Chapter 14

Changes in Marine Biodiversity as an Indicator of Climate Change

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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 from all sources [1], originated in the oceans and most of the larger taxonomic groups still reside there today. Over evolutionary time scales, there have been massive changes to the ocean's biodiversity, including several mass extinctions [2–4] that have shaped planetary diversity over millions of years [5]. Some, if not most of these events are thought to correlate with large-scale climate change that perturbed ocean temperature, chemistry, currents and productivity [6].

Today, we are living through another episode of rapid climate change, which is causing global changes in weather patterns and ocean temperature [7] that are beginning to change thermal stratification, currents and productivity [8–12]. Most studies on the ecological effects of climate change, whether on land or in the sea, have concentrated on individual species [13–16], as discussed elsewhere in this volume. Only quite recently have community metrics such as species diversity been studied in direct relation to climate change [17–19]. Here, we will build on this emerging literature while discussing how marine biodiversity may serve as an indicator of recent climate change. Biodiversity has three main components: diversity within species, between species and of ecosystems [1]. We will discuss changes in all three components, but note that studies to date have mostly focused on species composition and species richness, likely because these represent the most easily quantifiable aspects of biodiversity.

Despite its taxonomic prominence, marine biodiversity is sometimes overlooked in the climate change discussion undoubtedly because much of it is little known and less understood than its terrestrial counterpart. For example, Sala and others [20] projected ‘global biodiversity scenarios’ for the year 2100 but did not consider marine ecosystems at all. Yet, marine biodiversity needs to be accounted for, not just because of its geographic extent, but also as it provides important ecosystem goods and services such as fisheries yields, shoreline protection, carbon and nutrient cycling, detoxification of wastes and pharmaceuticals, to name a few [21,22]. 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 [23,24].

Here we consider the role of marine biodiversity as a response variable and indicator of recent climate change. We first discuss observed changes in biodiversity at various scales: local, regional and global, 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 and productivity 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 rely 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 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 such as overfishing or eutrophication.

2. CLIMATE CHANGE AND 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 via greenhouse gas forcing [7,25], increased climatic variability leading to more frequent extreme events [26] and changes in sea level, thermal stratification and ocean currents [8,27,28]. These processes can act on biodiversity directly (e.g. where local temperatures exceed individual species' physiological tolerances [29,30]) or indirectly (e.g. by altering habitat availability, species interactions or productivity [8,11,27]). Furthermore, potentially complex interactions between climate change and other global change aspects, notably those due to fishing, eutrophication, ocean acidification, habitat destruction, invasions and disease may also be important [27,31–33] and are briefly highlighted in this review. This latter point suggests an important difference between the current episode of climate change and previous climate perturbations in Earth's history: recent changes in climate are superimposed on other stressors that have already compromised biodiversity in many places [22]. From a scientific standpoint this added complexity can make it more difficult to clearly attribute observed changes in diversity to a single factor.

3. EFFECTS OF CLIMATE CHANGE ON 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 (0.1–10 km) to regional (10–1000 km) and global (1000–10 000 km), respectively. In Section 3.4, we discuss factors other than increases in temperature, that are related to climate. Observed effects are summarised in Table 1.

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 by local factors such as wave exposure, tidal mixing, upwelling and species composition. Nevertheless, some common patterns have been observed at local scales.

In temperate locations, slow changes in species composition have been observed that often lead to an overall net increase in diversity. Changes in species composition were first shown by Southward and colleagues in their classic long-term studies in the English Channel [34]. 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. The reverse patterns were observed during periods of cooling [34]. Similar changes occurred in the northwest Pacific (Monterey Bay, California) where 8 out of 9 southern species of intertidal invertebrates increased between the 1930s and 1990s, while 5 out of 8 northern species decreased [35]. This change tracked observed increases in both mean and maximum temperature and led to an overall

TABLE 1 Summarising observed direct effects of climate change on marine biodiversity

