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Authors	Sydeman, William J.;Poloczanska, Elvira;Reed, Thomas E.;Thompson, Sarah Ann
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University College Cork, Ireland
Coláiste na hOllscoile Corcaigh

Title: Climate Change and Marine Vertebrates

Authors: William J. Sydeman[1,2]*, Elvira Poloczanska[3,4], Thomas E. Reed[5], and Sarah Ann Thompson[1,6]

Affiliations:

[1]Farallon Institute for Advanced Ecosystem Research, Petaluma, California, 94952, USA

[2]Bodega Marine Laboratory/University of California Davis, Bodega Bay, California, 94923, USA

[3]CSIRO Oceans and Atmosphere, Ecosciences Precinct, Brisbane 4102, Australia

[4]Global Change Institute, University of Queensland, St Lucia, Brisbane 4072, Australia

[5]School of Biological, Earth and Environmental Sciences, University College Cork, Cork, Ireland

[6]Climate Impacts Group, University of Washington, Seattle, Washington, 98195, USA

*Correspondence to: wsydeman@faralloninstitute.org

Abstract:

Climate change impacts on vertebrates have consequences to marine ecosystem structures and services. We review marine fish, mammal, turtle, and seabird responses to climate change and discuss their potential for adaptation. Direct and indirect responses are demonstrated from every ocean. Due to variation in research foci, responses differ among taxonomic groups (redistributions for fish, phenology for seabirds). Mechanisms of change are: (1) direct physiological responses and (2) climate-mediated predator-prey interactions. Regional-scale variation in climate-demographic functions makes range-wide population dynamics challenging to predict. The nexus of metabolism relative to ecosystem productivity and food webs appears key to predicting future effects on marine vertebrates. Integration of climate, oceanographic, ecosystem, and population models that incorporate evolutionary processes is needed to prioritize the climate-related conservation needs for these species.

Main Text:

Introduction

Marine vertebrates are diverse and charismatic, capturing and impassioning societal interests due to their roles in food, educational, and recreational systems. Largely, this is due to their conspicuousness, a characteristic which makes them ideal for investigating the impacts of climate change on marine ecosystems. Fish provide protein to human populations and support economic and food security, while sea turtles, seabirds, and mammals contribute to regional economies (tourism) and cultures, as well as to human subsistence in remote areas. These animals are ecologically relevant, imparting top-down effects on marine food webs that may control community stability (*1*, *2*). Marine vertebrates, particularly seabirds, show great value as ecological indicators, and may play pivotal roles in assessments of marine ecosystem health (*3*).

Marine vertebrate - climate relationships have been studied for over a century. In the early 20th century, when studies of El Niño were in their infancy, clear effects were documented for Peruvian seabirds (*4*). Fish distributional shifts were particularly well documented in extratropical California during the 1957-1959 El Niño event (*5*). Effects of low frequency climate variability on trophic interactions and marine vertebrate populations were demonstrated in the late 1980s (*6*). It is now well established that fish, birds, and mammals regularly respond to climate phenomena, such as El Niño-Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO), and Atlantic Multi-Decadal Oscillation (AMO), which fluctuate on a range of temporal scales (*7*, *8*). For example, when the North Atlantic warmed in the early 20th century (~1920s-1940s) at rates comparable to contemporary warming (*9*), associated ecological changes included widespread northward shifts of fish and increases in fisheries productivity driven by bottom-up processes (*10*, *11*). Thus, changes in marine vertebrate life histories, demographic traits, and distribution have long been a subject of interest. Because marine vertebrates are ecologically important and vulnerable, clearly responsive to climatic factors, and provide extensive economic and aesthetic value to society, it is imperative to better understand the impacts of climate change on these key marine organisms.

Taxonomic Diversity

Huge challenges to understanding and prediction remain, however, not the least of which concerns the complexity of biological interactions that drive change (Fig. 1). Climate change can affect these animals directly, through physiological functions (*12*), or indirectly, through predator-prey interactions and other trophic mechanisms or through modification of critical habitats such as coral reefs and seagrass beds. Fish, the dominant marine vertebrate group, demonstrate complex life histories including, for many species, a planktonic life-stage in which habitat occupancy and prey use differs from adult life stages, resulting in different vulnerabilities to environmental change. Most fish are ectothermic and derive oxygen from seawater; thus, their responses to climate change are direct and physiological, with impacts on basic metabolic functions. Furthermore, changes in ocean productivity and prey availability are well demonstrated to drive fluctuations in fish populations. Sea turtles, generally considered ectothermic, are characterized by highly migratory life histories, long age-to-maturity (often decades), and nest on land (sandy beaches) where ambient temperatures determine the sex of embryos. In contrast, marine mammals and seabirds are endothermic; climatic effects on these groups are mostly indirect, influenced primarily by shifts in habitat or prey availability, though coastal inundation of low-lying nesting areas for tropical seabirds (and sea turtles) is also of concern. The high metabolic rate of some species (notably seabirds) necessitates regular access to food resources to maintain somatic condition. Thus, the nexus between metabolic shifts and nutritional needs, coupled with variation in ocean productivity and trophic interactions, may be a key predictor of the ability of marine vertebrates to cope with climate change. Moreover, while all marine vertebrates may be considered vagile, some conduct trans-oceanic or trans-hemispheric migrations

(*13*), while others are more sedentary (e.g., coral reef fish). Reproductive tactics also vary from batch-spawning semelparity (single reproductive episode during life, e.g., Pacific salmon) to long-term iteroparity (multiple reproductive cycles, e.g., albatrosses that live upwards of 80 years). While these fundamental differences result in varying responses among taxonomic groups to climate, a key similarity is that generally these animals derive sustenance from the oceans.

