

Chapter 18

Climate Change: Warming Impacts on Marine Biodiversity

Helmut Hillebrand, Thomas Brey, Julian Gutt, Wilhelm Hagen, Katja Metfies, Bettina Meyer, and Aleksandra Lewandowska

Abstract In this chapter, the effects of temperature change—as a main aspect of climate change—on marine biodiversity are assessed. Starting from a general discussion of species responses to temperature, the chapter presents how species respond to warming. These responses comprise adaptation and phenotypic plasticity as well as

H. Hillebrand (✉)

Institute for Chemistry and Biology of the Marine Environment (ICBM), Carl-von-Ossietzky University of Oldenburg, Wilhelmshaven, Germany

Helmholtz Institute for Functional Marine Biodiversity (HIFMB), Oldenburg, Germany

e-mail: helmut.hillebrand@uni-oldenburg.de

T. Brey • K. Metfies

Alfred Wegener Institute, Helmholtz Centre for Marine and Polar Research, Bremerhaven, Germany

Helmholtz Institute for Functional Marine Biodiversity (HIFMB), Oldenburg, Germany

e-mail: thomas.brey@awi.de; katja.metfies@awi.de

J. Gutt

Alfred Wegener Institute, Helmholtz Centre for Marine and Polar Research, Bremerhaven, Germany

e-mail: julian.gutt@awi.de

W. Hagen

BreMarE Bremen Marine Ecology, University of Bremen, Bremen, Germany

e-mail: whagen@uni-bremen.de

B. Meyer

Institute for Chemistry and Biology of the Marine Environment (ICBM), Carl-von-Ossietzky University of Oldenburg, Wilhelmshaven, Germany

Alfred Wegener Institute, Helmholtz Centre for Marine and Polar Research, Bremerhaven, Germany

Helmholtz Institute for Functional Marine Biodiversity (HIFMB), Oldenburg, Germany

e-mail: bettina.meyer@awi.de

A. Lewandowska

Institute for Chemistry and Biology of the Marine Environment (ICBM), Carl-von-Ossietzky University of Oldenburg, Wilhelmshaven, Germany

e-mail: aleksandra.lewandowska@uni-oldenburg.de

range shifts. The observed range shifts show more rapid shifts at the poleward range edge than at the equator-near edge, which probably reflects more rapid immigration than extinction in a warming world. A third avenue of changing biodiversity is change in species interactions, which can be altered by temporal and spatial shifts in interacting species. We then compare the potential changes in biodiversity to actual trends recently addressed in empirical synthesis work on local marine biodiversity, which lead to conceptual issues in quantifying the degree of biodiversity change. Finally we assess how climate change impacts the protection of marine environments.

Keywords Climate change • Adaptation • Marine conservation • Phenology • Range shift • Warming

18.1 Introduction

Climate change impacts on marine ecosystems are multifaceted, with strongly interdependent changes in CO₂ concentrations, temperature, mixing regimes, and biogeochemical cycles of elements and organic compounds. The response of marine communities to these non-point pressures requires dealing with the synergies of these changes. However, for marine biodiversity we still need to understand the basic mechanisms driving the responses to any single of these factors of which most are non-linear. Therefore, in this section, we address the different stressors in separate chapters, but interlink these closely. The present chapter focuses on the temperature aspect of climate change and its consequences on marine ecosystems and biodiversity. Acidification-related aspects are dealt with in Chap. 19 (Thor et al.), eutrophication in Chap. 22 (von Beusekom et al.).

In this chapter we mainly address the question of human-mediated changes in climate, disentangling it from climate change on geological time frame, which have less connection to marine environment protection. The anthropogenic causation of climate warming has been globally summarized by the latest report of the Intergovernmental panel on Climate Change (IPCC 2013). Initiated by human-induced increases in CO₂-emissions, the global atmospheric temperature increased by 0.85 °C in the period 1880 to 2012, whereas the global ocean warmed by 0.44 °C at the surface between 1971 and 2010. A warming of similar magnitude in the first 70 years of the twentieth century is discernible as well (Fig. 18.1, down right). Moreover, the ocean absorbed most of the energy stored in the climate system. It is predicted that the global ocean will continue to warm during the current century, predictions for global averages in the upper 100 m ranging between 0.6 and 2.0 °C. It is very likely that this heat will penetrate from the surface to the deep ocean and affect global ocean circulation (Balmaseda et al. 2013; Llovel et al. 2014; Roemmich et al. 2015).

This general pattern showed—and will continue to show—strong regional variation, e.g., IPCC predicts the strongest ocean warming for the surface in tropical and Northern Hemisphere subtropical regions and for greater depth in the Southern Ocean (IPCC 2013). At the same time, in addition to the overall warming trend,

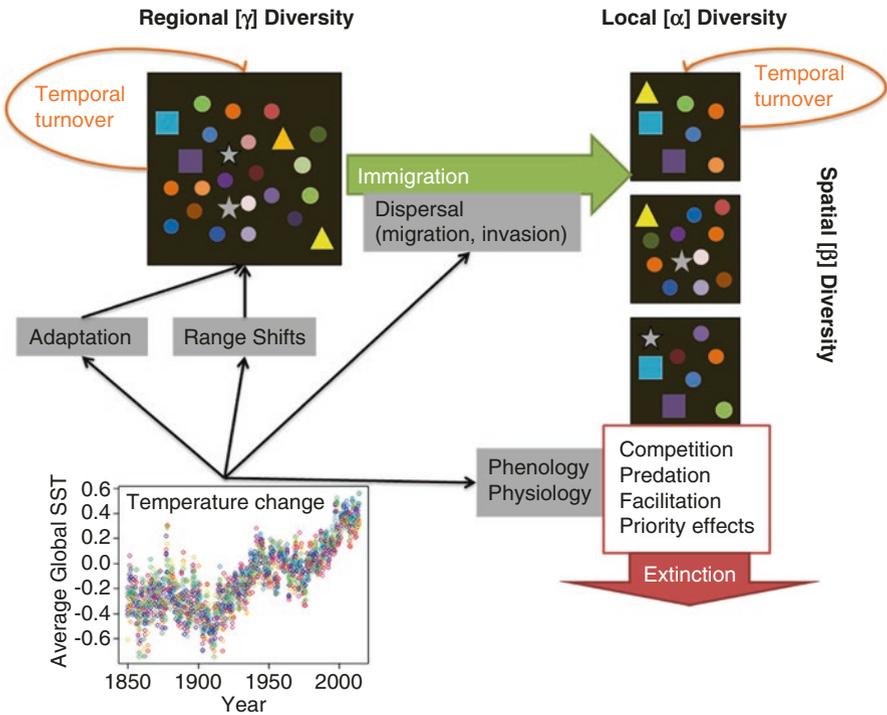


Fig. 18.1 Potential responses of marine communities under altered temperature regimes. Temperature change is presented as global average sea surface temperature (standardized to the period 1951–1980 as anomaly in °C), *different colours* are different month such that the degree of variation for each year gives an estimate of the seasonal variation in warming. Regional consequences of temperature change on biodiversity are mediated by species distribution shifts (see Sect. 18.4) and adaptation to altered temperature (see Sect. 18.3). These processes will also alter the patterns of immigration at the local scale. Interactions between species (such as competition, facilitation, and predation) and stochastic processes (such as priority effects) at the local scale constrain which species survive or go extinct in the assemblage (Sect. 18.5). These constraints of local biodiversity are affected by temperature through altered timing (phenology) and fitness (physiology) of the organisms (Sect. 18.2)

changes in the variability in temperature between years and with seasons is observable (Fig. 18.1). Thus, any marine region is affected by overlaying temporal patterns, comprising trends in mean temperature, altered variation around this trend in time and space, and extreme events, especially consisting of extraordinary heat waves. Each of these aspects of climate warming (trend, variation, and extreme events) can separately or jointly alter the composition, diversity and productivity of marine communities. Additionally, indirect effects from the warming driven changes in ocean circulation might alter, amplify or counteract the direct consequences of temperature change. Potential regional aspects include, e.g., the weakening of the Atlantic current (Rahmsdorf et al. 2015) and deep-water formation (Fahrbach et al. 2011), the amplification of the marine effects of the El-Nino Southern Oscillation (ENSO) phenom-

enon (Cai et al. 2014) or shifts in oceanic fronts, e.g. of the Polar Frontal System to the South (Sokolov and Rintoul 2009), shrinking and regionally advancing of polar ice caps (Arrigo and Thomas 2004; Cook et al. 2005; Comiso 2010; Turner et al. 2009) and the thinning and stabilizing of surface water layers (Sarmiento et al. 2004).

