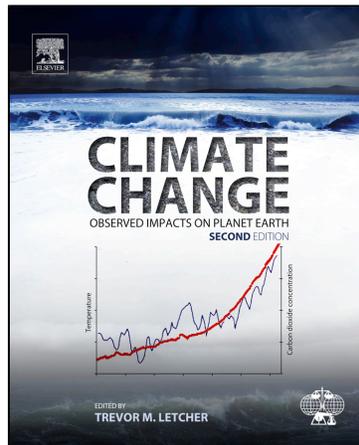


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MARINE BIODIVERSITY AND CLIMATE CHANGE

13

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1. INTRODUCTION

Our planet has a number of features that make it unique, namely the presence of large oceans and the evolution of life forms therein. Biodiversity, commonly defined as the variability among living organisms [1], likely originated in the oceans, and most of the larger taxonomic groups still reside there today. Over evolutionary timescales, there have been massive changes to the ocean's biodiversity, including several mass extinctions [2–4] that have shaped the diversity of life over millions of years [5,6]. Some, if not most, of these events are thought to correlate with large-scale climate change that perturbed ocean temperature, circulation, chemistry and productivity [6,7]. In general, observed patterns of biodiversity change are increasingly being understood in relation to variation in temperature, both over time [8] and space [9].

Today, we are living through another episode of rapid climate change [10], which is causing global changes in weather patterns, temperature and ice cover [11,12] that affect the sea level, thermal stratification regime, ocean circulation patterns and productivity [13–19]. Most attempts to trace the ecological effects of climate change, whether on land or in the sea, have concentrated on individual species [20–23], as discussed elsewhere in this volume. It is only quite recently that community metrics such as species composition and diversity have been studied in direct relation to climate change [24–29]. Here we attempt to summarize this emerging literature, to detect common patterns in the effects of climate change on marine biodiversity. Biodiversity has three main components: diversity contained within species, between species, and of ecosystems or habitats [1]. We will discuss

changes in all three components, but note that studies to date have mostly focused on species diversity, namely patterns and changes in species richness (the number of species in a given area), likely because it represents the most easily quantifiable aspect of biodiversity.

Despite its taxonomic prominence, marine biodiversity is sometimes overlooked in the climate change discussion, undoubtedly because much of it is less understood than its terrestrial counterpart. Yet, marine biodiversity needs to be accounted for, not just because of its different taxonomic composition and large geographic extent (oceans comprise >70% of the planet's surface and >90% of the living biosphere by volume), but also as it provides important ecosystem goods and services such as fishery yields, shoreline protection, carbon and nutrient cycling, climate regulation, among others [30–33]. The ocean's biodiversity should therefore be carefully studied in order to understand and project how it will change with climate change and what the consequences may be for human well-being [6,32,34,35].

In this chapter, we first discuss both observed and predicted changes in biodiversity at various scales and how they relate directly to warming and other climate-related factors. Then we outline some indirect effects of climate change that arise from complex interactions with biotic and abiotic factors, and the cumulative effects of climate and other global changes. Finally, we highlight the importance of biodiversity for maintaining ecosystem resilience in the face of climate change. We do not pretend to give a complete overview but instead discuss some prominent patterns by example, largely focusing on the effects of increasing temperature. Herein we shall focus on documented changes from the published literature and highlight how these effects are projected to develop into the future. The primary question we are asking is whether diversity, here defined as the number of genotypes, species or habitats in a location, changes in some predictable way with climate change. A secondary question is how climate effects on marine biodiversity are modified by and interact with other, co-occurring aspects of global change.

2. CLIMATE CHANGE IN THE OCEANS

Climate change has a range of effects on the abiotic marine environment, which are documented in detail elsewhere in this volume. From a biodiversity perspective, the prominent physical changes include ocean warming [11,36,37], increased climatic variability leading to more frequent extreme events [38,39] and changes in sea level, sea ice extent, thermal stratification and ocean circulation [13,40,41]. In addition, both warming and altered ocean circulation act to reduce subsurface oxygen (O₂) concentrations [42]. Carbon dioxide emissions, which in large part drive anthropogenic climate change, also cause ocean acidification (see Chapter 18, this volume for details). All of these processes can act on biodiversity directly (for example when local temperature exceeds individual species' physiological tolerances) or indirectly (for example by altering habitat availability, species interactions, or productivity). Furthermore, potentially complex interactions between climate change and other aspects of global change, notably those due to fishing, eutrophication, habitat destruction, invasions and disease can be important [40,43–46] and are briefly highlighted in this review. This latter point suggests an important difference between the current and previous episodes of climate change in Earth's history – recent changes in climate are superimposed on other stressors that have already compromised biodiversity in many places [6,30]. From a scientific perspective, this added complexity can make it more difficult to clearly attribute observed changes in diversity to a single factor. From a

conservation perspective, the loss of biodiversity already diminishes adaptive capacity and diversity of biotic responses to climate change [47].

