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# Climate-Driven Shifts in Marine Species Ranges: Scaling from Organisms to Communities

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## Keywords

climate change, colonization, extirpation, biogeography, food webs, marine–terrestrial comparison

## Abstract

The geographic distributions of marine species are changing rapidly, with leading range edges following climate poleward, deeper, and in other directions and trailing range edges often contracting in similar directions. These shifts have their roots in fine-scale interactions between organisms and their environment—including mosaics and gradients of temperature and oxygen—mediated by physiology, behavior, evolution, dispersal, and species interactions. These shifts reassemble food webs and can have dramatic consequences. Compared with species on land, marine species are more sensitive to changing climate but have a greater capacity for colonization. These differences suggest that species cope with climate change at different spatial scales in the two realms and that range shifts across wide spatial scales are a key mechanism at sea. Additional research is needed to understand how processes interact to promote or constrain range shifts, how the dominant responses vary among species, and how the emergent communities of the future ocean will function.

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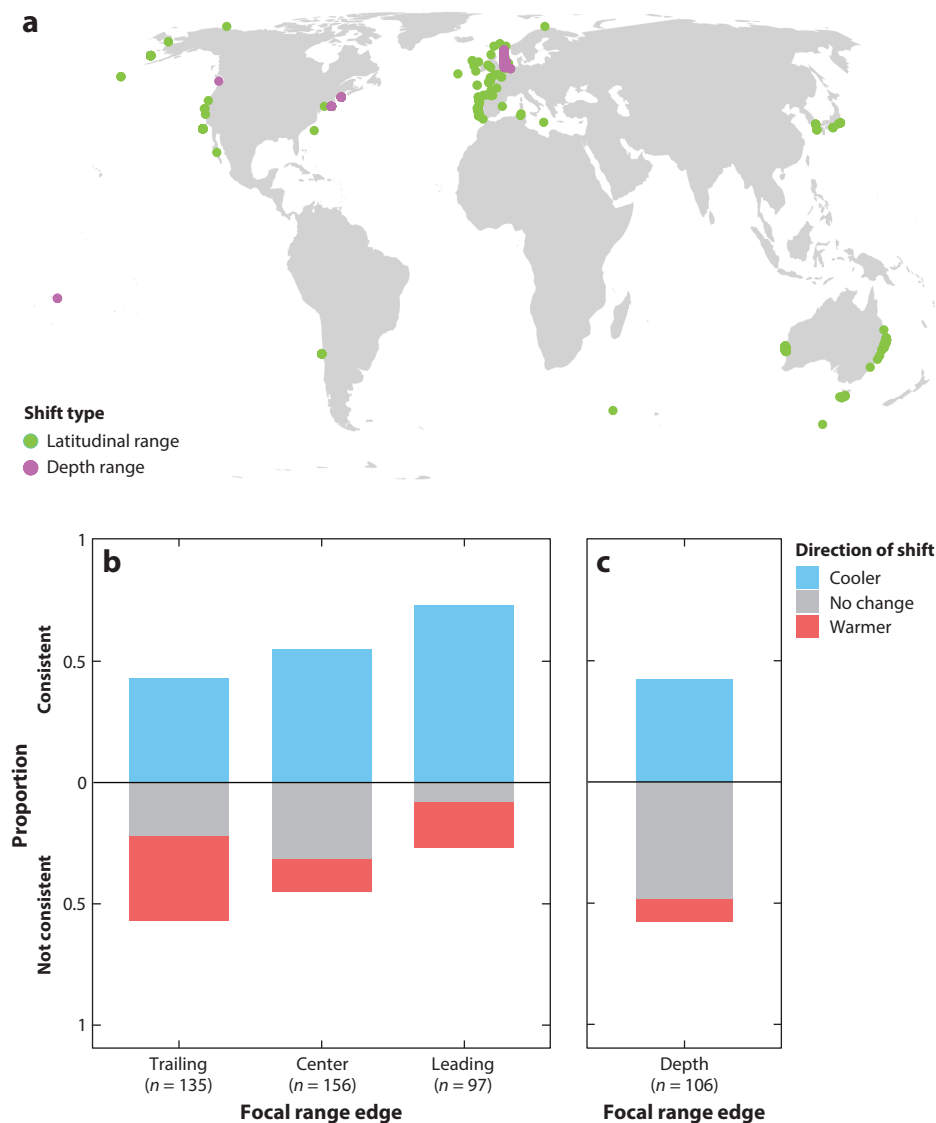
## 1. INTRODUCTION

More than 150 years ago, Dana (1853) laid out a biogeographic description of ocean life in terms of isocrymes (lines of equally cold winter temperatures), with the implicit suggestion that these maps of environment and biogeography would be relatively stable through time. The intervening decades of research, however, have shattered any sense of a stable ocean environment. Ocean conditions vary cyclically across temporal scales from years to decades, centuries, and beyond. Beyond that, human greenhouse gas emissions have driven ocean surface temperatures to rise 0.7°C and  $p\text{CO}_2$  to increase as well, with cascading effects on stratification, oxygen concentrations, pH (a 30% rise in hydrogen ion concentrations), primary productivity, circulation, and more (Hartmann et al. 2013, Rhein et al. 2013). Ocean warming is now accelerating, so both the rate and magnitude of future changes are likely to be even larger (Cheng et al. 2019). Perhaps ironically, Dana's publication came out right around the time that industrialization led to the emission of large quantities of the greenhouse gases responsible for these changes.

Any perception of stable marine biogeography has fallen away amid observations of dramatic shifts in species geographic distributions over timescales from years to decades, centuries, and millennia. Climate change is already driving poleward range edges of marine species to expand at an average of 72 km/decade, which is approximately an order of magnitude faster than observed rates on land (Poloczanska et al. 2013). Existing records have been sufficient to document hundreds of species moving to higher latitudes and greater depths with warming (**Figure 1**), though the complex mosaic of temperatures sometimes means that species have moved in other directions as they track preferred conditions (Dulvy et al. 2008, Pinsky et al. 2013). Climate velocity—defined as the rate and direction that isotherms move across the seascape—has been a useful concept for explaining some of the variation in rates and directions of range shifts across species and regions (Burrows et al. 2011, Pinsky et al. 2013, Sunday et al. 2015).

The modern shifts in marine species distributions are not unprecedented, though the pace of change in recent decades is likely much faster than it was over geological time. During the end-Permian mass extinction (approximately 252 Mya), for example, ocean warming and other changes precipitated the worst catastrophe in the history of complex life, eliminating nearly 80% of marine animal genera (Payne & Clapham 2012). Extinctions recorded during end-Permian warming were disproportionately clustered among high-latitude taxa, strongly suggesting that they ran out of climatically habitable space (Penn et al. 2018). By contrast, low-latitude animals were more likely to go extinct during rapid and severe climate cooling during the Late Ordovician mass extinction (approximately 445 Mya) (Finnegan et al. 2012), again suggesting that species shifted to new locations and ran out of habitat.

Shifts in marine species distributions have attracted substantial attention, particularly over the last decade once it became clear that marine species were shifting rapidly but had been understudied relative to similar processes on land (Murawski 1993, Perry et al. 2005, Richardson & Poloczanska 2008). In this review, we treat a shift as any change in the spatial distribution of a species that can be separated from sampling error, but we focus on shifts that can be reasonably attributed to climate change. Two chapters in the IPCC Fifth Assessment Report focused on ocean impacts of climate change (Hoegh-Guldberg et al. 2014, Pörtner et al. 2014), and other papers have reported global syntheses of observations (Molinos et al. 2017; Poloczanska et al. 2013, 2016) or projected future patterns across hundreds to tens of thousands of species (Cheung et al. 2009, Molinos et al. 2015, Morley et al. 2018). An exhaustive review of all related research is neither needed nor possible. Instead, this review focuses on the current state of knowledge regarding the key processes driving shifts in marine species distributions, the traits that can help generalize existing results to unstudied species, the ecological and evolutionary consequences of these shifts, and key areas for future research.



**Figure 1**

Global summary of studies on climate-driven range shifts of marine species. (a) Locations of latitudinal (green) and depth (purple) range shift studies. (b) Proportion of latitudinal range edges or centers shifting toward higher latitudes (blue), not shifting (gray), or shifting toward lower latitudes (red). (c) Proportion of depth range edges or centers shifting toward greater depths (blue), not shifting (gray), or shifting toward shallower depths (red). In panels b and c, bars above 0 are generally consistent with broad-scale climate change predictions, while those below 0 are generally not. Latitudinal data are from Poloczanska et al. (2016); depth data are from Poloczanska et al. (2013).