Temperature change thus is multi-layered in time and space, comprising global trends with regional patterns and variance as well as local heat-waves. Consequently, climate change impacts on biodiversity can only be understood, if processes affecting biodiversity are also analysed across different scales of space, time and organisation (Fig. 18.1). Therefore, it is useful to address consequences of climate change across different scales of biodiversity,¹ which have been introduced to classical ecology by Whittaker (1960): The smallest component of biodiversity is called α -diversity, which describes species composition, species richness and dominance in local assemblages of potentially interacting species. It can be characterized as within-habitat diversity, whereas the difference in species composition of local habitats within a region is called β -diversity or spatial species turnover. The composition and richness of all habitats in a region is called γ -diversity, which encompasses the entire regional species pool potentially colonizing a certain habitat.

In the following sections, we analyse different pathways of biodiversity change with special emphasis on temperature changes (see Chaps. 19 and 22), such as adaptation (see Sect. 18.3), range shifts (see Sect. 18.4), or the change in local interactions (see Sect. 18.5). We then compare the potential changes in biodiversity to actual trends recently addressed in empirical synthesis work on local marine biodiversity (see Sect. 18.6), which lead to conceptual issues in quantifying the degree of biodiversity change. Finally we assess how climate change impacts the protection of marine environments (see Sect. 18.7). Before doing so, however, we will present a short primer on species responses to temperature as a basis for potential changes in biodiversity. Obviously, a full accounting of the ecophysiology of temperature is beyond the scope of this Handbook, but section Sect. 18.2 clarifies some basics to help understand the biodiversity consequences of temperature change.

¹The term “biodiversity” comprises different aspects of biological differentiation. We explicitly use this term *sensu lato*, crossing scales from “diversity within species” (e.g. genotypic differences in a population) over “diversity between species” (e.g., number of species in a food web) to diversity at higher organisational scales (e.g., functional groups). At all these levels, biodiversity can be characterized by richness (number of entities, such as genotypes or species or functional groups), evenness (dominance structure, high evenness reflecting equal contribution of all entities to the community), and identity (taxonomic or functional characteristics [traits] of the entities).

18.2 Organismal Response to Temperature

Organisms physiologically respond to environmental gradients such as temperature with an optimum curve (Fig. 18.2a), where performance (e.g., a metabolic rate such as photosynthesis rate, growth rate) is maximized under optimum conditions (O in Fig. 18.2a), and survival is only possible in a certain range of temperature (between the pessima P in Fig. 18.2a). This is also the broadest ecological niche of this species for temperature, where niche is a set of conditions an organism can tolerate. Often, conditions sufficient not only for survival but for somatic growth or reproduction are narrower subsets of this niche. This type of niche is called fundamental, as it relies completely on the physiological capacity of the species. This contrasts to realized niches, which take other species into account, e.g. competitors, prey species or predator species, which may limit the occurrence of a species along the temperature gradient to an even narrower range of conditions (Fig. 18.2a).

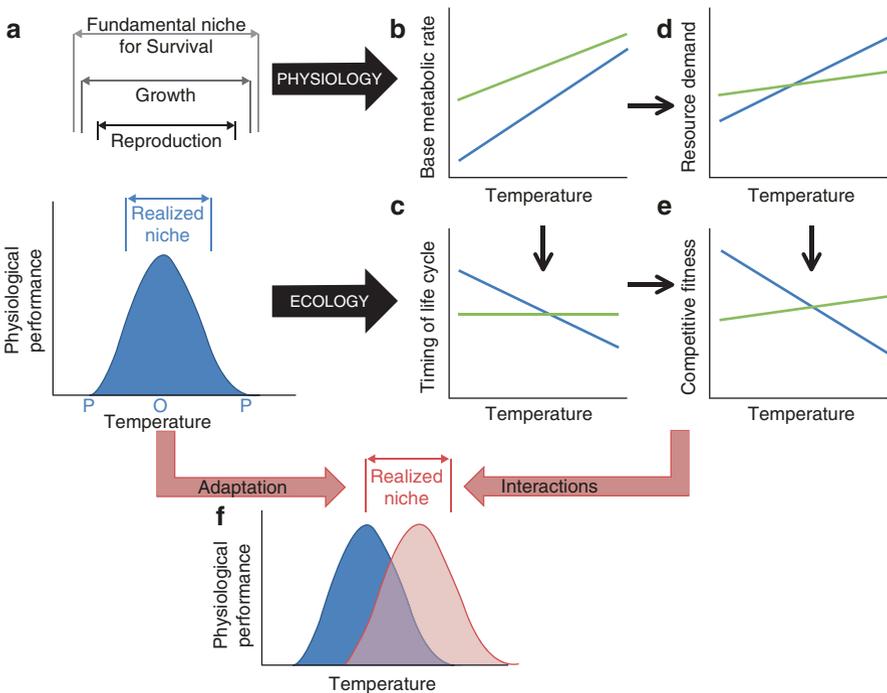


Fig. 18.2 Conceptual summary of species responses to temperature. (a) Optimum curve of a focal species to a temperature gradient with optimum and a fundamental niche constrained by pessima (P), and a realized niche. (b–e) Physiological and ecological processes to a small shift in temperature below the optimum of a focal species (blue) and an interacting species (green), which could be a consumer (panel c) or a competitor (panel e). (f) Adaptation (change in the fundamental niche) and altered interactions lead to a new realized niche in a warmed climate (depicted in red). More details see text

When addressing the warming effects on biodiversity, effects on fundamental and realized niches are possible. Warming might enhance temperature to an extent that minimum temperature requirements are met (entering the fundamental niche) or that maximum temperatures are exceeded (leaving the fundamental niche). It has been discussed how likely it is that warming (a global increase of ca. 1 °C) is sufficient to exceed the physiological tolerance of a species given that many species experience large temperature ranges in temporal (seasonal, tidal, upwelling) or spatial (depth) dimensions of their habitat. However, if temperature changes induce additional stressors, e.g. reducing the oxygen content of water, the fundamental niche in fact may be too small (Pörtner and Farrell 2008). Moreover, changes in biodiversity might occur at much more subtle changes of temperature given the temperature-dependence of species interactions and thus the realized niche. To understand this, the physiological and ecological responses to temperature ranges within the niche (or even below the optimum) have to be addressed (Fig. 18.2b-e).

Below the optimum, an increase in temperature leads to increased metabolic rates (Fig. 18.2b, for details, see e.g. the metabolic theory of ecology, Brown et al. 2004). Thus, physiological rates (enzyme kinetics, respiration, uptake of resources, development, or growth) increase, with the slope of the increase differing between species. This physiological response will also alter the phenology of a species (Fig. 18.2c), whereby the term phenology includes all temporal life-cycle events such as larval fall, end of hibernation, migration to winter or summer habitats, etc.. This are often triggered by physiological responses, and consequently differ between organisms. If interacting species show different phenological responses, temporal mismatches might occur (see Sect. 18.5).