Cause	Effect	Effect on diversity	References
Temperature increase (tropical)	Coral bleaching	↓	[38,39]
Temperature increase (temperate)	Warm-adapted species replace cold-adapted ones	↑	[19,35,45,47,52]
Temperature increase (polar)	Decline of polar endemics invasion of subpolar species	?	[41–44]
Increased climate variability (heat waves)	Increased rates of disturbance	↓	[67,68]
Increased upwelling intensity	Surface water hypoxia	↓	[69–71]
Increasing water column stratification	Lower nutrient supply and productivity	?	[8,11,12]
Sea level rise	Erosion of coastal habitat	↓	[74]
Changes in currents	Changes in larval transport	?	[96]

increase in invertebrate species richness by 7%, due to 3 species newly invading from the south [35]. A similar pattern of southern species invading and northern species declining was documented for a temperate reef fish community in southern California [36]. 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 [36]. These two contrasting examples illustrate that predictions based on temperature alone can be misleading, at least on a local scale, if concomitant changes in productivity are involved. Moreover, it has been shown that local differences in tidal exposure render some northern sites more thermally stressful than southern sites, counteracting the poleward shift of southern species discussed above, and possibly causing localised extinctions [37].

In tropical locations warming can lead to species loss and a decline in diversity, as maximum temperature tolerances are exceeded. So far, this applies particularly to tropical coral reefs that are affected by warming-related bleaching events (reviewed, for example, by Refs. [33,38,39] 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 [38]. The loss of coral species is likely to cause secondary losses of reef-associated fauna and flora through loss of critical habitat. This mirrors climate-related losses of tropical diversity on land [40]. Unfortunately, detailed estimates of how species richness and community structure have changed after bleaching events are scarce but such changes are suspected to be large [15].

Polar marine ecosystems are thought to be particularly sensitive to climate change because small temperature differences can have large effects on the extent and thickness of sea ice. Therefore, the rate of change in species abundances and composition has been very fast, much of it related to changes in sea ice cover. While sea-ice dependent species such as polar bears [41], krill [42] and some penguins [43,44] have sharply decreased in abundance at some locations, there are signs of increasing invasion of subpolar and ice-independent species in other places [43]. Little information on net changes in local species richness (increase or decrease in diversity) is available so far.

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 done in relation to fisheries or plankton monitoring data. As on the local scale, 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 [45,46], as well as fish communities [47]. These changes are not necessarily synchronised: Beaugrand and colleagues documented a growing mismatch between warming-related changes in zooplankton 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 as compared to fast-growing species [47]. This finding has implications for fisheries, as species with slower life histories are already more vulnerable to overexploitation [48] 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, among species that shifted their range the average rate of northward change was 2.2 $\mathrm{km{\cdot}a^{-1}}$, which is more than 3 times faster than observed range shifts in terrestrial environments, which reportedly average 0.6 $\mathrm{km{\cdot}a^{-1}}$ [14]. This may not be surprising, given the lesser extent of physical boundaries in marine, and particularly pelagic environments.

The net effect of these compositional changes on species richness was 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 [19]. This change correlated tightly with increasing water temperature during the same period [19]. The same trends have been found in the Bristol Channel, UK where fish species richness increased by 39% from 1982 to 1998 [49]. 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 on land, where species richness of British butterflies [18] and epiphytic lichen in the Netherlands [50] has increased with warming over time, mostly driven by southern species that were able to respond quickly to warming. The total magnitude of increase in species richness was quite variable, however: 10% increase in butterfly species, but a doubling in lichen richness over the last 2–3 decades.

