ANNUAL REVIEWS

Annual Review of Marine Science

How Do Marine Pelagic Species Respond to Climate Change? Theories and Observations

Grégory Beaugrand[1,2] and Richard R. Kirby[3]

[1] Laboratoire d'Océanologie et de Géosciences, CNRS UMR 8187 LOG, Université de Lille and Université du Littoral Côte d'Opale, F-62930 Wimereux, France; email: gregory.beaugrand@univ-lille1.fr

[2] Sir Alister Hardy Foundation for Ocean Science, Plymouth PL1 2PB, United Kingdom

[3] Secchi Disk Foundation, Yealmpton PL8 2HU, United Kingdom

Annu. Rev. Mar. Sci. 2018. 10:169–97

The *Annual Review of Marine Science* is online at marine.annualreviews.org

https://doi.org/10.1146/annurev-marine-121916-063304

Keywords

climatic variability, climate change, environment, marine species, communities, theories, observations, biodiversity

Abstract

In this review, we show how climate affects species, communities, and ecosystems, and why many responses from the species to the biome level originate from the interaction between the species' ecological niche and changes in the environmental regime in both space and time. We describe a theory that allows us to understand and predict how marine species react to climate-induced changes in ecological conditions, how communities form and are reconfigured, and so how biodiversity is arranged and may respond to climate change. Our study shows that the responses of species to climate change are therefore intelligible—that is, they have a strong deterministic component and can be predicted.

ANNUAL REVIEWS

Annual Review of Marine Science

How Do Marine Pelagic Species Respond to Climate Change? Theories and Observations

Grégory Beaugrand[1,2] and Richard R. Kirby[3]

[1]Laboratoire d'Océanologie et de Géosciences, CNRS UMR 8187 LOG,
Université de Lille and Université du Littoral Côte d'Opale, F-62930 Wimereux,
France; email: gregory.beaugrand@univ-lille1.fr

[2]Sir Alister Hardy Foundation for Ocean Science, Plymouth PL1 2PB, United Kingdom

[3]Secchi Disk Foundation, Yealmpton PL8 2HU, United Kingdom

Annu. Rev. Mar. Sci. 2018. 10:169–97

The *Annual Review of Marine Science* is online at marine.annualreviews.org

https://doi.org/10.1146/annurev-marine-121916-063304

Keywords

climatic variability, climate change, environment, marine species, communities, theories, observations, biodiversity

Abstract

In this review, we show how climate affects species, communities, and ecosystems, and why many responses from the species to the biome level originate from the interaction between the species' ecological niche and changes in the environmental regime in both space and time. We describe a theory that allows us to understand and predict how marine species react to climate-induced changes in ecological conditions, how communities form and are reconfigured, and so how biodiversity is arranged and may respond to climate change. Our study shows that the responses of species to climate change are therefore intelligible—that is, they have a strong deterministic component and can be predicted.

INTRODUCTION

Marine pelagic systems are strongly affected by the impact of climate on temperature (its mean and variability) through its influence on atmospheric circulation, wind direction, and the intensity of oceanic currents and upwelling (Bigg 1996). Climate also influences salinity (by affecting ocean currents, evaporation, precipitation, and sea ice extent), oxygen concentration (by altering the thermal regime and oceanic mixing), macronutrients (by controlling the mixing of the water column, upwelling, and river discharge), micronutrients (through the influence of atmospheric circulation on aeolian inputs), and pH (which is influenced seasonally by photosynthesis) (Comiso et al. 2008, Dickson et al. 1996, Feely et al. 2009, Sarmiento et al. 2004). Climatic variation, whether natural or resulting from anthropogenic causes, can therefore alter the local ecological conditions of pelagic habitats to affect the abundance of species and the composition of biological communities.

To appreciate how climatic variability and climate change affect biodiversity, we need a clear idea of the processes that shape living systems, which means that climate change biology should be founded in biogeography and macroecology. It was for this purpose that we developed the macroecological theory on the arrangement of life (METAL) to explain how marine species, communities, ecosystems, and the emergent biodiversity are organized in space and time, and so how they are reconfigured by changing environmental conditions (Beaugrand 2015). METAL therefore provides a unifying framework to understand how climate change can alter life from low to high organizational levels (Beaugrand et al. 2014, 2015). In this review, we show that the theory helps elucidate many of the biological changes that have already been ascribed to climate and show that they are connected through the interactions between the species ecological niche and the environmental regime.

METAL enables us to propose a hierarchical sequence of responses of species to climate change that involves, in the following order, behavior, physiology, phenology (seasonal dilatation or contraction), annual abundance, biogeography (biogeographical shifts and range expansion or contraction), extinction, and adaptation (**Figure 1**). Behavioral adjustment (also termed behavioral plasticity) enables a species to exploit the habitat microheterogeneity to remain in environmental conditions that are close to their ecological optimum, e.g., thermotaxis. Physiological adjustment enables an organism to acclimate to environmental conditions that depart from the ecological optimum of the species. When this type of adjustment becomes difficult, normal life is compromised and local abundance diminishes. When climate cannot be overcome by behavioral and physiological adjustments (acclimatization), it affects the seasonal distribution of the species locally. Phenological adjustment (also called phenological plasticity) is therefore the response of a species to changing local environmental conditions in order to remain in an environment that enables optimal growth and reproduction, and maintain annual abundance at the highest possible level. When phenological plasticity becomes difficult, annual average abundance diminishes, leading eventually to the local extirpation of a species. Annual average abundance changes resulting from the positive and negative effects of local climate can alter a species' spatial distribution. The sum of all local effects on annual average abundance that lead eventually to local extirpation or appearance can be perceived at a macroecological scale as a biogeographical shift. Extinction occurs eventually when range contraction is complete. Finally, adaptation, which can enable a species to avoid global extinction, is a modification in the genotype that enables an alteration of the biology of a species that modifies its ecological niche. [Note that we consider that (*a*) the niche is controlled by the genotype, and any alteration of the niche of a species results from a modification in its genotype, and (*b*) the norm of reaction is included within the ecological niche.] Adaptation to new environmental conditions, which might be impossible if the magnitude and speed of climate change are too great, is briefly discussed in our review because its effect is to alter the shape of a species' ecological niche and therefore the interaction between the organism and its environment.

Habitat: the place where a species lives

Environment: the sum of all conditions, including allogenic and autogenic factors; these factors may or may not affect living organisms

Niche: the sum of all environmental factors that enable a species to complete its life cycle

Phenology: the schedule of recurring biological events in plants and animals; it can be measured in several ways depending on the system under investigation

Extinction: the full disappearance of a species

Acclimatization: the adjustment of an organism to temporal environmental fluctuations

Extirpation: the local disappearance of a species

Norm of reaction: the range of phenotypes expressed across a large range of environmental conditions

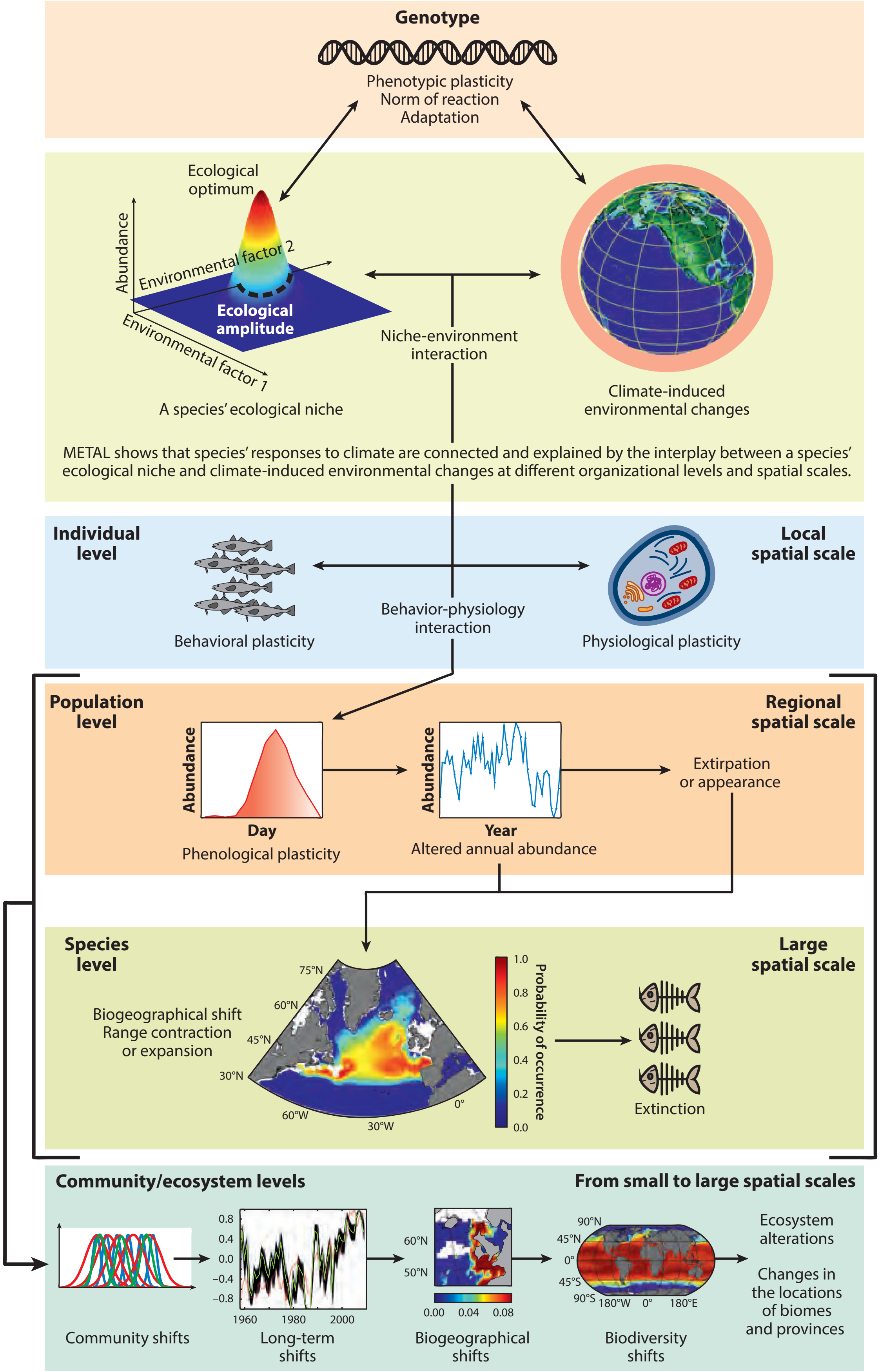

Figure 1

Theoretical diagram summarizing the different types of responses explained by the macroecological theory on the arrangement of life (METAL) from the species level to the community and ecosystem levels. METAL connects and explains climate-induced behavioral, physiological, and phenological shifts, as well as changes in annual average abundance, local extirpation and appearance, biogeographical shifts, range expansion and contraction, and extinction. Note that the norm of reaction is included in the ecological amplitude of the niche, whereas adaptation modifies the shape of the niche.

When METAL is applied at the community and ecosystem levels, the local species' individual responses to climate alter the pelagic community in a predictive way, resulting from the propagation of the interaction between the species' ecological niche and the ecological conditions at higher organizational levels. Here, the response includes seasonal succession, gradual and abrupt community shifts, the spatial distribution of species assemblages, biodiversity, ecosystems, and biomes (**Figure 1**). Changes in seasonal succession can sometimes trigger trophic mismatch, but provided no other important ecological dimensions or habitat requirements differ among species, METAL predicts that community reassembly should be limited. Gradual community shifts have been frequently reported, sometimes associated with abrupt community shifts, and arise from the individual species' responses to climate that reconfigure communities in a given region. Biogeographical shifts of species' assemblages suggest that community reconfiguration is limited. Biodiversity is affected by the reconfiguration of communities triggered by phenological and biogeographical shifts of species. Ecosystem-level changes affecting ecosystem functioning and associated goods and services are altered by biodiversity rearrangement. Finally, the spatial movements of provinces or biomes are the consequence of regional biodiversity rearrangements.

RESPONSES TO CLIMATE AT THE SPECIES LEVEL

Each species has its own unique ecological niche, which reflects the sum of all environmental factors that enable it to complete its life cycle. We propose that most responses of species to climate are linked through this concept (*sensu* Hutchinson 1957). We assume that the ecological niche is under the control of genes that determine a species' biology and therefore its response to environmental change (**Figure 1**). A species is capable of phenotypic plasticity (acclimatization) to extend its distributional range (i.e., its southern and northern boundaries) or to achieve seasonal acclimatization. Phenotypic plasticity can be accomplished in many ways, e.g., by a change in enzyme concentration or activity, homeoviscous adaptation, or the synthesis of new proteins or cryoprotective molecules. Phenotypic plasticity usually has limits, however, which explains why there are only a few pandemic species and why a subarctic species cannot become a temperate species on a short timescale. The species' niche integrates its norm of reaction (Shama et al. 2011) when its entire spatial distribution throughout the year is considered. METAL shows that the ecological niche is a fundamental macroscopic property of a species, which elucidates the response of living systems to climatic variability and climate change from the species to the community and higher organizational levels (Beaugrand 2015). Below, we review the different types of expected responses, from local to global adjustments, and integrate them into a unifying framework.

Local Adjustments

Here, we cover responses to climate change that take place from microscales to regional scales (<1 m to several kilometers), including (*a*) behavioral adjustments, (*b*) physiological adjustments, (*c*) phenological adjustments, and (*d*) changes in annual abundance. The initial response to adverse environmental conditions is likely to be acclimatization, involving first a behavioral change to exploit environmental conditions that are closest to the species' ecological optimum and then a physiological adjustment if behavioral adjustment is insufficient. Physiological adjustment requires energy, however, and therefore will be limited in time. If further acclimatization becomes impossible, phenological adjustment occurs. Together, these changes subsequently affect the annual average local abundance of the species, which is the fourth adjustment. All four types of adjustment result from the interaction between the ecological niche and environmental conditions from the individual to the population.