3. EFFECTS OF CLIMATE CHANGE ON MARINE BIODIVERSITY

What are the recently observed changes in biodiversity, and how do they relate to climate? In the following Sections 3.1–3.3, we first review evidence for the effects of climate warming that are emerging at increasing scales, from local (<10 km) to regional (10 km–1000 km) and global (>1000 km), respectively. In Section 3.4, we discuss factors other than changes in temperature. Observed effects are summarized in Table 1.

Cause	Effect	Net effect on diversity	Selected references
Temperature increase (tropical regions)	Local extinction of heat-sensitive species;	↓	[28,72,86]
	Coral bleaching and associated habitat change	↓	[53,54,57,137]
Temperature increase (temperate regions)	Warm-adapted species replace cold-adapted ones	↑	[26,49,69,71,77]
	Shifts of some habitat-forming species poleward and deeper	↓	[52,68,122]
Temperature increase (polar regions)	Invasion of subpolar species	↑	[64,66,67]
	Decline of endemics and sea ice dependents	↓	[60–63,66]
Increased climate variability (heat waves, storms)	Increased rates of disturbance	↓	[111,112]
Increased upwelling intensity	Mid-water hypoxia	↓	[106–108]
Increasing water column stratification	Lower nutrient supply and productivity	?	[13,16,17,110]
Sea level rise	Erosion of coastal habitats	↓	[115]
Changes in ocean circulation	Changes in larval transport	?	[138]

3.1 LOCAL SCALE

Changes in biodiversity at the local scale are often driven by the interplay of local and regional abiotic and biotic factors. The effects of a regional change in sea surface temperature (SST), for example, may be mediated or exacerbated by local factors such as wave exposure, tidal mixing, upwelling, and species composition. Nevertheless, some common patterns have been observed.

In temperate locations, slow changes in species composition often lead to an overall net increase in species richness. This was first shown by Southward and colleagues in their classic long-term studies in the English Channel [48]. Both intertidal and pelagic communities changed predictably during periods of climate warming, with warm-adapted species increasing in abundance and cold-adapted species decreasing, leading to overall increases in diversity. Reverse patterns were observed during periods of cooling [48]. Similar changes occurred in the northwest Pacific (Monterey Bay, California) where eight of nine southern species of intertidal invertebrates increased between the 1930s and 1990s, while five out of eight northern species decreased [49]. This change tracked observed increases in both mean and maximum temperature and led to an overall increase in invertebrate species richness by 7%, due to three species newly invading from the south [49]. A similar pattern was documented for a temperate reef fish community in southern California [50]. In this case, however, sudden warming in the 1970s also led to a decline in productivity, 80% loss of large zooplankton biomass and recruitment failure of many reef fish. This may explain why total biomass declined significantly, and total species richness also declined by 15%–25% at the two study sites [50]. These two contrasting examples illustrate that predictions based on temperature alone can be misleading, if concomitant changes in productivity or other overriding factors are involved. Moreover, it has been shown that local differences in tidal exposure rendered some northern sites more thermally stressful than southern sites, counteracting the poleward shift of southern species discussed above and possibly causing localized extinctions [51]. In addition to latitudinal shifts, species may also move into deeper, colder waters, as observed for example in fish [29] and seaweeds [52].

In tropical locations, warming can lead to species loss and a decline in diversity, as maximum temperature tolerances are exceeded. So far, this has been particularly documented in tropical coral reefs that are affected by bleaching events (reviewed for example by Refs [45,53,54] and in Chapter 13 of this volume). Poised near their upper thermal limits, coral reefs have experienced mass bleaching where sea temperatures have exceeded long-term summer averages by more than 1°C for several weeks [53,55]. The loss of sensitive coral species causes secondary changes of reef-associated fauna and flora [56]. For reef fish specifically, available studies so far indicate large changes in species composition after bleaching events, and a decline in species diversity that is linearly related to disturbance intensity [57] (see Ref. [58] for an exception).

Polar marine ecosystems are also thought to be particularly sensitive to climate change. In some parts of the Arctic and Antarctic atmospheric temperatures are rising at rates more than double the global average, and sea ice extent is shrinking rapidly, particularly in the Arctic [10]. Partly spurred by warmer climate and more open waters, there are other growing human impacts on polar regions such as pollution, exploitation and development. Therefore, the rate of change in species abundances and composition can be rapid [59]. While sea ice–dependent species such as polar bears [60], krill [61] and some penguins [62,63] have sharply decreased in abundance at some locations, there are signs of increasing invasion of subpolar and ice-independent species in other places [62]. For example, killer whale (*Orcinus orca*) sightings are increasingly almost exponentially in the Canadian Arctic, as sea ice retreats [64]. As these powerful consumers can set off trophic cascades [65], the resulting changes to the food web could be complex. However, only a few observations on net changes in species richness are available so far [66]; for example, surveys of Arctic macrobenthos suggest slow increases in species numbers at sites that are accessible to larval advection from southern locations [67]. Large uncertainties remain due in part to low sampling effort [66], and in part due to the complexity of this highly seasonal environment and the compounding effect of changes in sea ice, salinity, stratification, runoff and acidity [59].

