Global warming benefits the small in aquatic ecosystems

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Understanding the ecological impacts of climate change is a crucial challenge of the twenty-first century. There is a clear lack of general rules regarding the impacts of global warming on biota. Here, we present a metaanalysis of the effect of climate change on body size of ectothermic aquatic organisms (bacteria, phyto- and zooplankton, and fish) from the community to the individual level. Using long-term surveys, experimental data and published results, we show a significant increase in the proportion of small-sized species and young age classes and a decrease in size-at-age. These results are in accordance with the ecological rules dealing with the temperature–size relationships (i.e., Bergmann's rule, James' rule and Temperature–Size Rule). Our study provides evidence that reduced body size is the third universal ecological response to global warming in aquatic systems besides the shift of species ranges toward higher altitudes and latitudes and the seasonal shifts in life cycle events.

biological scale | body size | climate change | ectotherms | metaanalysis

At the biogeographical scale, the most noticeable ecological impact of global warming is a shift of species' ranges toward higher altitudes and latitudes in accordance with their thermal preferences (1–3). This observation has been used extensively to forecast the effect of climate change on biota by modeling future species distributions according to climate-change scenarios (4). However, such patterns and pattern-related predictions do not elaborate specific underlying ecological mechanisms. As a consequence, our understanding and, in turn, our ability to forecast the impacts of climate change on biota remains limited (e.g., it seems possible to forecast species' ranges, but it remains difficult to predict the relative abundances of species within a community). Besides the shifts in species' ranges, the second well-known ecological response to global warming is a change in phenology (3). Such patterns could lead to a decoupling of the dynamics of predators and prey (5). This mechanism-oriented hypothesis, generally referred to as the match–mismatch hypothesis (6), offers perspectives in forecasting the ecological impacts of climate change (5, 7, 8). Nevertheless, all of the components of the food web can be affected by dissimilar changes in phenology, leading to complex dynamics that are difficult to predict (5). The match–mismatch hypothesis and the shifts of species' ranges are key tools when evaluating the ecological consequences of global warming, but they are thus far insufficient to provide clear views on future ecological changes. Further general rules dealing with the impacts of a global rise in temperature on biota are needed.

Body size is a fundamental biological characteristic that scales with many ecological properties (e.g., fecundity, population growth rate, competitive interactions) (9, 10). Surprisingly, few studies have dealt with changes in body size with global warming (10), especially for ectotherms, although they represent ≈99.9% of species on Earth (11). Furthermore, the biological scales (individual, population, community) at which global warming should act on body size have not been studied. Three rules concerning ecogeographical and ecothermal gradients (10) are relevant in this context. First, Bergmann's rule (12), states that warm regions tend to be inhabited by small-sized species.

Second, James' rule (13) states that, within a species, populations with smaller body size are generally found in warmer environments. Third, the temperature–size rule (TSR) states that the individual body size of ectotherms tends to decrease with increasing temperature (14). Combining these rules, we can build a set of 5 hierarchical and nonmutually exclusive hypotheses concerning the potential effect of climate change on size structures from the individual to the community scales (Fig. 1). The first hypothesis predicts a decrease in mean body size at the community scale under warming whatever the underlying mechanisms (community body size shift hypothesis). If there is a decrease in the mean body size at the community scale under warming, there are 4 subsequent hypotheses that could explain this decrease. According to Bergmann's rule, the first mechanism acts at the community scale is an increase in the proportion of small size species (species shift hypothesis) in terms of abundances of individuals and/or number of species. Second, according to James' rule, the decrease in size at the community scale could also be due to a decrease in mean body size at the population scale (population body size shift hypothesis). In turn, such a size decrease at the population scale could be due to 2 mechanisms. First, according to the TSR, the size-at-age (or size-at-stage; individual scale) should decrease with increasing temperature (size-at-age shift hypothesis). Note, however, that this decrease should not be observed for early ages or stages because the TSR predict a higher growth rate but a lower final size at higher temperature. In addition to this decrease in size-at-age/stage, an increase in the proportion of juveniles (population age-structure shift hypothesis) could also be expected at the population scale. The latter hypothesis does not correspond to the above-cited ecogeographical or ecothermal rules, but it is the default explanation if the population body size shift hypothesis applies whereas the size-at-age shift hypothesis does not apply. Note that, due to compensatory effects, the invalidation of a hypothesis does not imply that both subsequent hypotheses do not apply. For instance, no changes in mean size at the community scale can be due to a decrease in mean body size at the population scale and an increase in proportion of large species.