Behavioral adjustments. Behavioral adjustment is probably used by all pelagic organisms to attenuate the effects of environmental variability on physiological performance (Huey et al. 2003, Sunday et al. 2014, Zmiri et al. 1974). In particular, ectotherms exploit habitat heterogeneity by adjusting their time (e.g., day or night) or place of activity to maximize biological efficiency and save the cost of physiological adjustment, or to cope temporarily with extreme (damaging or lethal) hydrometeorological events (Perry et al. 2005, Sims et al. 2006). Behavioral adjustment is particularly relevant in places where the water column is heterogeneous either horizontally or vertically. Living close to a thermocline or a horizontal frontal structure may enable a species to exploit the heterogeneity of their thermal environment; this will depend on the species mobility and life history traits that control dispersal, foraging behavior (e.g., tuna and dogfish), or migration (e.g., herring and tuna). Behavioral adjustment to temperature must take place with respect to other environmental parameters, however, and trade-offs likely exist. For example, vertical migration to escape temperatures that are too warm is possible providing that other environmental variables remain suitable.

Distinct vertical distributions of two copepods, *Calanus finmarchicus* (a subarctic species) and *Calanus helgolandicus* (a temperate, pseudo-oceanic species), have been reported in Dogger Bank in the North Sea (Jónasdóttir & Koski 2011): The temperate species was observed at the surface, whereas the cold-water species occurred at depths of 30–50 m (**Figure 2**). Behavioral adjustment therefore enables species to occur in a habitat with environmental conditions close to those of their optimal ecological niche. The phytoplankton food of both copepod species lives near the surface, however, which will ultimately constrain the vertical distribution of these two species and therefore their local response to changing temperature. Other examples include marine organisms that migrate offshore to escape cold inshore winter temperatures and those, like seabirds, that migrate over long distances (Guilford et al. 2009, McQuinn 1997).

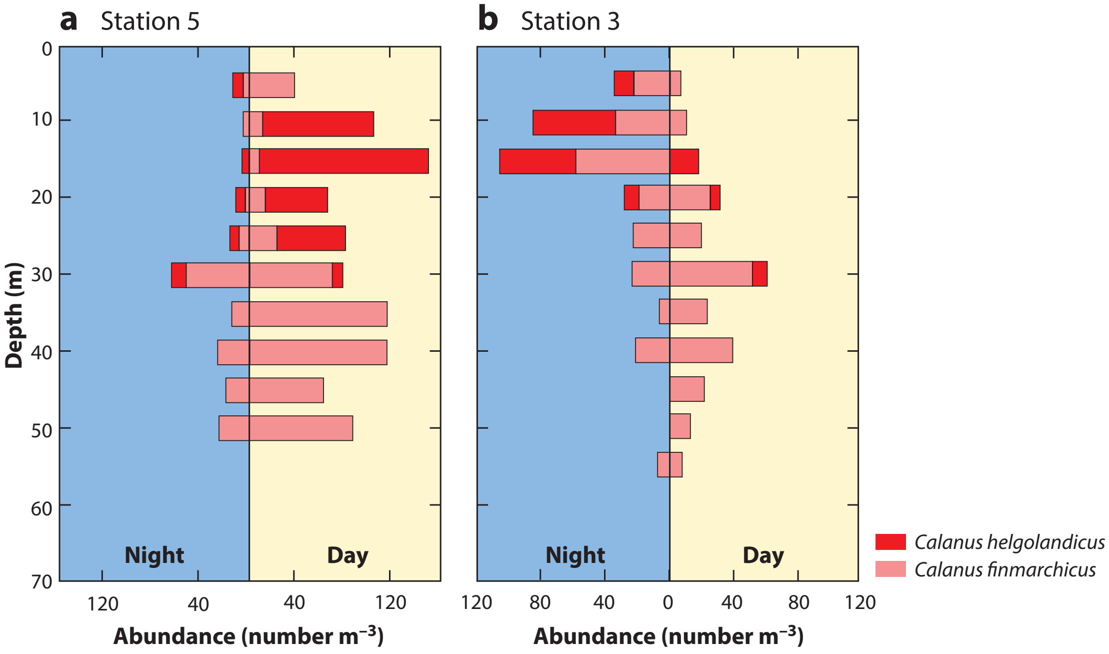

Figure 2

Vertical and diurnal changes in the abundance of female *Calanus helgolandicus* (*dark red bars*) and *Calanus finmarchicus* (*light red bars*) at day and night at two stations close to Dogger Bank in 2005: (*a*) station 5 (56°N, 4°E) and (*b*) station 3 (56.3°N, 3.7°E). Adapted from Jónasdóttir & Koski (2011).

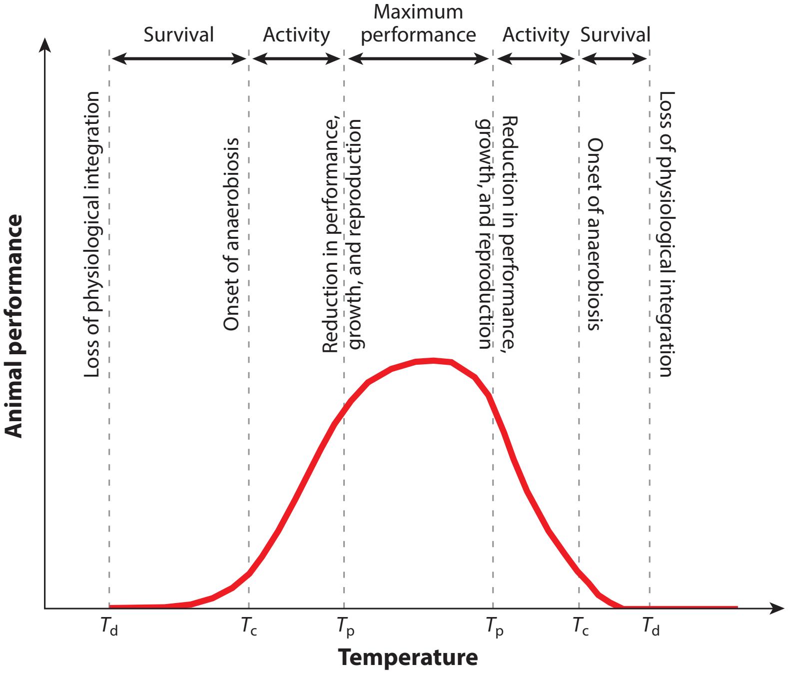

Figure 3

Physiological effects of temperature on an ectotherm. T_p is the pejus thermal threshold, at which aerobic metabolism begins to diminish; T_c is the critical thermal threshold, at which activity ceases; and T_d is the denaturation thermal threshold, at which denaturation begins.

Physiological adjustments. The normal activities of individual species take place within a range of thermal conditions, which vary from one species to another (**Figure 3**). Physiological adjustment occurs when thermal stress moves a species too far from its thermal optimum and behavioral plasticity can no longer compensate. At the individual level, thermal stress may be acute (resulting from an extreme hydrometeorological event, such as an El Niño event) or chronic (resulting from gradual, persistent climate change). Using the terminology defined by Shelford (1931) to describe the law of tolerance, Frederich & Pörtner (2000) described the changing performance of the spider crab *Maja squinado* by examining how hemolymph oxygen tensions, ventilation, and heart rate varied from 0°C to 40°C. They determined the range of optimum performance by identifying the pejus (meaning "turning worse") temperature thresholds (T_p) of the animal—the first threshold at which aerobic metabolism starts to diminish. T_p is thought to occur earlier at higher temperatures than it does at lower temperatures because adaptation to a hyperthermic stress seems to be more difficult (Frederich & Pörtner 2000). Physiological stress leads to immunodepression, making the species less resistant to parasites and pathogens. When the thermal stress reaches the critical temperature T_c, anaerobiosis starts and activity ceases. If the thermal stress continues, torpor takes over the organism, and survival is rapidly threatened. In the field, survival is further exacerbated by negative species interactions (e.g., parasitism, disease, and predation). When temperature attains the denaturation temperature threshold T_d, metabolic dysfunction has cascading effects at the cellular level. The thermal stress disrupts coordination between mutually dependent biochemical reactions, leading to a loss of physiological integration. Those physiological thresholds constrain species distribution and their response to climate change (Pörtner 2001).

In the case of climate change, the chronic effect of a thermal stress progressively perturbs an animal's biology and affects its population dynamics. The physiological adjustment of an individual species to temperature has an energetic cost that subsequently affects other functions, such as swimming, foraging activity, growth, and reproduction. Individuals become less competitive or resistant to predation, and mortality rapidly rises. When adverse environmental conditions become severe and frequent, reproduction and population growth decrease, reducing local population density.

Biotope: the set of dominant physical and chemical characteristics experienced by a community; an ecosystem results from the interaction between the biocoenosis and the biotope

A special case of physiological adjustment is dormancy, which is characterized by limited activity, growth, and development (Baumgartner & Tarrant 2017). A special type of dormancy in copepods is diapause, which enables them to endure temporary unfavorable environmental conditions. In pelagic ecosystems, diapause takes place mainly before or when environmental conditions become unsuitable for a species (Baumgartner & Tarrant 2017), and in some copepods, such as *C. finmarchicus*, it is facultative and may be modulated by the environment (Aruda et al. 2011). Copepods may diapause in two different ways. Some species (i.e., Calanidae and Eucalanidae) accumulate a large amount of lipids and diapause as juveniles or adults in deep waters, whereas others (i.e., Centropagoidea) produce resting eggs that sink on the sediments. These ways to diapause induce a dependence regarding the substrate-biotope component (van der Spoel 1994); in the first case, the copepod needs deep water, and in the second, it needs sediments in shallow (neritic) regions. For example, *C. finmarchicus* cannot diapause in the North Sea, and so its spring abundance in the North Sea results from individuals that overwinter in the Norwegian Sea Deep Water (Heath et al. 1999). Although much remains to be studied, it is also possible that climate change, by influencing the timing of diapause, may influence the number of generations that a species produces each year (the degree of voltinism) and thereby its phenology and annual abundance. Variations in the degree of voltinism resulting from the effect of climate on species physiology may either amplify or dampen the influence of climate change on seasonal species distribution and annual abundance (Beaugrand et al. 2007, Knell & Thackeray 2016).

Phenological shifts. Phenology is defined here as the seasonal pattern of the abundance of a species. Altering the phenology enables a species to occur in an environment that has optimal ecological conditions. We therefore think that the timing is driven primarily by environmental conditions such as temperature, photoperiod, and nutrient availability and the structure of the water column (Ji et al. 2010, Mackas et al. 2012, Thackeray et al. 2016, Visser & Both 2005) and only secondarily by prey availability (Visser & Both 2005, Winder et al. 2009).

Below, we show how changes in temperature can affect a species' phenology (Beaugrand et al. 2014). We first describe a simple theoretical example using a niche based on the single environmental parameter of mean sea surface temperature (SST). The thermal niche is calculated as follows (ter Braak 1996):

$$E_{i,j,s} = c_s e - \left[\frac{(x_{i,j} - u_s)^2}{2t_s^2} \right], \qquad 1.$$

where $E_{i,j,s}$ is the expected abundance of pseudospecies s at location i and time j, c_s is the maximum value of abundance for species s (here fixed to 1), $x_{i,j}$ is the SST at location i and time j, u_s is the thermal optimum for species s, and t_s is the thermal amplitude for species s. The thermal tolerance is an estimation of the breadth (or thermal amplitude) of the species' thermal niche (or bioclimatic envelope) (ter Braak 1996).

From Equation 1, we created a hypothetical species characterized by a Gaussian thermal niche with $u_s = 15°C$ and $t_s = 5°C$ (**Figure 4*a***). The corresponding spatial range of this pseudospecies was calculated by projecting its thermal niche onto the spatial domain (**Figure 4*b***) and gave a maximal abundance in the North Atlantic Drift Province (Longhurst 1998), between the northern part of the subtropical gyre and the oceanic polar front (Dietrich 1964).