Observations, Mechanisms, and Models

Information Base – Fisheries, endangered and iconic marine wildlife, seabird monitoring, and society's fascination with marine environments have produced many long-term observational data sets. Fisheries statistics, some exceeding a century, as well as interdecadal monitoring studies at important local habitats, such as nesting or breeding sites for seabirds, sea turtles, and marine mammal populations, are available for global syntheses (*14*). When coupled with environmental data on atmospheric and oceanographic conditions, this provides a rich database with which to examine biophysical relationships and potential climate change impacts on populations. Nonetheless, there remain many gaps in our knowledge; for example, most studies have been conducted in the temperate Northeast Atlantic and the temperate to subarctic North Pacific. Key studies also exist from southern Africa (e.g., *15*) and Antarctica (e.g., *16*), but many rich areas of the world's oceans remain largely under-studied. Additionally, fisheries-dependent data may be compromised by a non-random temporal and spatial distribution of fishing effort, and seabird, sea turtle and marine mammal data sets rarely exceed one period of decadal variability (e.g., the PDO or AMO). This means that, for the most part, statistical attribution of changes in marine vertebrate populations to anthropogenic climate change is difficult, as few data sets allow one to disentangle unidirectional climate change from low-frequency climate variability. Mechanistic understanding of change has also been elusive.

That said, recent global syntheses provide robust evidence of widespread impacts of climate change on marine vertebrates (*14*, *17*). Contemporaneous changes in coupled ocean variables and processes such as temperature and regional upwelling, nutrient supplies and primary production, and ocean acidification and de-oxygenation (*18*), indicate the potential for causal relationships and the inherent complexities of a 3-dimensional habitat. For example, discontinuities in physical and chemical components of the ocean are observed in vertical and horizontal domains. Potential pathways of marine vertebrate response are also complex and include classic climate to predator bottom-up food web dynamics (Fig. 1A), climatically-driven shifts in predation pressure on mesopredators (Fig. 1B), as well as other potential mechanisms including trophic cascades and terrestrial-marine coupling (Fig. 1C,D). Thus, understanding climate change impacts on marine ecosystem primary and secondary productivity and availability of prey to consumers is vital to predicting future responses to climate change. Responses in terms of phenology, distribution, and demography will also be mediated by climate change impacts on critical habitats, such as coral reefs and seagrass beds utilized by fish as adult foraging grounds or juvenile nurseries, sandy nesting

beaches for sea turtles and seabirds, and sea ice which provides foraging and breeding habitats for polar bears (Arctic) and penguin species (Antarctic).

Phenology - Phenology is the study of the timing of recurring biological events and how these are influenced by climate, such as the seasonal phasing of phytoplankton blooming in marine ecosystems or timing of egg-laying in seabirds. Climate change is causing variation in the peak and seasonality of both temperature and primary production in the oceans (*19*, *20*). Generally, warm seasons are arriving earlier and ending later (*21*) and are expected to advance the timing of spring migrations and breeding, delay autumn migrations, and alter the seasonal peak abundances of marine organisms (*22*). Phenological responses have been well demonstrated in many species of seabirds and zooplankton, including larval fish (*23*). Globally, spring phenologies of all marine species (including planktonic and nektonic species) have advanced by 4.4 ± 1.1 days per decade since the mid 20th century (*14*); responses are variable among taxonomic groups. For example, seabirds were not significantly different from zero due to regional advances and delays in breeding dates. Delayed breeding for emperor penguins (*Aptenodytes forsteri*) and other seabird species in the western Antarctic was linked to a delay in sea ice breakup, hypothesized to influence prey availability and limit access to prey resources (*24*). Similar delays were reported for northern gannets (*Sula bassana*) in the northeast Atlantic and linked to warmer temperatures, also presumably related to prey resources (*25*). No unidirectional trends in phenology were observed for several seabird species in the North Pacific (*26*, *27*), although the timing of breeding of seabirds in this region tracks phase shifts of the PDO. In contrast, earlier breeding for little penguins (*Eudyptula minor*) in Australia has been linked to ocean warming and improved prey availability (*28*). Similarly, nesting phenology in sea turtles has been linked to ocean temperature; however, evidence of climate change responses is weak and overshadowed by regional variations (*29*, *30*). The initiation of breeding migrations is likely driven by environmental conditions on distant feeding grounds (turtles deposit fat reserves that are mobilized later for breeding) (*31*), though to date remote climate effects have yet to be investigated.

Fish phenologies show similar complexities, although studies are rare. The phenology of adult salmon (*Oncorhynchus* spp.) migration in Alaska shows population-specific advances and delays (*32*); delays for sockeye (*O. nerka*) run timing may be related to warm river conditions and low summer stream flows. In the North Sea, advanced spawning of sole (*Solea solea*) corresponded to warmer winter temperatures, which likely accelerated gonadal development (*33*). Off California, both earlier and later seasonal peaks in larval fish abundance (n = 43 species) were observed, corresponding to the preferred habitat of each species (*34*); neritic species that reside near upwelling centers showed delays in peak abundance, whereas timing for peak abundance has advanced for more pelagic, offshore-dwelling species.

While research clearly shows a range of phenological responses to recent climate change, in general we lack clear ‘yardsticks’ for how marine vertebrates *should* change their phenology to avoid

loss of fitness (e.g., phenological responses of food species or predators against which to compare focal species responses) (*35*). Few models project anticipated changes in phenology (*36*), however, a rare study (*37*) presents an individual-based modeling framework for characterizing climate change effects on phenology and there is scope for adapting such models to other species and contexts (*38*). Phenological shifts can maintain alignment of predator and prey or other resources in time or space as climate changes (*39*), but there is no reason to assume perfect tracking across trophic levels (*40*); indeed, some phenological responses may disadvantage individuals. In summary, most studies, including those showing both advances and delays in breeding date and peak abundance, hypothesize phenological responses via metabolic shifts or prey resources, but few have demonstrated matching of vertebrate needs with prey availability relative to climate change (*41-43*).