3.2 REGIONAL SCALE

A growing number of studies have examined changes in species composition and diversity at regional scales. Much of this work was conducted using fisheries or plankton monitoring data, but recent work has extended to other species groups, such as seaweeds [68]. Again, a dominant observation is the replacement of cold-adapted by warm-adapted species. This appears to occur simultaneously at various levels in the food web, for example in North Atlantic zooplankton [69,70], as well as fish communities [27,71]. These changes are not necessarily synchronized; Beaugrand and colleagues documented a growing mismatch between warming-related changes in North Sea zooplankton communities since the 1980s and the emergence of cod larvae and juveniles. Cod populations were directly affected by changes in temperature but also indirectly by changes in their planktonic prey that compromised growth and survival of cod larvae. Perry et al. observed that larger species with slower life histories (such as cod) adapted their range much more slowly to changing conditions compared to fast-growing species [71]. This finding has implications for fisheries, as species with slower life histories are already more vulnerable to overexploitation [72] and may also be less able to compensate for warming through rapid demographic responses. Constraints to range shifts, however, appear to be less important than on the land. In the North Sea, the average rate of northward change was 2.2 km a^{-1} (where 'a' refers to annum), which is more than three times faster than observed range shifts in terrestrial environments, which reportedly average 0.6 km a^{-1} [21]. Likewise, a meta-analysis of species range shifts showed that marine species fill their thermal niches more fully and move more readily at both cold and warm range boundaries compared to terrestrial species [73]. These findings may not be surprising, given the absence of hard physical boundaries in marine, and particularly pelagic, environments.

The net effect of such temperature-induced compositional changes on species richness can be surprisingly large – an almost 50% increase in the number of species recorded per year in North Sea bottom trawl surveys was documented between 1985 and 2006 [26]. This change correlated tightly with increasing water temperatures [26]. Similar trends have been found in the Bristol Channel, UK, where fish species richness increased by 39% from 1982 to 1998 [74]. In both cases, increases in richness were mainly driven by invasion of small-bodied southern species. It is noteworthy that similar regional changes have been observed nearby on land, where the species richness of British butterflies [25] and epiphytic lichen in the Netherlands [75] have increased with warming over time.

Such decadal changes in species richness and diversity are superimposed on significant year-to-year variation in temperature and other climatic factors. For example, in the NW Atlantic there is a well-documented latitudinal gradient in fish species richness that covaries with temperature [76]. This latitudinal gradient in diversity was previously treated as static. Recently it has been shown how temperature variability readjusts diversity gradients year by year [77]. Temperature variability is linked to large-scale pressure differences across the North Atlantic, known as the North Atlantic Oscillation (NAO) [78]. Positive NAO anomalies cause temperature gradients in the NW Atlantic to steepen, which leads to rapid adjustments in species diversity – northern areas decline and southern areas increase in diversity [77]. During NAO-negative years, the gradients flattens – northern areas increase and southern areas decrease in diversity. Although the north-south trend of increasing fish diversity does not reverse, there are substantial differences in its slope. This dynamic pattern is mostly driven by expansions and contractions of species at their northern or southern range limits [77]. Again, warming waters increase overall diversity in temperate regions; cooling waters have the opposite effect.

Similar mechanisms have been shown to affect pelagic fish diversity across the tropical to temperate Pacific Ocean. Here, pressure differences in the central Pacific lead to periodic warming and cooling of surface waters in the eastern tropical Pacific, the well-known El Niño Southern Oscillation (ENSO) that affects weather patterns around the planet [79]. Positive ENSO years are characterized by regional warming of the eastern tropical Pacific and an increase in species diversity in the following year [24]. Regional cooling leads to decreases in diversity. Single species such as blue marlin [24] or skipjack tuna [80] appear to readjust their distribution year by year in response to these temperature changes. These studies show how species diversity not only serves as an indicator of long-term climate change but accurately tracks short-term variability in climate as well. A caveat for many fish populations is of course that intense exploitation can override climate signals on diversity. For example, in the Atlantic and Indian Oceans there has been a long-term decline in tuna and billfish species richness, which is most likely explained by fishing [24]. In the Pacific, however, a similar decline is counteracted by increasing warming after 1977 [24].