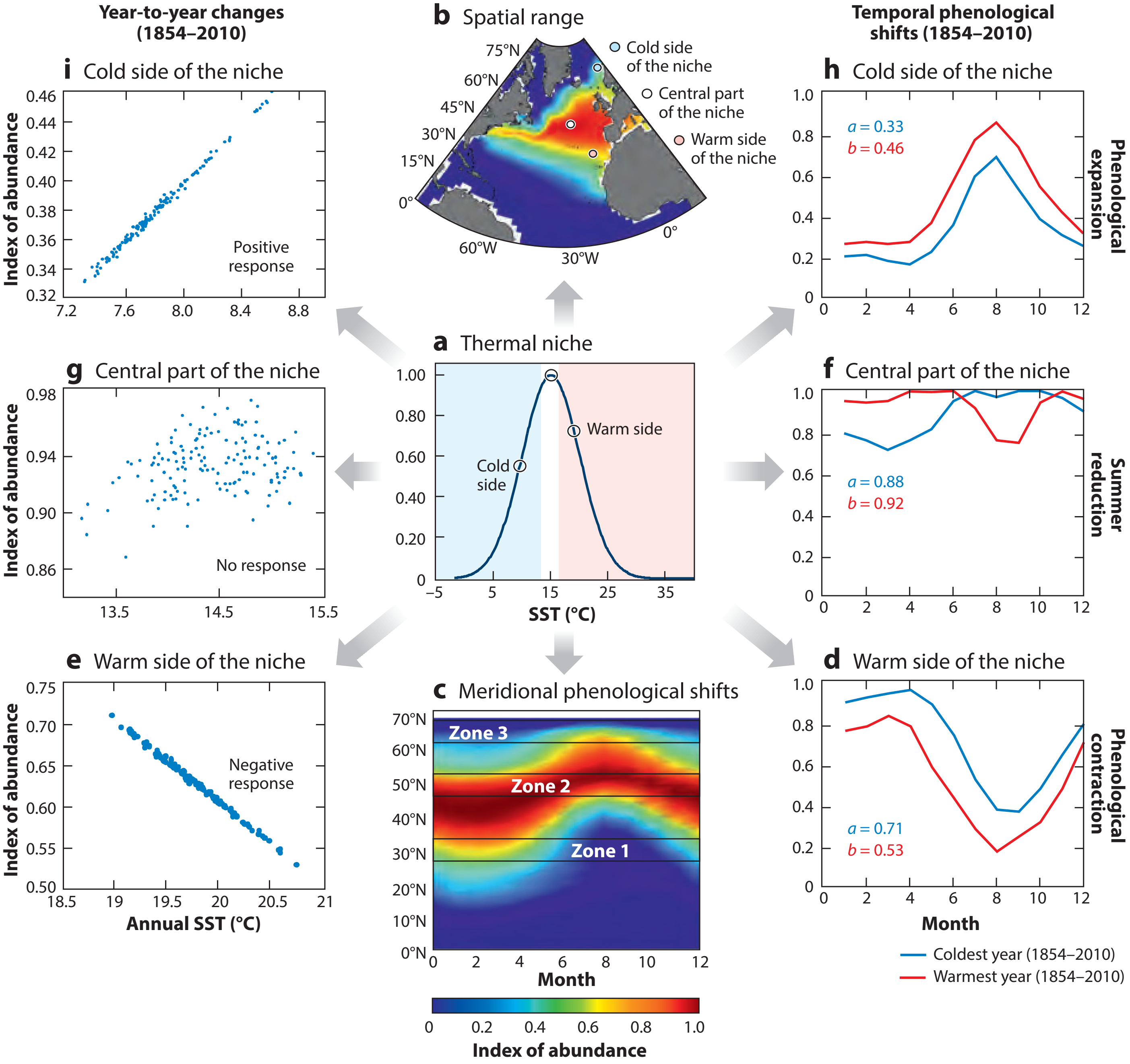

Figure 4

Relationships among species niche, spatial distribution, phenology, and long-term changes in abundance. (*Center column*) The thermal niche of a hypothetical cold-water species (panel *a*), its spatial distribution (panel *b*), and theoretical changes in abundance as a function of latitude and month (i.e., phenological shifts as a function of latitude) (panel *c*). The circles in panels *a* and *b* denote the three parts of the niche or zones that are considered in other panels. Zone 1 is the part of the distribution where the seasonal maximum occurs in spring or winter, zone 2 is the part of the distribution where the seasonal extent is highest, and zone 3 is the part of the distribution where the seasonal maximum is located at the end of summer. (*Right column*) The phenology of the pseudospecies in a region with a thermal regime corresponding to the warm side (panel *d*), central part (panel *f*), and cold side (panel *h*) of the niche. Changes in abundance are for the coldest (*blue*) and warmest (*red*) years based on the reference period 1854–2010; here, *a* and *b* are the average abundances for the coldest and warmest years, respectively. (*Left column*) Relationships between year-to-year changes in the abundance of the pseudospecies and annual sea surface temperature (SST) in a region with a thermal regime corresponding to the warm side (panel *e*), central part (panel *g*), and cold side (panel *i*) of the niche.

The calculation of the expected species abundance as a function of latitude and month allows the distinction of three main phenological zones (**Figure 4*c***). First, in the southern part of its range, the pseudospecies has a seasonal maximum in winter or spring, the latter time period being more likely when parameters such as photosynthetically active radiation (PAR) affect the species either directly through its influence on photosynthesis (e.g., phytoplankton) or indirectly through the food web (e.g., herbivorous zooplankton). The influence of PAR on primary production is prominent toward higher latitudes (Behrenfeld 2010). At its extreme southern range, such a species is unlikely to adjust its phenology in response to an increase in sea temperature, resulting in a local reduction of its annual abundance (i.e., average abundance $a = 0.71$ for the coldest year versus $b = 0.53$ for the warmest year during the period 1854–2010) and a northward biogeographical shift (**Figure 4*d***); conversely, if conditions become colder, the species is likely to increase in abundance.

Two situations may theoretically take place in the case of an increase in temperature. If winter phenology is achievable, the species experiences an earlier phenology (**Figure 4*d***). By contrast, species that cannot be present in winter may be unable to move toward an earlier phenology at the same rate that they disappear at the end of their phenological period; this may occur if the photoperiod in high latitudes limits the development of the species in winter. Note that in both cases, the species exhibits a phenological contraction (**Figure 4*d***). An earlier phenology associated with a phenological contraction has been shown for *Neocalanus plumchrus* in the northeast Pacific (Batten & Mackas 2009). At the southern limit of the pseudospecies' range (zone 1, **Figure 4*a*–*c***), both its resistance and its resilience to warming are expected to be low (**Figure 4*e***), but the opposite is expected in the case of cooling.

At the center of its range (zone 2, **Figure 4*a*–*c***), the pseudospecies exhibits its maximum seasonal extent, with the duration being modulated by its thermal amplitude t_s (Equation 1). Here, the species can be observed throughout the year as long as other niche dimensions, such as PAR, length of day, or nutrients, do not exert a controlling influence. A small reduction in the abundance of the pseudospecies can be observed in summer if temperatures warm (**Figure 4*f***). At an annual scale, all else being held constant, the erosion of the seasonal period of occurrence in late summer should be compensated by higher abundance toward spring or early summer, and consequently, no substantial alteration of the species annual mean should be expected ($a = 0.88$ for the coldest year and $b = 0.92$ for the warmest year during the period 1854–2010; **Figure 4*f***); because species resistance and resilience to warming and cooling are greatest in zone 2, no relationship between long-term changes in abundance and annual temperature should be seen (**Figure 4*g***). Note that in the case of a phytoplankton species, an annual maximum in summer might be divided into two maxima because macronutrients are also important in shaping phenology, the first maximum in spring and the second later in the year if a low nitrate concentration (the law of the minimum) or grazing limits phytoplankton growth in summer. In the same way, winter phenology may be impossible because of the limitation induced by the photoperiod. The calculation of phenological index may reveal an earlier phenology, but the annual abundance may not change substantially.

At the northern edge of its distributional range (zone 3, **Figure 4*a*–*c***), the pseudospecies is likely to peak in summer. In this case, the cold-water species can extend its occurrence in both early summer and spring if temperatures warm and also in late summer and the beginning of autumn, resulting in an increase of its annual mean abundance ($a = 0.33$ for the coldest year and $b = 0.46$ for the warmest year during the period 1854–2010; **Figure 4*h*,*i***). The pseudospecies experiences a phenological expansion, with both earlier and later phenology. Therefore, METAL explains why studies have sometimes reported a later phenology for late-summer species, although even for those species, an earlier phenology is just as likely (Ji et al. 2010). It is possible that another environmental factor, such as nutrient concentrations or food availability, limits the phenological adjustment toward summer.

Thermophily: the aptitude of a species to develop at a high temperature

If SST increases north of the northern species boundary, a biogeographical shift will take place, although the species' presence will first be detected in late summer, when sea temperatures are highest. This example shows that warm-water species arriving in a new area should be first detected in late summer or the beginning of autumn, when local temperatures warm. This prediction has been confirmed by the arrival of warm-water species such as *Centropages typicus*, *Centropages violaceus*, and *Temora stylifera* along European coasts in late summer (Lindley & Daykin 2005). Arrival time is expected to be earlier for eurytherms than for stenotherms, both of which have the same degree of thermophily. According to METAL, the most frequently documented phenological adjustment in the context of current climate change should be toward an earlier phenology (Menzel et al. 2006, Poloczanska et al. 2013, Thackeray et al. 2016). Although some studies have estimated an earlier phenology of approximately 4.4 days per decade for marine species (Poloczanska et al. 2013), METAL shows that this pattern represents only a part of a more complex temporal adjustment of a species to climate involving phenological contraction/expansion and an increase/decrease in seasonal maximum of abundance.

Sometimes a species does not exhibit a phenological shift, or the magnitude and the timing of a phenological shift may vary among different taxonomic groups and trophic guilds (Thackeray et al. 2016, Visser & Both 2005). The first case is expected under METAL when a species lives in zone 2, where changes in phenology are limited, the phenomenon being amplified under high local variability and/or stochasticity related to sampling (Beaugrand & Kirby 2016). The second case is predicted by METAL when the degrees of eurythermy or thermophily differ among species or taxonomic groups. Spring and summer species are likely to exhibit an earlier phenology but also a phenological contraction, whereas late-summer species may exhibit a phenological expansion associated with both earlier and later phenology (**Figure 4**).

Latitudinal shifts in phenology are expected from the poleward to the equatorward part of the spatial distribution of a species. This can be demonstrated when we model the latitudinal shift in the phenology of *C. finmarchicus* using a four-dimensional niche that includes PAR, bathymetry, chlorophyll *a* concentration, and mean SST (Beaugrand et al. 2014) (**Figure 5**). Although both the duration and timing of predicted phenology are smaller than observed owing to population dynamics (**Figure 5*a*,*b***), the expected timing (revealed by the center-of-gravity index) and maximum and mean annual abundance and seasonal duration are significantly correlated positively and explain 67–96% of the variance of the observed parameters (**Figure 5**). Our example therefore shows that changes in the seasonal extent of a species from zone 1 to zone 2 (as in **Figure 4*c***) are associated with a shift in annual abundance and that a shift toward an earlier phenology is limited by PAR and chlorophyll *a* concentration (**Figure 5*a*,*b***); these two parameters, included in the model, were responsible for the absence of phenology in winter. The net effect is a phenological contraction toward zone 1 (as in **Figure 4*c***). The degree of voltinism diminishes when the seasonal extent shortens (Knell & Thackeray 2016), which reduces the resilience of the species to warming. Duration is therefore a key phenological parameter to monitor, although it is rarely assessed (Batten & Mackas 2009, Beaugrand et al. 2007).

Interestingly, in studies of long-term phenological shifts of the North Sea plankton, Edwards & Richardson (2004) found no phenological shift for spring diatoms. They proposed that the phenology of these diatoms did not shift because the reproduction of the taxonomic group was controlled mainly by the photoperiod. According to METAL, however, spring North Sea diatoms cannot shift their phenology in winter because they are at their southern boundary (zone 1, as in **Figure 4*c***) and therefore cannot compensate for an increase in sea temperature in winter because reduced winter PAR limits their growth. Spring North Sea diatoms should therefore decline in the future if the warming continues, exhibiting a pattern similar to the one observed for *C. finmarchicus* (**Figure 5*a*,*b***). METAL also predicts that summer diatoms and dinoflagellates will

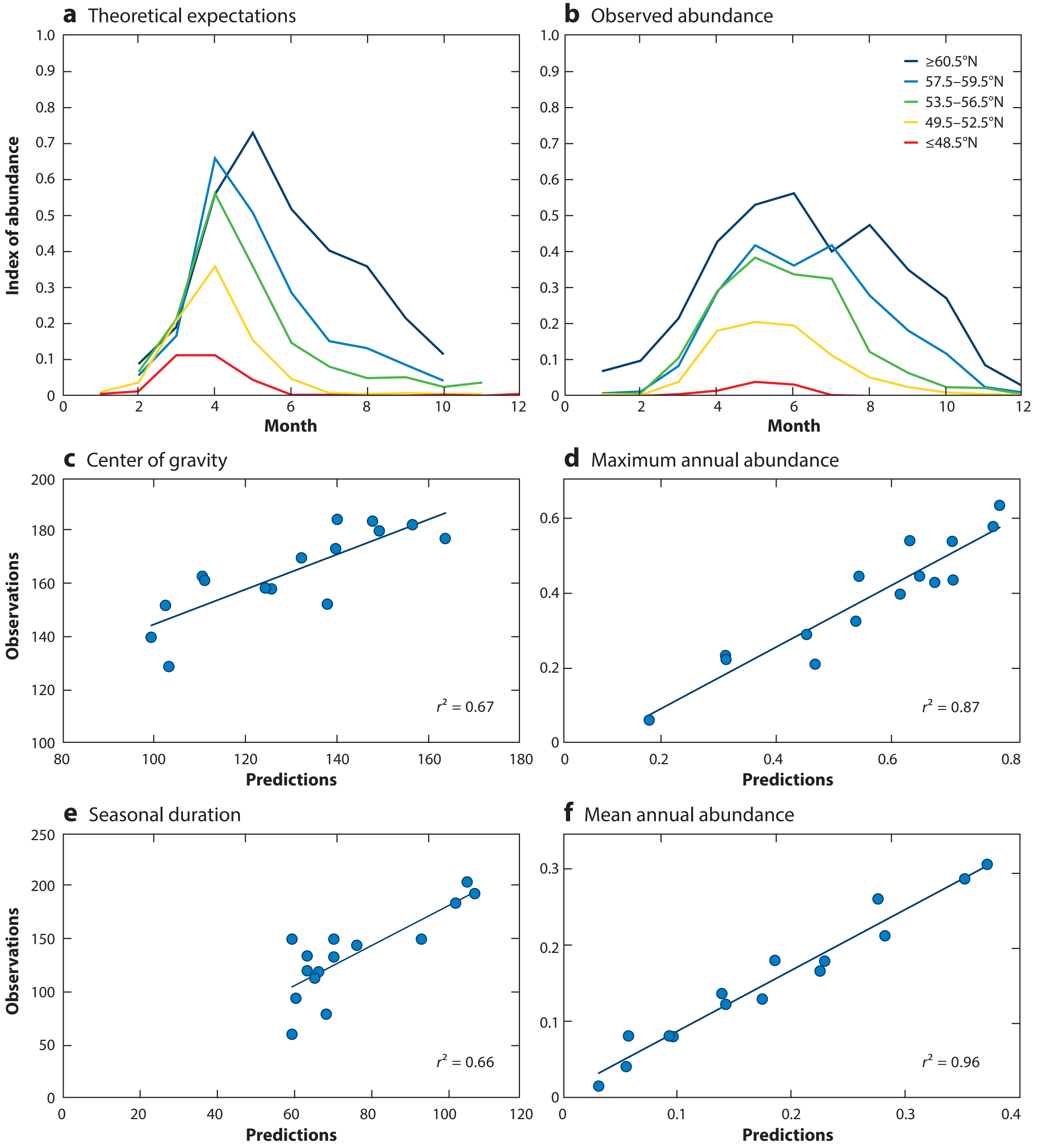

Figure 5

Predicted and observed phenological shifts in a zonal band (10–30°W) from 48.5°N to 62.5°N. (*a*,*b*) Predicted (panel *a*) and observed (panel *b*) phenological shifts for five latitudinal bands: ≥60.5°N, 57.5–59.5°N, 53.5–56.5°N, 49.5–52.5°N, and ≤48.5°N. (*c*–*f*) Predicted and observed center of gravity (panel *c*), maximum annual abundance (panel *d*), seasonal duration (panel *e*), and mean annual abundance (panel *f*) for every latitude between 48.5°N and 62.5°N (15 pairs of observation). The center of gravity measures the timing of the peak of abundance (i.e., timing weighted by the monthly abundance). Seasonal duration was assessed by calculating the duration above half of the maximum annual abundance.

exhibit an earlier seasonal occurrence, a pattern observed by Edwards & Richardson (2004, their figure 1).