These decadal changes in species richness and diversity are superimposed on significant year-to-year variation in temperature and diversity. In the NW Atlantic there is a well-documented latitudinal gradient in fish species richness that co-varies with temperature [51]. This latitudinal gradient in diversity has previously been treated as static. Recently it has been shown how temperature variability readjusts diversity gradients year-by-year [52]. Temperature variability is linked to large-scale pressure differences across the North Atlantic, known as the North Atlantic Oscillation (NAO) [53]. Positive NAO anomalies cause temperature gradients in the NW Atlantic to steepen, which leads to rapid adjustments in species diversity: northern areas decline, southern areas increase in diversity [52]. During NAO-negative years the gradient flattens: northern areas increase, southern areas decrease in diversity. Although the north–south trend of increasing diversity does not reverse, there are substantial differences in its slope. This dynamic pattern is mostly driven by expansions and contractions of species ranges at their northern or southern range limits [52]. 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 [54]. Positive ENSO years are characterised by regional warming of the eastern tropical Pacific and an increase in species diversity in the following year [17]. Regional cooling leads to decrease in diversity [17]. Single species such as Blue Marlin [17] or skipjack tuna [55] are seen to readjust their distribution year-by-year in response to these temperature changes. These studies show how species diversity does not only serve as an indicator of long-term climate change, but accurately tracks short-term variability in climate as well. A caveat for exploited fish populations is of course that intense exploitation can override climate signals on diversity. In the Atlantic and Indian Oceans, for example, there has been a long term decline in tuna and billfish species richness, that is most likely explained by fishing [17]. In the Pacific, however, a similar decline is counteracted by increasing warming after 1977 [17].

In contrast to marine fish, plankton communities are not affected by exploitation, except maybe indirectly through trophic cascades [56]. For both phyto- and zooplankton phenological changes (e.g. the timing of the spring bloom), range shifts and changes in species composition have been shown to track changes in climate [9,57]. Recently, it has been suggested that plankton communities may in fact be more sensitive indicators of climate change than the environmental variables (like SST) themselves, because of non-linear responses of biological communities that may amplify subtle environmental perturbations [58]. Thus, plankton communities are increasingly used as indicators of recent climate change [57].

3.3. Global Scale

There are few global scale studies of marine biodiversity and its response to climate variability and global change. 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 [59]. Whether to expect global marine extinctions due to climate change is yet unclear, although much concern is focusing on coral reefs worldwide that are simultaneously threatened by warming and acidifying waters [33]. Dulvy and co-workers [48] 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. Moreover, some coral-associated fish have also disappeared over the course of recent bleaching events [48].

Although the question of projected extinctions due to climate change is contentious [60,61], there is little doubt that temperature is a major driver of marine diversity at the global scale. Global diversity patterns have so far been synthesised for single-celled (foraminiferan) zooplankton [62], tropical reef organisms [63], tuna and billfish [17], and most recently, marine mammals [64,65]. Global reef diversity peaks at tropical latitudes in the Philippine–Indonesian triangle [63], whereas fish, foraminifera and mammals all peak at intermediate latitudes, around 20–30° North or South [17,62,64,65]. These patterns are all most parsimoniously explained by variation in SST (Fig. 1a), which explains between 45 and 90% of the variation in species diversity for these groups [17,62,65]. As mentioned above, variation in SST well explains not just the broad spatial patterns but also much of the inter-annual variation in tuna and billfish richness in the Pacific [17] as well as seasonal variation in mammal diversity in the Atlantic [65]. Moreover, the global richness pattern of tuna and billfish could be independently reconstructed from individual species' temperature tolerances [30]. Therefore, it appears that temperature might indeed be a powerful and general determinant of species richness at