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**Acclimation:**

the physiological adjustments of an organism in response to a single environmental change, usually in laboratory conditions

**Extirpation:**

the disappearance of a species from a region or location (i.e., local extinction)

**Oxygen- and capacity-limited thermal tolerance (OCLTT):**

the hypothesis that the ability to acquire and distribute oxygen to tissues sets organismal thermal limits

**Critical thermal minima and maxima:**

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the temperatures at which organisms lose the ability to maintain orientation and position

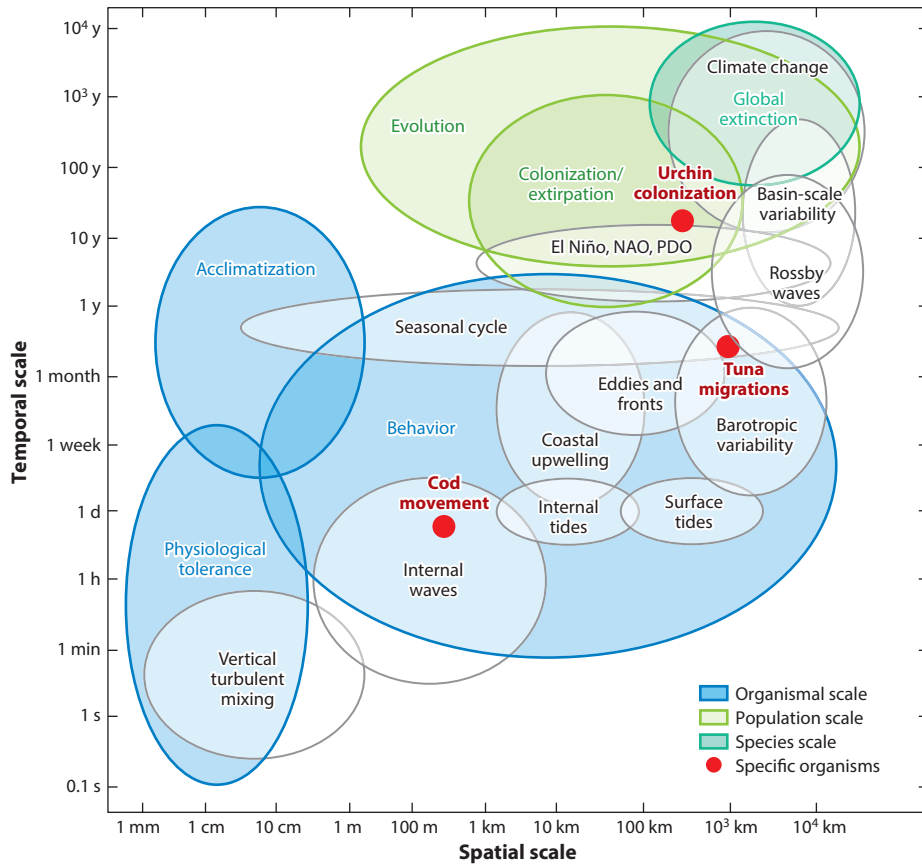
Overall, we find that marine species have high sensitivity to climate change at the organismal and population level, balanced by relatively strong abilities to colonize new territory. These mechanisms of response to climate change and variability contrast with those on land, where species often have lower colonization abilities but greater behavioral adaptation options and less physiological sensitivity (Kinlan & Gaines 2003, Pinsky et al. 2019, Robinson et al. 2011). These differences suggest that range shifts across wide spatial scales are a key way in which marine species cope with climate change. Even though the same ecological and evolutionary processes are at work in the ocean and on land, shifts in species distributions in these two realms occur in dramatically different fluid environments, with different physical properties, geographic patterns, evolutionary histories, and patterns of human impacts (Denny 1993, McCauley et al. 2015). It should therefore be no surprise that the consequences and impacts of climate change differ in important ways as well.

## 2. SCALING FROM PHYSICS TO BIOGEOGRAPHY

Understanding shifts in species distributions is fundamentally a problem of scaling. Individual organisms interact with their environment at scales from millimeters to 100 m or even  $10^4$  km (Figure 2), but species distributions are determined by the locations of thousands to billions of organisms across hundreds to thousands of kilometers. How do individual organisms cope with environmental change? How do individual responses scale up to affect species distributions? Answering these questions requires knowing how organisms interact with their environment across fine spatial and temporal scales and also which of those processes are most relevant for driving wide-scale changes in the spatial distributions of many organisms at once.

It is useful to think of relevant processes spread across scales of time, space, and biological organization (Figure 2). For individuals at a single location, a certain amount of environmental change is physiologically tolerable. Behavior helps mobile organisms avoid stressful conditions. Over slightly longer periods of time, acclimation allows individuals to modify their physiological tolerance. At the population level, evolution can alter tolerance across generations. Across space, processes of colonization and extirpation allow populations to move into new locations and vacate historical territories. If all of these are insufficient, a species suffers global extinction.

Marine organisms are directly influenced by their environment through temperature, oxygen, and food availability, while other factors, such as carbonate chemistry, are important but have been less often implicated in shifting species distributions. Changing temperatures alter protein structures and membrane fluidity, speeding or slowing cellular processes like metabolism. One idea—known as the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis—posits that physiological systems interact such that, at temperatures that are too low or too high, the metabolic demand for oxygen exceeds the oxygen supply from the surrounding water and an organism's ability to distribute that oxygen to tissues (Deutsch et al. 2015, Pörtner & Knust 2007) (see the sidebar titled Oxygen), though there is active debate on the most relevant mechanisms (Lefevre et al. 2017). Organisms have critical thermal minima and maxima ( $CT_{\min}$  and  $CT_{\max}$ , respectively) at which they lose the ability to maintain their orientation and position (Cowles & Bogert 1944), as well as hypoxic thresholds ( $PO_2^{\text{crit}}$ ) below which aerobic metabolism declines (Deutsch et al. 2015). Tolerance varies by life stage and environmental experience, with indications that larvae and juveniles are most sensitive in many taxa (Harvey et al. 2013). Sublethal effects, such as constraints on feeding times, that combine to limit growth or reproduction may be even more important (Gunderson & Leal 2016). In this way, food availability, temperature, and hypoxia may all interact, with sublethal impacts of high temperature or low oxygen mitigated by greater food availability and exacerbated by lesser food availability.



**Figure 2**

Scales of oceanographic variation (gray) overlaid by scales of organismal (blue), population (green), and species (blue-green) processes for responding to this variation. Specific organisms are highlighted in red. Abbreviations: NAO, North Atlantic Oscillation; PDO, Pacific Decadal Oscillation.

## OXYGEN

Recent evidence suggests that the combined effects of warming and oxygen loss together limit geographic distributions for marine ectotherms. Equatorward range limits often match habitats where the oxygen supply is two to five times the oxygen demand set by a species' temperature-dependent resting metabolic rate (Deutsch et al. 2015). Warmer temperatures drive higher metabolic rates that exceed oxygen availability. Sufficient oxygen is needed for an organism to survive, feed, defend itself, grow, and reproduce. With warming expected by the end of the century, habitat losses will be particularly acute at equatorward boundaries where the metabolic scope is already close to the critical value for survival (Deutsch et al. 2015). Temperature-fueled changes in the location and extent of oxygen minimum zones can also vertically compress habitats (Prince et al. 2010) and increase overlap among competitors, between predator and prey (Stewart et al. 2014), and with fisheries (Prince et al. 2010). These results suggest that the synergistic impacts of both oxygen and warming are likely to strongly shape future species distributions, biomass production, and ecosystem function.

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**Spatial refuge:**

a feature of the landscape that continues to provide suitable habitat to an organism despite environmental change

**Behavioral****thermoregulation:**

the maintenance of body temperature through actions such as habitat selection or basking

**Acclimatization:**

the physiological adjustments of an organism to a change in its natural, multistressor environment

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However, the environment an organism experiences is not straightforward to measure. Oceanographic processes at scales from centimeters to  $10^4$  km drive spatial and temporal variation in temperature and oxygen (**Figure 2**). Solar heating drives the ocean surface to heat up by as much as 2–6°C each day, but 10 m or so deeper, temperatures are relatively constant throughout the day (Gentemann et al. 2008). Internal waves can bring cool, deeper, and oxygen-poor water into shallow water at scales of hours and kilometers, while upwelling can have similar impacts over months and tens of kilometers (Grantham et al. 2004). Bathymetry concentrates both processes in particular locations, creating a spatial mosaic of average and extreme temperatures across the three-dimensional ocean. This mosaic creates spatial refuges, such that an organism or a population in one location can hit stressful limits while another only kilometers away does not (Lima et al. 2016, Smith et al. 2017). Spatial refuges can be even smaller in the intertidal zone and can be found on the scale of a few centimeters (Lima et al. 2016).