In contrast to marine fish, plankton communities are not affected by exploitation, except maybe indirectly through trophic cascades [81]. For both phyto- and zooplankton phenological changes (for example the timing of the spring bloom), range shifts and changes in species composition have been shown to track changes in climate quite well [14,69,82]. For example, long-term Continuous Plankton Recorder data in central and European waters show that zooplankton communities there are gradually shifting away from cold-temperate and subarctic species to more species-rich warm-temperate and mixed assemblages [69]. Thus plankton communities are increasingly used as indicators of recent climate change [82].

Another approach used for macroalgae entailed the compilation of >20 000 herbarium records collected in Australia since the 1940s [68]. The study shows shifts in species distribution along both the coasts of the Indian and Pacific oceans consistent with rapid warming over the past five decades. If these waters continue to warm, hundreds of species could be pushed out of suitable habitats along the Australian coastline, with no place further south to go. These species (and others that depend on particular seaweed habitats) could face regional or even global extinction [68].

Recently, regional climate change has been discussed in the context of climate velocity, which is defined as the speed and direction of climate change across the landscape [83]. The advantage of this concept is that it tracks the spatial dimension of climate change and appears to predict very well the observed movements of surveyed fish populations around North America [29]. Interestingly, there was much variability in species responses in this region, with many populations moving northward but others tracking in the opposite direction, moving deeper, or further offshore. Climate velocity, however, was able to capture much of this variation and explained the recent shift in the distribution of individual species and entire communities better than individual species characteristics [29].

3.3 GLOBAL SCALE

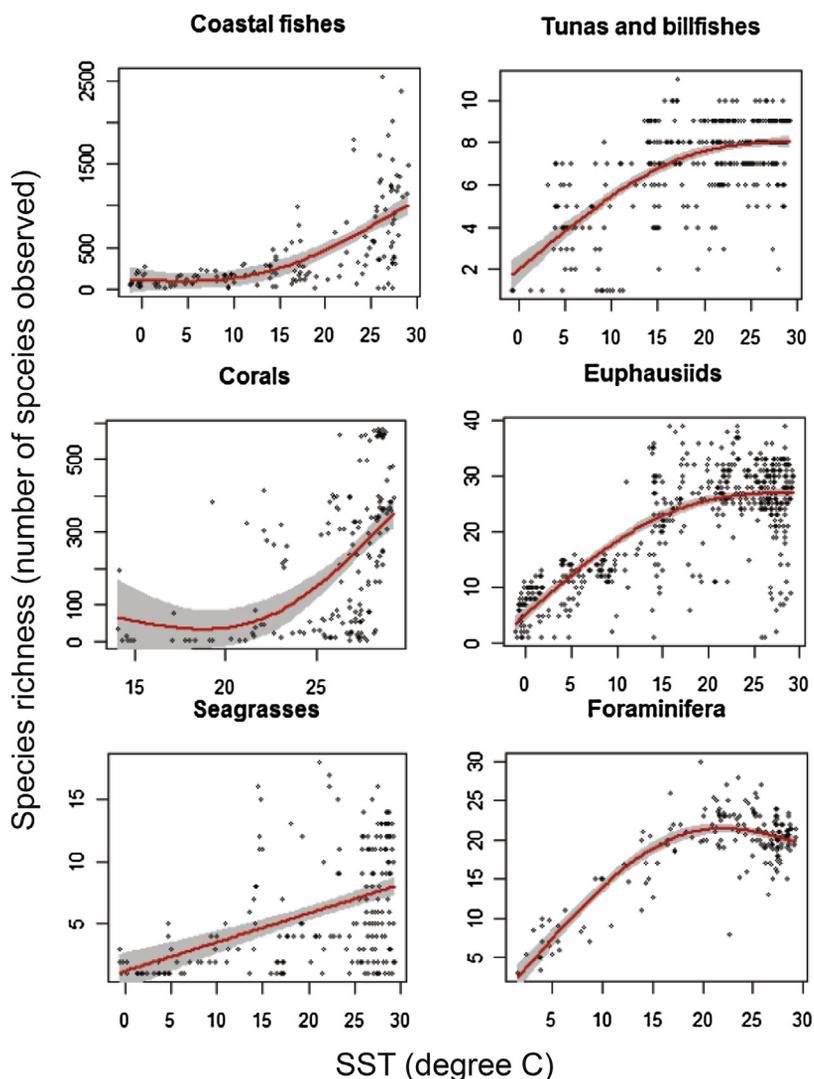
There are a growing number of global-scale studies analyzing the effects of global climate variability and change on marine biodiversity. The argument has been made on land, albeit controversially, that a large number of extinctions could be caused by climate change by compressing species thermal habitats, particularly for species of restricted ranges [84]. Whether to expect global marine extinctions due to climate change is yet unclear, although much concern is focusing on coral reefs that are simultaneously threatened by warming and acidifying waters [45,85]. Dulvy and co-workers [72] note

the possible global extinction of two coral species due to bleaching (*Siderastrea glynni*, *Millepora boschmai*), both of which have limited geographic ranges in the Eastern Pacific. Another study calculates that one-third of reef-building corals are faced with elevated extinction risk from climate change and other impacts [86]. Some coral-associated fish have also disappeared over the course of recent bleaching events [72]. Other habitat-forming species, such as sea grasses, mangroves and some seaweeds, also face elevated extinction risk due to warming and sea level rise [52,87,88], with consequences for communities dependent on these habitats.