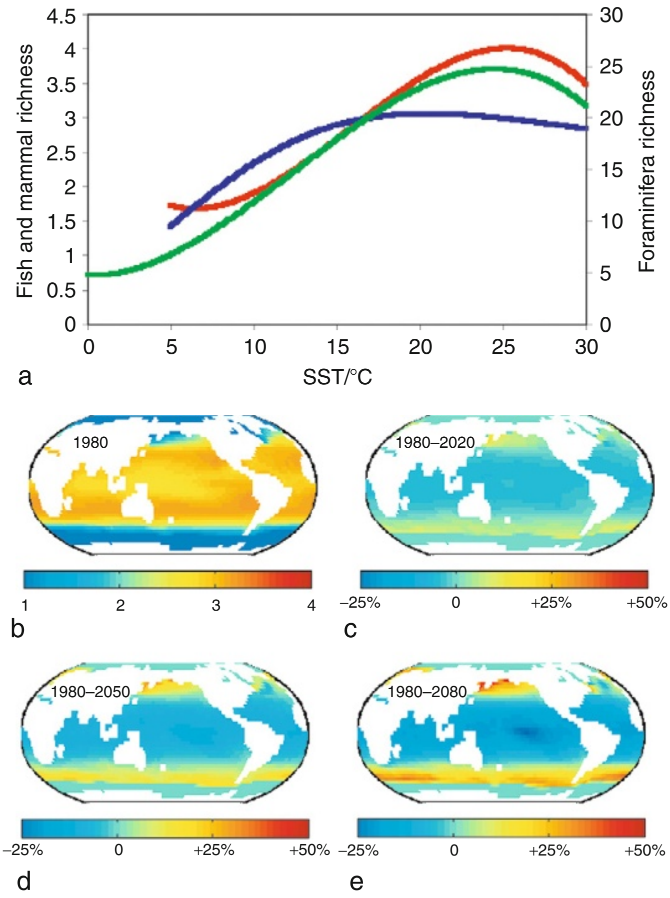

FIGURE 1 Effects of sea surface temperature (SST) on marine pelagic biodiversity. (a) Empirical relationships between SST and the observed species richness of foraminiferan zooplankton (green, data from [62]), tuna and billfish (red, data from [17]) and genus richness of deep-water cetaceans (blue, data from [65]). Maps depict projected mean genus richness of deep water cetaceans in (b) 1980, and relative changes in richness projected to occur between (c) 1980 and 2020, (d) 1980 and 2050 and (e) 1980 and 2080 are shown. Changes are expressed as percents of the mean (over all ocean areas <65° latitude) diversity in 1980 minus one (as the minimum diversity is 1.0). Panels b–e are reprinted with permission from Ref. [65].

global scales. The empirically derived relationships between SST and species richness can be used to derive hypotheses about the potential effects of warming on large-scale patterns of species richness. An example is shown in Fig. 1, displaying the global pattern of deep-water cetacean genus richness (Fig. 1b) as derived from the empirical SST relationship (blue line in Fig. 1a), along with projected changes due to moderate warming (Fig. 1c–e, see Ref. [65] for more detail). Climate data were derived from the Intergovernmental Panel on Climate Change CGCM1 model using scenario A2a. Given the observed relationship with SST, diversity is projected to increase substantially at high latitudes, but to decrease in the tropical ocean. So far, the low availability of time series data does not allow testing this prediction for marine mammals, but this may change with improved tracking and monitoring capabilities.

3.4. Other Factors Relating to Climate Change

Despite the strong observed effects of temperature discussed above 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 ml·l^{-1} at 100 m depth [17,66]). Many marine animals may also concentrate in areas of high productivity [64]. These factors are both directly and indirectly affected by climate change (Table 1). Increasing climate variability, for example, can affect biodiversity through extreme events, such as intense storms or heat waves, which can lead to large-scale die-offs, as recently seen in shallow-water corals or seagrass meadows [38,39,67,68]. Such events are likely leading to substantial losses in local diversity, at least on short to intermediate time scales. Similarly, increased variability in wind stress has been shown to affect the intensity of upwelling, leading to periodic hypoxia and death of marine organisms [69–71]. Furthermore, climate change is implicated in the observed shallowing of oxygen minimum zones in the tropical ocean [72], which is likely compromising local biodiversity at intermediate depths. Primary productivity is also affected by global warming, particularly through increased stratification and lower nutrient supply to the photic zone [8,9,11]. Because there are strong relationships between productivity, biomass and diversity in plankton [73], changes in stratification, nutrient supply and productivity are likely altering species diversity patterns.