The changed metabolic rates are closely related to altered resource requirements as well (Fig. 18.2c), such that some species need to take up more nutrients or prey in order to meet the higher energetic demands (Fig. 18.2d). Consequently, competitive dominance might shift along a small temperature gradient, if competing species show different shifts in competitive fitness along a temperature gradient (Fig. 18.2e). A species winning in a competitive situation at low temperature might lose at slightly higher temperatures, if the change is sufficient to alter resource requirements or is beyond the optimum of one of the species. Additionally, changes in phenology might alter competition as well, if e.g. an earlier larval fall allows one species to occupy space (pre-emption of a limiting resource).

These changes in interactions will impact the realized niche, which might be compressed or expanded and shifted along the temperature axis in a warmed world depending on the actual change in the interactions (see Sect. 18.5). However, the realized niche might also change by adaptation (see Sect. 18.3), which can shift the fundamental niche by, e.g. physiological acclimatization, selection from standing genetic variation (favouring genotypes with higher optimal temperature) or novel mutations. The biogeographic consequence of a shifted realized niche then often is a range shift (see Sect. 18.4).

18.3 Adaptation to Altered Temperature Regimes

Thermal adaptation to a shifting climate—as well as acclimatization between seasons—requires shifting thermal niches and adjusting niche widths (Pörtner 2010, see also Fig. 18.2). Irrespective whether we deal with adaptation within species (changing allele frequencies in a population) or between species (changing species frequencies in a community), adaptation can comprise novel mutations or—normally on a much shorter time scale—selection from standing genetic (or species) variation. The latter is called phenotypic plasticity. Hence, depending on environmental conditions the genotype may adjust phenotypic characteristics of an organism according to the requirements in a habitat. Reusch (2013) differentiates between phenotypic plasticity and phenotypic buffering. This definition refers to classical plasticity as response within the usual performance range of an individual selecting for enhanced opportunity under novel conditions. In contrast, phenotypic buffering represents a special case and implies maintenance of a functional phenotype under conditions of increasing stress close to the tolerance limits of an organism.

Phenotypic plasticity includes modifications in e.g., life-history traits, behaviour and physiological performance and is a key mechanism allowing organisms to adapt rapidly to changing environmental conditions (acclimation). Developmental plasticity in behavioural and life-history traits is a common phenomenon in marine animals and climatic stimuli during early ontogeny may be an essential trigger to express plasticity (O'Connor et al. 2007, Munday et al. 2013). Eurythermal organisms from temperate regions or coastal systems exhibit a more pronounced plasticity than rather stenothermal organisms from tropical or polar regions (Somero 2005; Reusch 2013; Storch et al. 2014). However, plasticity is not limited to individuals. Climatic effects, e.g. elevated temperatures, experienced by the parents may result in a better performance of the offspring, e.g. juvenile damselfish fully coping with increased temperatures (Donelson et al. 2012). Evidence of such accelerated trans-generational plasticity effects is accumulating in marine systems. These non-genetic mechanisms open a new avenue of experimental research and need to be considered, when predicting climate change implications (Munday et al. 2013).

The greatest risk of extinction is experienced by species with longer generation cycles, small population size as well as ecological specialists and overexploited species (Dulvy et al. 2003). Especially more complex species (but also larger species) have to “buy time” to persist in a climate change scenario (Chevin et al. 2010; Storch et al. 2014), as their genetic modifications usually require more extended time scales for DNA-fixed adaptive changes. Munday et al. (2013) point out that even in long-lived species genetic adaptation should not be dismissed as an adaptive option during times of rapid environmental changes, based on advances in theoretical understanding of phenotypic plasticity and genetic evolution (Chevin et al. 2010). Thus, both phenotypic plasticity and evolutionary potential of organisms must be considered, when predicting the consequences of climate change for marine organisms. However, few data are available on evolutionary responses from marine systems, due to a “weak tradition” of marine biology in this field, fewer model

organisms and difficulties with multi-generational experimental studies. Reusch (2013) argues that fisheries data on recruitment, maturity, reproductive effort and growth of individuals may provide the best evidence of plastic versus adaptive responses, with harvesting inducing evolutionary change (Olsen et al. 2004), although possibly selecting for different life-history traits than climate change (Munday et al. 2013).

Phenotypic plasticity, trans-generational plasticity, genetic adaptation, and species sorting will all play a role in the alteration of biodiversity under climate change, but the relative importance and the time-frame for these different response mechanisms is not easily addressed (Litchman et al. 2012). Litchman et al. (2012) conclude that assessing these issues requires a combination of experimentally derived data on major functional traits (and their plasticity) with data on species distributions along temperature gradients to better characterize thermal niches. At the same time, molecular approaches, quantitative genetics and (long-term) evolution experiments need to address temperature effects on selection and mutation in isolation and in combination with other stressors (e.g., acidification). The potential in predicting species occurrence and performance by combining ecological and evolutionary constraints has already been shown in model approaches (Follows et al. 2007; Thomas et al. 2012).

18.4 Range Shifts Alter Regional Marine Diversity under Altered Temperature Regimes

Biogeographic studies on climate change effects focused on the observation and prediction of range shifts with latitude or other spatial gradient correlated to temperature (Wilson et al. 2004; Hampe and Petit 2005; Jump and Penuelas 2005; Parmesan et al. 2005; Thuiller et al. 2005; Wilson et al. 2005). Also in marine organisms, substantial shifts in spatial distribution ranges have been observed in organism groups from passively transported plankton to mobile top-predators (Beaugrand et al. 2002; Atkinson et al. 2008, Beaugrand et al. 2009; Montes-Hugo et al. 2009, Block et al. 2011; Hazen et al. 2013). In an unprecedented meta-analysis across locations and marine organism groups, Poloczanska et al. (2013) summarized 360 studies on distributional shifts and found an average shift of 30.6 [± 5.2] km dec⁻¹, with the leading edge of the range moving faster (72.0 [± 13.5] km dec⁻¹) than the trailing edge (15.4 [± 8.7] km dec⁻¹). These results have two major implications: First, this shift is substantially faster than comparable estimates for the leading edge across terrestrial organisms (6.1 [± 2.4] km dec⁻¹) or terrestrial plus freshwater organisms (19.7 [± 3.7] km dec⁻¹) (Parmesan and Yohe 2003; Chen et al. 2011). Second, there is a huge discrepancy between the shifts of leading and trailing edges of the ranges, which partly can be explained by different warming scenarios in the different data sets used for these edge estimates (Poloczanska et al. 2013). However, differences in the lower and upper margin of climate-induced range shifts are also congruent with observations of a time-lag between immigration and

extinction at the regional scale. Comparisons within single animal groups such as marine fish and invertebrates shows that projected immigration rates (species arriving per area) were an order of magnitude higher than local extinction rates (Cheung et al. 2008a). This discrepancy reflects the time needed for immigration and extinction: Moving forward in space entering a new regional pool (i.e., moving the leading edge) is fast as it is an immediate consequence of successful colonization. Local extinction of poleward-moving species at the trailing edge, however, requires time, as displacement by immigrating species is not instantaneous. This phenomenon has been called “extinction debt” and is well described in terrestrial ecology (Tilman et al. 1994; Wearn et al. 2012). The impact of immigrations such as bioinvasions (see Chap. 25 by Kuhlenskamp and Kind) on native biodiversity cannot be observed in short time, which has led to the conclusion that the time since invasion in many parts of the world is insufficient to record regional extinctions (Gilbert and Levine 2013). In the context of climate change impacts on biodiversity, this means that we are prone to observe increases in species richness in a warming climate for a long period of time (see Sect. 18.6) before decreases in biodiversity are to be expected.