Conover & Schultz (1995) have proposed that latitudinal compensation may take place for life history traits such as growth rate. This apparent evidence for a countergradient variation (i.e., an ecogeographical pattern where latitudinal change in a phenotypic trait is minimized by the genotype) is explained well by a phenological shift that places the individuals of a species in months that experience similar environmental conditions. Therefore, countergradient variation is also well explained by METAL when the species' ecological niche (assumed to be constant at least at decadal scales) interacts with the environment to select the temporal window that corresponds to the optimum section of the ecological niche. As a result, only minor changes in some life history traits, such as growth rate and body size, should be expected, without the need to invoke an alteration of the genotype. When considering only the thermal niche, growth rate would not change and body size would not be affected because variations in body size result from the temperature-size rule (Atkinson 1994). Our framework therefore suggests that phenological shifts are not exclusively the result of evolutionary adaptation or phenotypic plasticity (Przybylo et al. 2000). Rather, they can simply reflect the adjustment of a species to the environmental regime that corresponds to their ecological niche (Beaugrand 2009).

Alterations in local annual abundance. Annual abundance is the outcome of the environmental conditions experienced by a species and represents the integration of behavioral, physiological, and phenological adjustments (**Figure 1**). Although McGinty et al. (2011) noticed that the long-term relationship between annual abundance and temperature may be inconsistent between different locations, it can be described by one of three scenarios (see **Figure 6** and the sidebar titled Expected Responses of Species' Annual Abundance to Temperature Changes): a nil, negative, or positive relationship (Beaugrand & Kirby 2016).

EXPECTED RESPONSES OF SPECIES' ANNUAL ABUNDANCE TO TEMPERATURE CHANGES

Using a mixed deterministic/stochastic model, with stochasticity representing 20% of the amplitude of the deterministic signal, Beaugrand & Kirby (2016) explored the different types of relationships expected between the abundance of a cold-water species (such as *Calanus finmarchicus*) and temperature at four different thermal regimes (**Figure 6*b*–*e***) corresponding to the following key points along the thermal niche (**Figure 6*a***):

1. T_{opt}, the optimal zone between the T_{S} points, where both reproduction and growth are maximal and the variability in species abundance as a function of temperature is low. In this zone, correlations are not expected with or without stochasticity because the thermal regime is unlikely to trigger large changes in abundance (**Figure 6*b***).
2. T_{HV} (cold and warm edges), the points around which the sensitivity to temperature is highest. In this zone, the deterministic signal related to the niche-temperature interaction is strong, and only high stochasticity can affect the relationship between abundance and temperature (**Figure 6*c*** for the cold side and **Figure 6*d*** for the warm side). Although the effect of stochasticity is minimal in this region of the niche, it significantly affects the percentage of variance explained.
3. T_{D} (warm edge), the threshold from which temperature effects are unlikely to be detected in the field because the thermal influence on the species becomes too small compared with stochasticity (**Figure 6*e***).

Note that, for some thermophile species (those with an upper thermal limit higher than 30°C and some tropical species), a negative relationship may not be currently observable with the contemporaneous climate.

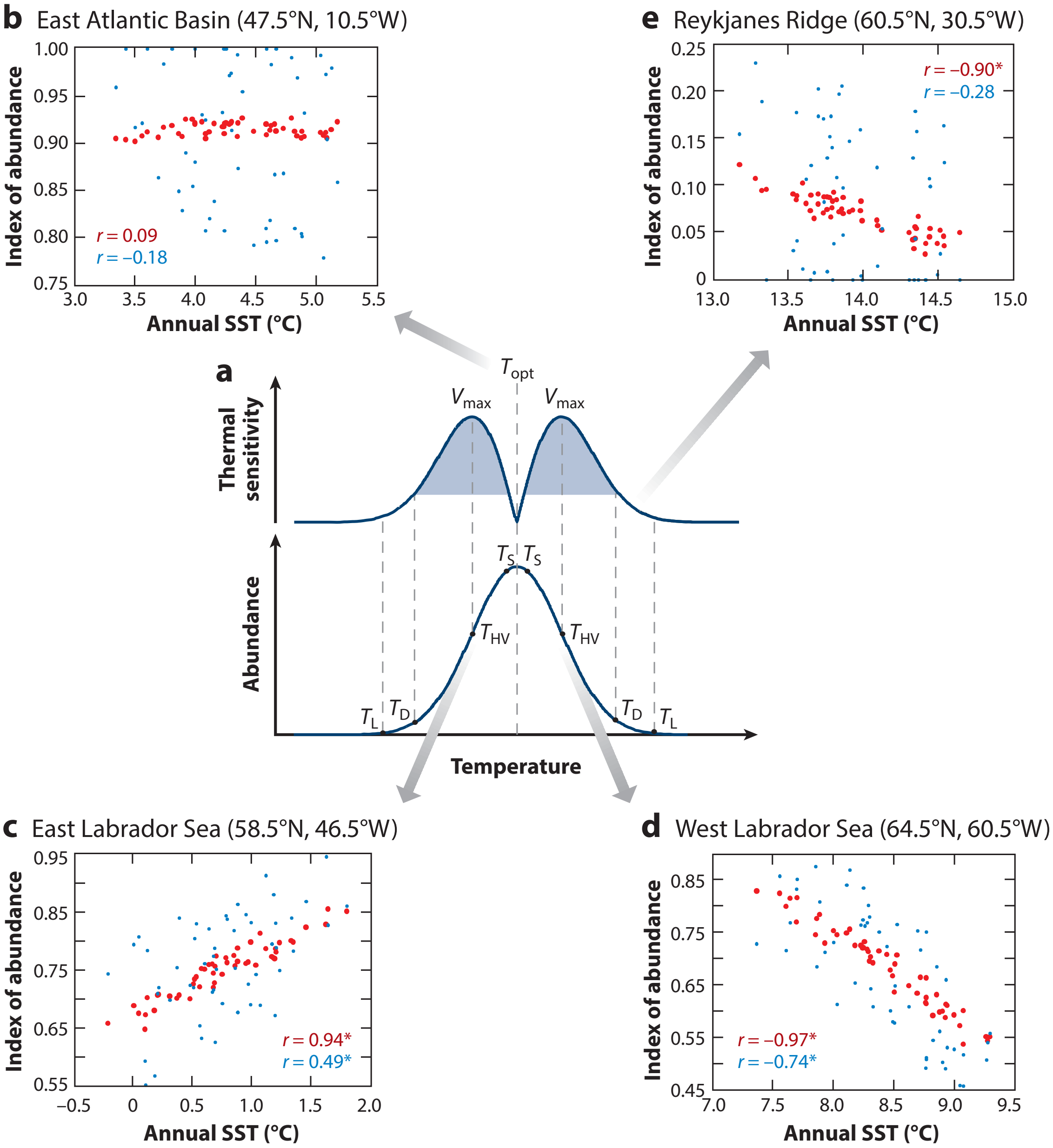

Figure 6

(*a*) The thermal niche of a hypothetical species (*bottom*) and the species' theoretical response to climate-induced changes in temperature (*top*). The optimal part of the thermal niche (T_{opt}) corresponds to the center of the species' distributional range between T_{S} (where S stands for stable) and is associated with low year-to-year variability. The bimodal distribution of the year-to-year variability exhibits a maximal variability $V_{\max}$ corresponding to the greatest slopes of the thermal niche (T_{HV}, where HV stands for high variability). T_{D} (where D stands for detectability) is the threshold from which temperature effects are unlikely to be detected because the species' thermal sensitivity becomes too small. T_{L} (where L stands for lethal) represents the temperatures below (toward the northern part of the distributional range) and above (toward the southern part of the distributional range) which temperatures become lethal. The blue areas indicate the regions where the response of the species to climate-induced temperature changes is expected to be strong. (*b*–*e*) Theoretical long-term (1958–2009) changes in the standardized abundance of *Calanus finmarchicus* and relationships with annual sea surface temperatures (SSTs) in four areas of the North Atlantic using a deterministic model (*red*) and a mixed deterministic/stochastic model (*blue*). Correlation coefficients are based on a deterministic model only (*red*) and a mixed deterministic/stochastic model (*blue*). The asterisks indicate where correlations are significant. The deterministic model was based on four environmental parameters: temperature, bathymetry, photosynthetically active radiation, and chlorophyll *a* concentration. Adapted from Beaugrand (2012) and Beaugrand & Kirby (2016).

For a temperate boreal species, year-to-year changes in abundance are negatively correlated with changes in temperature toward the warmer limit of its spatial distribution (**Figures 4*e*** and **6*d***). Because the seasonal extent of the species is restricted to a short time period (**Figure 4*c***), it may have limited generations per year (zone 1; some species may even be univoltine in this region), making it sensitive to exceptional meteorological events that may have persistent negative effects at the population level, such as heat waves (Sunday et al. 2014); note that the opposite is true for a cold wave. (This region goes from T_{HV} to T_{L} on the right side of the niche in **Figure 6*a***.)

A species is not influenced by temperature at the center of its range (**Figures 4*g*** and **6*b***), and its seasonal extent is large as long as no other environmental factors have an effect (zone 2 in **Figure 4*c***; many species are likely to be multivoltine in this zone). When the thermal regime is along the part of the niche located between the two T_{S} thresholds around T_{opt}, the sensitivity of the species to climate is lowest and the effects of exceptional meteorological events are likely to be insignificant.

At the cold edge of a species' range, the relationships between year-to-year changes in abundance and fluctuations in temperature are positive (**Figures 4*i*** and **6*c***). (This region goes from T_{HV} to T_{L} on the left side of the niche in **Figure 6*a***.) Again, the degree of voltinism is lowest here, and exceptional meteorological events may have strong effects on the species' abundance. At the edge of the spatial distribution of a species, strong blooming or collapse can be expected to occur relatively rapidly in response to an exceptional meteorological event.

Where the thermal regime corresponds to the side of the thermal niche ranging from T_{D} to T_{L} (**Figure 6*a***), we can expect to see fluctuations in abundance that appear to be independent of temperature because annual fluctuations have only a small amplitude in comparison with local stochasticity (see the sidebar titled Expected Responses of Species' Annual Abundance to Temperature Changes). It is not self-contradictory, however, for a strong signal to be observed in the case of an exceptional event, because the intensity of this type of event may be such that it moves the thermal regime away from the insensitive region between T_{D} and T_{L} to the region between T_{L} and T_{HV}, which is highly sensitive to changes in temperature (**Figure 6*a***).

Beaugrand & Kirby (2016) used METAL to test whether a part of the long-term changes in the abundance of *C. finmarchicus* could be attributed to a multidimensional niche-environment interaction by modeling the niche of the calanoid with a mixed deterministic/stochastic model (**Figures 6** and **7**). The deterministic component of the model was the result of the application of the Non-Parametric Probabilistic Ecological Niche model based on four environmental parameters: monthly SSTs (1958–2009), bathymetry, and climatologies of monthly chlorophyll *a* concentration and PAR. The niche of *C. finmarchicus* was therefore four-dimensional, but only annual SSTs varied on a year-to-year basis. The stochastic component of the model was represented by a random noise that was fixed to 20% of the total amplitude of species abundance. METAL predictions were subsequently tested against observed data of *C. finmarchicus* collected from the Continuous Plankton Recorder survey in three regions of the North Atlantic corresponding to the warm edge of the niche because no data were available for the cold edge of the niche. Expected and observed long-term changes in the abundance of *C. finmarchicus* were significantly correlated (**Figure 7*a–c***), and although the correlations may seem weak, they are in the range of values expected when stochasticity is moderate. Stochasticity had a larger effect at a local scale than at the macroscale of the species' spatial distribution. Although locally, the correlations were close to 0.5, when the niche was assessed from both expected and observed abundance of *C. finmarchicus* at the scale of the North Atlantic, the correlation increased substantially, to 0.7 (**Figure 7*d***). Schwartzman & Lineweaver (2005) also suggested that determinism is likely to diminish at smaller scales because the ratio of stochasticity to determinism increases when the spatial scale decreases. This may also explain the success of macroecology (Brown 1995, Gaston & Blackburn 2000).