Finally, climate change leads to sea level rise (Chapter 18, this volume) and changes in ocean currents (Chapter 20, this volume). Sea level rise in concert with increasing climate variability can lead to increasing coastal erosion and the loss of coastal habitats. This may compromise the diversity of species depending on wetlands, saltmarshes or mangroves [74]. 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 [74]. Ocean currents, fronts and upwelling zones are changing in response to alterations in temperature, precipitation, runoff, salinity and wind. These water movements strongly influence larval supply, species migrations and productivity [74]. So far, effects of changing currents on ocean diversity have not been studied, however, with the exception of upwelling studies mentioned above [69–71]. It can be concluded that both temperature as well as other climatic factors can modify patterns of diversity which may lead to interactive effects. 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. Up to this point we have reviewed the direct effects of increasing temperature and climate variability, and resulting changes in upwelling, stratification, sea level 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 are highlighting such indirect effects, pointing towards some well-documented examples for illustration (Table 2).

TABLE 2 **Examples of some indirect and interactive effects of climate change with other drivers of marine biodiversity**

Primary cause	Secondary cause	Effect on species group	Effect on diversity	References
Increased upwelling intensity	Decline in keystone predator	Release of competitive dominant	↓	[76]
Warming	Disease	Increased pathogen development, disease transmission, and host susceptibility	↓	[32,77]
Increase climate variability	Fishing pressure	Fish more vulnerable to overexploitation	↓	[24]
Warming	Nutrient pollution	Increase in algal and jellyfish blooms	↓	[31,85–87]
Warming	Acidification and fishing	Coral reef loss due to bleaching, algal overgrowth and lower calcification	↓	[33,88]
Warming	Invasion	Faster establishment of invaders	?	[90]

Consider the classic example of a keystone predator, the starfish *Pisaster ochraceus*, which maintains intertidal diversity by feeding on competitively dominant mussels *Mytilus californianus* [75]. This interaction, however, is temperature-dependent: increases in upwelling lead to colder waters, lower predation rates and higher mussel cover [76]. Therefore, possible effects of climate change on diversity are mediated by a powerful 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 (reviewed in Refs. [32,77]). This has become evident both in the sea and on land following large-scale warming events associated with ENSO, which are implicated with increases in several coral diseases, oyster pathogens, crop pathogens, rift valley fever and human cholera [32,77]. These effects occurred both in tropical and temperate location, with some documented range shifts of pathogens towards higher latitudes.

Climate change can also affect the interaction between humans and marine biodiversity. Over the past centuries human impacts have already had a marked impact on marine biodiversity, including a number of local, regional and global extinctions [48]. To date, exploitation and habitat destruction have probably had the most severe impacts [48,78]. The existing rate of habitat destruction will likely be accelerated by climate-driven habitat losses due to sea level rise, acidification and bleaching [33,74]. 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 young (often immature) individuals to the fishery. Recruitment, however, is strongly affected by climate variability [79]. Removing the older age classes removes resilience to recruitment failure, and increases susceptibility both of the stock and the fishery to climatically induced fluctuations [24]. Another important factor is the removal of stock diversity by intense fisheries, which again increases vulnerability to climate by removing life-history variation and local adaptations [80]. Reducing fishing mortality in the majority of fisheries, which are currently fully exploited or overexploited, is the principal feasible means of managing fisheries for increased robustness to climate change [24,81].

Apart from fishing and habitat destruction, humans are affecting marine biodiversity through pollution, including nutrient pollution leading to eutrophication of coastal waters, algal blooms and hypoxic conditions [82]. These factors have documented negative effects on diversity, primarily by reducing susceptible species, but also by increasing dominance of fast-growing opportunists. The potential for complex indirect effects of climate change has been explored, for example, with respect to eutrophication and algal blooms [31]. Field and laboratory experiments have shown that increased nutrient availability (e.g. through sewage or fertilizer runoff) can trigger algal blooms, especially where herbivore populations are depressed [83,84]. Climate warming further accelerates algal growth but also feeding rates by grazers. The effect of climate warming on algal blooms depends therefore on the magnitudes of both nutrient input, and the composition and abundance of grazers [31]. Observation and experiments both suggest that as rates of nutrient input and climate warming grow, these could synergistically enhance bloom-forming species such as algae [31,85] and jellyfish [86,87].