Predictions on future regional biodiversity under a warming climate are often inferred from fundamental or realized temperature niches of species. This assumes that species are able to track the changing geographic location of their “climate envelopes”, which are calculated from their present-day distribution. Potential shifts in regional biodiversity are then derived from calculating the area change within a certain climate envelope and using species-area relationships to predict the change in regional diversity (Thomas et al. 2004; Araujo et al. 2005; Xenopoulos et al. 2005; Lewis 2006). This approach has been mainly used—and critically discussed—in terrestrial assessments of climate change effects on biodiversity. Critics of this approach point to the extinction debt discussed above and the absence of temporal dynamics of dispersal and migration (He and Hubbell 2011) as well as the lack of acknowledging the non-uniformity of species-area relationships (Drakare et al. 2006; Gutt et al. 2012). More fundamentally, climate envelope modelling in its most basic form does not include adaptation and species-co-dependencies. An example for a marine model, which considers some of these biological processes, is that of Cheung et al. (2008b).

Most indirect effects of thermal change, which is mostly but not exclusively temperature increase, result in range shifts, which can be much faster than those affected by the heating of the oceans through the atmospheric warming. In case of changing current dynamics, transportation vectors for pelagic organisms and pelagic larvae of benthic sedentary species are changed. Such changes in hydrodynamic pattern result in sudden changes in environmental conditions and, thus, potentially affect diversity patterns considerably. A temperature-driven increase in the stability of pelagic stratification and thinning of surface waters leads to changes in the nutrient and food supply and in the underwater light environment, resulting in altered species interactions (see Sect. 18.5). In some marine ecosystems a shift from larger to smaller phyto- and zooplankton organisms (Moline et al. 2004; Hays et al. 2005) with cascading effects on higher trophic levels (Montes-Hugo et al. 2009) and even on the abyssal benthos is observed or expected (Smith et al. 2008). In polar areas,

warming might shift species composition and functional biodiversity (e.g., via reduced ventilation of the deep-sea or melting of sea-ice alter), which potentially alters primary production as well as particle flux to the sea-bed, and thereby destructs essentially important habitats (Boetius et al. 2013; Gutt et al. 2015).

18.5 Species Interactions in Altered Temperature Regimes

Local assemblage biodiversity can respond to changing temperature regimes especially through altered species interactions (Fig. 18.1). Local biodiversity increases if species disperse into the community, either as new immigrants (see Sect. 18.4 on range shifts and Chap. 25 on invasions) or from the regional species pool via colonization from neighbouring habitats. Immigration might be inhibited if previously arrived species occupy space or ecological niches (so-called priority effects). When established in a local habitat, species can go extinct based on competitive exclusion, predator-prey dynamics or the lack of facilitating/mutualistic interactions. All of these (priority effects as well as competitive, predator-prey-, and mutualistic interactions) are sensitive to temperature changes as the organisms' fitness in these interactions depend on the one hand on potentially temperature-dependent physiological traits, on the other hand on their phenology, i.e., their seasonal appearance (Fig. 18.1).

The majority of spring and summer events, such as spring phytoplankton bloom, have advanced in response to climate change (Thackeray et al. 2010; Poloczanska et al. 2013). Poloczanska et al. (2013) summarized 50 data sets on marine phenology shifts in spring and in summer, and found on average an earlier onset of phenological aspects by $4.4 [\pm 0.7]$ days decennium^{-1} . As a result of differences in thermal physiology (e.g. between ectotherms and endotherms or autotrophs and heterotrophs) organisms vary in phenological responses to climate warming. This variation can disorder the synchrony of ecological interactions among species, functional groups and trophic levels (Fig. 18.3), potentially disrupting ecosystem resilience. For example, the dominance of small phytoplankton species increases with warming, because smaller cells have a competitive advantage at higher temperatures through high nutrient uptake and growth rates (Reuman et al. 2014). Such dominance shift results in changes in food chain length and hence reduced energy transfer to higher trophic levels. Furthermore, temperature-driven shifts in species composition might lead to the dominance of toxic species or species having low nutritional value with potentially negative consequences for upper trophic levels. Depending on physiological traits, increasing temperature can also dampen or enhance oscillations in predator-prey interactions (Amarasekare 2015). Warming enhances the negative impact of a keystone predator on prey communities if higher temperatures increase predator occurrence (Harley 2011) or consumption rates (Isla et al. 2008; O'Connor 2009). Differential phenological shifts of prey and predator in response to temperature change might induce temporal mismatches in the occurrence (Fig. 18.3), leading to altered marine trophodynamics (Philippart et al.

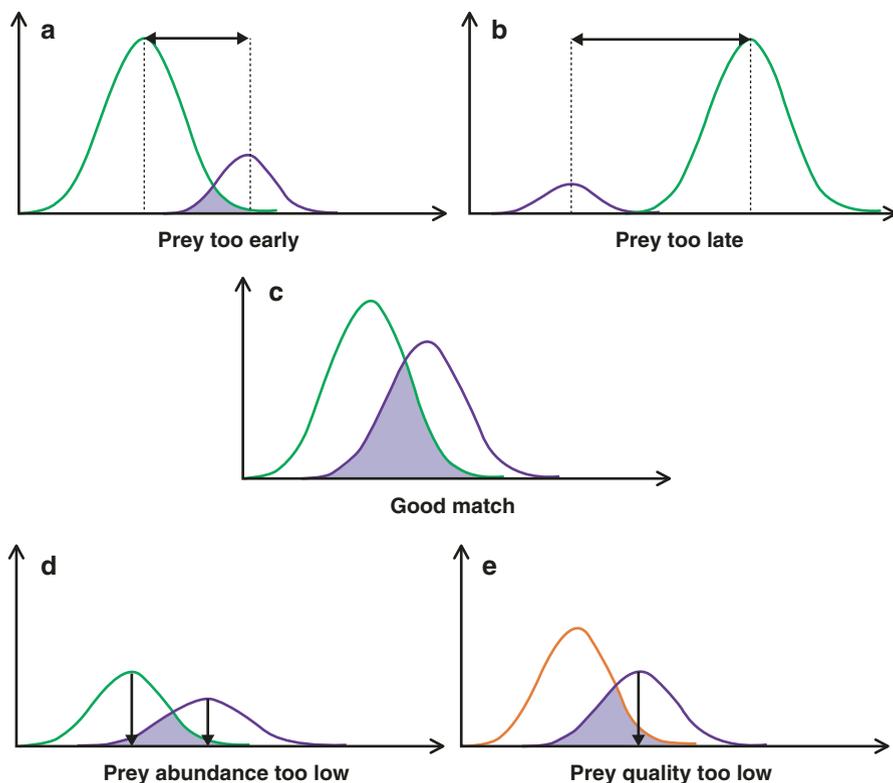


Fig. 18.3 Match (c) and mismatch (a, b, d, e) in trophic interactions in response to climate warming. Too early (a) or too late (b) prey development (*green and orange curves*) can lead to trophic mismatch resulting in a decrease of consumer biomass (*violet curves*). Similarly, lower prey abundance (d) or low food quality (e.g. low nutritional value, toxic species; e) can limit consumer growth. Combined mismatch scenarios (e.g. earlier development and low abundance of the prey) can occur as well

2003; Edwards and Richardson 2004; Durant et al. 2005; Burthe et al. 2012; Sommer et al. 2012) and consequent declines in commercially important fish stocks such as cod (Beaugrand et al. 2003).

An important aspect of mismatch occurs when temperature-induced changes in phenology meet endogenous rhythms which are stimulated by other variables such as day-length. A wide range of organism from cyanobacteria to humans have developed a circadian rhythm with an endogenous timing system, for which day length (photoperiod) is the most widely used environmental stimulus. In marine organisms in general, little is known about the principles of endogenous clocks and how these clocks interact with environmental cycles and this is particularly true for high latitude pelagic organisms. The polar pelagic environment is particularly characterized by extreme seasonal changes in environmental factors such as day length, light intensity, sea ice extent and food availability and a rapid change in these conditions

in the face of climate warming (Atkinson et al. 2004; Pörtner et al. 2009; Schofield 2010). Not surprisingly, many polar pelagic organisms have evolved endogenous rhythmic physiological and behavioral functions, which are synchronized with these cyclic changes (e.g. Kawaguchi et al. 1986; Marcus and Scheef 2010; Meyer 2012; Jørgensen and Johnsen 2014).