Harnik et al. have more broadly compared the patterns and drivers of extinction across both the fossil record and the recent Anthropocene [6]. They found a fundamental difference in drivers of extinction, with climatic changes, perturbations in ocean chemistry, acidity and oxygen content explaining most marine extinctions across the fossil record, while combinations of human-driven overharvesting, habitat loss and pollution tended to explain more recent (last 400 years) extinctions. The authors speculated, however, that climate change is poised to recreate some of the conditions that led to previous mass extinctions, and hence may again become a dominant driver of extinction in the future, in combination with other cumulative stressors [6].

Although the question of projected extinctions due to climate change is contentious [89,90], there is little doubt that temperature is a major driver of marine diversity at the global scale. Global diversity patterns have so far been synthesized for 13 major taxa ranging from zooplankton to whales [9]. Two fundamental patterns emerged. For coastal species such as corals, sea grasses, coastal fish, among others, global reef diversity peaked at tropical latitudes in the Western Pacific [91], with a secondary hotspot in the Caribbean [9]. Pelagic plankton, fish and mammals, however, all peaked at intermediate latitudes, around 20°–30° North or South [24,92–94]. These patterns were most parsimoniously explained by spatial variation in sea surface temperature, which explained 45%–90% of the variation in species diversity for these groups (Fig. 1, showing examples of 6 out of 13 taxa analyzed). As mentioned above, variation in sea surface temperature well explains not just the broad spatial patterns but also much of the interannual variation in tuna and billfish richness in the Pacific [24] as well as seasonal variation in cetacean diversity in the Atlantic [94]. Moreover, the global richness pattern of tuna and billfish could be independently reconstructed from individual species' temperature tolerances [95]. Thus, it appears that temperature might be a powerful and general predictor of species richness at global scales. A prominent ecological theory supports this observation: the metabolic theory of ecology [96] predicts well-known relationships between body size, temperature and metabolic rate, which also correlates with the rate of mutation and speciation across long time horizons [97,98]. Taken together, these processes may explain higher diversity in the tropics but fail to account for the different pattern of diversity in pelagic species.

The empirical relationships between SST, species distributions and species richness can be used to derive hypotheses about the potential effects of future warming on species richness. For example, deep-water cetaceans show a unimodal relationship with SST, which under future warming scenarios projects substantial diversity increases at high latitudes but decreases in the tropical ocean [94]. This prediction was verified by a more detailed species-by-species habitat model that tracks preferences for temperature, sea ice and depth across all species of marine mammals to predict a synthetic diversity pattern [99]. In a warming ocean, the highest latitudes increased dramatically in species richness, but tropical locations showed fewer marine mammal species. Substantial turnover in species composition was predicted for temperate locations, but the effect on net richness remained small.

**FIGURE 1**

Temperature is a dominant environmental predictor of marine biodiversity. Shown are relationships as richness for six species with global coverage plotted against sea surface temperature (SST/°C). Species richness is the number of species present per grid cell across a global 880 × 880 km equal-area grid. (Redrawn from data in Ref. [9] with permission.)

These patterns for mammals broadly agree with similar predictions for 1066 exploited fishes and invertebrates, which were also modelled in relation to their temperature, salinity, depth and sea ice preferences, as well as their association with habitat features such as coastal upwelling, coral reef,

estuaries and seamounts [28,100]. The authors mapped predicted changes in species invasions (Fig. 2(a)), extinctions (Fig. 2(b)) and turnover (Fig. 2(c)) across the world oceans. Invasions and turnover of species composition were predicted to occur particularly frequently at high latitudes, and