Distribution - Climate change and ocean warming is predicted to cause shifts in marine vertebrate distributions, and thus diversity (patterns in the richness of communities) (*22*, *44*). Anticipated impacts include increases in species richness in temperate-subarctic biomes, local species extinctions in tropical biomes, and the emergence of no-analog communities (*44-46*). Small-ranged species, which dominate in the tropics, and polar communities may be at highest risk from warming (*44*). Climate related redistributions are best studied in fish. Recent decadal increases in fish community diversity and productivity observed in the high-latitude northeast Atlantic (*47*) and Bering Sea (*48*) have been linked to regional warming. Whether or not boreal/sub-polar fish production will continue to increase as a function of climate change is a key question. Latitudinal shifts will induce changes in photoperiodic responses (day length differs in newly colonized areas), in some cases enhancing growth due to longer day lengths for feeding (*49*) and in others disrupting trophic synchronies or, particularly in polar oceans, resulting in shorter windows of food availability (*50*).

Across the globe, distribution shifts of, on average, 30.6 ± 5.2 km per decade have been reported and the fastest responses are for fish and zooplankton, including larval fish (*14*). Differences in the speed and direction of shifts among fish and invertebrate populations may be explained by local rates of isotherm shifts (*51*). Shifts in depths occupied have also been documented as cold-water species take refuge in cooler, deeper waters, particularly where latitudinal shifts are blocked (*52*, *53*). For example, in the northern Gulf of Mexico, where the coastline prohibits poleward distributional shifts, demersal fish assemblages shifted deeper instead (*51*). Fishing complicates interpretations of climate-driven redistributions (*54*) and can amplify or obscure responses to climate change (*55*, *56*). As an example, cod distribution in the North Sea has shifted northward, eastward, and deeper over the past century; the northward shift and deepening have been linked to warming, however, the shift eastward was linked to fishing pressure, complicating interpretations and attribution to climate change (*57*).

Warming combines with other oceanographic processes to influence species redistributions. Numerous range extensions have been observed in fish of temperate waters of southeast Australia and

linked to regional warming as well as a strengthening of the East Australian Current; the mechanism includes enhanced transport of larvae and juveniles (*58*). In the northwest Atlantic, changes in silver hake (*Merluccius bilinearis*) distribution were correlated with the position of the Gulf Stream, although the hake respond to changes in bottom temperatures arising from the same changes in circulation patterns that influence the Gulf Stream (*59*).

Ocean acidification, in addition to changes in temperature, presents risks to larval fish in particular, while oxygen availability is an important determinant of fish metabolic rates and their ability to cope with warming, ultimately affecting growth and body size (*12*). Oxygen declines also are projected to result in poleward and vertical contractions of habitats and a reduction in fish body size (*60-62*). Humboldt squid off California, however, appear to have responded to warming and deoxygenation with a recent range expansion, increasing predation pressure on commercial fish species (*63-65*; Fig. 1C).

Distribution shifts of air-breathing marine vertebrates are also expected as a consequence of warming temperatures, primarily through modification of prey availability or critical habitats. Declining sea ice has forced polar bears to utilize terrestrial food resources as sea ice foraging habitats decline and denning is driven into coastal areas (*66*, *67*; Fig. 1B). Seabird redistributions have been documented for South African and Australian breeding colonies in relation to changes in prey availability (*68*, *69*). One climate model analysis suggests shifts in North Pacific albatrosses corresponding to a poleward shift of the Transition Zone Chlorophyll Front (*46*); albatross observations in Alaska corroborate these results by showing a northward shift in the center of distribution and increased albatross density in the subarctic Bering Sea (*70*).

Demography – Numerous demographic responses (e.g., vital rate statistics such as reproductive success and survival) have been shown for seabirds, sea turtles, and fish, and contrasting responses to environmental measurements are apparent. For example, Antarctic sea ice extent (SIE) has a positive effect on adult survival and a negative effect on egg hatching rates in emperor penguins (*Aptenodytes forsteri*; *71*, *72*), and negative or non-significant relationships with snow petrel survival (*Pagodroma nivea*; *73*, *74*). Additionally, there is evidence that "moderate is better", with intermediate SIE related to the highest survival rates for Adélie penguins (*Pygoscelis adeliae*; *75*, see also *76*); moderate ice cover promotes primary productivity and facilitates access to prey resources by foraging seabirds.

In general, ocean warming correlates negatively with seabird breeding success and survival; examples include puffins from Norway (*77*) and shags and auks in the U.K. (*78*), but this is not always the case. Positive relationships have been demonstrated between breeding success and temperature for little penguins off Australia (*79*), as well as two Antarctic albatross species (*80*) and puffins off Russia (*81*). An example highlighting the link between foraging success and breeding success is the recent poleward shift in wandering albatross (*Diomedea exulans*) distributions as westerly wind fields in the Southern Ocean have strengthened and moved poleward (*82*). As a result,

albatross foraging trips have shortened in duration and breeding success has improved. Variation in survival may also relate to sea surface temperature (SST); for example, Waugh et al. (*83*) documented a negative relationship between the survival of rare Westland petrels (*Procellaria westlandia*) and SST anomalies in areas frequented by the birds during the breeding season, but a positive relationship between those two factors in foraging areas used in the non-breeding season. In sea turtles, the sex of hatchlings is determined by incubation temperatures of eggs in nests dug above sandy beaches (female biases arise above ~29°C). Air temperatures on many beaches worldwide have already warmed to, or are close to, all female-producing temperatures and temperature projections indicate further biases (*84*). However, population units may span many beaches in a region and temperatures fluctuate during nesting seasons (for example, reduced with rainfall), so the necessary males may still be produced.