Mobile organisms also use the spatial mosaic for behavioral thermoregulation, potentially avoiding stressful conditions when spatial refuges are available in ways that can mitigate adverse demographic impacts (Fey et al. 2019). For example, Atlantic cod (*Gadus morhua*) in Norway prefer prey-rich shallow habitats when water temperatures are cool but retreat to deeper, cooler waters when shallow-water temperatures increase above 16°C (Freitas et al. 2016). Bigeye tuna (*Thunnus obesus*) do the opposite: They feed in cold, deep waters but return to surface waters to warm up (Holland et al. 1992). Movements of dentex (*Dentex dentex*) (Aspillaga et al. 2017) and bonefish (*Albula vulpes*) (Brownscombe et al. 2017) across depths also appear to regulate body temperatures. Whether mobile marine organisms hit physiological limits in a given location therefore depends not only on their tolerance but also on their mobility and the accessibility of thermal refuges. Moving deeper can allow species to avoid hot surface temperatures but may not help them avoid hypoxic limits, because oxygen availability also decreases with depth (Deutsch et al. 2015). Larger marine organisms tend to be more mobile and have access to a wider range of conditions (McCauley et al. 2015), though tiny pelagic zooplankton can also move hundreds of meters vertically each day (Elder & Seibel 2015).

Over longer periods of time, organisms also alter their physiological tolerance through acclimatization. Acclimatization can be reversible for an organism or may be set developmentally or even transgenerationally (Munday et al. 2017). Reversible thermal acclimation is insufficient to fully offset future warming, though it can help organisms cope with certain stressful conditions (Gunderson & Stillman 2015, Gunderson et al. 2017). Over generations, natural selection can favor individuals that tolerate new environmental conditions, allowing a population to evolve and therefore persist under conditions that would otherwise drive it to extirpation (Gomulkiewicz & Holt 1995). However, fine-scale habitat variation and gene flow across environmental gradients can constrain or promote evolution through processes such as gene swamping and local adaptation (Gonzalez et al. 2013).

Populations can also respond to changes in their environment by colonizing new areas, though to do so, organisms first need to disperse there. For both larvae and adults, individuals will choose behaviors and movement patterns based on signals in their immediate environment, not large-scale knowledge of where newly suitable locations can be found (Allen et al. 2018). Diffusive movement may randomly transport some individuals to suitable locations where they can survive and reproduce, but active movement is a more complex process guided by the fine-scale cues that organisms use. Tunas, for example, move north seasonally with local changes in temperature and productivity (Block et al. 2011).

Beyond abiotic conditions, organismal behavior, movements, and abundances are also set in part by food availability, and these indirect effects also raise scaling challenges. At a coarse level, warming oceans generally become more stratified, which reduces the flux of nutrients into the

photic zone and reduces food web production in many ecosystems (Sarmiento et al. 2004). However, local oceanographic processes like fronts and eddies concentrate nutrients, prey, and predators; increase interaction rates; and increase productivity and nutrient cycling (Woodson & Litvin 2015). Differences in prey preferences, foraging strategies, and handling times among species create idiosyncratic consumer responses to changes lower down in the food web. Food web processes also amplify changes in primary productivity such that effects become stronger higher up in the food web, in part through changes in growth efficiency (Stock et al. 2014).

On one level, we have millions of fine-scale interactions over short periods of time between organisms and their thermal, oxidic, and biotic environments. On another level, these processes lead to species disappearing from one location, appearing in another, and shifting their distribution over longer timescales and large spatial scales. A shift in distribution is therefore not a direct outcome of climate change but the emergent consequence of fine-scale interactions between an organism and its immediate environment, which in turn are influenced by both climate variability and climate change. Most observations of species range shifts have not been individually attributed to climate change—and likely cannot be—but the aggregate consistency of patterns across species and geographies strongly implicates climate change as the major driving factor (Poloczanska et al. 2013). Understanding how these pieces connect across scales is an ongoing challenge, but the next section describes the progress that has been made so far.

### 3. CHANGING RANGE BOUNDARIES

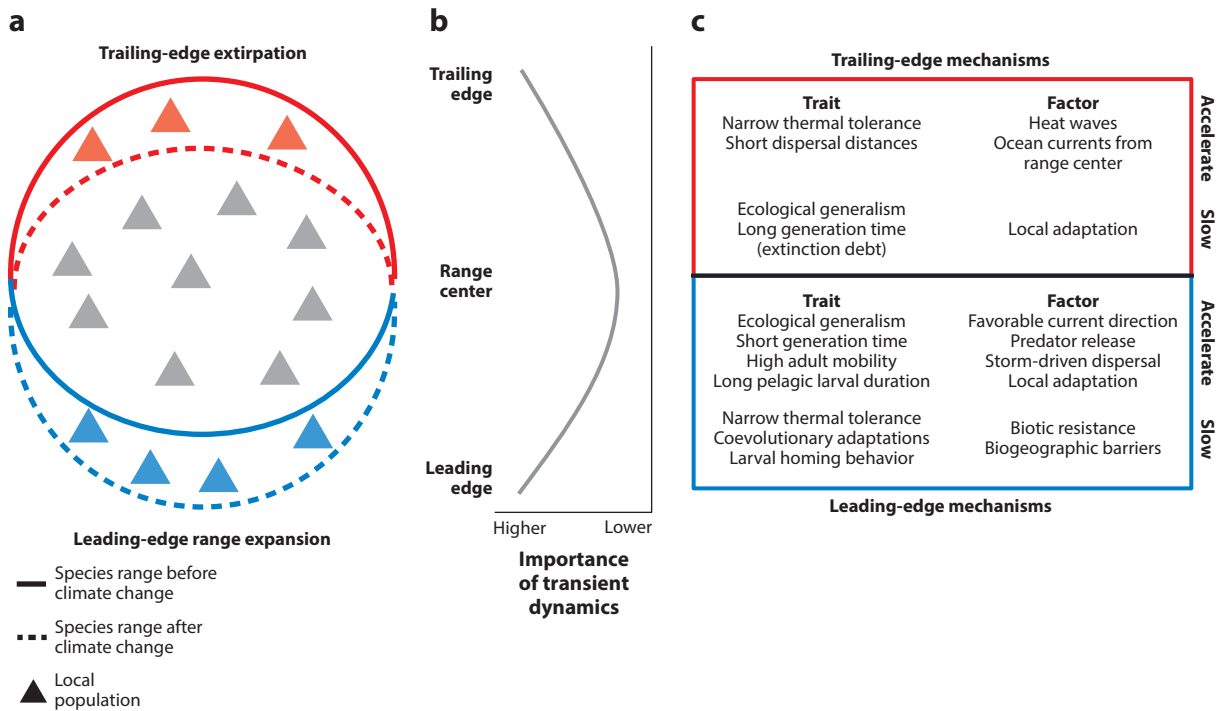
The dynamics of species geographic distributions can be decomposed partly into changes at the two range boundaries (**Figures 1, 3, and 4**). At leading range boundaries, species extend into new regions as environmental conditions become more favorable. At trailing edges, population extirpations cause ranges to contract (Thomas et al. 2001). Processes at both boundaries are inherently transient and far from equilibrium dynamics (Hastings et al. 2018). Distinct processes operate at leading and trailing edges, however, and it is therefore useful to consider them separately (**Figures 1, 3, and 4**). Darwin (1859) and others have proposed that abiotic factors shape poleward range edges, while biotic constraints form equatorward boundaries. In the ocean, both high- and low-latitude marine species range limits correspond relatively well to those predicted from physiological thermal limits, suggesting that abiotic conditions are important at both edges (Sunday et al. 2012). This pattern may mean that some or perhaps many marine species can be found in waters that reach stressful temperatures, though additional research is needed to test this hypothesis.

#### 3.1. Leading-Edge Expansions

Invasion ecology provides a useful framework to explore processes that shape the leading edge. For a species to invade, and for a species to advance poleward in response to climate change, populations must colonize new regions. A successful invasion or colonization requires a species to disperse to a new location and maintain positive growth through either self-persistence or ongoing immigration (Bridle & Vines 2007). The invasion framework also usefully links a species' colonization capacity to species traits, revealing how these traits work in concert with biotic and abiotic habitat characteristics (Kolar & Lodge 2001). For example, while dietary generalism may help a species persist in a new region with novel prey, environmental conditions must also facilitate the movement of individuals to the habitable region (**Figure 3**).