In this article, we studied changes in body size from individuals to communities under climate warming by testing the 5 hypotheses described above. The tests of the hypotheses were based on (*i*) the analysis of the effects of increasing temperature on long-term fish data sampled in French rivers and in the Baltic Sea, (*ii*) the analysis of experimental plankton data (bacteria, phyto- and zooplankton) collected in light- and temperature-controlled mesocosms (15), and (*iii*) on a review of related published work based on data collected in mesocosms and in the
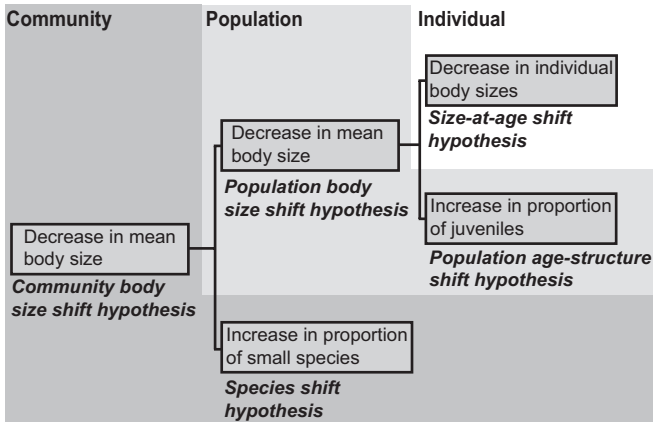
Fig. 1. The tested hypotheses regarding the impact of warming on body size at different biological scales.

Fig. 3. Mean effect sizes (i.e., mean weighted temporal trend statistic S; $\pm95\%$ confidence intervals). Negative or positive trend values indicate temporal decrease or increase, respectively. Mean temporal trends are significant if their 95% confidence intervals did not contain 0. Community body size shift and species shift hypotheses were tested by using 4 freshwater fish communities. To test the species shift hypothesis, small species were defined as species with a maximum size below the first quartile of the maximum size of all of the species in the community. Proportions of small species are calculated in terms of species richness (SR) and abundances (Ab.). Population body size shift and population age-structure shift hypotheses were tested by using 28 and 18 fish populations, respectively. Size-at-age shift hypothesis was tested by using 28 age classes. Significantly different means for marine (M) vs. freshwater (F) populations are represented. To increase readability some effect sizes are divided by a factor x (indicated in the figure as /x).

North Sea (Fig. 2). Impacts of potential confounding factors, and especially of fisheries, were considered. Our results support the hypothesis that reduced body size is a third universal or very general ecological response to global warming among ectotherms in aquatic systems, besides the shift of species ranges toward higher altitudes and latitudes and the seasonal shifts in life-cycle events.

Results

We found that increased temperature acts on communities, populations and individuals through changes in species composition, growth and reproduction.