Owing to the availability of excellent data on seabirds, a number of climate-dependent population models have been implemented by coupling demographic data with climate system models. These studies assume that climatic-demographic relationships will remain the same into the future, a bold assumption given developing novel climate states (*85*) and well-documented breakdowns in climate-demographic relationships for fish (*86*). Nonetheless, population viability studies have been revealing. For example, population declines of 11-45% by 2100 have been projected for Cassin's auklet (*Ptychoramphus aleuticus*), a planktivorous seabird; this model was based on established relationships between demographic rates (breeding success and adult survival) and upwelling intensity and ocean temperatures (*87*). In the Antarctic, continent-wide declines of emperor penguins have been projected based on local SIE in relation to breeding success and survival estimates (*76*). Interestingly, at the continental scale, interannual variability in SIE promotes population stability because of opposing functions between SIE and breeding success and survival. Climate-dependent models also highlight the complexity of responses in fish. For example, for south Pacific albacore tuna (*Thunnus alalunga*), application of a 2-D coupled physical-biological-fisheries model at the ocean basin scale predicts an initial population decline followed by an increase in biomass as a new spawning ground is established towards the end of the 21st century (*88*). However, population dynamics are also sensitive to simulated changes in optimal spawning temperatures; accounting for potential evolutionary processes favouring albacore with preferences for higher optimal ambient spawning temperature suppresses the emergence of a new spawning ground and stock abundance remains low.

Capacity for Adaptation

The albacore example underscores a crucial yet relatively understudied issue: the potential for evolutionary adaptation and/or phenotypic plasticity to modulate population responses to climate change. The former involves genetic change across generations driven by natural selection on heritable phenotypes whereas the latter occurs when individuals employ existing genes to express

different phenotypes in changing environments. Plasticity typically occurs more rapidly than evolution and thus represents the "first line of defense" in a changing environment. Indeed, a large body of work demonstrates that marine vertebrates have a broad capacity to adjust their behaviors, physiology, and morphology in response to short-term changes in environmental conditions via plasticity in labile (where phenotype changes at least as fast as the environment) and non-labile traits (*89-91*). Tagging studies of seabirds, marine mammals, and pelagic fish offer opportunities for measuring individual reaction norms - the range of phenotypes produced across environments due to phenotypic plasticity - and fitness correlates, and relating these to population-level trends. For example, individual common murres (*Uria aalge*) adjust egg-laying dates in response to climate-related cues, allowing them to track interannual changes in the seasonal peak in forage with benefits for breeding success (*92*). The need for plasticity in some traits, however, is balanced by selection for relative constancy ("canalization") in others that are more closely correlated with fitness (*91*). Many long-lived pinnipeds and seabirds, for example, maximize fitness by minimizing interannual variance in adult survival and breeding propensity, which in turn dampens the demographic consequences of changing climate (*93*). Antarctic fur seals (*Arctocephalus gazella*) breeding on South Georgia have lost some of this capacity for life history buffering, however, likely due to lack of plasticity in breeding schedules in the face of reduced food predictability (*93*).

More generally, plasticity has its limits and evolutionary adaptation of reaction norms themselves may be required for populations to persist in rapidly changing (or increasingly variable) climates. Empirical evidence for evolutionary responses to contemporary climate change in marine vertebrates (indeed most taxa) is almost completely lacking, but this may reflect detection problems rather than a lack of evolutionary potential (*90*, *91*). Most populations harbor substantial genetic variation for traits affecting fitness, but the key unknown is whether evolution can unfold rapidly enough to prevent extinction (*94*). Phenological traits in particular may experience strong selection; for example, timing of peak nesting of adjacent genetic stocks of the flatback sea turtle *Chelonia depressa* in northern Australia have diverged to coincide with local temperature regimes compatible with high incubation success and suitable hatchling sex ratios, but this likely occurred over thousands of years (*95*). Whether marine vertebrates can keep evolutionary pace with unprecedented (at least in their recent evolutionary history) rates of environmental change is of great concern, and 'space-for-time' substitutions may be a poor guide in this respect. In theory, transgenerational adaptation to climate change can also occur via epigenetic mechanisms or inherited environmental effects (*96*), but the importance of these mechanisms is uncertain. Laboratory experiments for the few vertebrate species which lend themselves to captive breeding (e.g., *97*), or observations of fine-grained population responses (e.g., *98*), can be used to infer the potential for phenotypic plasticity and microevolution.

Clearly, marine vertebrate species do not have equal scope for adaptive responses. For example, species that evolved in relatively stable climates are expected to have narrow thermal

tolerances (e.g., stenothermal Antarctic fishes; *99*) and less capacity for thermal or other types of plasticity than populations inhabiting more variable environments. Similarly, historically large, widespread, or well-connected populations may possess greater evolutionary potential than small, localized or isolated populations (*100*). Aside from these general rules of thumb, it is difficult to predict *a priori* which marine vertebrates will be most capable of adapting to climate change. The strongest generalizations that can be made are that: (a) all else being equal, species with shorter generation times will evolve faster than those with longer generation times, at least initially (at evolutionary equilibrium both are predicted to track a moving optimum at the same annual rate) and (b) species capable of rapid population growth are more likely to be rescued by evolution (*94*). Marine vertebrates with slow life histories and low annual fecundity, i.e., most seabirds, sea turtles, and marine mammals, as well as many sharks, are thus expected to be less evolutionarily resilient to rapid climate change, despite the fact that they have substantial capacity for adaptive plasticity. Note however that life histories themselves may evolve due to climate-induced selection, although again the pace of such changes will be critical.

Thus, a major challenge remains to understand how the resilience of species, communities, and ecosystems is affected by the plasticity of individuals and microevolution (or a lack thereof) of populations. It is useful in this respect to distinguish among factors affecting exposure to changing environments and those affecting sensitivity to given changes, which together determine vulnerability at each level of biological organization (*101*; Fig. 2). It is also important to realize that plasticity and evolutionary adaptation by no means guarantee population persistence and can even lead to declines in abundance (*102*). On the other hand, populations and species may respond to climate change idiosyncratically and such diversity can enhance the resilience of species and communities via portfolio effects (where the dynamics of biological systems are less variable than their individual components; *103*). For example, the overall numbers of sockeye salmon *Oncorhynchus nerka* returning to Bristol Bay, Alaska, annually are much less volatile than the numbers returning to individual rivers within the bay, due to asynchronous dynamics among local populations (*104*). Given the limitations on our forecasting abilities, adaptable conservation strategies that spread risk and maintain genetic and ecological heterogeneity and connectivity are most prudent (*103*, *105*).