To undergo range expansion, species must first enter a new region. Many marine ectotherms spend a period of their life cycle suspended in the water column and transported by ocean





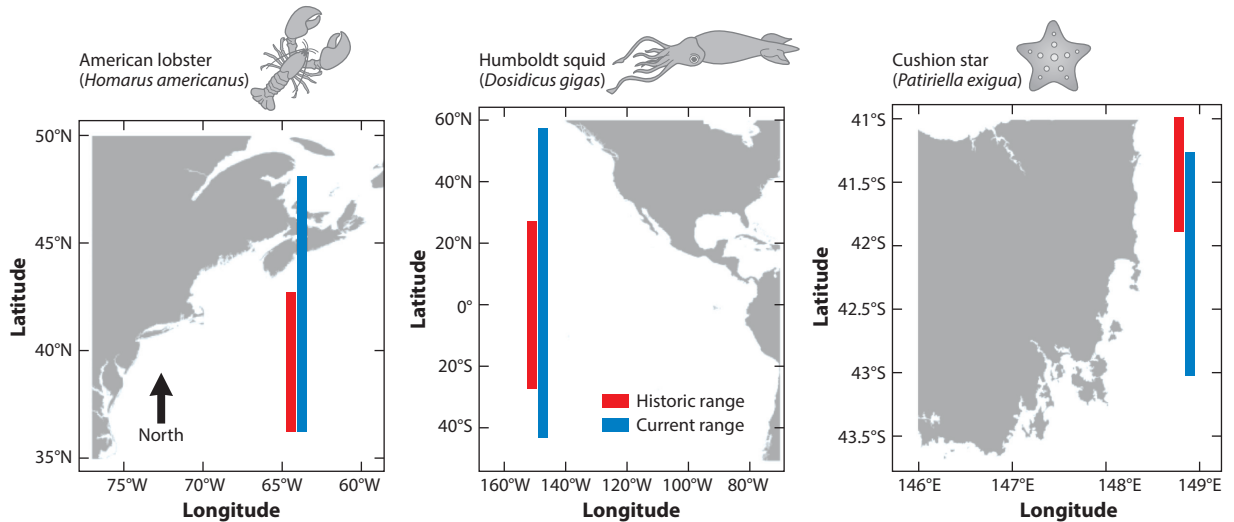
**Figure 3**

Processes of species range shifts. (a) Depiction of a possible species range shift in response to climate change. Red triangles represent populations that have experienced extirpation at the equatorward range boundary, gray triangles represent core populations, and blue triangles represent populations that have colonized at the poleward range boundary. (b) Transient (nonequilibrium) dynamics. While pervasive throughout ecological systems, these dynamics are especially important at range edges. (c) Traits and other factors that can slow or accelerate shifts.

currents before settlement. For species that have small adult home ranges—such as corals, smaller invertebrates, and reef fishes—this early life stage serves as the primary opportunity to expand their range and, as such, may be strongly influenced by the prevailing currents (Figure 3). As an example, corals have expanded northward more quickly on the south than on the north coast of Japan, aided by the strong, warm, poleward Kuroshio current (Kumagai et al. 2018). However, in other regions, opposing current patterns may predominantly carry larvae equatorward and hinder expansion toward suitable habitat (Molinos et al. 2017). In addition, coastal ocean currents that turn offshore can act as biogeographic barriers to dispersal and limit range expansions. Examples include the intersection of the Indian and Atlantic Oceans at Cape Agulhas, the Labrador Current and Gulf Stream at Cape Hatteras, and the Kuroshio and Oyashio Currents near Cape Inubo (Pappalardo et al. 2015, Teske et al. 2006). Rare long-distance dispersal events may also be important at expanding range boundaries and are often facilitated by extreme climatic episodes and anomalous current patterns. For example, more frequent storm-driven kelp raft dispersal events are already breaking down the relative ecological isolation of Antarctica (Fraser et al. 2018).

Beyond larval dispersal, adult mobility dominates range expansion in many species. Large marine fishes, such as whale sharks, exhibit immense mobility as adults, moving tens of thousands of kilometers over a handful of years (Guzman et al. 2018). Subsequently, for many of these species adult mobility serves as a better predictor of the rate of range expansion than larval dispersal strategy (Sunday et al. 2015). Species with high mobility as adults (e.g., swimming) tend to extend





**Figure 4**

Recent latitudinal range shifts of three marine species, highlighting asymmetric changes in leading and trailing edges. Offshore populations of the American lobster in the northeast Atlantic (historic: 1964; present: 2009) experienced range expansion without apparent range contraction near the equator. The Humboldt squid in the eastern Pacific (historic: common range throughout the twentieth century; present: 2004–2006) experienced range expansion toward both poles without apparent range contraction near the equator. The cushion star in Tasmania (historic: 1950s; present: 2007–2008) experienced leading-edge range expansion and some trailing-edge range contraction. Data are from Alarcón-Muñoz et al. (2008), Pinsky et al. (2013), and Pitt et al. (2010); species icons are from the Noun Project.

their ranges faster than less mobile species (e.g., crawling or sessile) (Brooker et al. 2007, Luiz et al. 2011, Sunday et al. 2015) (**Figure 3**).

Arrival in a new region does not guarantee establishment and subsequent positive population growth (Burgess et al. 2012, Sadowski et al. 2018). Species that thrive in new habitats tend to be ecological generalists that have flexibility in habitat and diet, such as omnivores as opposed to herbivores or predators (Sunday et al. 2015) (**Figure 3**). For example, a potential location for poleward expansion may provide suitable temperatures or oxygen levels for a species, but suitable benthic habitat may not be present. The northern range limit of an intertidal limpet, for example, appears to be set by a gap in suitable rocky habitat despite suitable environmental conditions even farther north (Gilman 2006). By contrast, the rapid range expansion of the Indo-Pacific lionfishes (*Pterois volitans* and *Pterois miles*) across ecosystems in the western Atlantic is often linked to their diverse diet and ability to persist across depths and substrates (Grieve et al. 2016).

The link between range expansions and abiotic conditions has been demonstrated most clearly for temperature, particularly winter temperatures. Northward expansion of Atlantic croaker (*Micropogonias undulatus*) along the east coast of the United States in the 1990s has been linked to sequential warm winters that allowed cold-sensitive juveniles to survive through the winter and subsequently establish north of the species' historical range (Hare & Able 2007). Lionfish juveniles, by contrast, have appeared as far north as New York (implying no lack of dispersal abilities) but have not become established above Cape Hatteras because they fail to survive through the winter (Grieve et al. 2016). Continued warming is likely to enable Atlantic croaker, lionfish, and other species to survive year-round at higher latitudes (Grieve et al. 2016, Hare & Able 2007).

Beyond abiotic drivers, high species richness and diversity in the resident ecological community may slow the establishment of new species through biotic resistance (Angert et al. 2011,

Stachowicz et al. 2002) (**Figure 3**). For example, tropical species have colonized temperate marine protected areas (MPAs) more slowly than they have colonized neighboring unprotected areas. The exact mechanisms preventing the infiltration of warm-water species in MPAs remain unclear, but the disparity likely results from a lack of tropical settlement cues and higher predation rates from large-bodied predators inside MPAs (Bates et al. 2014). It is important to consider both biotic and abiotic drivers in facilitating or limiting range expansions, though the relative importance of these processes remains poorly understood (Louthan et al. 2015).

At the leading edge, evolutionary processes in addition to ecological processes can accelerate range expansion through evolution of species traits (**Figure 3**). Novel biotic interactions and habitat conditions associated with range expansions apply selective pressures to populations (Hoffmann & Sgro 2011). In the terrestrial realm, experiments with beetles and plants have revealed that range expansion leads to the accumulation of individuals with enhanced dispersal strategies at the leading edge (Szűcs et al. 2017, Williams et al. 2016). Selective pressures can also lead to morphological divergence. Comparisons of fossil and extant specimens of the marine gastropod *Acanthinucella* suggest that changes in shell morphology are associated with poleward expansion during Pleistocene climatic fluctuations (Hellberg et al. 2001). Similarly, genetic studies of the red coral *Corallium rubrum* suggest that the species may be locally adapted at range boundaries, and therefore alleles unique to marginal populations may provide the architecture to accelerate poleward expansion (Ledoux et al. 2015).

### 3.2. Trailing-Edge Contractions

While successful colonization at the leading edge causes range expansions, extirpations at the trailing edge drive range contractions. Populations undergo local extinction when they can no longer maintain positive growth rates (Cahill et al. 2014, Louthan et al. 2015). As one example, the temperate seaweed *Scytothalia dorycarpa* experienced a rapid range contraction of 100 km in response to a marine heat wave that exposed populations at the warm edge to extended periods of sea surface temperatures up to 5°C above normal (Smale & Wernberg 2013).

While climate-driven extirpations have occurred in the ocean (Wiens 2016), these contractions appear to be five times slower than the rate of range expansions (Poloczanska et al. 2013). In addition, the proportion of leading range edges that are expanding is greater than the proportion of trailing edges that are contracting (**Figure 1**). For example, the Humboldt squid (*Dosidicus gigas*), an opportunistic species with short generation times, has rapidly expanded toward both poles, yet there is no record of population declines near the equator (Alarcón-Muñoz et al. 2008, Zeidberg & Robison 2007) (**Figure 4**).

Potential explanations for this asymmetry between leading and trailing edges (**Figures 1 and 4**) include difficulties detecting extirpation, stronger regional climate change at higher latitudes, and extinction debt (**Figure 3**). Determining whether a species has become extirpated is challenging in part because it can be confused with imperfect detection and in part because equatorward range boundaries often occur within tropical regions underrepresented in the biodiversity literature (Hampe & Petit 2005, Smale & Wernberg 2013, Thomas et al. 2006, Tydecks et al. 2018). Statistical methods to account for the sampling process can help alleviate the first issue and are becoming more widely used (MacKenzie et al. 2006, Thorson et al. 2016). In addition, climate change has occurred faster in temperate than tropical regions, which could explain why species experience fewer changes at their equatorward boundaries (Poloczanska et al. 2013). Finally, extinction debt may be accumulating for long-lived species that exhibit a delayed response to environmental changes (Jackson & Sax 2009) (**Figure 3**). Analyses of marine species across the North Atlantic reveal a positive correlation between temperature change and increases in species richness,

suggestive of transient dynamics driven by rapid colonization of new species but slower extirpation of resident species after environmental change (Batt et al. 2017, Hiddink et al. 2015, Magurran et al. 2015).