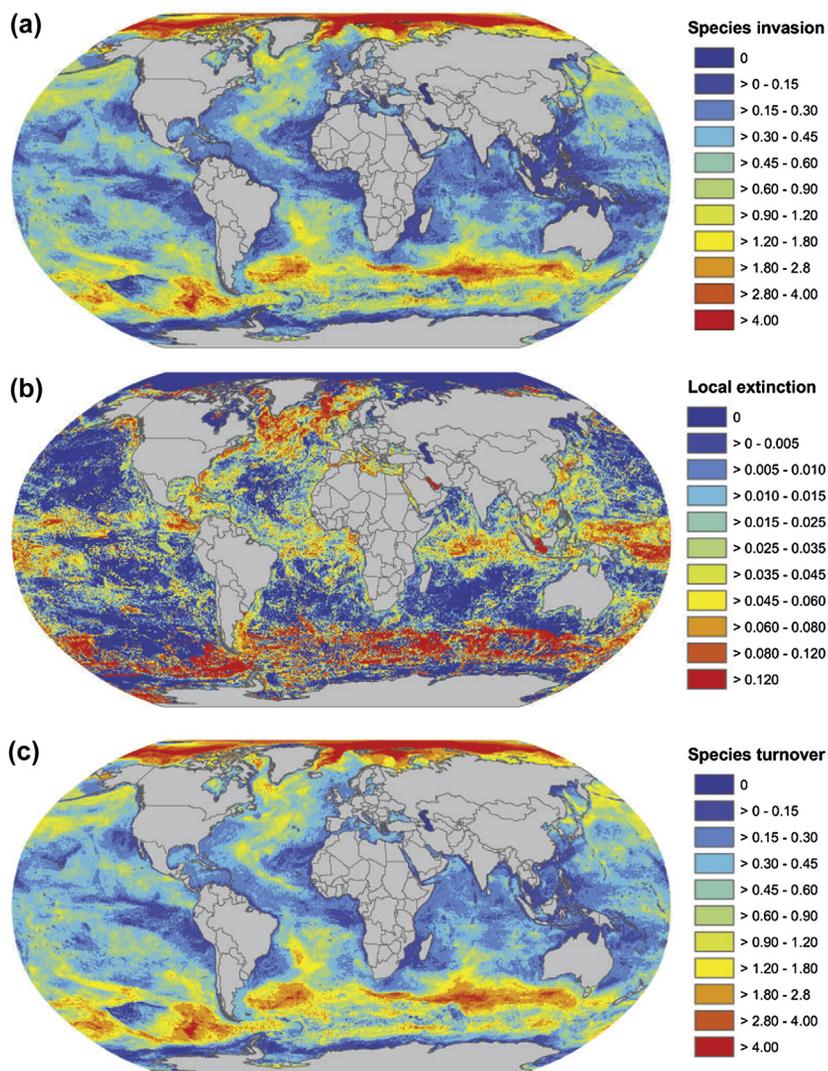


FIGURE 2

Predicted impact of ocean warming on biodiversity of 1066 species of fish and invertebrates. Predicted changes are expressed in terms of: (a) invasion intensity; (b) local extinction intensity; and (c) species turnover in 2050 relative to the mean of 2001–2005 (high-range climate change scenario). Intensity is expressed proportional to the initial species richness in each $0.5^\circ \times 0.5^\circ$ cell. (Reprinted with permission from Ref. [28].)

extinctions were especially common in the tropics, the North Atlantic and the Southern Ocean. Again, net loss of species richness was most commonly predicted at tropical latitudes.

Finally, a global modelling study of plankton communities again reached similar conclusions, with large predicted losses of diversity in warm waters (assuming the lack of a rapid evolutionary response) and gains at high latitudes [101]. It is striking how plankton, fish and whales show similar current patterns in diversity relating to global temperature fields [9], and also similar predicted responses to climate change.

So far, most of these projections exclude the possibility of significant evolutionary change or other adaptive changes altering temperature or other habitats preferences for species faced with significant warming. Yet, the evidence for both short-term acclimatory and longer-term adaptive acquisition of climate resistance is mounting, for example in corals [102] and phytoplankton [103].

3.4 OTHER FACTORS RELATING TO CLIMATE CHANGE

In addition to the strong observed and predicted effects of temperature on biodiversity, there are clearly other factors that are important in influencing diversity on local, regional and global scales. For tuna and billfish, for example, the availability of thermal fronts that act to concentrate food supply is of great importance, as is the availability of sufficient oxygen concentrations ($>2 \text{ mL L}^{-1}$ at 100 m depth) [24,104]. Many marine animals may also concentrate in areas of high productivity [93], and export productivity appears to be a major correlate of deep-sea species richness [105]. However, all of these factors (fronts, oxygen, surface-ocean and export productivity) are both directly and indirectly affected by climate change (Table 1). For example, increased variability in wind stress has been shown to affect the intensity of upwelling, leading to periodic hypoxia and death of marine organisms [106–108]. Furthermore, climate change is implicated in the observed shallowing of oxygen minimum zones in the tropical ocean [109], which is likely compromising local biodiversity at intermediate depths. Surface-ocean biomass and productivity is also affected by global warming, particularly through increased stratification and lower nutrient supply to the photic zone [13,14,16,18,19]. This will most likely have direct effects on surface diversity [82,101] but also indirect effects on deep sea ecosystems that are extremely food limited and depend almost entirely on export production [110].