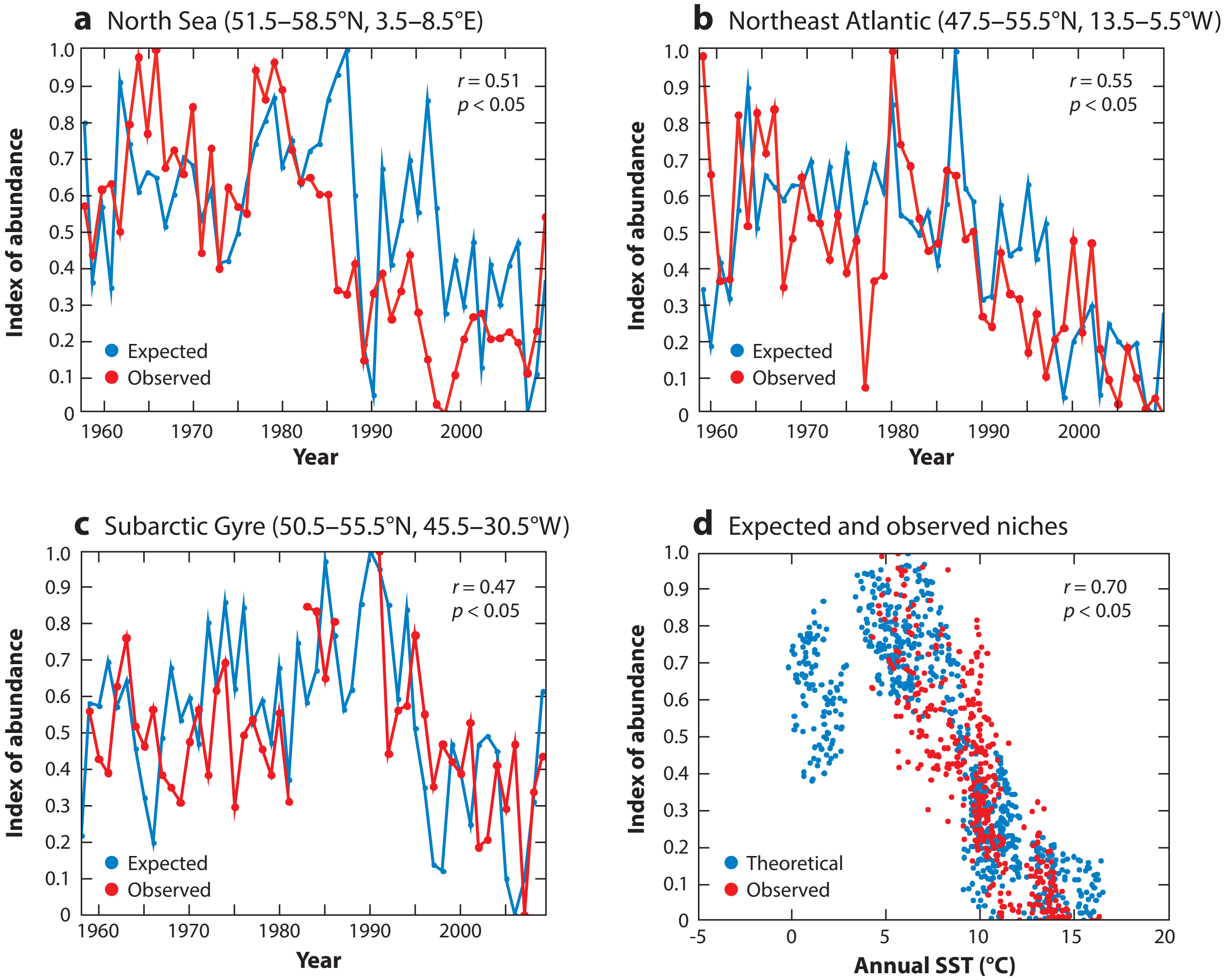

Figure 7

Predicted and observed year-to-year changes in the abundance of *Calanus finmarchicus* in the North Atlantic using a niche model based on four ecological dimensions: temperature, bathymetry, photosynthetically active radiation, and chlorophyll *a* concentration. Observed data originate from the Continuous Plankton Recorder survey. (*a–c*) Long-term expected (*blue*) and observed (*red*) changes in the North Sea (panel *a*), northeast Atlantic (panel *b*), and Subarctic Gyre (panel *c*). (*d*) Relationships between theoretical (*blue*) and observed (*red*) long-term (1958–2009) changes in the standardized abundance of *C. finmarchicus* as a function of annual sea surface temperature (SST). Correlation coefficients and their corresponding values of probability are indicated. Adapted from Beaugrand & Kirby (2016).

Global Adjustments

The local or regional responses of species reshape their distributional range at a macroecological/biogeographical scale. Here, we show the connection between these changes and those at larger spatial scales. We show that latitudinal shifts are only a part of more complex biogeographical alterations that have both meridional and zonal components. Range contraction may lead eventually to global extinction in some extreme cases. We also discuss potential adaptation (genetic change) in the context of current climate change because it may alter the shape of the species' ecological niche to modify the niche-environment interaction.

Biogeographical shifts. Changes in the local annual abundance of a species result from the sum of the negative and positive effects of climate on species abundance (**Figure 1**). When the climatic forcing is too great, however, a species may spend too much time outside its ecological niche and may diminish or even disappear from a region. Local extirpation or appearance is perceived at a macroecological scale as a biogeographical shift (**Figure 1**). Many authors have suggested that the geographical range of a species reflects its ecological niche (Brown 1984, Lomolino et al. 2006), which explains the relative success of ecological niche modeling because it allows the past, current, and future spatial distributions of a species to be predicted from environmental conditions (Fromentin et al. 2014, Lenoir et al. 2011, Raybaud et al. 2013). Biogeographical shifts have been documented in both the terrestrial and marine realms (Beaugrand et al. 2002, Parmesan & Yohe 2003, Perry et al. 2005, Thomas & Lennon 1999). Hickling et al. (2006) investigated the responses of freshwater and terrestrial species (e.g., millipedes, spiders, herptiles, birds, and mammals) to climate change in Britain. Of the 329 species they examined, 275 (84%) exhibited a northward shift, in agreement with global warming expectation. A meta-analysis performed on 129 marine species that exhibited a shift revealed that 97 (75%) moved poleward, an observation consistent with climate change scenarios (Sorte et al. 2010). In the METAL theory (Beaugrand 2015), the concept of the niche is also central to explaining species biogeographical shifts.

Contemporaneous biogeographical movements are generally regarded as latitudinal species shifts in response to warming (Beaugrand et al. 2002, Parmesan & Yohe 2003, Perry et al. 2005, Thomas 2010, Thomas & Lennon 1999). Using an average rate of latitudinal shift for a species is misleading, however, because those shifts should be envisioned in a two-dimensional (biogeographical) space and not only in a one-dimensional (latitudinal) space. **Figure 8** shows the modeled past (Last Glacial Maximum), present (1960–1969), and future (2090–2099) spatial distributions of *C. finmarchicus* in the North Atlantic. This figure demonstrates the complexity of the biogeographical movements, showing that the shifts have both meridional and zonal components, that there are zones of nil or small shifts (e.g., the oceanic polar front in the northwest Atlantic), and that there are zones where substantial shifts take place (e.g., the northeast Atlantic). Perry et al. (2005) showed a northward movement of 15 out of 36 species in the North Sea that paralleled an increase in sea temperature. They also provided evidence that some species that did not move latitudinally migrated vertically. For example, the plaice (*Pleuronectes platessa*) and the cuckoo ray (*Leucoraja naevus*) were two among six species that responded to sea warming by moving deeper into the water column.

As a result of climate change, species may exhibit range contractions and expansions (Cheung et al. 2009, MacLeod 2009), although quantifying these contractions and expansions remains challenging. They are particularly difficult to quantify for equatorial or tropical species, for which the thermophilic section of the niche is often unknown and cannot be estimated reliably from our current knowledge of the warm edges of species' spatial distributions; as a result, we may underestimate their resistance and resilience to climate warming. Nevertheless, the ranges of tropical species are likely to expand, whereas those of temperate and polar species are likely to contract.

Global extinction. For some species, range contraction may take place to such an extent that it results in extinction. Periods of global warming have been associated with major extinction events in the past (Gaston & Spicer 2004, Jablonski 1991) and so anthropogenic climate change may cause species extinctions in the future (Thomas et al. 2004). Estimating the magnitude of such climate-induced extinctions is difficult, however. Based on an examination of 1,103 species of animals and plants, Thomas et al. (2004) provided a rough assessment of the potential effects of anthropogenic climate change on terrestrial species extinction by 2050. Their estimates were based on bioclimatic models and species-area relationships for three levels of warming and for scenarios of nil or full (universal) dispersal. For a high level of warming, they found that climate-caused species extinctions may range between 21% and 32% when there is no limitation in species dispersal and between 38% and 52% when there is no possibility of dispersal. For moderate climate change, the percentage of species committed to extinction ranged between 15% and 20% for universal

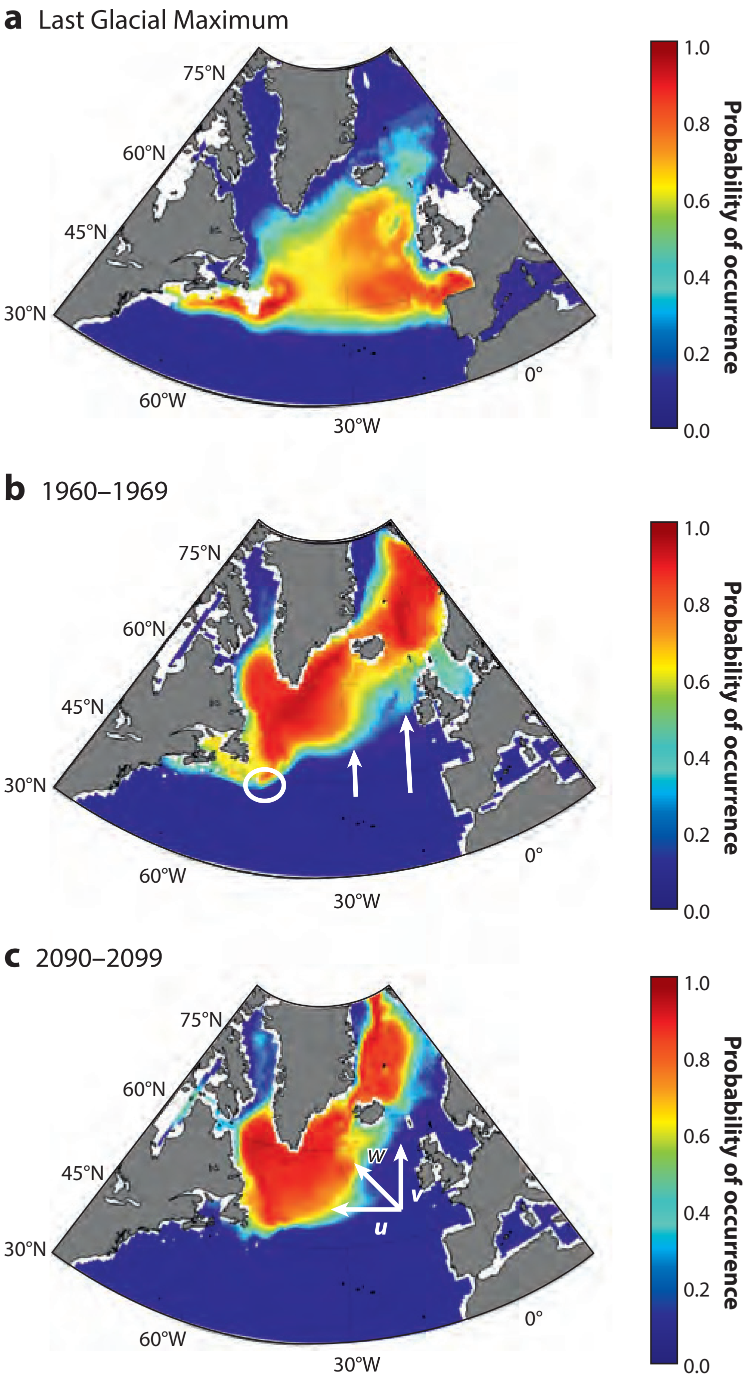

Figure 8

Modeled probability of occurrence of *Calanus finmarchicus* for (*a*) the Last Glacial Maximum, (*b*) the 1960s, and (*c*) the 2090s. The Non-Parametric Probabilistic Ecological Niche model, based on both sea surface temperature and bathymetry, was applied. The future spatial distribution was modeled using a pessimistic scenario (preindustrial $CO_2 \times 4$). In panel *b*, the white circle indicates an absence of northward movement between the Last Glacial Maximum and the 1960s, and the white arrows indicate the magnitude of the northward movement. In panel *c*, *u* and *v* are the zonal and meridional components, respectively, and *w* is the vectorial sum of *u* and *v*. Adapted from Beaugrand (2015).

dispersal and between 26% and 37% for no dispersal. For optimistic climate change scenarios, the percentages ranged between 9% and 13% for universal dispersal and between 22% and 31% for no dispersal. Rates of species committed to extinction varied among taxonomic groups and ecoregions.

We do not know whether anthropogenic climate change has resulted in any extinctions in the marine realm; none have been documented as yet. Although some marine species, such as the Mediterranean mysid *Hemimysis speluncola* (a marine cave species), may become at risk (Chevaldonné & Lejeusne 2003), extinction is unlikely at present for most pelagic species.

Adaptation. We consider the species' phenotypes seen throughout its range to be its norm of reaction, i.e., the phenotypes that are associated with the full ecological conditions it experiences; therefore, the norm of reaction is fully included within the species' ecological niche. Adaptation is viewed as the outcome of natural selection on the genotype that enables the species to alter its behavior and physiology so that it modifies the shape of its niche (**Figure 1**). Therefore, adaptation is not fully excluded from the present framework. It is unclear whether adaptation will enable ectotherms to overcome the environmental alterations induced by the current global climate change (Gunderson & Stillman 2015).