Characteristics and conditions that favor extirpation include specialization and the inability to tolerate a wide range of abiotic and biotic conditions (**Figure 3**). Short dispersal distances also make it unlikely that declining populations can recover through metapopulation rescue (**Figure 3**), as has been suggested to explain seaweed extirpations (Smale & Wernberg 2013). In a meta-analysis across many marine species, it also appears that ocean currents whose direction opposes the direction of range contraction promote extirpation, possibly by transporting maladapted genes and impeding local adaptation (Molinos et al. 2017).

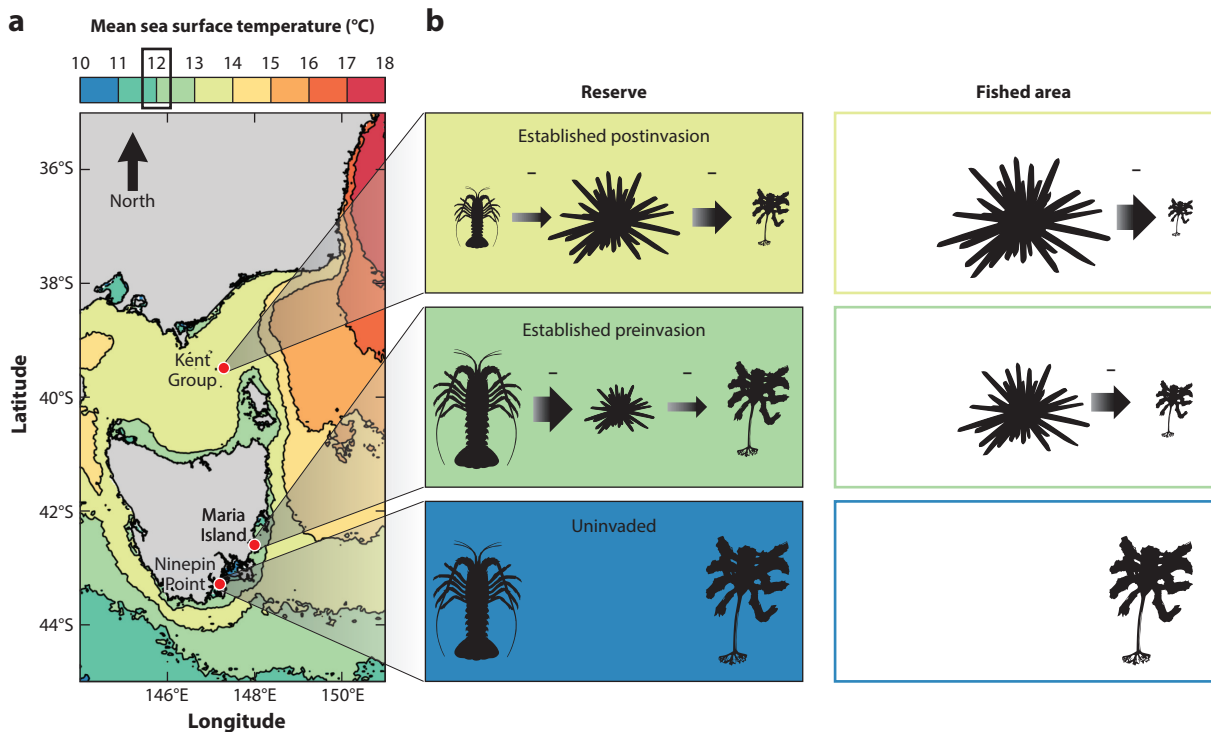
While evolution at the leading edge allows rapid range expansion, evolution at the trailing edge slows range contraction (Ledoux et al. 2015, Wiens 2016) (**Figure 3**). Theory tells us that while excessive gene flow can reduce the potential for local adaptation through gene swamping, moderate gene flow from the core of the population toward the edges can improve fitness by reducing homozygosity (Bontrager & Angert 2019, Bridle & Vines 2007). Marine species often have high levels of standing genetic variation because of large population sizes and gene flow across environmental gradients (DeWoody & Avise 2000), and extant populations may therefore contain the raw genetic material to respond to a changing environment. Few examples exist for recent climate change-driven evolution due to the challenges in providing strong evidence that allele frequency has shifted in response to a climate driver (Merilä & Hendry 2014). However, comparing maximum temperature tolerance in *Daphnia* hatched from eggs spanning generations revealed that water fleas evolved increased heat tolerance as resident lakes warmed (Geerts et al. 2015). While species with similarly short generation times—such as marine phytoplankton—may be able to evolve in time to overcome the effects of climate change, it is unclear whether evolution can occur fast enough in long-lived keystone species to maintain ecosystem function at low latitudes (Beaugrand & Kirby 2018, Geerts et al. 2015, Thomas et al. 2012, Wiens 2016).

#### 4. ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES

The previous sections highlighted that variation in ecological and evolutionary processes is likely to alter how an individual species responds to warming oceans by shifting its range. As a result, a species within an ecological community may shift more or less quickly than another species with which it interacts, setting up the potential for warming to create ecological mismatches that drive large changes in community composition or dynamics.

By driving extirpation from historical ranges and allowing species into new habitats, climate change can disrupt historical species interactions and communities. However, empirical evidence suggests that species demonstrate remarkable adaptability to changing conditions that promotes stability in food web properties (McCann & Rooney 2009). This evidence suggests that it is the network of interactions between species—and not species identity or diversity per se—that underlies the structure and function of ecosystems (McCann 2007) or the potential resilience of food webs in the face of shifting species composition. Here, we highlight how shifting ranges are likely to alter species interactions, the consequences for ecology and evolution, and how knowledge of ecological network structure could be leveraged to anticipate effects on ecosystem function.

The past, present, and future assemblage of species will constitute a network of interactions, from competition and predation to mutualism and facilitation. The astonishing complexity of interaction networks can make projections under future range shifts a daunting prospect. However, some insight may be gained by considering these interactions with respect to their reciprocal effects on the partner species. When range shifts result in losses of antagonistic interactions like



**Figure 5**

Community consequences of climate-driven range shifts illustrated by marine protected areas. (a) Mean sea surface temperatures during austral winter (June–August) 2001–2010. The outline around 12°C represents the cold limit for successful larval development of the barrens-forming urchin *Centrostephanus rodgersii*. (b) The community impact of the climate-driven range expansion of *C. rodgersii* inside (filled boxes) and outside (open boxes) of marine reserves in Tasmania. The fill color of the boxes represents the sea surface temperature at the site from 2001 to 2010, and the size of each icon represents its relative abundance. (Top) Urchins were first sighted in the Kent Group of islands in the 1960s, and by 2000, urchin barrens were continuous across all sites with little macroalgae (Johnson et al. 2005). Reserves established in 2005 have not yet resulted in restored macroalgae (Bates et al. 2017). (Middle) Large lobsters present in the Maria Island Marine Reserve prevent the establishment of urchin populations and maintain macroalgae (Ling et al. 2009), while deforestation has occurred in nearby fished areas. (Bottom) Urchins have yet to establish at sites in the vicinity of the Ninepin Point Marine Reserve, where winter temperatures are still below the cold limit. Species icons are from PhyloPic and were created by Joanna Wolf (lobster) and Jake Warner (urchin).

competition and predation, new species assemblages represent an opportunity for prey population growth (**Figure 5**). On the other hand, when changes in species distribution lead to losses in positive interactions like mutualism, facilitation, and feeding, species are likely to fare worse under future ocean conditions and may be driven extinct in the most extreme cases.

The consequences of gains (or losses) in species interactions due to past climate shifts provide insight into changes to come. These impacts have been widespread in marine ecosystems across latitudes. Warming-induced expansion of Atlantic cod into Arctic waters resulted in increased overlap with prey and a 20% increase in cod biomass (Howell & Filin 2014) as greater resource availability increased cod reproductive potential. Conversely, increased overlap with arrowtooth flounder (*Atheresthes stomias*), a predator, led to higher mortality of juvenile walleye pollock (*Gadus chalcogrammus*) (Hunsicker et al. 2013). Increased overlap with a poleward-expanding Humboldt squid population may have driven a large decline in populations of hake (*Merluccius productus*) (Zeidberg & Robison 2007). Finally, poleward expansion of tropical corals and herbivorous fishes

is driving a macroalgal-to-coral shift across Japan through enhanced herbivore pressure and increased competition between corals and kelps (Kumagai et al. 2018).