Unfortunately, the range of conditions in which the clocks are operating in polar pelagic key organisms, such as krill, is not well understood. It is also not known which physiological and behavioral consequences might emerge when the daily and seasonal timing systems in these animals exceed their normal limits, protected from changes in temperature and pH. Increasing sea water temperature and changing sea ice dynamics may cause a change in the seasonal pattern of food availability in the environment leading to an earlier onset of biological production such as plankton spring blooms (Jørgensen and Johnsen 2014). The ovary of female krill begins to mature at this time, and the spring bloom is an important fuel for this process. However, whereas the phenology of environmental conditions to which the life cycle of key organisms is synchronized may change, the dominant stimulus (photo-period) of endogenous driven cycles will not. The ongoing environmental alterations might desynchronize previously matched interactions between the endogenous seasonal rhythms of key species such as krill (e.g. metabolic regulation, sexual maturation, and lipid accumulation) and its environment (e.g. seasonal sea ice dynamic, spring diatom blooms), which have evolved over millions of years.

Climate change driven modifications of organism performance, population size and species inventory add up to the overall changes in biodiversity observed at the community/ecosystem level. Assuming that the emergent behaviour of an ecosystem depends on the properties and behaviour of the species it is composed of, such change in biodiversity should cause responses at the ecosystem level. To understand these causal relationships and their implications for ecosystem functioning, goods and services, the response of the entire ecological network has to be analyzed (Woodward et al. 2010). Feeding relationships constitute the dominant type of organism-to-organism interaction in ecosystems, and hence the network approaches focus on food webs. Generally, environmental variability is buffered by system resilience, which is provided by organism adaptive capacity, functional biodiversity and functional redundancy, i.e. the networks' capacity for functional compensation (Bellwood et al. 2003; Fonseca and Ganade 2001; Johnson 2000; Naeem 1998). Hence, a system's capacity to buffer stress is likely to be correlated with biodiversity, because the more species a network is composed of, the greater trophic variety as well as redundancy among species might become (McCann 2000; Hooper et al. 2005).

Among the multitude of functional traits, species vulnerability to food web-mediated alterations seems to play a particularly important role (Petchey et al. 2008). Vulnerability of a species is expected to increase with predator diversity and to decrease with prey diversity (e.g. Jacob et al. 2011; Memmott et al. 2000; Mintenbeck et al. 2012). Hence, trophic network analysis facilitates the identification of species that may be particularly sensitive to food web alterations such as the Antarctic silverfish *Pleuragramma antarctica* in the Antarctic Ocean fish commu-

nity (Mintenbeck et al. 2012). Furthermore, we have to consider whether such secondary effects are isolated events or, through feedback and cascading mechanisms, may ripple through the whole network. Jacob et al. (2011) studied network robustness in relation to species functional traits in a 489 species marine food web from the Antarctic Weddell Sea. Their modeling approaches indicate that the initial, e.g., temperature induced loss of a few species may cause a cascade of secondary extinctions up to a network collapse to half its initial size. The severity of this secondary loss of biodiversity depends to a large extent on the functional traits of the primary extinctions, and effects are most severe when the most vulnerable species are lost initially. Jacob et al. (2011) hence reinforce the view that highly connected species are essential for network robustness (e.g., Dunne et al. 2002; Petchey et al. 2008) and thus for maintaining biodiversity under environmental change.

18.6 Expected and Observed Trends in Local Diversity Under Changing Climate

The net change in marine biodiversity at the local scale is a product of these counteracting temperature-dependent changes in immigration, phenology, physiology and interactions- and consequently extinctions. This net change comprises the change in local composition (temporal turnover) and the change in emergent biodiversity properties such as species richness. Recently, two major meta-analyses have analysed long-term trends in local marine species richness across ecosystems and organisms. Across 100 time series from terrestrial, freshwater and marine systems, no systematic loss of local species richness (α -diversity) was observed (Dornelas et al. 2014). Most data sets showed no net change in richness, however, the change in biotic composition (the shift in the identity of species present) was faster than predicted from null models in their data set (see Sect. 18.4). In an analysis of 471 time series, exclusively from coastal marine ecosystems, species richness showed predominantly positive trends (Elahi et al. 2015). Only for habitats for which locally an adverse human impact was reported (ca 3% of the studies), a clear negative trend in richness was observed. By contrast, time series from locations where positive effects were performed (e.g. via protection) showed a strong positive trend in richness. The habitats with equivocal or no information on environmental trends showed a weaker but on average positive richness trend.

A different picture arises from warming experiments: here, most experiments showed a decrease in species richness with increasing temperature across all three major realms, but especially pronounced in marine ecosystems (Gruner et al. 2017). The loss of species scaled directly to the degree of warming, i.e., higher warming resulted in more pronounced species loss. The difference between these experimental results and the observational time series warrants an explanation. Whereas methodological issues might contribute to these differences (duration of experiments versus time series, the latter also being affected by other environmental changes beyond warming), the major discrepancy is immigration: most experiments pre-

cluded or inhibited dispersal, thus measured temperature effects on coexistence via competition, facilitation and predation (see Fig. 18.1). The conclusion from these experiments thus is that local loss of species via these interactions is accelerated at higher temperature. This net negative effect of warming becomes visible if analysed in isolation, but not in natural time series, because there (re-) immigration counteracts species loss. As discussed for regional biodiversity, immigration effects are immediate, whereas extinction takes time, precluding the observation of richness decline in natural systems even if there is ample evidence that a warmer climate accelerates metabolic rates as well as population dynamics and consequently leads to faster effects of species interactions (Hillebrand et al. 2012).

In addition to the discrepancy between immediate immigration and delayed extinction, our current knowledge on biodiversity trends also suffers from a strong focus on species richness. The measured species richness in a habitat strongly depends on sampling effort (sample size and the completeness of the census), the size of the species pool (γ -diversity), and the dominance distribution in the community. Chase and Knight (2013) provide an excellent analysis of these issues and suggest that conclusions based on the relative change in species richness alone are prone to suffer from large uncertainties even if sampling effort is standardized. Consequently, species richness estimates have to be amended by other measures of biodiversity to reflect biodiversity change. Evenness, a measure of the relative dominance structure, has been proposed as a useful—and statistically more or less independent—measure of biodiversity (Hillebrand et al. 2008). The advantage of evenness is that it has a closed scale from 0 to 1, allowing easy comparison between sites. The disadvantage, however, is that species identity is not reflected - a shift to different species (e.g. from large long-lived to small short-lived) does not necessarily shift evenness even if the ecological consequences can be dramatic. Integrative indices combining information on dominance and number of taxa (e.g., Shannon, Simpson) are useful if complete knowledge of rare species is lacking, especially in extremely species-rich systems like coral reefs and the deep-sea. These indices as well as cumulative dominance plots are driven by dominance patterns with a focus on abundant species and down-weighted rare species. Still, these indices are crude simplifications of biodiversity and by definition do not address the role of rare species, which might have disproportionate impacts on ecosystem functions (Bracken and Low 2012).