The tendency of a species to preserve ancestral ecological traits and environmental distribution is known as niche conservatism, and it means that species rarely change biomes (Crisp et al. 2009). In a study of 11,000 plant species at timescales of tens of millions of years and at large spatial scales, Crisp et al. (2009) found only 396 cases (3.6%) where a biome shift was associated with evolutionary divergence; interestingly, this occurred only between biomes with a high ecological similarity. Crisp et al. (2009) concluded by stating that species' evolutionary success relies not on adapting to a new biome but rather on tracking biomes with similar environmental conditions, and they compared this with introduced species, which generally tend to invade regions with ecological characteristics similar to those of their native range (niches, *sensu* Hutchinson 1957).

Overpeck et al. (2003) noted that only a small amount of macroevolution was apparent during the Quaternary, which was a period of repeated climate change. Today, rates of climate change are probably much higher than past rates of climatic niche evolution, however (Quintero & Wiens 2013). Quintero & Wiens (2013) estimated that the rate of niche evolution for terrestrial vertebrates should be 10,000 times faster than those normally observed to overcome the effects of anthropogenic climate change. For species with very short generation times, evolution may be faster, however. Studies of the phytoplankton *Chlorella vulgaris* have shown that growth rates evolved rapidly after just 10 generations when the temperature was raised from 20°C to 30°C (Padfield et al. 2016). However, if evolution can be so quick, why have species in the past not adapted to changes in the thermal regime more readily, and instead retreated to refugia (Dobrowski 2011)?

RESPONSES TO CLIMATE AT HIGHER ORGANIZATIONAL LEVELS

Below, we illustrate briefly how individualistic responses to climate change can propagate at the community level and propose some predictions about how communities may reconfigure in response to climate change.

Ecological Succession

Gleason and Ramensky observed that species respond individualistically to environmental changes and called this response the principle of species individuality (Whittaker 1975). As a consequence, it has been suggested that changes in seasonal succession may desynchronize species interactions and trigger trophic mismatch (Beaugrand et al. 2003, Edwards & Richardson 2004, Parmesan

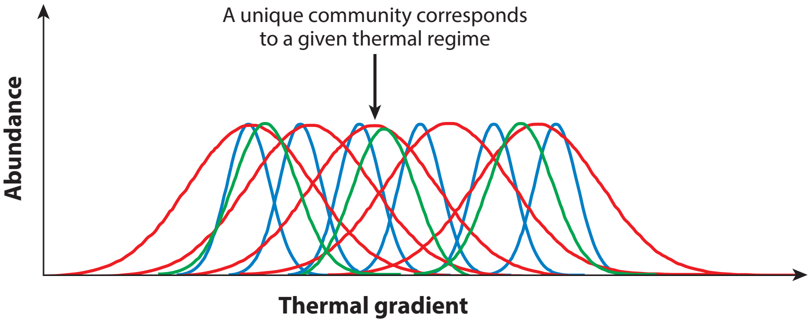

Figure 9

A pseudocommunity composed of pseudospecies, each of which is characterized by a thermal niche. For a given temperature (e.g., the one indicated by the *vertical arrow*), community structure is invariant as long as no other ecological factor affects a pseudospecies. It follows that community reconfiguration is limited by the ecological niche of each species.

2005). Although this remains to be investigated in depth, our framework suggests that reassembly should be limited because interacting species have at least a part of their ecological niche in common, providing that no other important ecological dimensions or habitat requirements differ among them. Because a synusia should remain similar for a given thermal regime (**Figure 9**), a certain degree of reconfiguration is expected only when the degree of eurythermy among interacting species differs substantially, when species strongly depend on each other (e.g., a specialized predator), and when the habitat is strongly influenced by engineer species, which is not generally the case in the pelagic environment.

Synusia: a part of a community characterized by relative life homogeneity (e.g., zooplankton in a given pelagic ecosystem)

Long-Term and Abrupt Community Shifts

Many reports have shown that temperature is a key driver of changes in communities at different spatial scales (Beaugrand et al. 2008, 2013a; Burrows et al. 2011, 2014; Kirby & Beaugrand 2009; Kirby et al. 2008; Luczak et al. 2011; Richardson & Schoeman 2004). Because the responses of species to climate change are determined in large part by the interaction between the thermal niche and temperature, we can create pseudospecies that each have a different thermal niche. Those species are subsequently allowed to colonize a given oceanic region as long as they can survive changes in the environmental regime at different timescales. Niche overlapping is allowed, but no species can have the same ecological niche in a given region, following the principle of competitive exclusion (Gause 1934). By constructing pseudocommunities, we can then investigate how climate may influence pelagic communities. Because pseudocommunities generally have more species than actual communities, we can select only a number of pseudospecies that corresponds to the community's species richness. By repeating the procedure 10,000 times, we can examine the long-term changes in these pseudocommunities and investigate how they are correlated with actual communities. This work was carried out in the North Sea using data from the Continuous Plankton Recorder survey (Beaugrand 2014, Beaugrand et al. 2014). Modeled changes in pseudocommunities are highly correlated with observed community shifts in the North Sea (**Figure 10**). In addition, the abrupt shift observed at the end of the 1980s in Continuous Plankton Recorder data is also predicted by METAL.

Changes in the Location of Species Assemblages

As stated above, community reconfiguration is likely to be limited because species occurring in the same place at the same time have overlapping niches, and therefore we should not expect

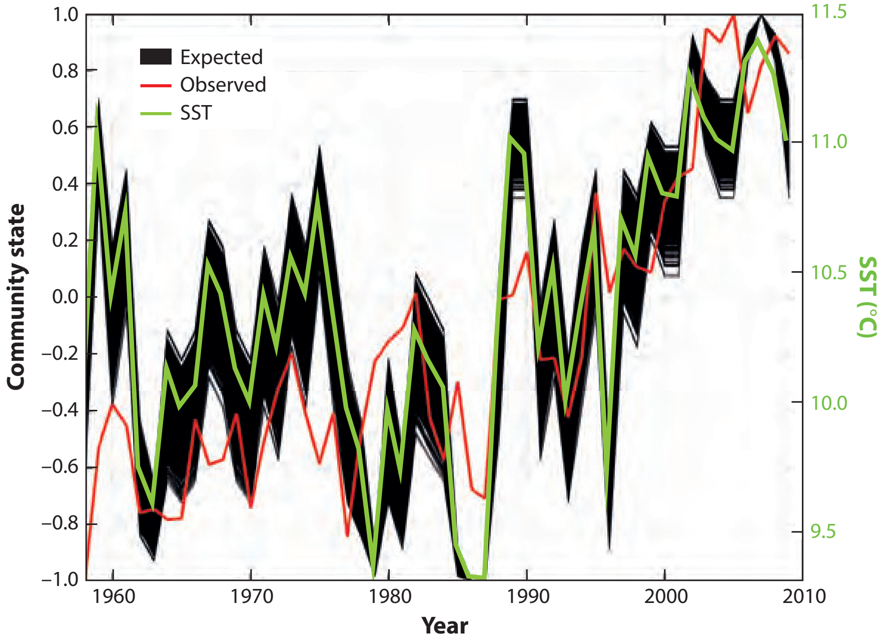

Figure 10

Test of the hypothesis that climate-caused abrupt community shift may be triggered by the interaction between changes in temperature and the thermal niche of each species composing a community. A total of 10,000 long-term expected changes were simulated (*black*) and compared with the first component of observed long-term copepod abundance changes for 1958–2009 (*red*) and annual sea surface temperature (SST) for 1958–1999 (*green*). Adapted from Beaugrand et al. (2014).

a substantial alteration of pelagic synusiae (**Figure 11**); we consider the ecological niche of a species to be controlled by the genotype (**Figure 1**) and therefore stable at a relatively long timescale (e.g., greater than decadal scale). In the northeastern region of the North Atlantic, major biogeographical shifts took place from 1960 to 2005 (Beaugrand 2009, Beaugrand et al. 2002). For example, a northward movement of warm-water calanoid copepod species has been observed, which is associated with a reduction in the number of colder-water species. Those biogeographical movements have deeply altered pelagic biodiversity (Beaugrand et al. 2009).

Changes in Biodiversity

Biodiversity shifts have already been observed or predicted to occur as the climate warms at regional and global scales, and examples exist from plankton to commercially exploited fish (Beaugrand et al. 2010, 2015; Brander et al. 2003; Burrows et al. 2014; Cheung et al. 2009; Hiddink & ter Hofstede 2008; Jones & Cheung 2015; Perry et al. 2005; Wernberg et al. 2011). METAL suggests that shifts in biodiversity are likely to result from the individual rearrangement of species as the climate changes, which takes place through the interaction between the ecological niche of each species and changes in the environmental regime (Beaugrand et al. 2013b, 2015).

Because temperature is a top parameter from the molecular level to the biosphere (Brown et al. 2004, Lineweaver & Schwartzman 2004), using a thermal niche can significantly help us to understand and anticipate climate-induced shifts in biodiversity. To reconstruct biodiversity, we applied the same type of model we used to investigate long-term community shifts. Each pseudocommunity results from the aggregation of pseudospecies, each of which is characterized by a unique niche. A total of 39,218 thermal (Gaussian) niches were generated at a year-to-year scale,

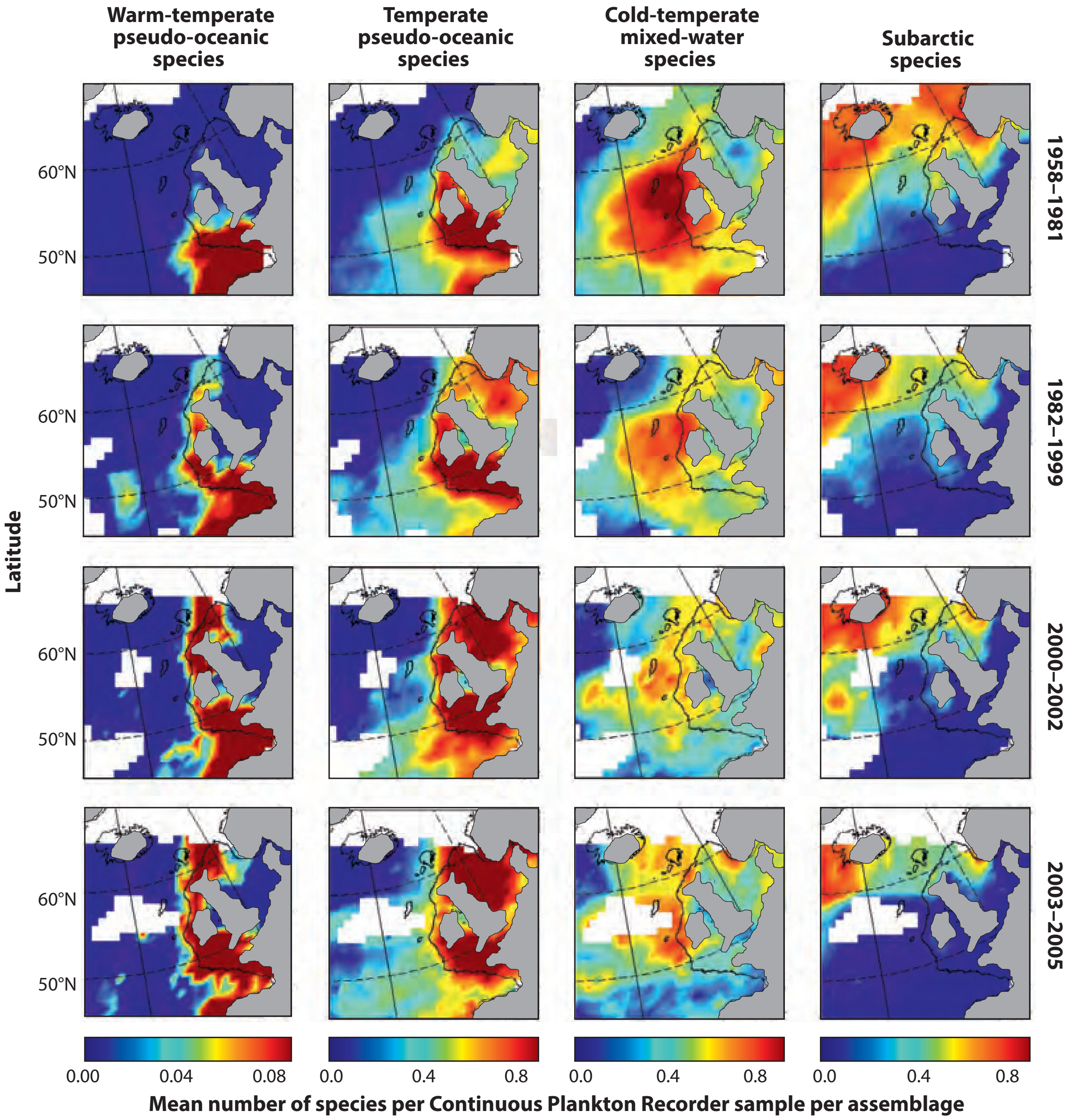

Figure 11

Long-term biogeographical shifts in calanoid copepods in the northeastern part of the North Atlantic. The mean number of species per sample is small because sampling is based on approximately 3 m^3 of seawater filtered and includes both day and night surface samples. Adapted from Beaugrand et al. (2009).

but only half (19,609) were chosen randomly to consider niche vacancy (Rohde 2005). All species were able to colonize a given region of the global ocean providing that they could withstand the local temperature (annual SST) regime (Beaugrand et al. 2015). Reconstructed biodiversity patterns from the past (Last Glacial Maximum and mid-Pliocene) and the contemporary period were highly correlated with observed patterns of biodiversity for a variety of taxonomic groups. Predictions of biodiversity shifts were carried out for the North Sea, and METAL explained well the long-term biodiversity shifts observed from 1960 to 2009 (Beaugrand et al. 2015), demonstrating that the currently observed increase in biodiversity results from a climatic effect, i.e., the increase in the thermal regime of extratropical oceans and seas (Beaugrand et al. 2010, Hiddink & ter Hofstede 2008).

