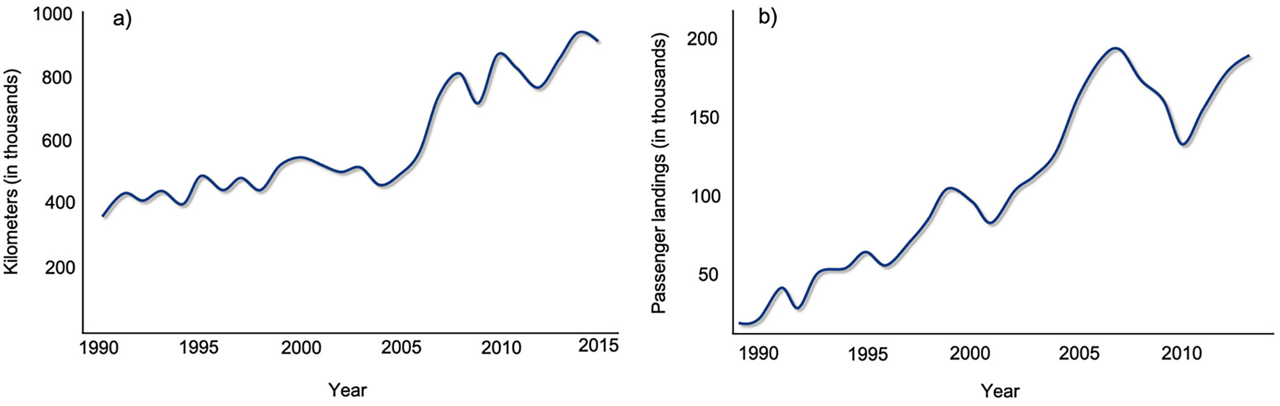

Fig. 4. Increases in anthropogenic activities in the polar regions since 1990 as a result of climate change. (a) Total distance traveled by all vessels (tug, tanker, passenger, fishing, etc.) in the Canadian Arctic (adapted from Dawson et al. 2018). (b) Total passenger landings during the tourist season of each year in Antarctica (adapted from Bender et al. 2016)

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 walrus 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 Barrer 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)

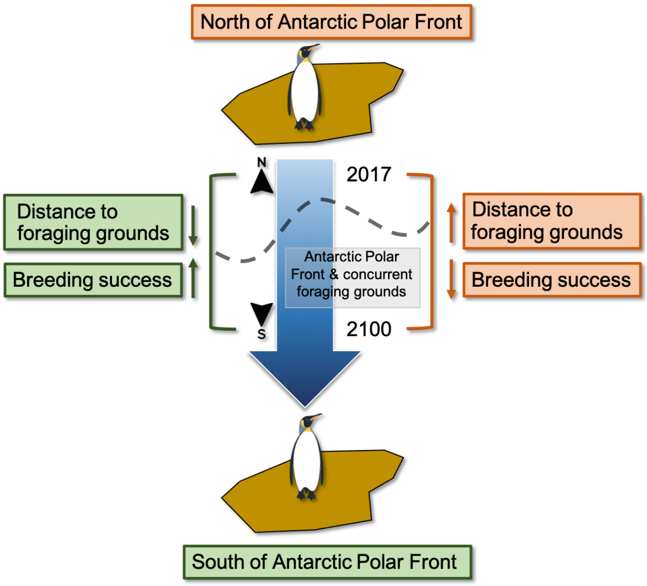

Fig. 5. Fragmented nature of king penguin habitat compounds climate change impacts on land and sea habitats: as the Antarctic Polar Front (APF) shifts southward over the next century, populations north (orange) and south (green) of the APF will be impacted differently. Downward arrows: decreasing; upward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

(Thorne et al. 2015, Cristofari et al. 2018). 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.

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 sea-based 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.

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