Community Body Size Shift. A metaanalysis revealed that the mean temporal trend (S) of mean body size of fish in large French rivers was significantly negative during the last 2–3 decades under gradual warming (Fig. 3). A decrease in mean body size with increasing temperature was also observed for bacteria in temperature-controlled mesocosms [extended linear mixed-effect (LME) model, coefficient estimate $= -1.06 \times 10^{-3}$, t value $= -5.51$, number of observations $= 68$, $P = 3.1 \times 10^{-2}$;
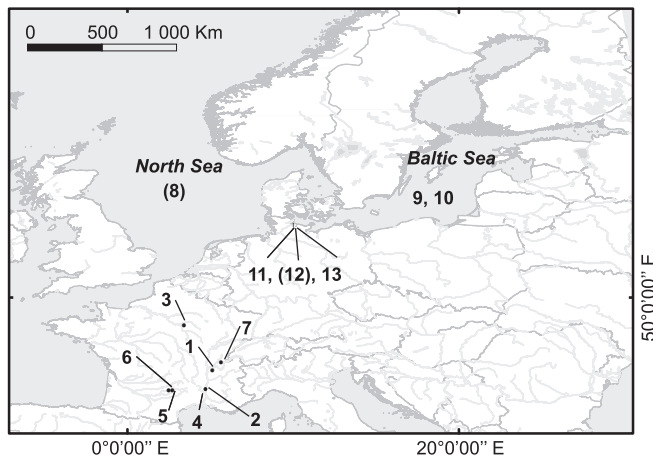

Fig. 2. Location of the study areas. 1–4: Long-term survey of freshwater fish communities in large rivers. 5–7: Long-term survey of brown trout populations. 8: Long term survey of North Sea fish community. 9–10: Long term survey of herring and sprat populations in the Baltic Sea. 11–13: Sampling of bacteria and phytoplankton communities and of *Pseudocalanus* sp. (zooplankton) in temperature-controlled mesocosms. Numbers in brackets refer to published climate–size relationships reviewed in this article (16, 17).
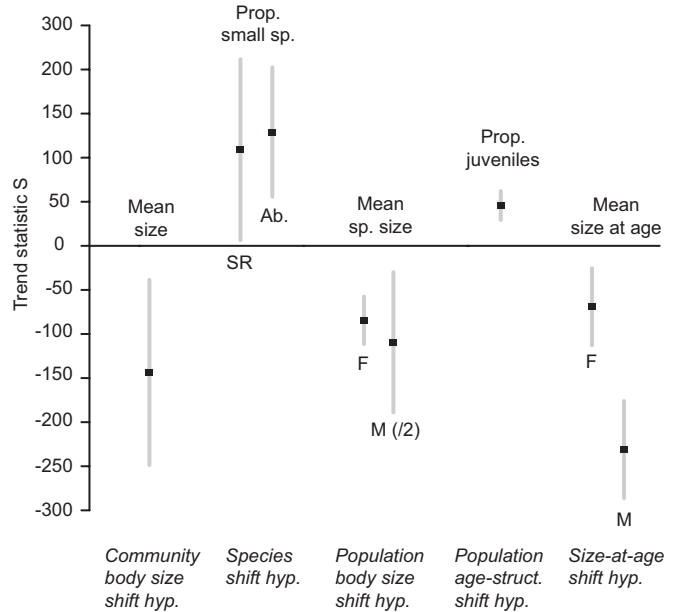
Fig. 4*A*]. The mean cell size of phytoplankton also tended to decrease with increasing temperature in the same mesocosms (16) (Fig. 4*B*).

Species Shift. Supporting the species-shift hypothesis, the proportion of small-sized species significantly increased in communities of large French rivers (Fig. 3) both in terms of species richness and abundance. Similar patterns were also observed for the fish community of the North Sea where the geographical ranges of small species expanded, whereas those of large species shrank due to warming (17) (Fig. 4*C*). In this way, the more even distribution of small species and the patchier distribution of large species should result locally in an average temporal increase in the number of small species and an average decrease in the number of large species. Finally, because the same size s_i was attributed to all individuals from a given phytoplankton taxon i in ref. 16, the observed decrease in mean size described above (community body size shift; Fig. 4*B*) is entirely due to an increase in proportion of abundances of small-sized taxa.

Population Body Size Shift. Besides interspecific patterns, our metaanalysis revealed a negative temporal trend in the mean body size of individual fish populations under global warming (Fig. 3). Herring and sprat populations in the Baltic Sea showed merely significant stronger decrease in mean size than freshwater species populations (coefficient $Qb = 2.67$, $P = 0.10$), underlining the potential additive effect of fisheries.