Therefore, ecologists seek to get more complete information including shifts in taxon identity (e.g., species replacing each other), richness (number of taxa) and dominance into measures of temporal turnover (Fig. 18.1). While the meta-analysis by Dornelas et al. (2014) failed to show an overarching trend in species richness, a simultaneous analysis of temporal turnover showed a significant increase in species replacements over time. Another example, more closely related to climate change, is the analysis of the thermal effluent of a nuclear power plant in the Baltic Sea: along the gradient of >9 °C above ambient temperature, species richness was unaffected, but temporal turnover significantly accelerated with increasing temperature (Hillebrand et al. 2010). Thus, the number of species remained constant, but species were replaced faster (see also Guinder et al. 2010; Widdicombe et al. 2010). In a recent article, Hillebrand et al. (2017) used marine, freshwater and terrestrial time

series data to show that zero change in richness could be related to anything from none to full exchange of species composition. They argue strongly to base assessments of biodiversity change on multiple measures of composition.

The pitfalls of estimating biodiversity change have potentially dramatic consequences for ecosystem evaluation and management. The Marine Strategy Framework Directive by the European Union lists biodiversity as first descriptor of ecosystem status. Any substantial conclusion on biodiversity change, however, needs well-resolved and long-term continuous observation. Such a comprehensive overview of marine biodiversity and how it responds to natural and anthropogenic stressors is critical in our quest to understand the consequences of climate change for marine ecosystems and to develop management strategies. This requires the development and implementation of new multidisciplinary observation strategies that allow year-round long term observation of marine biodiversity with adequate spatial and temporal resolution, in parallel to physical and biogeochemical measurements. Here special emphasis should be put on integrating observations of marine microbial biodiversity, which has been understudied in the past due to technological constraints. Marine microbes account for 90% of ocean biomass, form the basis of marine food webs and regulate important biogeochemical cycles. Expected climate change related perturbation of marine microbial communities will have important consequences for higher trophic level productivity. Developing an observational framework to establish a baseline for the spatial and temporal variability of microbial biodiversity and community composition is therefore critical to understand consequences of climate change in the marine environment. During the past decades numerous publications successfully demonstrated the potential of molecular methods for refined high resolution assessment of marine microbial biodiversity (e.g. De Vargas et al., 2015; Sunagawa et al., 2015). It is expected that these methods will become progressively more integrated into the day-to-day repertoire of marine long term monitoring sites. Furthermore, combination of molecular biodiversity assessments with cutting edge automated underway sampling on-board ships, and moored sampling technology such as sediment traps or automated water samplers allows year round collection of marine microbes from the surface to the depths, even in remote marine environments. In the long run, molecular-based observation methods have strong potential to be part of multidisciplinary marine long term observation strategies in order to generate information on marine microbial biodiversity with adequate high spatio-temporal resolution (biodiversity and biogeography).

18.7 Protection

It is beyond doubt that marine biodiversity will change in the future. Temperature driven shifts in geographic distribution of species will probably lead to increase of biodiversity in high latitudes and decrease of biodiversity in tropics (Beaugrand et al. 2015; Thomas et al. 2012) with consequences for marine ecosystem

productivity. Decrease of the number of cold water species and increasing dominance of warm water species might lead to homogenisation of communities among the globe. Furthermore, disproportionately higher proportion of extinctions at the top of the trophic cascade together with spreading invasions at the bottom of the trophic cascade (Lotze et al. 2006) will potentially change functioning and structure of marine food webs.

The only way to avoid degradation of ecosystems in the face of climate change is reduction of anthropogenic pressure. It becomes clear that we need to radically reduce greenhouse gases emissions and avoid irreversible losses of biodiversity. However, it is not yet clear how to avoid biodiversity loss and whether we only should protect hot spots of an exceptionally high diversity or also places with unique species composition, which contribute considerably to the maintenance of co-existence of species and the ecosystem services and goods they could sustainably provide.

There is strong evidence that marine protected areas and fisheries closures improve biodiversity. In areas where negative impacts were alleviated or positive measures taken, species richness increased in the global analysis of coastal marine biodiversity time series (Worm et al. 2006; Elahi et al. 2015). Moreover, increased diversity enhanced ecosystem functions and had a positive impact on ecosystem recovery after climatic extremes (Worm et al. 2006). Increasing coastal vegetation by restoration of mangroves, salt marshes and seagrass meadows is another promising approach to improve local ecosystem health. Coastal vegetation does not only provide habitat for many aquatic and terrestrial organisms, but it also reduces soil erosion and has a great capacity to sequester atmospheric CO₂ (Bruno et al. 2014).

To understand adaptive capacity of species to climate warming and to identify ecosystem attributes that promote ecosystem resilience, we need effective long-term monitoring programs which would provide practical information for conservation and ecosystem-based management. Management strategies should focus on dominant anthropogenic stressors such as eutrophication and overfishing accompanying climate warming (Sale 2008) and should assess cumulative impact of both natural and human-driven perturbations (Halpern et al. 2007). Unfortunately, governance and decision processes are often organized around single-sectors (e.g. fisheries, tourism), challenging holistic approaches to ecosystem-based management (see Chaps. 5, 6 and 7).

References

- Amarasekare P (2015) Effects of temperature on consumer-resource interactions. *J Anim Ecol* 84:665–679
- Araujo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species-climate impact models under climate change. *Glob Chang Biol* 11:1504–1513
- Arrigo KR, Thomas DN (2004) Large scale importance of sea ice biology in the Southern Ocean. *Antarct Sci* 16:471–486
- Atkinson A, Siegel V, Pakhomov EA, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–103
- Atkinson A, Siegel V, Pakhomov EA, Rothery P, Loeb V, Ross RM, Quentin LB, Schmidt K, Fretwell P, Murphy EJ, Tarling GA, Fleming AH (2008) Oceanic circumpolar habitats of Antarctic krill. *Mar Ecol Prog Ser* 362:1–23

- Balmaseda MA, Trenberth KE, Källén E (2013) Distinctive climate signals in reanalysis of global ocean heat content. *Geophys Res Lett* 40:1754–1759
- Beaugrand G, Edwards M, Raybaud V, Goberville E, Kirby RR (2015) Future vulnerability of marine biodiversity compared with contemporary and past changes. *Nat Clim Change* 5:695–701
- Beaugrand G, Luczak C, Edwards M (2009) Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Glob Chang Biol* 15:1790–1803
- Beaugrand G, Reid PC, Ibanez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296:1692–1694
- Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. *Nature* 426:661–664
- Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecol Lett* 6:281–285. doi:10.1046/j.1461-0248.2003.00432.x
- Block BA et al (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature* 475:86–90
- Boetius A, Albrecht S, Bakker K, Bienhold C, Felden J, Fernández-Méndez M, Hendricks S, Katlein C, Lalande C, Krumpfen T, Nicolaus M, Peeken I, Rabe B, Rogacheva A, Rybakova E, Somavilla R, Wenzhöfer F, RV Polarstern ARK27-3-Shipboard Science Party (2013) Export of algal biomass from the melting Arctic sea ice. *Science* 339:1430–1432
- Bracken MES, Low NHN (2012) Realistic losses of rare species disproportionately impact higher trophic levels. *Ecol Lett* 15:461–467
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789
- Bruno JF, Harley CDG, Burrows MT (2014) Climate change and marine communities. In: Bertness MD, Bruno JF, Silliman BR, Stachowicz JJ, Bertness MD, Bruno JF, Silliman BR, Stachowicz JJ (eds) *Marine community ecology and conservation*. Sinauer Associates, Inc., Sunderland, MA
- Burthe S et al (2012) Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web. *Mar Ecol Prog Ser* 454:119–133
- Cai W, Borlace S, Lengaigne M, van Rensch P, Collins M, Vecchi G, Timmermann A, Santoso A, McPhaden MJ, Wu L, England MH, Wang G, Guilyardi E, Jin F-F (2014) Increasing frequency of extreme el nino events due to greenhouse warming. *Nature Clim. Change* 4:111–116.
- Comiso JC (2010) Variability and trends of the global sea ice cover. In: Thomas DN, Dieckmann GS (eds) *Sea ice*, 2nd edn. Wiley-Blackwell, Oxford, UK, pp 205–246
- Chase JM, Knight TM (2013) Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecol Lett* 16:17–26
- Chen IC, Hill JK, Ohlemuller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026
- Cheung WWL, Lam VWY, Sarmiento JL, Kearny K, Watson R, Pauly D (2008a) Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish* 10:235–251
- Cheung WWL, Lam VWY, Pauly D (2008b) Dynamic bioclimate envelope model to predict climate-induced changes in distribution of marine fishes and invertebrates. *Fish Centre Res Rep* 16:5–50
- Chevin LM, Lande R, Mace GM (2010) Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biol* 8:e1000357
- Cook AJ, Fox AJ, Vaughan DG, Ferrigno JG (2005) Retreating glacial fronts on the Antarctic Peninsula over the past half-century. *Science* 308:541–544
- Donelson JM, Munday PL, McCormick MI, Pitcher CR (2012) Rapid transgenerational acclimation of a tropical reef fish to climate change. *Nat Clim Chang* 2:30–32
- Dornelas M et al (2014) Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344:296–299
- Drakare S, Lennon JJ, Hillebrand H (2006) The imprint of the geographical, evolutionary and ecological context on species-area relationships. *Ecol Lett* 9:215–227
- Dulvy NK, Sadovy Y, Reynolds JD (2003) Extinction vulnerability in marine populations. *Fish Fish* 9:261–285