Concluding Remarks

Changing climate creates systemic effects that ripple through marine food webs, affecting all trophic levels. As mid to upper trophic level species, most climatic effects on seabird and mammalian consumers will be indirect, operating via changes in ocean productivity and food webs. In contrast, ectothermic fish may respond immediately and substantially to relatively small changes in temperature and oxygen concentrations and potentially ocean acidification, factors which may affect their metabolism. Endothermic organisms, such as birds and mammals, may not respond directly to physical changes, and only to changes in food supplies over time, but once they respond, changes are

likely to be substantial and difficult to reverse. Thus, indirect responses, while perhaps delayed, are powerful and potentially long-lasting, hence a challenge for management and conservation. Some impacts may be mediated by phenotypic plasticity or evolutionary change, but the capacity for marine vertebrates to respond in this manner is variable and unpredictable based on the information at hand. Anthropogenic global warming is anticipated to increase physical and ecosystem variability and bring ecological surprises, as novel species interactions and communities form, which further confounds assessment of risks to marine vertebrates.

A variety of new modeling approaches are emerging, from species distribution models (SDMs) and population models to complex ecosystem models operating across varying temporal and spatial scales, all of which involve balancing tradeoffs in realism against uncertainties in model parameters and structures (*106*). The latest wave of SDMs better account for interactions between evolution and dispersal (as well as biotic interactions), but their parameterizations are limited by data availability and increases in model complexity can come at the expense of tractability (*107*). International coordination of modeling efforts (e.g., fisheries under the framework of the Inter-sectoral Impact Model Intercomparison Project; *108*) may provide consistent estimates of uncertainties (*109*). The availability of high-quality data on marine vertebrates, however, facilitates comparative studies of similar species between ecosystems, as well as coupling climate and ecosystems models with genetic and population models, which are feasible approaches to improve understanding and forecasting the future for these key marine animals.

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Fig. 1. Four case studies illustrating the complex mechanisms by which climate change can indirectly affect marine vertebrates via trophic interactions. (A) Bottom-up effects of climate change in the North Sea; the reduction in lipid-rich copepods results in declines in sandeel recruitment and poor seabird breeding success (*110*). (B) Climate-mediated top-down effects of polar bears in the Arctic with positive impacts (reduced predation) hypothesized for Arctic seals and negative (increased predation) impacts on sub-Arctic seals, nesting eiders, and terrestrial resources (*111-113*). (C) Potential climate-mediated trophic cascade in the California Current System driven by range expansion of Humboldt squid, with increasing predation on hake and mesopelagic fishes cascading to decreased predation on krill (*63-65*). (D) Marine-terrestrial coupling and ecological cascade on Coral Sea Islands, south-west Pacific, driven by climate change simultaneously affecting the ocean and land, lessening food availability and reducing nesting habitat quality for seabirds (*114*, *115*). Each case study is a simplified schematic and does not include all potential food web links and interactions. Light blue arrows: direct climate controls, dark blue arrows: bottom-up interactions, red arrows: top-down interactions; solid lines: well supported, dashed lines: hypothesized.

Credits: Øystein Paulsen (krill, via https://commons.wikipedia.org); https://commons.wikipedia.org (puffin, sandeel, herring, copepod, mesopelagic fish, eider, polar bear, squid, and hake); Freshwater and Marine Image Bank (harp seal, ringed seal).

Fig. 1A.