Even in the absence of directional trends in mean climate variables, increasing climate variability can affect biodiversity through extreme events, such as intense storms or heat waves, which can lead to large-scale die-offs such as in shallow-water corals or sea grass meadows [53,54,111,112]. Particularly when habitat-forming species such as sea grasses and corals are affected, such events can lead to substantial changes in local diversity, including genetic, species and habitat diversity, at least on short to intermediate timescales. Similarly, ocean acidification is occurring as a direct consequence of increasing CO_2 emissions, independent of trends in other climate variables. Observations at naturally acidified sites [113] as well as experiments [114] so far suggest that acidification forces substantive shifts in community composition but not necessarily large reductions in the number of species.

Finally, climate change leads to sea level rise (Chapter 16, this volume) and changes in ocean circulation (Chapter 17, this volume). Sea level rise in concert with increasing climate variability and more frequent storms can lead to increasing coastal erosion and the loss of coastal habitats (Chapter 20, this volume), which may affect the diversity of coastal species that depend on wetlands, salt marshes or mangroves [87,115]. Shorelines are increasingly fortified against rising water levels thereby preventing

the adaptive inland movement of wetlands and upward movement of intertidal habitats, which decline or disappear over time together with their associated flora and fauna [52,115]. Further away from the coastlines, ocean circulation patterns can be sensitive to changes in temperature, precipitation, runoff, salinity and wind. So far, the effects of changing circulation and currents on ocean diversity have not been studied in any detail, with the exception of upwelling studies mentioned above [106–108].

We conclude that climate change leads to a range of physical changes, many of which are known to have effects on species diversity not directly mediated by changes in temperature. These effects may further interact with other aspects of global change that are unrelated to climate. Such complexities are discussed in more detail below.

4. CUMULATIVE IMPACTS AND INDIRECT EFFECTS OF CLIMATE CHANGE

A major challenge in ecological research is the disentanglement of multiple factors that are driving ecological change [46]. Up to this point we have reviewed the direct effects of increasing temperature and climate variability, and resulting changes in upwelling, stratification, sea level, oxygen and currents (Table 1). In reality, however, these processes are likely interacting with other impacts on biodiversity, such as exploitation, eutrophication, disease, and physical disturbance, among others. Species composition and abundance are also influenced to a large degree by local species interactions, such as predation, competition and facilitation. Through changing species interactions, and by interacting with other drivers, climate change can have a number of indirect effects that are sometimes surprising and difficult to predict. Here we highlight such indirect effects, giving some well-documented examples for illustration.

Consider the classic example of a keystone predator, the starfish *Pisaster ochraceus*, which maintains intertidal diversity by feeding on competitively dominant mussels *Mytilus californianus* [116]. This interaction, however, is temperature dependent – increases in upwelling lead to colder waters, lower predation rates and higher mussel cover [117]. Therefore, possible effects of climate change on diversity are mediated by a strong interaction between a predator and a competitively dominant prey.

Another well-documented complexity concerns the interaction between warming temperatures and disease. There is good evidence that climate warming can increase pathogen development and survival, disease transmission and host susceptibility [44,118]. This has become evident both in the sea and on land following large-scale warming events associated with ENSO, which are implicated in several coral diseases, oyster pathogens, crop pathogens, Rift Valley fever and human cholera [44,118]. These effects occurred both in tropical and temperate locations, with some documented range shifts of pathogens toward higher latitudes. In some cases, such temperature-mediated disease outbreaks may contribute to observed shifts in the latitudinal distribution of species. The range centroid of American lobster, for example, has shifted northward by about 2° latitude since 1970 [29]. In all likelihood, this is not caused by the northward migration of individuals but by a shifting balance of growth and mortality at the fringes of the present range. In the case of lobster populations, both paramoebic [119] and fungal diseases [120] have recently contributed to the collapse of populations at the southern range limit, and may be moving north, as temperatures continue to warm.

Climate change can also affect the interaction between our own species and marine biodiversity. Over the past two centuries humans have already had a marked impact on marine biodiversity, including a number of local, regional and global extinctions [6,72]. To date, exploitation and habitat

destruction have probably had the most severe effects [121]. The existing rate of coastal habitat destruction will likely be accelerated by climate-driven losses due to warming, sea level rise, acidification and bleaching [45,87,88,115,122]. Similarly, the effects of exploitation are likely exacerbated by climate change. This is because most fisheries effectively truncate the age structure and size structure of target fish, by preferentially removing larger, older individuals. The fishery then becomes increasingly dependent on the recruitment of new individuals into the fishery. Recruitment however is strongly affected by climate variability [123] and change [124]. Removing the older age classes increases susceptibility both of the stock and the fishery to climatically induced fluctuations [34]. In addition, documented changes in temperature and plankton concentration have already affected the capacity of major fish stocks to produce new recruits [124]. Reducing fishing mortality and rebuilding spawning stock biomass may be the only feasible means of mitigating the impacts of climate change on recruitment [34,124,125].