- Dunne JA, Williams RJ, Martinez ND (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol Lett* 5:558–567
- Durant JM et al (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecol Lett* 8:952–958
- Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430:881–883
- Elahi R et al (2015) Recent trends in local-scale marine biodiversity reflect community structure and human impacts. *Curr Biol* 25:1938–1943
- Fahrbach E, Hoppema M, Rohardt G, Boebel O, Klatt O, Wisotzki A (2011) Warming of deep and abyssal water masses along the Greenwich meridian on decadal time scales: the Weddell gyre as a heat buffer. *Deep-Sea Res II* 58:2509–2523
- Follows MJ, Dutkiewicz S, Grant S, Chisholm SW (2007) Emergent biogeography of microbial communities in a model ocean. *Science* 315:1843–1846
- Fonseca CR, Ganade G (2001) Species functional redundancy, random extinctions and the stability of ecosystems. *J Ecol* 89:118–125. doi:[10.1046/j.1365-2745.2001.00528.x](https://doi.org/10.1046/j.1365-2745.2001.00528.x)
- Gilbert B, Levine JM (2013) Plant invasions and extinction debts. *Proc Natl Acad Sci U S A* 110:1744–1749
- Gruner DS, Bracken MES, Berger SA, Eriksson BK, Gamfeldt L, Matthiessen B, Moorthi S, Sommer U, Hillebrand H (2017) Effects of experimental warming on biodiversity depend on ecosystem type and local species composition. *Oikos* 126:8–17
- Guinder VA et al (2010) Long-term changes in phytoplankton phenology and community structure in the Bahia Blanca Estuary, Argentina. *Mar Biol* 157:2703–2716
- Gutt J, Zurell D, Bracegirdle TJ, Cheung W, Clarke MS, Convey P, Danis B, David B, De Broyer C, di Prisco G, Griffiths H, Laffont R, Peck L, Pierrat B, Riddle MJ, Saucedo T, Turner J, Verde C, Wang Z, Grimm V (2012) Correlative and dynamic species distribution modelling for ecological predictions in the Antarctic: a cross-disciplinary concept. *Polar Res* 31:11091. doi:[10.3402/polar.v31i0.11091](https://doi.org/10.3402/polar.v31i0.11091)
- Gutt J, Bertler N, Bracegirdle TJ, Buschmann A, Comiso J, Hosie G, Isla E, Schloss IR, Smith CR, Tournadre J, Xavier JC (2015) The Southern Ocean ecosystem under multiple climate stresses – an integrated circumpolar assessment. *Glob Chang Biol* 21:1434–1453. doi:[10.1111/geb.12794](https://doi.org/10.1111/geb.12794)
- Halpern BS, Selkoe KA, Micheli F, Kappel CV (2007) Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. *Conserv Biol* 12:1301–1315
- Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecol Lett* 8:461–467
- Harley CDG (2011) Climate change, keystone predation, and biodiversity loss. *Science* 334:1124–1127
- Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. *Trends Ecol Evol* 20(6):337–344
- Hazen EL et al (2013) Predicted habitat shifts of Pacific top predators in a changing climate. *Nat Clim Chang* 3:234–238
- He FL, Hubbell SP (2011) Species-area relationships always overestimate extinction rates from habitat loss. *Nature* 473:368–371
- Hillebrand H, Blasius B, Borer ET, Chase JM, Downing JA, Eriksson BK, Filstrup CT, Harpole WS, Hodapp D, Larsen S, Lewandowska AM, Seabloom EW, Van de Waal DB, Ryabov AB (2017) Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *Journal of Applied Ecology*, online early. doi:[10.1111/1365-2664.12959](https://doi.org/10.1111/1365-2664.12959)
- Hillebrand H, Bennett DM, Cadotte MW (2008) Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89:1510–1520
- Hillebrand H, Burgmer T, Biermann E (2012) Running to stand still: temperature effects on species richness, species turnover, and functional community dynamics. *Mar Biol* 159:2415–2422
- Hillebrand H, Soininen J, Snoeijs P (2010) Warming leads to higher species turnover in a coastal ecosystem. *Glob Chang Biol* 16:1181–1193
- Hooper DU, Chapin Iii F, Ewel J, Hector A, Inchausti P, Lavorel S, Lawton J, Lodge D, Loreau M, Naem S (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35

- Jacob U, Thierry A, Brose U, Arntz WE, Berg S, Brey T, Fetzer I, Jonsson T, Mintenbeck K, Möllmann C, Petchey O, Riede JO, Dunne JA (2011) The role of body size in complex food webs: a cold case. *Adv Ecol Res* 45:182–223. doi:[10.1016/B978-0-12-386475-8.00005-8](https://doi.org/10.1016/B978-0-12-386475-8.00005-8)
- IPCC (2013) Summary for policymakers. In: Stocker TF et al (eds) *Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge University Press, Cambridge and New York, pp 1–18
- Isla JA, Lengfellner K, Sommer U (2008) Physiological response of the copepod *Pseudocalanus* sp. in the Baltic Sea at different thermal scenarios. *Glob Chang Biol* 14:895–906
- Johnson KH (2000) Trophic-dynamic considerations in relating species diversity to ecosystem resilience. *Biol Rev Camb Philos Soc* 75:347–376
- Jørgensen EH, Johnsen HK (2014) Rhythmic life of the Arctic charr: adaptations to life at the edge. *Mar Genomics* 14:71–81
- Jump AS, Penuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol Lett* 8:1010–1020
- Kawaguchi K, Ishikawa S, Matsuda O (1986) The overwintering strategy of Antarctic krill (*Euphausia superba* Dana) under the coastal fast ice off the Ongul Islands in Lützow-Holm Bay, Antarctica. *Mem Nat Inst Polar Res Spec Iss* 44:67–85
- Lewis OT (2006) Climate change, species–area curves and the extinction crisis. *Philos Trans R Soc B Biol Sci* 361:163–171
- Litchman E, Edwards KF, Klausmeier CA, Thomas MK (2012) Phytoplankton niches, traits and eco-evolutionary responses to global environmental change. *Mar Ecol Prog Ser* 470:235–248
- Llovel W, Willis JK, Landerer FW, Fukumori I (2014) Deep-ocean contribution to sea level and energy budget not detectable over the past decade. *Nat Clim Chang* 4:1031–1035
- Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–1809
- Marcus NH, Scheef LP (2010) Photoperiodism in copepods. In: Nelson RJ, Denlinger DL, Somers DE (eds) *Photoperiods – the biological calendar*. Oxford University Press, New York, pp 193–217
- McCann KS (2000) The diversity–stability debate. *Nature* 405:228–233
- Memmott J, Martinez ND, Cohen JE (2000) Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *J Anim Ecol* 69:1–15
- Meyer B (2012) The overwintering of Antarctic krill *Euphausia superba*, from an ecophysiological perspective – a review. *Polar Biol* 35:15–37
- Mintenbeck K, Barrera-Oro ER, Brey T, Jacob U, Knust R, Mark FC, Moreira E, Strobel A, Arntz WE (2012) Impact of climate change on fishes in complex Antarctic ecosystems. *Adv Ecol Res* 46:351–426. doi:[10.1016/B978-0-12-396992-7.00006-X](https://doi.org/10.1016/B978-0-12-396992-7.00006-X)
- Moline MA, Claustre H, Frazer TK, Schofield O, Vernet M (2004) Alternation of the food web along the Antarctic Peninsula in response to a regional warming trend. *Glob Chang Biol* 10:1973–1980
- Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE, Schofield O (2009) Recent changes in phytoplankton communities associated with rapid regional climate change along the Western Antarctic Peninsula. *Science* 323:1470–1473
- Munday P, Warner RR, Monro K, Pandolfi JM, Marshall DJ (2013) Predicting evolutionary responses to climate change in the sea. *Ecol Lett* 16:1488–1500
- Naem S (1998) Species redundancy and ecosystem reliability. *Conserv Biol* 12:39–45
- O’Connor MI (2009) Warming strengthens an herbivory-plant interaction. *Ecology* 90:388–398
- O’Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP et al (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proc Natl Acad Sci U S A* 104:1266–1271
- Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B, Dieckmann U (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428:932–935
- Parmesan C et al (2005) Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos* 108:58–75
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42