METAL revealed that changes in marine biodiversity around the world will be nonuniform: Biodiversity will decrease in warm-water regions between 40°S and 40°N (from the equator to the subtropics) and will increase in temperate and polar regions. The increase in biodiversity projected by METAL and expected from other studies (Jones & Cheung 2015) has already been observed among copepods and fish in the extratropical regions of the Atlantic (i.e., the North Sea) (Beaugrand et al. 2010, Hiddink & ter Hofstede 2008). METAL also suggests a reduction in biodiversity in permanently stratified regions, an observation that is also projected by a multi-ensemble model based on niche modeling (Jones & Cheung 2015). Using 194 strains belonging to more than 130 species from major phytoplankton groups, Thomas et al. (2012) showed that global climate change may reduce phytoplankton biodiversity considerably in tropical regions by the end of this century.

We next investigated the potential consequences of global warming for the pelagic biodiversity at the end of the century, comparing those changes with the ones that occurred between the Last Glacial Maximum and the 1960s, between the mid-Pliocene and the 1960s, and between the 1960s and the 2000s (**Figure 12**). If future global warming remains below 2°C [Representative Concentration Pathway (RCP) 2.6], which is the amount of warming the international community considers to be below the threshold that would place natural systems at risk of grave damage, only 42% ± 26% of the global ocean would experience a substantial shift in biodiversity (**Figure 12*a***). More alarming is that the three other levels of global warming that were examined each indicated that they would place the marine biosphere at risk of increasingly significant changes (**Figure 12*b–d***). When warming reaches the dangerous threshold of 2°C, our model predicts that 78–94% of the surface ocean would experience a change in marine biodiversity. Such percentages should be compared with biodiversity shifts experienced as part of natural year-to-year variability during the last five decades or changes that already took place between the 1960s and the 2000s (**Figure 12*e*,*f***). These levels of biodiversity shifts would be higher than those experienced between the Last Glacial Maximum (or even the warmer period of the mid-Pliocene) and the 1960s (**Figure 12*g*,*h***). Biodiversity shifts between the Last Glacial Maximum and the 1960s took place over a period much longer than a century (∼5,000 years). When global warming rises above the dangerous threshold of 2°C, between 50% and 70% of the global ocean may experience a change in marine biodiversity equivalent to or greater than that experienced between the Last Glacial Maximum or mid-Pliocene and the 1960s, indicating a major effect of climate warming on marine biodiversity.

Consequences at the Ecosystem Level

Changes in biodiversity will inevitably affect ecosystem functioning (e.g., trophodynamics and species interaction, benthic-pelagic coupling, and sea-land interactions), provisioning (e.g., fisheries and aquaculture), and regulating services (e.g., the biological carbon pump) (Beaugrand et al. 2010; Cheung et al. 2009; Doney et al. 2012; Jones & Cheung 2015; Kirby & Beaugrand 2009; Kirby et al. 2007; Luczak et al. 2011, 2012). Although some of the consequences may be predicted from METAL, the relationships between the characteristics of the species' ecological niches and their life history traits remain to be understood and parameterized. For example, the increase in the biodiversity of calanoid copepods observed in areas that experienced an increase in temperature in the northeastern part of the North Atlantic and its adjacent seas has been accompanied by a phenomenon of dwarfism. The shift northward of warm-water species has reconfigured the synusia in such a way that it is now composed of smaller species, which may significantly alter

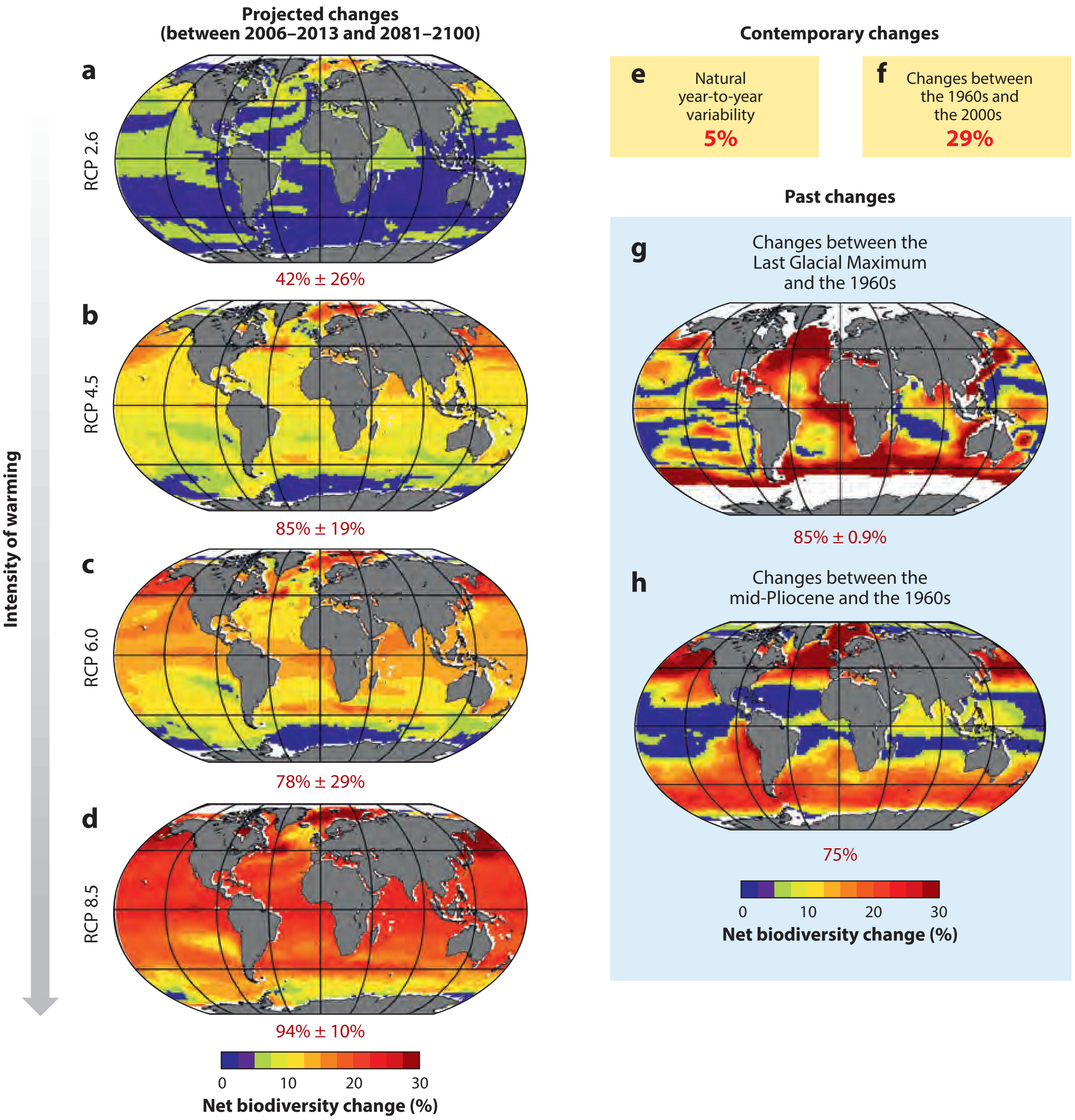

Figure 12

Expected future mean vulnerability of biodiversity in relation to past and contemporary changes. (*a–d*) Net biodiversity changes between 2006–2013 and 2081–2100 for scenarios under Representative Concentration Pathway (RCP) 2.6 (panel *a*), RCP 4.5 (panel *b*), RCP 6.0 (panel *c*), and RCP 8.5 (panel *d*). (*e*,*f*) Vulnerability of biodiversity related to natural year-to-year fluctuations in mean sea surface temperature (SST) (panel *e*) and to changes in mean SST between the 1960s and the 2000s (panel *f*). (*g*,*h*) Vulnerability of biodiversity related to changes in mean SST between the Last Glacial Maximum and the 1960s (panel *g*) and between the mid-Pliocene and the 1960s (panel *h*). All biological changes were based on quantitative measures of biodiversity and were subsequently expressed as percentages. Adapted from Beaugrand et al. (2015).

biological carbon exportation in those areas (Beaugrand et al. 2010). Understanding the relationships between the thermal amplitude and optima of species and their size could therefore help elucidate the effect of community reconfiguration on ecosystem-level processes, such as biological carbon exportation.

Coenocline: a gradient of communities

Ecocline: a gradient of ecosystems

Benthic-pelagic coupling in coastal seas is another ecosystem-level response that may be strongly affected by changes in temperature induced by anthropogenic climate change (Doney et al. 2012). In shallow seas, when stratification breaks down, the seabed and surface may be thermally similar, and therefore changes in sea surface temperature can affect the benthos. In the North Sea, this appears to have influenced the reproduction of benthic species whose meroplanktonic larvae may affect interactions in the plankton (Kirby et al. 2007, 2008). Kirby et al. (2007, 2008) suggested that those changes in trophic interactions reflected a shift in energy partitioning between the benthos and the pelagos that involved many species, from invertebrates to vertebrates, and several direct and indirect pathways.

Climate change may also alter sea-land interactions. The changes in North Sea decapods described above were also associated with an outburst in swimming crabs (*Necora puber*, *Liocarcinus depurator*, and *Polybius henslowii*) (Luczak et al. 2012). Because swimming crabs are a significant food source for lesser black-backed gulls during the breeding season, Luczak et al. (2012) suggested that this proliferation may have led to the increase in some North Sea colonies. Inhabiting the land but feeding mainly at sea, these gulls provide a link between marine and terrestrial ecosystems because the bottom-up influence of allochthonous nutrient input from seabirds to coastal soils can structure terrestrial trophodynamics. In this way, climate-caused marine ecosystem changes may have some consequences for coastal terrestrial ecosystems.

Shifts in Biomes and Provinces

A major ecological compartment (a biome) is by definition in equilibrium with a climatic regime. Therefore, climate change is expected to unbalance these large ecosystems (Lomolino et al. 2006). METAL predicts climate-induced shifts in the locations of biomes and provinces. Beaugrand et al. (2008) showed that a northward movement of North Sea isotherms triggered a poleward shift of the boundary between temperate and Arctic biomes (*sensu* Longhurst 1998). They showed that the average spatial distribution of upper-ocean chlorophyll concentration [as measured by the Sea-Viewing Wide Field-of-View Sensor (SeaWiFS)], the diversity and mean size of calanoid copepods (as measured by the Continuous Plankton Recorder survey), and the modeled occurrence of Atlantic cod exhibited a pronounced nonlinearity in their individual responses to temperature change between 9°C and 10°C. The critical thermal boundary of 9–10°C coincided with the transitional region between the Atlantic Polar biome and the Atlantic Westerly Winds biome. Beaugrand et al.'s (2008) analysis revealed that biome boundaries are highly sensitive to climate change and that climate-induced modifications in their geographical locations may have caused pronounced community/ecosystem shifts.

Pelagic biomes are primary biological units that can be fairly separated from each other (Longhurst 1998), although their geographical limits are dynamic at multiple timescales (Reygondeau et al. 2013). However, provinces are imbricated, and they are constituted of a mosaic of coenoclines and therefore ecoclines (Whittaker 1975). At a large scale, many studies suggest that provinces may be reconfigured as a consequence of global climate change. METAL suggests that there are strong constraints that will limit the rearrangement of provinces, especially in the pelagic domain (**Figure 9**). Some studies have proposed that new provinces may emerge from climate change in permanently stratified regions. This is indeed a possibility, but caution is needed because the upper thermal limits of the species inferred from their current distribution may be underestimated. In the past, higher temperatures may have occurred in those regions, and many species may have the potential to occur in warmer thermal regimes; here, this is the norm of reaction of species that may be underestimated. The determination of the upper thermal limit of pseudospecies in METAL has strong consequences for the modeled patterns of biodiversity, showing that the estimation of the upper thermal limit of species is fundamental. The only way to understand this is to reexamine warmer periods or to estimate this parameter through individual physiological experiments.

CONCLUSION

A unifying ecological theory to understand and predict how biodiversity is organized and how it responds to climate change is important. Our METAL framework is based on the concept of the ecological niche of Hutchinson (1957), which integrates genetic, molecular, and other biological processes that are difficult to parameterize in classical approaches because of the many variables that need to be estimated. Our theory shows that most responses of species documented so far can be explained by the ecological niche-environment interaction, which subsequently propagates to higher organizational levels. Our study shows that the responses of species to climate change are therefore intelligible—i.e., they have a strong deterministic component and can be predicted. A unifying ecological theory should also be able to guide future research by defining research priorities and identify both weaknesses and strengths in our current scientific knowledge, which we hope is a role METAL will fulfill.

DISCLOSURE STATEMENT

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

ACKNOWLEDGMENTS

G.B. thanks the Centre National de la Recherche Scientifique and the Sir Alister Hardy Foundation for Ocean Science.