Mismatches in the rates of range shifts between predator and prey are likely to have the most acute consequences for specialist predators. Impacts on a generalist predator may be more muted if the overall prey biomass remains similar. However, the availability of alternate prey alone may not be sufficient to mitigate effects on predators. Warming-driven shifts in prey species composition toward less energy-dense species led to poor growth of walleye pollock (*Gadus chalcogrammus*) in the eastern Bering Sea (Siddon et al. 2013). Likewise, a massive die-off of Cassin's auklets (*Ptychoramphus aleuticus*) during the Pacific "warm blob" of 2013–2015 was driven by a shift toward relative "junk food" species with low energy content (Jones et al. 2018). The stomachs of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) during the same oceanographic phenomenon were often empty or full of warm-water taxa—both of which are associated with poor future returns of adult salmon (Daly et al. 2017). Declines in prey quality can detrimentally affect predators in particular if they are unable to compensate with increased foraging (Harvey & Moore 2017).

The gain or loss of a key species interaction due to a range shift may also drive adaptation (including evolutionary adaptation) in one or both of the partners. For species that compete for resources, this competitive release or intensification may drive a shift in the species niche. New overlap between potential predator and prey may result in adaptations that allow the predator to consume the new prey or, conversely, for the prey to defend itself against the new predator. Responses to and by invasive species may guide expectations for the magnitude and time course of evolution in response to climate-driven range shifts. For introduced species, the likelihood of an evolutionary response is affected by the demographic effects of the new species interaction, the type of genetic variation in both species pairs, and the consistency of selection (Strauss et al. 2006). The evolution of traits that reduce competitive exclusion between two species is more likely where populations are large and well connected (Stotz et al. 2016), and populations are more likely to be well connected for range shifts than for species introductions (Sorte et al. 2010). In terms of new predator–prey interactions, marine prey may be more likely to respond appropriately to new predators, even if that predator has a different foraging mode, because most predator archetypes have global distributions in marine systems (Cox & Lima 2006). However, apparent prey naivete to Indo-Pacific lionfish (*Pterois volitans*) has contributed to the lionfish's devastating impact in the Caribbean (Lönnerstedt & McCormick 2013). If the resulting mortality rates from the new interaction are not high enough to cause prey extinction, those prey can evolve behavioral and structural defenses. Interestingly, there may be a trade-off between adaptations to new species interactions and adaptations to new environmental conditions, such as the trade-off between high temperature tolerance and competitive abilities that has been observed in copepods (Willett 2010).

Warming-driven range shifts also have the potential to alter ecological network structure to such an extent that these climate change cascades lead to new ecosystem regimes (Johnson et al. 2011) (**Figure 5**). Tropical herbivores invading temperate reefs have converted productive macroalgal habitats into low-diversity barrens in Japan (Verges et al. 2014), the Mediterranean (Verges et al. 2014), and Tasmania (Ling et al. 2009). Tropicalization may lead to a complete ecosystem transformation: In temperate seagrass meadows, invasion by tropical herbivorous fishes may facilitate future colonization of herbivorous megafauna that results in the replacement of a seagrass-detritus food web with one based on direct consumption of seagrass (Hyndes et al. 2016). Comparatively simple Arctic systems are particularly susceptible to climate-driven changes in species composition. Warming-fueled increases in macroalgal coverage in an Arctic fjord resulted in a benthic invertebrate community reorganization (Kortsch et al. 2012) that characterized a new, stable ecosystem state. Poleward expansion of boreal generalists altered the network properties of Arctic food webs by increasing connectance (i.e., the fraction of realized food web links) and

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**Tropicalization:**  
the transformation of a  
community from  
midlatitude to  
low-latitude biotic and  
abiotic characteristics

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reducing modularity (i.e., the division of food webs into subgroups of strongly interacting species) (Kortsch et al. 2015). Both changes may increase the synchrony of responses to perturbations.

Speciose food webs with high trait diversity may resist warming-induced species invasions and their impacts on ecosystem structure and function (**Figure 5**). Restored food webs in MPAs resisted colonization by subtropical vagrants on temperate reefs in Tasmania (Bates et al. 2013). In particular, a high abundance of lobsters in MPAs prevented the establishment of a range-expanding urchin (Ling et al. 2009) in macroalgal habitats (**Figure 5**). In southern California kelp forests, the restoration of urchin predators indirectly facilitated higher biomass of a native algae, which could then resist the invasion of a southern species of algae (Caselle et al. 2018). Likewise, the presence of a particular keystone species can stabilize communities in the face of warming: Limpet herbivory facilitated the persistence of the barnacle foundation species and its associated community (Kordas et al. 2017), which in turn meant that recovery was more rapid from acute warming events. On the other hand, biotic interactions may actually act to enhance further food web change. Positive interactions between range-expanding species and other warm-temperature-associated species can facilitate further tropicalization across the food web: The successful establishment of a range-expanding urchin led to communities of macroalgae, invertebrates, and fishes that are associated with warmer temperatures (Bates et al. 2017). The structure of ecological networks is therefore critical to understanding the broader impact of range shifts on ecosystem function.

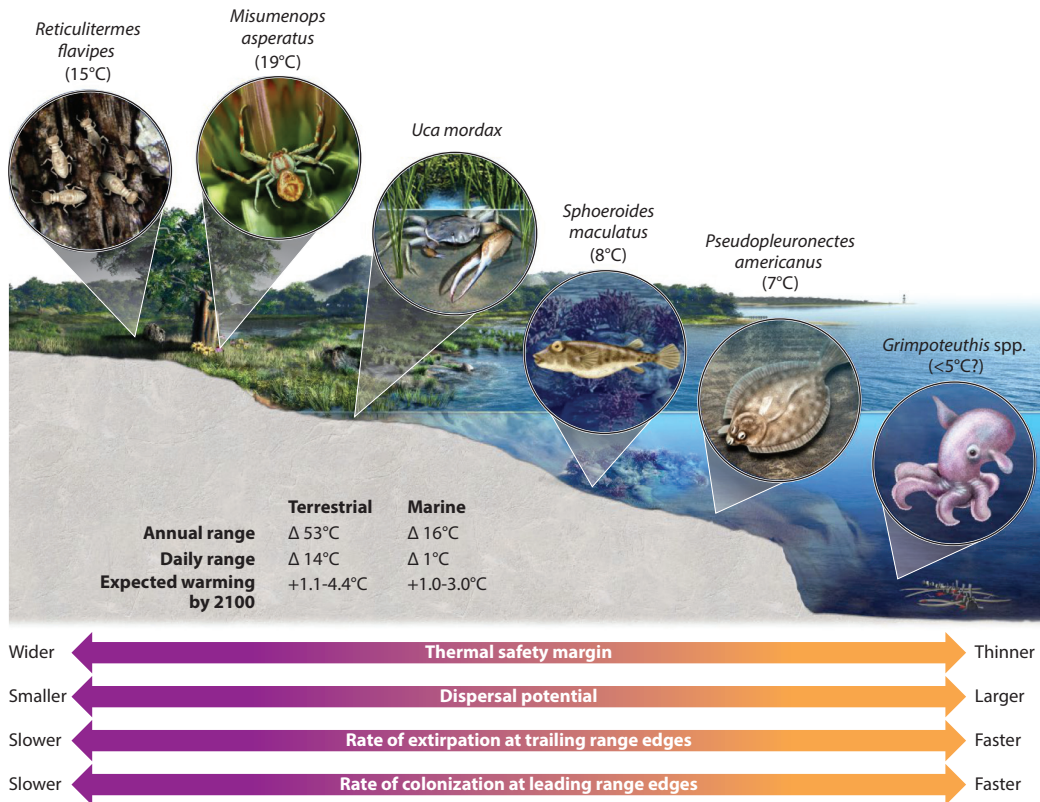
## 5. SIMILARITIES TO AND DIFFERENCES FROM RANGE SHIFTS ON LAND

Most research on shifting species ranges to date has been conducted on land, and so it is relevant to ask the extent to which shifts in the ocean and on land are similar. The distinct differences in physical conditions, geographic patterns, and evolutionary histories between the two realms provide important opportunities to test ecological and evolutionary theory (Steele 1985), including our understanding of climate impacts (**Figure 6**). At first glance, the entire ocean can appear to be a refuge from climate change. Water has a specific heat four times higher than air's, making the ocean in effect a 1.3-sextillion-liter water bath whose surface has warmed only half as fast as the land, even though the ocean has absorbed more than 90% of global warming's excess heat (Rhein et al. 2013).

However, this thermal inertia also mutes thermal variation across time and space, such that ongoing and future magnitudes of warming are large relative to the variation experienced by individual organisms or by entire evolutionary lineages. The daily temperature variation of the ocean surface, for example, can be an order of magnitude less than that of the land surface (**Figure 6**). Seasonal variation in temperature is on average six times higher on land than in the ocean, accentuated by particularly large differences at higher latitudes (Pinsky et al. 2019). Sea surface temperatures, for example, vary seasonally by 16°C off the coast of South Carolina, United States, but inland air temperatures swing by 53°C during the year (**Figure 6**). Variation at millennial timescales in the ocean is half the magnitude of that on land (Shakun et al. 2012). Oxygen, a fundamental requirement of aerobic life, is approximately 30 times less available in seawater than in air and often limits thermal tolerance (Giomi et al. 2014).