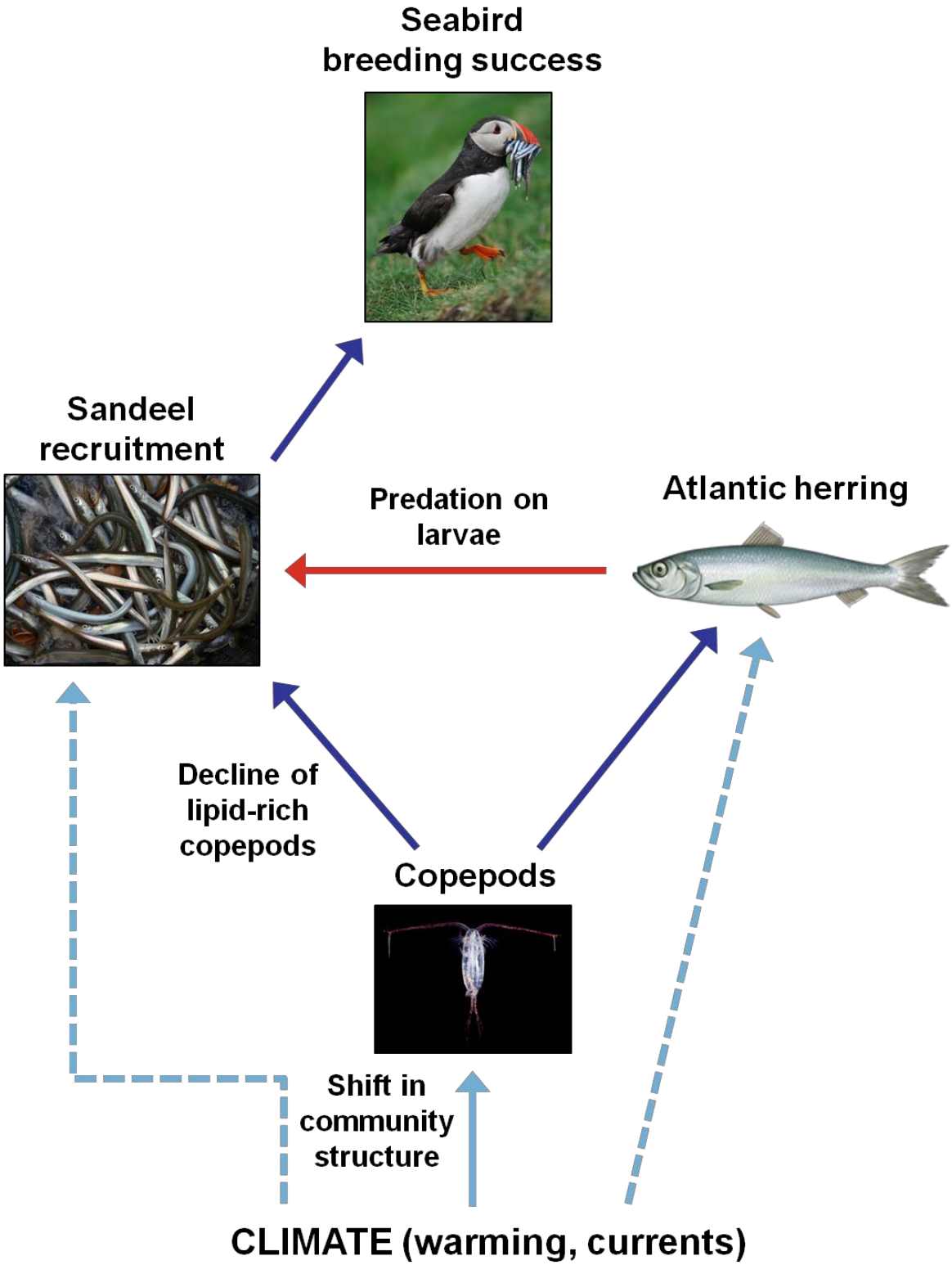

Seabird
breeding success
Sandeel
recruitment
Predation on
larvae
Atlantic herring
Decline of
lipid-rich
copepods
Copepods
Shift in
community
structure
CLIMATE (warming, currents)

Fig. 1B.

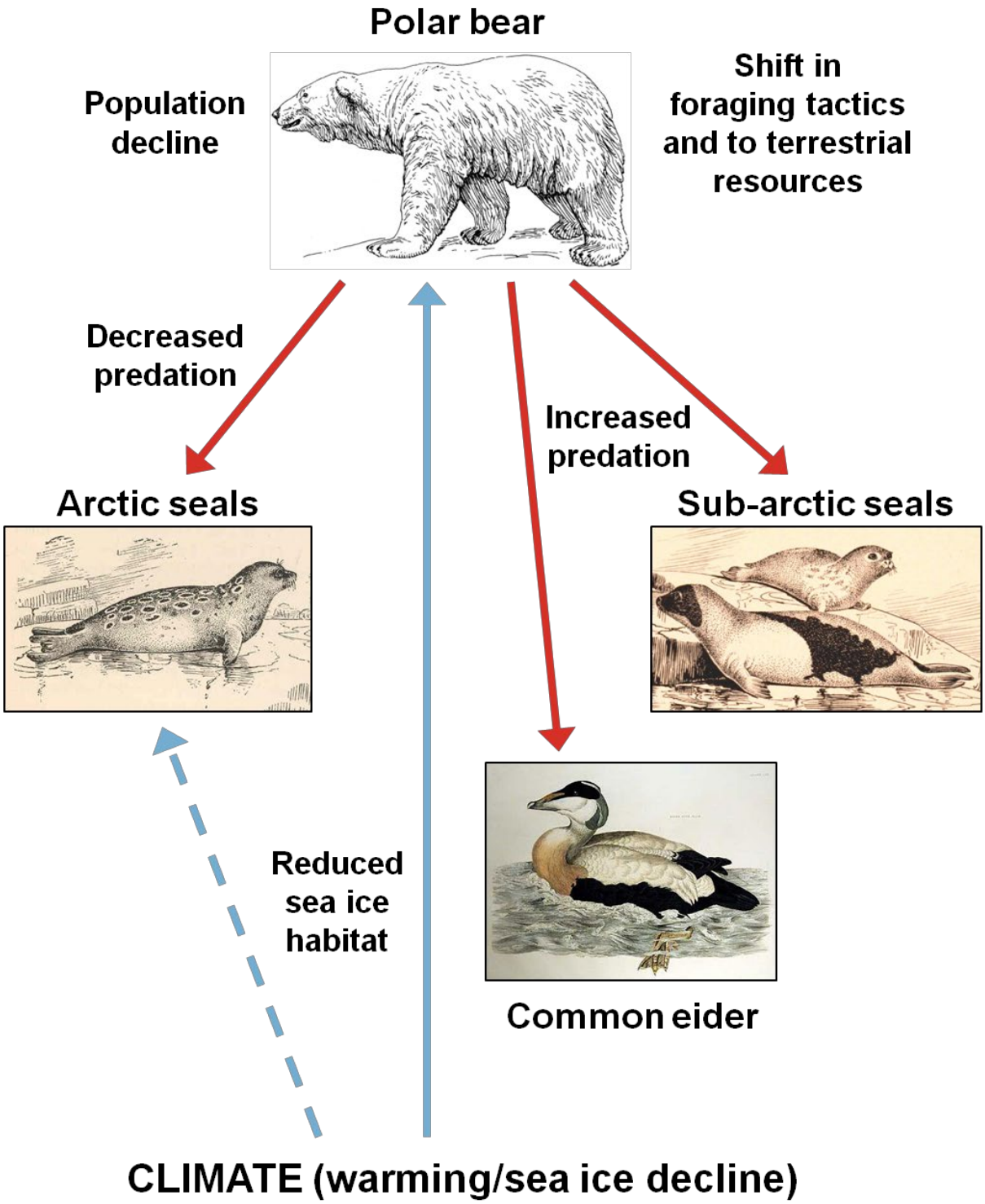

Polar bear
Population decline
Shift in foraging tactics and to terrestrial resources
Decreased predation
Increased predation
Arctic seals
Sub-arctic seals
Reduced sea ice habitat
Common eider
CLIMATE (warming/sea ice decline)

Fig. 1C.