Population Age-Structure Shift. The decrease in fish mean body size at the population scale was partially due to a significant
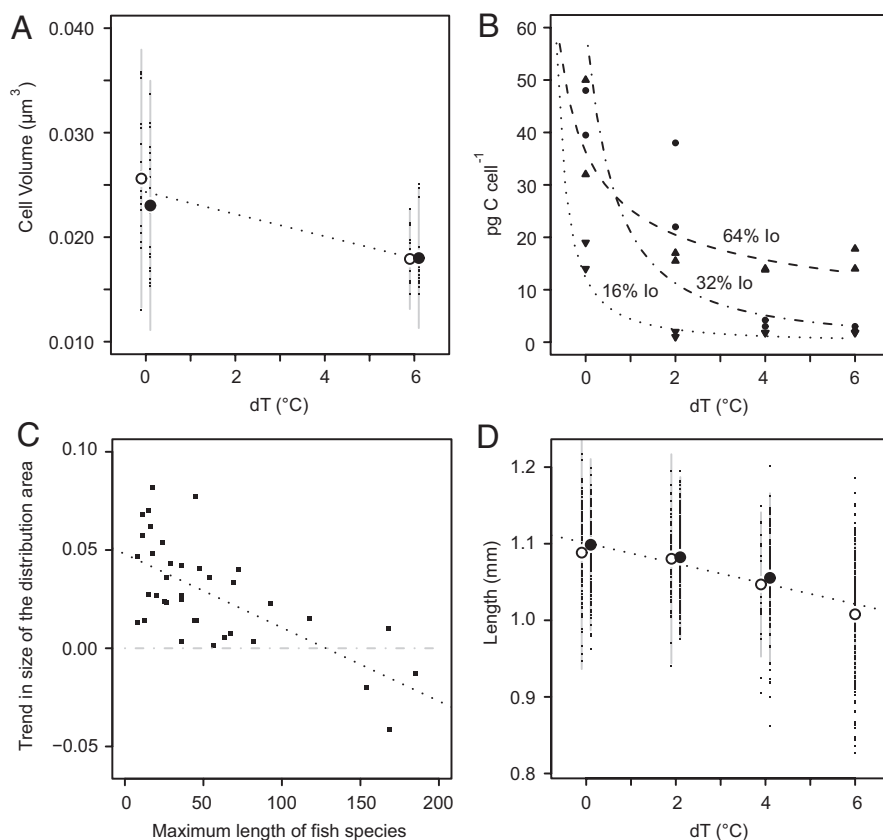
Fig. 4. Change in size structures under warming. (*A*) Cell size of bacteria subjected to different level of warming (+0, +2, +4, and +6 °C) compare to a reference thermal regime (dT) [means (open and closed circles), standard errors (gray lines), and raw data (closed rectangles) in the different replicates are represented]. (*B*) Mean cell size of phytoplankton at different level of warming (dT) and different light conditions [percentage of the natural light intensity above cloud cover (Io); 16% Io: hanging triangles; 32% Io: circles; 64% Io: standing triangles] (after figure 3c of ref. 16). (*C*) Effect of maximum length on distribution trends (expansion or shrinkage) of fish species in the North Sea during the past 20 y (after figure 4b of ref. 17). (*D*) Size of female adult *Pseudocalanus* sp. at different level of warming (dT) (symbols as for *A*).

increase in proportion of juveniles (Fig. 3), emphasizing the change in age structure of the populations. No specific response of herring and sprat populations was found (coefficient Qb = 2.1, P = 0.15).