The evolution of wider thermal tolerance involves energetic and other trade-offs, and in an environment that varies less through time, marine species have evolved narrower ranges of temperature tolerance than terrestrial species. For example, the Antarctic fish *Lepidonotothen nudifrons* can tolerate an 11°C range in the laboratory, whereas its terrestrial neighbor, the sub-Antarctic caterpillar (*Pringleophaga marioni*), can tolerate a 45°C range, measured as the difference between  $CT_{min}$  and  $CT_{max}$  (Sunday et al. 2011). Globally, physiological experiments suggest that thermal





**Figure 6**

A comparative view of climate change vulnerability from terrestrial to marine ecosystems. Representative species are shown with their thermal safety margins. The thermal safety margin is a relative (not absolute) proxy for the amount of warming an organism can tolerate. Lower annual and daily temperature variation in the ocean has left many marine species less evolutionarily conditioned to cope with climate warming, which is reflected in narrower safety margins. These vulnerabilities are exacerbated by reduced access to thermal refuges in the ocean. The numbers at the bottom show the average annual and daily range of temperatures from local monitoring stations, as well as the expected warming by 2100. The examples here are drawn from the east coast of North America, including weather stations and oceanographic buoys in South Carolina. Illustration by N.R. Fuller of Sayo-Art LLC.

tolerance breadth ( $CT_{\max} - CT_{\min}$ ) is, on average, approximately  $10^{\circ}\text{C}$  narrower for ectotherms in the ocean compared with those on land (Sunday et al. 2011). These differences become especially pronounced at the poles, where marine ectotherm tolerance breadths can be less than half those of climate-sensitive tropical ectotherms (Sunday et al. 2011). Narrow thermal tolerance may help explain why marine range edges also appear to be more tightly linked to temperature than are range edges on land (Sunday et al. 2012).

Another consequence of narrow thermal tolerance is that marine species live in habitats closer to their thermal limits than do terrestrial species. To understand sensitivity to warming, the difference between body temperatures and upper thermal tolerance limits (the thermal safety margin) is particularly relevant. Thermal safety margins for marine species are on average only 80% as wide as those of terrestrial species (Pinsky et al. 2019) (Figure 6).

It is also more difficult to avoid warming in the ocean: Water has a heat transfer rate that is 100 times that of air, and conduction and convection therefore maintain most ocean ectotherms near thermal equilibrium with their environment (Denny 1993). On land, species can use



convection, evaporative cooling, and microclimate refuges like shade or underground burrows to avoid hot air temperatures (Sunday et al. 2014). While poorly characterized, such thermal escapes appear to be less common in the ocean. Temperature gradients are generally weaker in the ocean (Burrows et al. 2011), and an organism therefore must move farther in the ocean than on land to experience an equivalent drop in temperature.

These differences in thermoregulatory options may explain why marine species have approximately double the plasticity in thermal tolerance compared with terrestrial species (Gunderson & Stillman 2015). The Bogert effect is the idea that behavior can buffer organisms from environmental variation and hence limit selection pressures on other traits (Bogert 1949). Applied to thermal variation, it suggests that fewer options for behavioral thermoregulation at sea may have led to the evolution of larger acclimation abilities, though even in the ocean, acclimation appears too small to fully offset the stress of future warming (Gunderson & Stillman 2015).

These conditions suggest that marine species are both more sensitive to warming temperatures and unable to avoid such warming through behavior. In combination, these factors imply that population extirpations in response to long-term increases in maximum temperatures may be more common in the ocean than on land (**Figure 6**). It is therefore perhaps no surprise that the existing global data on historical range contractions attributable to warming also suggest that contractions are twice as common in the ocean as on land (Pinsky et al. 2019).

Marine species, however, also have generally greater dispersal abilities than do species on land (**Figure 6**). Home range sizes are larger in the ocean than on land for a given body size (McCauley et al. 2015). The buoyancy provided by water means that it takes approximately eight times less energy to swim a given distance in the ocean than to run an equivalent distance on land (Schmidt-Nielsen 1972). Offspring dispersal distances are often longer in the ocean, facilitated by planktonic larval stages that float on ocean currents (Kinlan & Gaines 2003). Habitat features also impede dispersal for many terrestrial organisms, limiting colonization of new territory (Schloss et al. 2012). These differences suggest that climate-driven range extensions would occur faster or more commonly in marine organisms than on land (**Figure 6**). A synthesis across observations supports this, with range edges extending 10 times faster in the ocean than on land (Poloczanska et al. 2013).

Many marine species are also distinguished by exceptionally large population sizes, including phytoplankton, zooplankton, and some fishes. Bristlemouths (genus *Cyclothone*), for example, are mesopelagic fishes that may number 100 trillion individuals per species and are likely the most abundant vertebrates on the planet (Irigoin et al. 2014). High abundance can translate to high standing genetic variation, which provides raw material for evolution in the face of environmental change, particularly for species with short generation times. Gene flow across environmental gradients also means that genetic variation in marine species is widely dispersed and available for selection to act upon (Bernatchez 2016). In comparison, barriers to dispersal on land create more genetic divergence and greater potential for local adaptation to environmental conditions. Despite examples of evolution playing a role in range shifts and responses to hot temperatures in both marine and terrestrial systems (Bridle et al. 2013, Hellberg et al. 2001, Palumbi et al. 2014), the extent to which ongoing and future evolution will play different roles across realms remains unclear.

Overall, the picture emerging is one of higher organismal and population sensitivity to climate change but greater abilities to colonize new territory in the ocean, with somewhat less physiological sensitivity but greater behavioral adaptation options on land (**Figure 6**). These differences suggest that dominant climate change responses occur at different spatial scales in marine and terrestrial realms: Range shifts across wide spatial scales appear to be a key mechanism by which marine species cope with environmental change, while local mechanisms like physiological tolerance and behavior appear to play a larger role on land. Even though the same ecological and

evolutionary processes operate both in the ocean and on land, the consequences and impacts of climate change appear to differ in important ways.

## 6. ANTICIPATING FUTURE ECOSYSTEMS

The previous sections highlighted our understanding of how species ranges have responded to climate variability on land and in the seas, and the ecological and evolutionary consequences of these changes. Anticipating future range shifts requires integrating that knowledge effectively. Much progress has been made in using high-resolution projections of environmental variables and increasingly sophisticated approaches to project future species distributions at global (Cheung et al. 2009, Molinos et al. 2015) or regional scales (Morley et al. 2018) by the end of the century. These models suggest future shifts of approximately 50–100 km/decade, though with substantial variation across species and regions (Cheung et al. 2009, Morley et al. 2018). These models also suggest differential impacts across latitudes, with major losses of marine diversity and biomass in the tropics and gains in poleward regions that will experience substantial species turnover (Cheung et al. 2009) and homogenization (Molinos et al. 2015). Ensembles across global climate models show reasonable consistency in the direction and magnitude of predicted shifts in habitat for many species (Morley et al. 2018), and historical observations suggest that species distributions generally follow shifting habitat (Pinsky et al. 2013), building moderate confidence in projections of future species distributions at century scales (Cheung et al. 2016).

Such predictions, however, intentionally average over interannual and decadal climate variability. We are confident that many species will generally move poleward by the end of the century in response to long-term warming, but the interaction of anthropogenic warming with multiannual to multidecadal climate variability (e.g., El Niño or the Pacific Decadal Oscillation) can introduce substantial variation in the rate and direction of temperature change and the resulting shifts in distribution. Marine heat waves have already and will continue to become more frequent and last longer (Frölicher et al. 2018), and these events are associated with rapid range shifts and community shifts (Harley & Paine 2009, Wernberg et al. 2016). Extreme climatic events can further enhance invasions by decreasing the resistance of native communities (Diez et al. 2012). Population and evolutionary dynamics and their consequences for extirpation and extinction are very different in this scenario than with a slow and steady poleward march.

Even with accurate projections of species distributions, anticipating the structure and dynamics of future ecosystems remains a challenge. Future distributions may be smaller than those estimated based on the climate alone if current distributions are facilitated by another species, and larger where predators or competitors constrain the current realized niche. Incorporating biotic interactions directly into species distribution models can improve their predictive power (Araújo & Luoto 2007). However, there is evidence that the strength or even nature of interactions between two species may change in their new range (Menéndez et al. 2008), and synergistic effects of warming on existing species interactions can lead to population collapse (Mouritsen et al. 2005). Furthermore, biotic and abiotic conditions can alter the direction and magnitude of global change effects on biotic interactions (Tylianakis et al. 2008), and novel ecosystems may emerge where species interact for the first time. While projections under these no-analog conditions may seem impossible, insights from bioenergetics and theory for food web assembly can be informative.