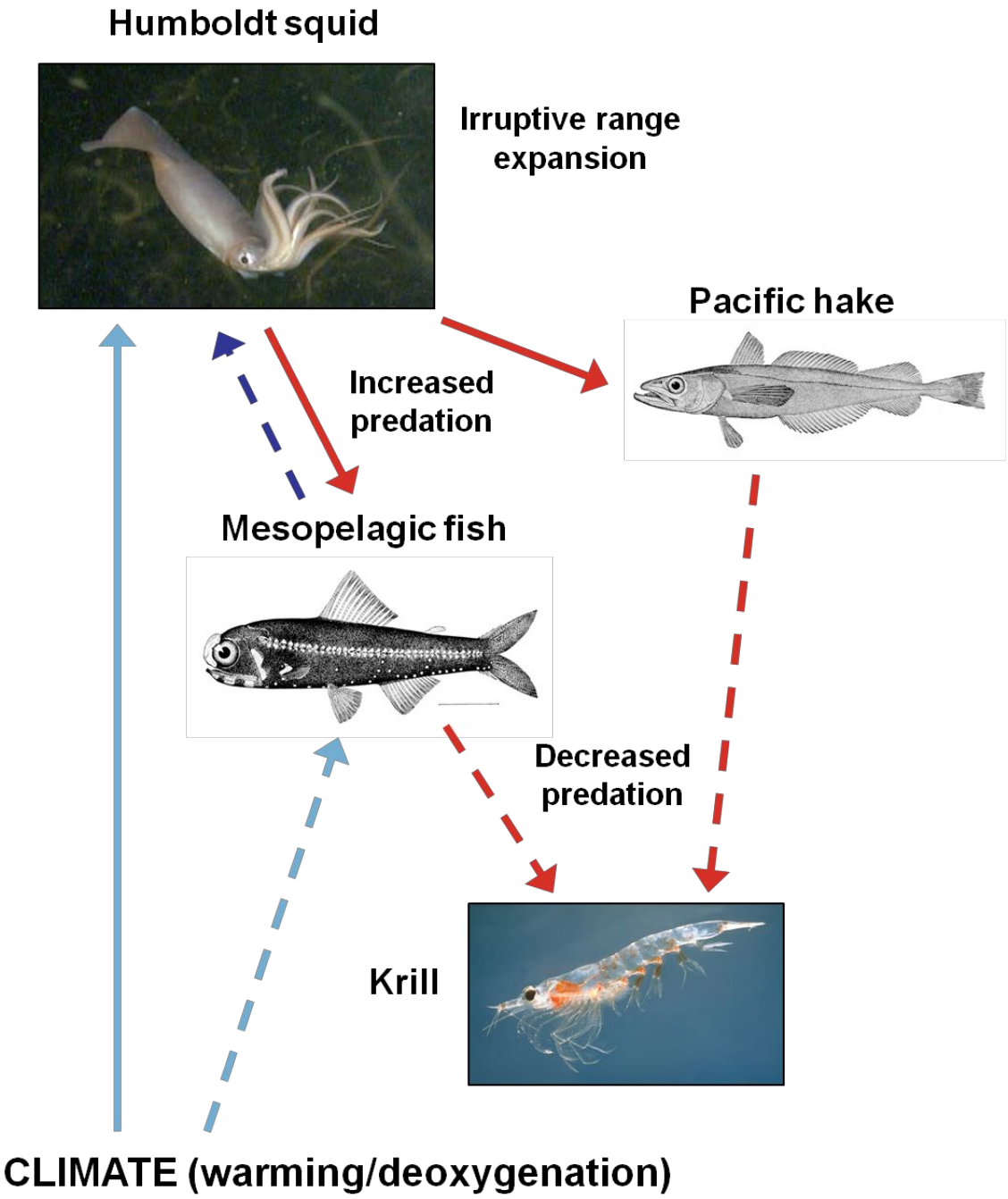

Humboldt squid
Irruptive range expansion
Pacific hake
Increased predation
Mesopelagic fish
Decreased predation
Krill
CLIMATE (warming/deoxygenation)

Fig. 1D.