Algal growth, particularly on tropical reefs can also be accelerated by the exploitation of herbivorous fishes, particularly parrotfish. This can synergistically enhance the effects of warming and acidification, which lead to bleaching and increase dissolution of calcareous exoskeletons, respectively [33]. Those disturbances open up new space for algae to colonise, which in the absence of herbivores can grow unchecked until they dominate reef structure and permanently alter the state of that community, as shown in recent field experiments [88].

Finally, human vectors are re-arranging marine biodiversity through the transport and release of non-indigenous organisms, both intentionally (as in aquaculture) and unintentionally (as in ship ballast water) [89]. Whether those species then become established or invasive in their new environment depends on a number of factors, such as temperature and salinity, habitat availability, predation and competition [89]. There is some evidence that ocean warming favours the establishment of invaders and hastens the displacement of native species [90]. Whether such invasions lead to a net loss of species, or even an increase in species richness as observed in some places [91], is not generally clear.

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 and species variation enhances the diversity of possible responses, and adaptive ability in the face of environmental variation [92,93]. For example, in a study on seagrass loss after the 2003 European heat wave, high genetic diversity (manipulated experimentally) led to faster recovery of damaged habitat [67]. This was driven both by selection of heat-adapted genotypes and by some form of facilitation that led to increased survival [67]. This observation was independently verified by laboratory experiments that manipulated temperature and genetic diversity in a controlled environment [68]. Another field study documented that high genetic diversity in seagrass also increased resilience to physical disturbance from overgrazing [94]. Theoretical studies have come to similar conclusions. For example, Yachi and Loreau [95] 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 studies follows the prediction that a loss in biodiversity should lead to a loss in productivity and resilience, which would enhance any effect of climate change (or other disturbances) on marine ecosystems. An increase in biodiversity should have the opposite effect. Evidence in support of this prediction comes from a series of meta-analyses examining local experiments, regional time series and global fisheries data [23]. The vulnerability to climate change in particular was examined by a regional study of Alaskan salmon fisheries that have been carefully managed to avoid loss of stock diversity [80]. 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 [80].

6. CONCLUSIONS

In this short (and necessarily incomplete) review, we examined whether marine biodiversity can serve as a useful indicator of climate and global change. It appears that indeed changes in diversity often indicate changes in climate, especially warming and increased climate variability. This is particularly true at large (regional and global) scales where diversity patterns are strongly linked to temperature. On local scales, this is less obvious because other factors may modify or override the underlying effects of climate change: (1) natural abiotic and biotic factors may alter the diversity response through changes in productivity, disturbance or species interactions and (2) other aspects of climate and global change may add complexity to the cumulative response of diversity. On a global ocean scale, it appears that, as on land, the tropics loose diversity, temperate regions show increased diversity, whereas polar environments so far mostly show declines in ice-dependent species as the climate warms. Underlying these dynamic patterns is a redistribution of species ranges, with range expansions of warm-adapted and range contractions of cold-adapted species towards the poles, as well as local extirpations and new invasions. On local scales, climate-change driven habitat losses, for example, through sea level rise, bleaching or acidification can accelerate the local loss of biodiversity. As a result, species communities and food webs on all scales reorganise. Sometimes this involves decoupling of predator populations from their prey or other mismatches in species interactions due to shifts in phenology and physiology. Little is known about how entire communities or food webs re-assemble with climate change; this should be a germane topic for further research.

From a biodiversity management perspective little can be done to change the shifting of species ranges and the reorganisation of ecosystems. It is important, however, to maintain as much as possible the response diversity both within and between species and habitats that is evidently so important for adaptation and resilience. This can be achieved by carefully adjusting the impacts of other factors that may reduce biodiversity and by minimising cumulative impacts. In an era of rapid climate change, complex and surprising effects are to be expected and any form of management must necessarily be highly adaptive and precautionary.

ACKNOWLEDGEMENTS

The authors wish to thank H. Whitehead and D. Tittensor for discussion and insight, as well as The Sloan Foundation (Census of Marine Life, FMAP Program) and NSERC for support.

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