Size-At-Age Shift. Finally, long-term analysis of fish populations highlighted a significant decrease in size-at-age (Fig. 3) with a significantly stronger effect for herring and sprat populations in the Baltic Sea (coefficient Qb = 20.4, P = 6.34×10^{-6}). The decrease in size-at-age was also detected in experimental data. We observed a decrease in size of adult females of *Pseudocalanus* sp. with temperature in the temperature-controlled mesocosms (extended LME model, coefficient estimate = −13.46, t value = −8.41, number of observations = 807, P = 4.00×10^{-4}; Fig. 4*D*).

Discussion

Observed patterns are consistent with our hypotheses, emphasizing a negative effect of global warming on the body size of aquatic ectotherms from the individual to community structure levels. Given that the biota and ecosystems considered in this study were diverse with regard to the potential confounding factors affecting body size, our results suggest that a common mechanism (or set of mechanisms) links size structure and thermal energy at all biological scales considered. Of course, other factors may have additive or multiplicative effects on size. For instance, it has been shown that body size of fish decreases with fishery activities (18, 19). By targeting large individuals, fisheries are considered as a selective pressure favoring early

maturation at smaller size. Thus, fishery activities could explain the observed decrease in size of herring and sprat in the Baltic Sea. On the other hand, regarding freshwater ecosystems, recreational fishing tended to decrease over the study periods in France (e.g., −38,703 fishermen/year from 1993 to 2008; data source: Federation Nationale de la Peche en France et de la Protection du Milieu Aquatique, www.federationpeche.fr). In addition, the species considered in our study (mostly cyprinid species) are not specially targeted by fishermen who prefer top predators. Similarly, the commercial fishing mostly concerns migratory species, eels, and top predators that accounted together for 79% of the total catches over the 1999–2001 period (data source: Suivi National de la Peche aux Engins/Resultats Professionnels; Conseil Superieur de la Peche/Office National de l'Eau et des Milieux Aquatiques, www.onema.fr). Finally, the number of professional fisherman was low at our study areas (e.g., on average 4, 3, 0, and 3 in the vicinity of site 1, 2, 3, and 4, respectively, over the 1999–2002 period; data source: Suivi National de la Peche aux Engins/Resultats Professionnels). Therefore, fishery pressure can be considered of minor impact in the freshwater areas studied in this article. Thus, the impact of fisheries cannot fully explain the decrease in size observed in rivers. In addition, obviously, fisheries cannot explain the patterns observed in the mesocosms. As a consequence, the overall consistency of the observed patterns emphasizes the role of temperature. Such results underline the importance of taking into account thermal constraints as potential confounding factors when studying changes in size structures. Indeed, early

maturation at smaller size has systematically been attributed to fishery activities in marine ecosystems (18, 19), although this pattern perfectly fits the TSR in environments that have been subjected to gradual warming. Although not underestimating the impact of fisheries, our results stressed that fishery pressure cannot be considered as the unique trigger of observed changes in size structures in marine ecosystems. Further analyses would be needed to evaluate the relative merit of global warming and fisheries in explaining changes in body size of marine fish. The TSR predicts a negative effect of warming on size at maturity but a positive effect on growth rate. As a consequence, warming leads to smaller sizes late in the ontogeny but to larger sizes early in the ontogeny. Thus, by only considering young-of-the-year individuals fish in rivers when testing the size-at-age shift hypothesis, we probably underestimated the impact of climate change on individual body size under no or low fishery pressure.

Cascading effects could also contribute to the changes in size. For instance, we cannot exclude that the decrease in size of *Pseudocalanus* sp. is partially due to low food quality of small-sized phytoplankton in warmer mesocosms (Fig. 4B). However, this effect can, again, not fully explain the observed changes because the other decreases in size (e.g., for freshwater fish or for phytoplankton) were not observed under decreasing food quality. Regarding fish communities, top-down constraints can also influence size structures. In particular, change in the abundance of predators can influence the abundance of smaller prey (20, 21). Nevertheless, in the large rivers studied, no special change in the predator abundance was observed (22, 23). Thus, we can safely conclude that temperature clearly negatively impacts body sizes at all biological scales.