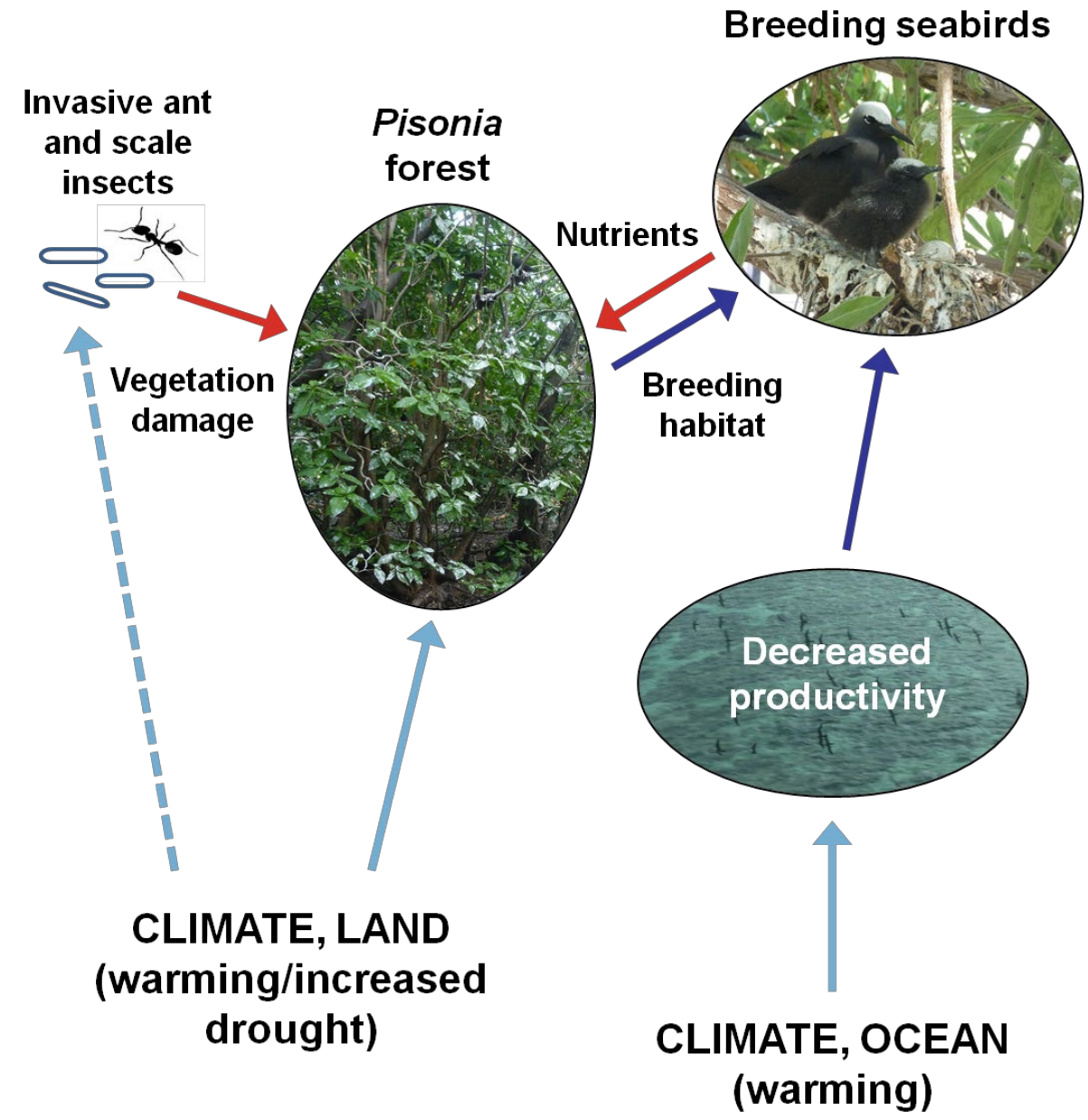
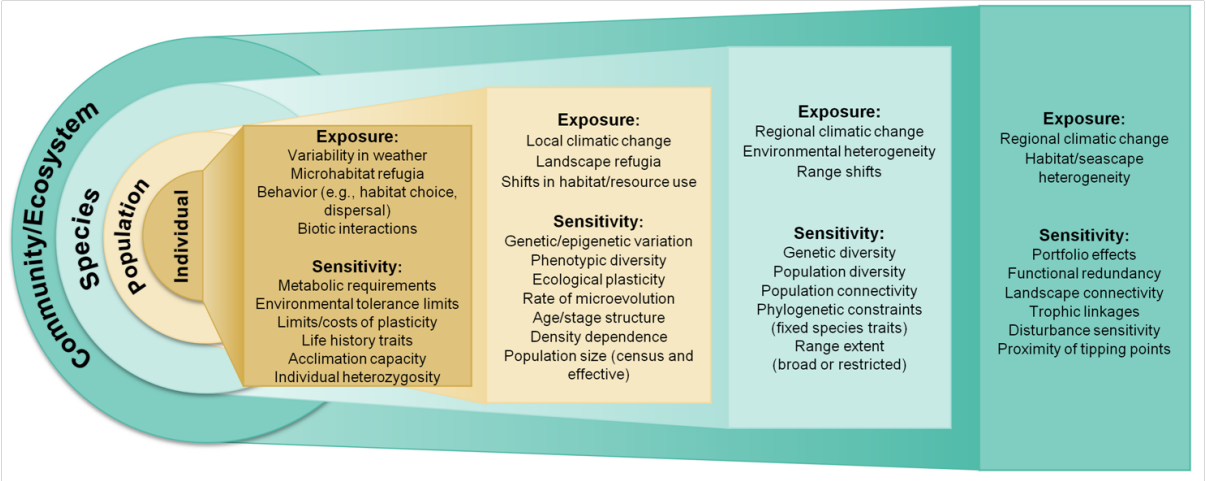

Breeding seabirds
Invasive ant and scale insects
Pisonia forest
Nutrients
Vegetation damage
Breeding habitat
Decreased productivity
CLIMATE, LAND (warming/increased drought)
CLIMATE, OCEAN (warming)

Fig. 2. Intrinsic properties of individuals, populations, species, and communities, together with extrinsic properties of the environments they inhabit, shape their exposure and sensitivity to climate change. Exposure is a function of climatic change and the degree of buffering due to habitat heterogeneity (e.g., refugia) and behavioural adjustments. **Sensitivity** is affected by intrinsic factors such as physiological tolerances and (relatively) fixed population/species traits and will be mediated by evolutionary changes, plastic ecological responses and resilience (the capacity of systems to persist and recover from disturbance). Vulnerability and emergent dynamics at each level of biological organization depend on processes operating at lower levels. For example, phenotypic plasticity and evolutionary adaptation (or lack thereof) propagate up from individuals and populations to affect the resilience of species and communities, and thereby ecosystem function. Additional human stressors and conservation management will further affect ecological and evolutionary resilience by modifying these and other factors. Adapted from *101*, *116*.

Fig. 2


Community/Ecosystem
Species
Population
Individual
Exposure:
Variability in weather
Microhabitat refugia
Behavior (e.g., habitat choice, dispersal)
Biotic interactions
Sensitivity:
Metabolic requirements
Environmental tolerance limits
Limits/costs of plasticity
Life history traits
Acclimation capacity
Individual heterozygosity
Exposure:
Local climatic change
Landscape refugia
Shifts in habitat/resource use
Sensitivity:
Genetic/epigenetic variation
Phenotypic diversity
Ecological plasticity
Rate of microevolution
Age/stage structure
Density dependence
Population size (census and effective)
Exposure:
Regional climatic change
Environmental heterogeneity
Range shifts
Sensitivity:
Genetic diversity
Population diversity
Population connectivity
Phylogenetic constraints (fixed species traits)
Range extent (broad or restricted)
Exposure:
Regional climatic change
Habitat/seascape heterogeneity
Sensitivity:
Portfolio effects
Functional redundancy
Landscape connectivity
Trophic linkages
Disturbance sensitivity
Proximity of tipping points