LITERATURE CITED

Aruda AM, Baumgartner MF, Reitzel AM, Tarrant AM. 2011. Heat shock protein expression during stress and diapause in the marine copepod *Calanus finmarchicus*. *J. Insect Physiol*. 57:665–75

Atkinson D. 1994. Temperature and organism size—a biological law for ectotherms? *Adv. Ecol. Res.* 3:1–58

Batten SD, Mackas DL. 2009. Shortened duration of the annual *Neocalanus plumchrus* biomass peak in the northeast Pacific. *Mar. Ecol. Prog. Ser.* 393:189–98

Baumgartner MF, Tarrant AM. 2017. The physiology and ecology of dipause in marine copepods. *Annu. Rev. Mar. Sci.* 9:387–411

Beaugrand G. 2009. Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. *Deep-Sea Res. II* 56:656–73

Beaugrand G. 2012. Unanticipated biological changes and global warming. *Mar. Ecol. Prog. Ser.* 445:293–301

Beaugrand G. 2014. Theoretical basis for predicting climate-induced abrupt shifts in the oceans. *Philos. Trans. R. Soc. B* 370:20130264

Beaugrand G. 2015. *Marine Biodiversity, Climatic Variability and Global Change*. London: Routledge

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC. 2003. Plankton effect on cod recruitment in the North Sea. *Nature* 426:661–64

Beaugrand G, Edwards M, Brander K, Luczak C, Ibañez F. 2008. Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecol. Lett.* 11:1157–68

Beaugrand G, Edwards M, Legendre L. 2010. Marine biodiversity, ecosystem functioning and the carbon cycles. *PNAS* 107:10120–24

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, Goberville E, Luczak C, Kirby RR. 2014. Marine biological shifts and climate. *Proc. R. Soc. B* 281:20133350

Beaugrand G, Kirby RR. 2016. Quasi-deterministic responses of marine species to climate change. *Clim. Res.* 69:117–28

Beaugrand G, Lindley JA, Helaouët P, Bonnet D. 2007. Macroecological study of *Centropages typicus* in the North Atlantic Ocean. *Prog. Oceanogr.* 72:259–73

Beaugrand G, Luczak C, Edwards M. 2009. Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Glob. Change Biol.* 15:1790–803

Beaugrand G, McQuatters-Gollop A, Edwards M, Goberville E. 2013a. Long-term responses of North Atlantic calcifying plankton to climate change. *Nat. Clim. Change* 3:263–67

Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296:1692–94

Beaugrand G, Rombouts I, Kirby RR. 2013b. Towards an understanding of the pattern of biodiversity in the oceans. *Glob. Ecol. Biogeogr.* 22:440–49

Behrenfeld MJ. 2010. Abandoning Sverdrup's critical depth hypothesis on phytoplankton blooms. *Ecology* 91:977–89

Bigg GR. 1996. *The Oceans and Climate*. Cambridge, UK: Cambridge Univ. Press

Brander K, Blom G, Borges MF, Erzini K, Henderson G, et al. 2003. Changes in fish distribution in the eastern North Atlantic: Are we seeing a coherent response to changing temperature? *ICES Mar. Sci. Symp.* 219:261–70

Brown JH. 1984. On the relationship between abundance and distribution of species. *Am. Nat.* 124:255–79

Brown JH. 1995. *Macroecology*. Chicago: Univ. Chicago Press

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–89

Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, et al. 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334:652–55

Burrows MT, Schoeman DS, Richardson AJ, Molinos JG, Hoffmann A, et al. 2014. Geographical limits to species-range shifts are suggested by climate velocity. *Nature* 507:492–96

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D. 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish.* 10:235–51

Chevaldonné P, Lejeusne C. 2003. Regional warming-induced species shift in north-west Mediterranean marine caves. *Ecol. Lett.* 6:371–79

Comiso JC, Parkinson CL, Gersten R, Stock L. 2008. Accelerated decline in the Arctic sea ice cover. *Geophys. Res. Lett.* 35:L01703

Conover DO, Schultz ET. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends Ecol. Evol.* 10:248–53

Crisp MD, Arroyo MTK, Cook LG, Gandolfo MA, Jordan GJ, et al. 2009. Phylogenetic biome conservatism on a global scale. *Nature* 458:754–56

Dickson R, Lazier J, Meincke J, Rhines P, Swift J. 1996. Long-term coordinated changes in the convective activity of the North Atlantic. *Prog. Oceanogr.* 38:241–95

Dietrich G. 1964. Oceanic polar front survey. *Res. Geophys.* 2:291–308

Dobrowski SZ. 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Glob. Change Biol.* 17:1022–35

Doney SC, Ruckelshaus M, Duffy JE, Barry JP, Chan F, et al. 2012. Climate change impacts on marine ecosystems. *Annu. Rev. Mar. Sci.* 4:11–37

Edwards M, Richardson AJ. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430:881–84

Feely RA, Doney SC, Cooley SR. 2009. Ocean acidification: present conditions and future changes in a high-CO_2 world. *Oceanography* 22(4):36–47

Frederich M, Pörtner HO. 2000. Oxygen limitation of thermal tolerance defined by cardiac and ventilatory performance in the spider crab, *Maja squinado*. *Am. J. Physiol.* 279:R1531–38

Fromentin J-M, Reygondeau G, Bonhommeau S, Beaugrand G. 2014. Oceanographic changes and exploitation drive the spatio-temporal dynamics of Atlantic bluefin tuna (*Thunnus thynnus*). *Fish. Oceanogr.* 23:147–56

Gaston KJ, Blackburn TM. 2000. *Pattern and Process in Macroecology*. Padstow, UK: Blackwell

Gaston KJ, Spicer JI. 2004. *Biodiversity: An Introduction*. Hong Kong: Blackwell

Gause GF. 1934. *The Struggle for Coexistence*. Baltimore, MD: Williams & Wilkins

Guilford T, Meade J, Willis J, Phililips RA, Boyle D, et al. 2009. Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. *Proc. R. Soc. B* 276:1215–23

Gunderson AR, Stillman JH. 2015. Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proc. R. Soc. B* 282:20150401

Heath MR, Backhaus JO, Richardson K, McKenzie E, Slagstad D, et al. 1999. Climate fluctuations and the invasion of the North Sea by *Calanus finmarchicus*. *Fish. Oceanogr.* 8(Suppl. 1):163–76

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Glob. Change Biol.* 12:450–55

Hiddink JG, ter Hofstede R. 2008. Climate induced increases in species richness of marine fishes. *Glob. Change Biol.* 14:453–60

Huey RB, Hertz PE, Sinervo B. 2003. Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat.* 161:357–66

Hutchinson GE. 1957. Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.* 22:415–27

Jablonski D. 1991. Extinctions: a paleontological perspective. *Science* 253:754–57

Ji R, Edwards M, Mackas DL, Runge JA, Thomas AC. 2010. Marine plankton phenology and life history in a changing climate: current research and future directions. *J. Plankton Res.* 32:1355–68

Jónasdóttir SH, Koski M. 2011. Biological processes in the North Sea: comparison of *Calanus helgolandicus* and *Calanus finmarchicus* vertical distribution and production. *J. Plankton Res.* 33:85–103

Jones MC, Cheung WWL. 2015. Multi-model ensemble projections of climate change effects on global marine biodiversity. *ICES J. Mar. Sci.* 72:741–52

Kirby RR, Beaugrand G. 2009. Trophic amplification of climate warming. *Proc. R. Soc. Lond. B* 276:4095–103

Kirby RR, Beaugrand G, Lindley JA. 2008. Climate-induced effects on the meroplankton and the benthic-pelagic ecology of the North Sea. *Limnol. Oceanogr.* 53:1805–15

Kirby RR, Beaugrand G, Lindley JA, Richardson AJ, Edwards M, Reid PC. 2007. Climate effects and benthic-pelagic coupling in the North Sea. *Mar. Ecol. Prog. Ser.* 330:31–38

Knell RJ, Thackeray SJ. 2016. Voltinism and resilience to climate-induced phenological mismatch. *Clim. Change* 137:525–39

Lenoir S, Beaugrand G, Lecuyer E. 2011. Modelled spatial distribution of marine fish and projected modifications in the North Atlantic Ocean. *Glob. Change Biol.* 17:115–29

Lindley JA, Daykin S. 2005. Variations in the distributions of *Centropages chierchiae* and *Temora stylifera* (Copepoda: Calanoida) in the north-eastern Atlantic Ocean and western European shelf waters. *ICES J. Mar. Sci.* 62:869–77

Lineweaver CH, Schwartzman D. 2004. Cosmic thermobiology: thermal constraints on the origin and evolution of life in the universe. In *Origins*, ed. J Seckbach, pp. 233–48. Dordrecht, Neth.: Kluwer

Lomolino MV, Riddle BR, Brown JH. 2006. *Biogeography*. Sunderland, MA: Sinauer

Longhurst A. 1998. *Ecological Geography of the Sea*. London: Academic

Luczak C, Beaugrand G, Jaffré M, Lenoir S. 2011. Climate change impact on Balearic shearwater through a trophic cascade. *Biol. Lett.* 7:702–5

Luczak C, Beaugrand G, Lindley JA, Dewarumez J-M, Dubois PJ, Kirby RR. 2012. North Sea ecosystem changes from swimming crabs to seagulls. *Biol. Lett.* 8:821–24

Mackas DL, Greve W, Edwards M, Chiba S, Tadokoro K, et al. 2012. Changing zooplankton seasonality in a changing ocean: comparing time series of zooplankton phenology. *Prog. Oceanogr.* 97–100:31–62

MacLeod CD. 2009. Global climate change, range changes and potential implications for the conservation of marine cetaceans: a review and synthesis. *Endanger. Species Res.* 7:125–36

McGinty N, Power AM, Johnson MP. 2011. Variation among northeast Atlantic regions in the responses of zooplankton to climate change: not all areas follow the same path. *J. Exp. Mar. Biol. Ecol.* 400:120–31

McQuinn IH. 1997. Metapopulations and the Atlantic herring. *Rev. Fish Biol. Fish.* 7:297–329

Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, et al. 2006. European phenological resonse to climate change matches the warming pattern. *Glob. Change Biol.* 12:1969–76

Overpeck J, Whitlock C, Huntley B. 2003. Terrestrial biosphere dynamics in the climate system: past and future. In *Paleoclimate*, *Global Change and the Future*, ed. KD Alverson, RS Bradley, TF Pedersen, pp. 81–111. Heidelberg, Ger.: Springer-Verlag

Padfield D, Yvon-Durocher G, Buckling A, Jennings S, Yvon-Durocher G. 2016. Rapid evolution of metabolic traits explains thermal adaptation in phytoplankton. *Ecol. Lett.* 19:133–42

Parmesan C. 2005. Biotic response: range and abundance changes. In *Climate Change and Biodiversity*, ed. TE Lovejoy, L Hannah, pp. 41–55. New Haven, CT: Yale Univ. Press

Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42

Perry AI, Low PJ, Ellis JR, Reynolds JD. 2005. Climate change and distribution shifts in marine fishes. *Science* 308:1912–15

Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, et al. 2013. Global imprint of climate change on marine life. *Nat. Clim. Change* 3:919–25

Pörtner HO. 2001. Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften* 88:137–46

Przybylo R, Sheldon BC, Merilä J. 2000. Climatic effects on breeding and morphology: evidence for phenotypic plasticity. *J. Anim. Ecol.* 69:395–403

Quintero I, Wiens JJ. 2013. Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. *Ecol. Lett.* 16:1095–103

Raybaud V, Beaugrand G, Goberville E, Delebecq G, Destombe C, et al. 2013. Decline in kelp in west Europe and climate. *PLOS ONE* 8:e66044

Reygondeau G, Longhurst A, Beaugrand G, Martinez E, Antoine D, Maury O. 2013. Toward dynamic biogeochemical provinces. *Glob. Biogeochem. Cycles* 27:1046–58

Richardson AJ, Schoeman DS. 2004. Climate impact on plankton ecosystems in the northeast Atlantic. *Science* 305:1609–12

Rohde K. 2005. *Nonequilibrium Ecology*. Cambridge, UK: Cambridge Univ. Press

Sarmiento JL, Slater R, Barber R, Bopp L, Doney SC, et al. 2004. Response of ocean ecosystems to climate warming. *Glob. Biogeochem. Cycles* 18:1–23

Schwartzman D, Lineweaver CH. 2005. Temperature, biogenesis and biospheric self-organization. In *Non-Equilibrium Thermodynamics and the Production of Entropy: Life, Earth and Beyond*, ed. A Kleidon, R Lorenz, pp. 207–17. Berlin: Springer

Shama LNS, Campero-Paz M, Wegner KM, de Block M, Stoks R. 2011. Latitudinal and voltinism compensation shape thermal reaction norms for growth rate. *Mol. Ecol.* 20:2929–41

Shelford VE. 1931. Some concepts of bioecology. *Ecology* 12:455–67

Sims DW, Wearmouth VJ, Southall EJ, Hill JM, Moore P, et al. 2006. Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *J. Anim. Ecol.* 75:176–90

Sorte CJB, Williams SL, Carlton J. 2010. Marine range shifts and species introductions: comparative spread rates and community impacts. *Glob. Ecol. Biogeogr.* 19:303–16

Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, et al. 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *PNAS* 111:5610–15

ter Braak CJF. 1996. *Unimodal Models to Relate Species to Environment*. Wageningen, Neth.: DLO Agric. Math. Group

Thackeray SJ, Henrys PA, Hemming D, Bell JR, Botham MS, et al. 2016. Phenological sensitivity to climate across taxa and trophic levels. *Nature* 535:241–45

Thomas CD. 2010. Climate, climate change and range boundaries. *Divers. Distrib.* 16:488–95

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, et al. 2004. Extinction risk from climate change. *Nature* 427:145–48

Thomas CD, Lennon JJ. 1999. Birds extend their ranges northwards. *Nature* 399:213

Thomas MK, Kremer CT, Klausmeier CA, Litchman E. 2012. A global pattern of thermal adaptation in marine phytoplankton. *Science* 338:1085–88

van der Spoel S. 1994. The basis for boundaries in pelagic biogeography. *Prog. Oceanogr.* 34:121–33

Visser ME, Both C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc. B* 272:2561–69

Wernberg T, Russell BD, Moore PJ, Ling SD, Smale DA, et al. 2011. Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. *J. Exp. Mar. Biol. Ecol.* 400:7–16

Whittaker RH. 1975. *Communities and Ecosystems*. New York: Macmillan

Winder M, Shindler DE, Essington TE, Litt AH. 2009. Disrupted seasonal clockwork in the population dynamics of a freshwater copepod by climate warming. *Limnol. Oceanogr.* 54:2493–505

Zmiri A, Kahan D, Hochstein S, Reiss Z. 1974. Phototaxis and thermotaxis in some species of *Amphistegina* (Foraminifera). *J. Eukaryot. Microbiol.* 21:133–38

Annual Review of
Marine Science

Volume 10, 2018

Contents

Errata

An online log of corrections to *Annual Review of Marine Science* articles may be found at http://www.annualreviews.org/errata/marine

Annual Review of
Marine Science

Volume 10, 2018

Contents