Taken together, these results have implications for priority setting in global conservation initiatives. Tropical regions are predicted and observed to suffer most from species loss due to climate change, while often lacking resources and capacity for mitigation and adaptation [126]. At the same time, these regions are hotspots of fisheries-induced pressures, coincident with low management capacity [127]. Four out of five global fisheries–conservation hotspots identified in a recent meta-analysis [127] coincide with areas of high predicted extinction intensity to climate change (Fig. 2), namely the Red Sea, Canary Current, Gulf of California and Indonesian Sea large marine ecosystems. The combination of multiple and intensifying threats, low capacity to meet these threats and high reliance of coastal populations on seafood and other marine goods and services motivate a strong management and conservation focus on tropical developing countries. Polar ecosystems also range high on the priority list due to the extraordinary rapid rate of change observed there, the possible extinction of polar specialist and ice-dependent species, and the growing pressures from development [59].

5. BIODIVERSITY AS INSURANCE AGAINST CLIMATE CHANGE IMPACTS

There is now good evidence that in addition to being a response variable to changes in temperature and climate, biodiversity may also provide resilience against climate change. This is because high genetic, species and habitat variation enhance the diversity of possible responses and adaptive capacity in the face of environmental variation [47,128,129]. For example, in a study on sea grass loss after the 2003 European heat wave, high genetic diversity (manipulated experimentally) led to faster recovery of damaged habitat [111]. This was driven both by selection of heat-adapted genotypes and by some form of facilitation that led to increased survival [111]. This observation was verified by laboratory experiments that manipulated temperature and genetic diversity in a controlled environment [112]. Another field study documented that high genetic diversity in sea grass also increased resilience to physical disturbance from overgrazing [130]. Theoretical studies have come to similar conclusions. For example, Yachi and Loreau [131] showed two major insurance effects of species richness on ecosystem productivity: (1) a reduction in the temporal variance of productivity, and (2) an increase in the temporal mean of productivity despite stochastic disturbances.

From these mechanistic studies follows the prediction that a loss in biodiversity should lead to a loss in productivity and resilience, which could magnify any effect of climate change (or other disturbances) on marine systems. An increase in biodiversity should have the opposite effect.

Broad evidence in support of this prediction comes from a series of meta-analyses examining local experiments, regional time series and global fisheries data [32]. The vulnerability to climate change in particular was examined by regional studies of Alaskan salmon fisheries that have been carefully managed to avoid loss of stock diversity [129,132]. These stock complexes show a remarkable resilience to climatic change due to a large number of local life-history adaptations that are preserved within the stock complex. As environmental conditions changed, overall productivity was maintained by different sub-stocks that were adapted to thrive under those conditions [132]. This 'portfolio effect', which is analogous to the effects of asset diversity on the stability of financial portfolios, was recognized as an important insurance against climate-driven fluctuation in exploited fish stocks [129]. Maintaining population, species and habitat diversity is now generally seen to be of critical importance in stabilizing ecosystem services in a variable and changing world [30,32,133].

6. CONCLUSIONS

In this short review, we examined the relationship between marine biodiversity and climate change. It appears that temperature changes (both warming and cooling) produce predictable changes in marine biodiversity, both on ecological [27,29] and evolutionary timescales [6]. This effect is particularly visible at large spatial scales where diversity patterns are strongly linked to temperature [9]. On a global scale, it appears that as oceans warm, the tropics lose diversity, temperate regions show species turnover and sometimes increases in net diversity, whereas polar environments so far mostly show declines in ice-dependent species and some invasion of subpolar taxa. Underlying these dynamic patterns is a redistribution of species ranges, with range expansions of warm-adapted and range contractions of cold-adapted species toward the poles, as well as local extirpations and new invasions that are driven by local climate velocity. On local scales, however, other factors may modify the effects of temperature change depending on local context. As a result, species communities and food webs on all scales reorganize. Sometimes this involves the loss of particular habitats and their associated communities, the decoupling of predator populations from their prey, or other changes in species interactions due to shifts in phenology and physiology. Little is known about how entire communities or food webs reassemble with climate change; this should be a germane topic for further research.

From a biodiversity management perspective, concerns about climate change as a threat to biodiversity focus on tropical and polar regions because of the documented and anticipated species losses there, often exacerbated by growing population pressures, cumulative impacts and scarce management capacity. But even in regions with well-developed science and management capacity, little can be done to control the shifting of species ranges and the reorganization of ecosystems. There is some debate about assisted migration, for example in helping warm-adapted coral species to spread more widely [134], but this strategy is controversial [135]. It is generally accepted, however, to maintain as much as possible the existing diversity both within and between species and habitats that is evidently so important for adaptation and resilience. This can be achieved by controlling the impacts of other factors that may compromise biodiversity and by minimizing cumulative impacts [32,136]. In an era of rapid climate change, however, complex and surprising effects on biodiversity are to be expected, and any form of management must necessarily be highly adaptive and precautionary.

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