Quantifying the interaction between energetic requirements and prey fields, for example, may serve as a useful tool for future projections of predator populations (Amélineau et al. 2018). Incorporating not only differences in prey quality but also prey population turnover rates can mean the difference between projected increases or decreases in predator populations. For example, warming is projected to result in the replacement of large-bodied copepods by smaller-bodied boreal

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**Size-spectrum**

**theory:** the idea that the body size distribution of organisms (rather than individual species identities) drives food web function

**Space-for-time**

**substitution:** using spatial patterns across environmental gradients to predict temporal changes in the same environmental conditions

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species with lower individual lipid content in Arctic marine ecosystems. However, the higher population growth rates of the smaller species actually could lead to higher lipid production available to predators (Renaud et al. 2018). Dynamic energy budget models (Sousa et al. 2010) may provide a useful framework for predicting ecosystem outcomes of future range shifts.

In addition, interest in using traits to assess the structure and function of food webs is growing (Gravel et al. 2016). Allometric approaches and size-spectrum theory may be particularly useful in aquatic ecosystems, where the strength of interactions is largely dependent on body size. Coupling information on body sizes and either rule-based or empirically driven prey size preferences is a powerful approach to assemble the topology of novel food webs and assign potential interaction strengths. Comparisons to historical food webs can suggest where ecosystem function may be conserved or altered (Tylianakis et al. 2010). Likewise, the resulting modularity of the interaction networks may suggest new keystone species roles. The structure of these new food webs and their relative function could be validated with space-for-time substitution by examining how specific ecosystems change across gradients in environmental conditions (McCann & Rooney 2009). Linking these observed changes to mechanistic process-based models derived from bioenergetics and network theory may serve as a powerful tool to project and anticipate future ecosystems and how they might differ in structure and function from their historical counterparts.

## 7. OPEN RESEARCH QUESTIONS

The last decade has witnessed a dramatic improvement in our understanding of climate-driven marine range shifts, but in many ways, this research has raised more new questions than it has answered. Here, we highlight knowledge gaps related to demographic mechanisms, species traits, rapid evolution, and the future of marine biodiversity.

A fundamental challenge in research on shifting marine species ranges is to understand the demographic mechanisms that create these shifts. Most research attention so far has been focused on why species are shifting, with attempts to identify the environmental changes responsible and develop appropriate methods for doing so. However, what is the relative importance of larval dispersal, adult movement, or changes in survival, reproduction, or other rates in driving the colonization patterns observed so far? What is the relative importance of adult emigration, increased mortality, or reduced reproduction in driving observed range contractions? For some species, the mechanisms are highly constrained. Larval dispersal, for example, must be the large-scale movement mechanism for sessile species, such as corals. The geographic ranges of large pelagic species like tunas, by contrast, are defined largely by adult movement and migration paths. For a wide range of species, however, both larval dispersal and adult movement are possible explanations. In addition, many of the apparently observed colonization events could represent the growth of a previously unrecognized population rather than an actual colonization, as was discovered for anchovy in the North Sea (Petitgas et al. 2012). If larval dispersal is the dominant mechanism, then colonization requires the growth and maturation of settled juveniles. If adult movement is the dominant mechanism, then questions of habitat connectivity, sensory environments, and movement ecology become highly relevant. Similarly, range contraction is a behavioral question if driven by adult movement but a demographic process if mortality and reproduction are dominant. Trade-offs among mechanisms may also exist, such as between evolution and colonization: Large-bodied organisms tend to have long generation times (and slow evolution) but greater adult dispersal abilities. Research on the mechanisms of colonization and extirpation would also create a strong foundation for understanding how other demographic processes, such as interactions among species, contribute to or constrain species range shifts. Uncovering the relevant demographic mechanisms will require new research, such as the use of electronic tags to observe adult

movement or the use of genetics and otolith chemistry to reconstruct larval dispersal pathways. New statistical methods to fit mechanistic models to observational data also have promise for testing alternative hypothesized mechanisms (Zurell et al. 2016).

Detecting shifts in marine species distributions and understanding the relative importance of alternative underlying mechanisms are reliant on long-term and consistent monitoring across large spatial, taxonomic, and temporal scales. At the moment, such monitoring efforts are concentrated in temperate zones, the Atlantic Ocean, and wealthier countries (Poloczanska et al. 2016, Wiens 2016) (**Figure 1**), constraining our understanding in particular of tropical responses to climate change, where, for example, evolution may be of relatively greater importance (Norberg et al. 2012). The development and use of novel observing technologies can likely help expand our ability to detect shifts, including environmental DNA, acoustics, citizen science, and paleorecords (Edgar et al. 2016, Gibb et al. 2019, Jonkers et al. 2019, Pikitch 2018), though the continuation of existing programs will also be exceptionally important.

As case studies of marine range shifts accumulate, a challenge becomes to understand why rates, magnitudes, and patterns are similar or different among species. In this context, a trait-based approach is useful because it generalizes beyond individual species to characteristics that can be measured on any species in any part of the world. Despite challenges in identifying range shift-related traits (Angert et al. 2011), linking traits to specific demographic mechanisms like range extension or range contraction is likely to be more productive than focusing on aggregate patterns like shifts in range centroids (**Figures 1** and **4**). Traits can also help inform mechanistic models. While trait databases are reasonably complete for marine fishes, those for invertebrates other than corals are generally poor, and greater attention to these species will likely prove productive for research.

Another key area for future research will be whether and (if so) to what extent rapid evolution contributes to or constrains colonization and extirpation. The quickly falling cost and effort for whole- or subgenome DNA sequencing makes research on rapid evolution possible in a way that it has not been to date. The extensive stores of otolith, scale, and other tissue samples from marine species (though biased toward commercially valuable species) make it possible to track allele frequencies through time and directly test for natural selection across the genome (Holmes et al. 2016). Ongoing research challenges are to make the link all the way from genetic change to phenotypic change to environmental change, or, alternatively, to show that climate-induced phenotypic change has been genetic rather than the result of phenotypic plasticity (Merilä & Hendry 2014).

With observed range shifts across so many species and geographic locations, colonization and extirpation appear to be key mechanisms by which marine species cope with a changing climate (**Figure 1**). But for how many species and for which species will colonization of new habitat be insufficient to avoid extinction? Predictions of extinction rates on land are substantial and increase with rising temperatures to more than 15% of all taxa under high greenhouse gas emissions scenarios, but the only estimates available for marine species are regional and apply to relatively few species (Urban 2015). The high dispersal rates of marine species might suggest less extinction in the ocean as species shift poleward, except for polar species that have nowhere else to go. Massive extinctions of marine life in the geological record are associated with large changes in temperature and oxygen. Are we facing a future of massive species loss in the ocean, or a future of relatively little extinction? While predicting the future is inherently difficult, the lack of global estimates of climate-driven marine extinctions is nonetheless surprising. Further efforts to integrate oceanographic projections with an understanding of marine food webs, species environmental tolerances, and dispersal abilities are needed to make progress on this challenging yet important problem.

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**Range centroid:**

the middle of a species range, often calculated as the geographic center of biomass or abundance

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## SUMMARY POINTS

1. A wide range of marine species are colonizing new territory and also being extirpated from historical locations as their environments change.
2. Marine species are more sensitive to changing climate but have greater colonization abilities than do many species on land, and shifts in species distribution in the ocean are generally occurring faster and more frequently than has been observed on land.
3. Shifts in distribution restructure marine communities, including food webs, but food web properties are often more stable than species identities.
4. Distinct ecological and evolutionary processes operate at leading and trailing edges of species distributions, shaping the transient dynamics at each edge and the variation in rates among species.
5. Future shifts in species distributions of 50–100 km/decade are projected in many cases, and impacts on marine communities are likely to be dramatic.

## FUTURE ISSUES

1. An ongoing challenge is to understand the relative importance of different demographic mechanisms and factors that create shifts in species distributions, including larval dispersal, adult movement, survival, reproduction, predators, prey, and competitors.
2. Both direct effects of the environment (including temperature and oxygen) on organismal function and indirect effects mediated through species interactions can be important in driving shifts in distribution, but we still lack a mechanistic understanding of the effects and their relative importance for the vast majority of marine species.
3. To understand how range shifts vary across species and how unstudied species are likely to respond, greater efforts to link colonization and extirpation dynamics to species traits rather than species identities will be helpful.
4. Likewise, using traits to infer future species interactions is likely to be a fruitful approach to making predictions about the structure and function of novel ecosystems created by differential range shifts of interacting species.
5. While evolution can be important for colonization and extirpation, we lack a strong understanding of the role it has already played or will play in the future. Both genomic and experimental approaches are likely to be helpful.
6. With the rate of ocean warming now accelerating, we still understand little about what ongoing climate change will mean for global rates of extinction among marine species, though the geological record suggests that rates may be high.
7. To enable future research and to inform conservation and management efforts, the continuation of existing biogeographic monitoring programs and expansion into new regions—particularly the tropics—through new programs or new technologies is especially important.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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