- Petchey OL, Eklöf A, Borrvall C, Ebenman B (2008) Trophically unique species are vulnerable to cascading extinction. *Am Nat* 171:568–579
- Philippart CJM, van Aken HM, Beukema JJ, Bos OG, Cadee GC, Dekker R (2003) Climate-related changes in recruitment of the bivalve *Macoma balthica*. *Limnol Oceanogr* 48:2171–2185
- Poloczanska ES et al (2013) Global imprint of climate change on marine life. *Nat Clim Chang* 3:919–925
- Pörtner HO, Farrell AP (2008) Physiology and climate change. *Science* 322:690–692
- Pörtner H, Farrell A, Knust R et al (2009) Adapting to climate change – response. *Science* 323:876–877
- Pörtner HO (2010) Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *J Exp Biol* 213:881–893
- Rahmsdorf S, Box JE, Feulner G, Mann ME, Robinson A, Rutherford S, Schaffernicht EJ (2015) Exceptional twentieth-century slowdown in Atlantic Ocean overturning circulation. *Nat Clim Chang* 5:475–480
- Reuman DC, Holt RD, Yvon-Durocher G (2014) A metabolic perspective on competition and body size reductions with warming. *J Anim Ecol* 83:59–69
- Reusch TBH (2013) Climate change in the oceans: evolutionary versus phenotypically plastic responses of marine animals and plants. *Evol Appl* 7:104–122
- Roemmich D, Church J, Gilson J, Monselesan D, Sutton P, Wihffels S (2015) Unabated planetary warming and its ocean structure since 2006. *Nat Clim Chang* 5:240–245
- Sale PF (2008) Management of coral reefs: where we have gone wrong and what we can do about it. *Mar Pollut Bull* 56:805–809
- Sarmiento JL, Slater R, Barber R, Bopp L, Doney SC, Hirst AC, Kleypas J, Matear R, Mikolajewicz U, Monfray P, Soldatov V, Spall SA, Stouffer R (2004) Response of coean ecosystem to climate change. *Glob Biogeochem Cycles* 18:GB3003. doi:[10.1029/2003GB002134](https://doi.org/10.1029/2003GB002134)
- Schofield O (2010) How do polar marine ecosystems respond to rapid climate? *Science* 328:1520–1523
- Smith GR, De Leo FC, Bernardino AF, Sweetman AK, Martinez Arbizu P (2008) Abyssal food limitation, ecosystem structure and climate change. *Trends Ecol Evol* 23:518–528
- Sokolov S, Rintoul SR (2009) Circumpolar structure and distribution of the Antarctic circumpolar current fronts: 2. Variability and relationship to sea surface height. *J Geophys Res Oceans* 114. doi:[10.1029/2008JC005248](https://doi.org/10.1029/2008JC005248)
- Somero GN (2005) Linking biogeography to physiology: evolutionary and acclimatory adjustments of thermal limits. *Front Zool* 2:1. doi:[10.1186/1742-9994-2-1](https://doi.org/10.1186/1742-9994-2-1)
- Sommer U, Aberle N, Lengfellner K, Lewandowska A (2012) The Baltic Sea spring phytoplankton bloom in a changing climate: an experimental approach. *Mar Biol* 159:2479–2490
- Storch D, Menzel L, Frickenhaus S, Pörtner HO (2014) Climate sensitivity across marine domains of life: limits to evolutionary adaptation shape species interactions. *Glob Chang Biol* 20(10):3059–3067
- Sunagawa S et al (2015) Structure and function of the global ocean microbiome. *Science* 348:6237
- Thackeray SJ et al (2010) Trophic level synchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Glob Chang Biol* 16:3304–3313
- Thomas CD et al (2004) Extinction risk from climate change. *Nature* 427:145–148
- Thomas MK, Kremer CT, Klausmeier CA, Litchman E (2012) A global pattern of thermal adaptation in marine phytoplankton. *Science* 338:1085–1088
- Thuiller W, Lavorel S, Araujo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. *Proc Natl Acad Sci U S A* 102:8245–8250
- Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt. *Nature* 371:65–66
- Turner J, Bindschadler R, Convey P, di Prisco G, Fahrbach E, Gutt J, Hodgson D, Mayewsky P, Summerhayes C (2009) Antarctic climate change and the environment. SCAR, Scott Polar Research Institute, Cambridge. 526p
- Vargas D et al (2015) Eukaryotic plankton diversity in the sunlit ocean. *Science*:348. doi:[10.1126/science.1261605](https://doi.org/10.1126/science.1261605)

- Wearn OR, Reuman DC, Ewers RM (2012) Extinction debt and windows of conservation opportunity in the Brazilian Amazon. *Science* 337:228–232
- Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol Monogr* 30:279–338
- Widdicombe C et al (2010) Long-term phytoplankton community dynamics in the Western English Channel. *J Plankton Res* 32:643–655
- Wilson RJ, Gutierrez D, Gutierrez J, Martinez D, Agudo R, Monserrat VJ (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecol Lett* 8:1138–1146
- Wilson RJ, Thomas CD, Fox R, Roy DB, Kunin WE (2004) Spatial patterns in species distributions reveal biodiversity change. *Nature* 432:393–396
- Woodward G, Benstead JP, Beveridge OS, Blanchard J, Brey T, Brown L, Cross WF, Friberg N, Ings TC, Jacob U, Jennings S, Ledger ME, Milner AM, Montoya JM, Pichler DE, O’Gorman E, Petchey OL, Olesen JM, Reuman DC, Thompson MS, Van Veen FJF, Yvon-Durocher G (2010) Ecological networks in a changing climate. *Adv Ecol Res* 42:71–138. doi:[10.1016/S0065-2504\(10\)42002-4](https://doi.org/10.1016/S0065-2504(10)42002-4)
- Worm B et al (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787–790
- Xenopoulos MA, Lodge DM, Alcamo J, Marker M, Schulze K, Van Vuuren DP (2005) Scenarios of freshwater fish extinctions from climate change and water withdrawal. *Glob Chang Biol* 11:1557–1564