One of the most surprising results of our analysis is the increase in proportion of young age classes under warming. Actually, to our knowledge, such a pattern has never been suggested before to explain the decrease in mean body size at the population scale under warming. However, it is important to note that this hypothesis has been mostly tested by using European freshwater fish populations where cyprinidae was the dominant family. The positive effect of high temperature and/or low flow conditions on recruitment is well known for many cyprinidae (24–30). Even though the underlying mechanisms are unclear, we cannot exclude that this effect is specific to cyprinids. From this viewpoint, we may agree that it is necessary to test the population age-structure shift hypothesis with other biota to consider it as a rule.

We have shown that ecological rules represent important tools when evaluating the ecological impacts of climate change. Symmetrically, climate change provides a good opportunity to test for the relative contribution of temperature in explaining ecogeographical rules. Explanations of Bergmann's and James' rules have invoked also latitude-related factors other than temperature, e.g., food availability, predation risk, distance from low-latitude refuges during ice ages, migration availability, and resistance to starvation (31). Although not negating the role of other factors, our study provides strong evidence that temperature actually plays a major role in driving changes in the size structure of populations and communities. More generally, it would be interesting to consider the impacts of global warming when studying any ecological rules based on size variability. For instance, according to Elton's rule [which states that body size decreases with decreasing trophic levels (32)], our results suggest that upper trophic levels could be more sensitive to climate warming than lower ones.

To conclude, we provide evidence that reduced body size is the third universal ecological response to global warming besides the shift of species ranges toward higher altitudes and latitudes and the seasonal shifts in life-cycle events. Further analyses would be necessary to identify the possible mechanism linking temperature and size across the different biological scales. If such a

mechanism exists, it should be linked to general theories in ecology. For instance the metabolic theory of ecology [MTE (33)] could help to understand at least part of the involved mechanisms. Indeed, according to this theory, the equilibrium number of individuals in a population (K) is predicted to vary as $K \propto [R]M^{-3/4}e^{E/kT}$, where R is the supply rate of the limiting resource, M is the mean mass of an individual, E is the activation energy of metabolism, k the Boltzmann's constant and T is the Kelvin temperature. Thus, $KM^{3/4}$ varies as $KM^{3/4} \propto [R]e^{E/kT}$. As a consequence, warming should lead to a decrease in the mean body mass and/or a decrease in abundance at equilibrium if $[R]$ does not concomitantly increase. In this way, the MTE could explain the population body size shift hypothesis and/or the species shift hypothesis. Further analyses of the relative sensitivity of the decreases in abundance and size to the species maximum size should help to evaluate the extent to which the MTE explains both hypotheses. Finally, we want to point out that it is critical to assess the evolutionary nature of the observed changes. Indeed, evolutionary responses to disturbances can be difficult (or impossible) to reverse and can lead to loss of genetic diversity (19). From this viewpoint, it would be important to distinguish evolutionary responses from plastic changes for conservation and management purposes (18, 19). Overall, knowing the triggers of changes in size with temperature from individual to community could greatly increase our understanding of ecosystem structuring and our ability to forecast impacts of anthropogenic pressures on biota.

Materials and Methods

Long-Term Data. *Large river fish communities.* We used data that were collected each year from 4 different study areas located on large French rivers (the Rhône and the Seine rivers) and over periods ranging from 14 to 27 years (22, 34). Fish were sampled 1–4 times per year [supporting information (SI) Table S1], from a boat, along banks and by using electrofishing techniques. Electrofished individuals were identified to species, measured and released. All study areas experienced a significant increase in temperature due to climate change (22, 34) (Table S2). We used yearly mean size (all individuals included) to test the community body size shift hypothesis. To test the species shift hypothesis, we used time series of proportion of small species in terms of (*i*) number of individuals (abundance) and (*ii*) number of species (species richness). For each study area, small species were defined as species with a maximum size (35) below the first quartile of the maximum size of all of the species in the community. The yearly mean sizes of the most abundant species were used to test the population body size shift hypothesis. At each study area, the most abundant species were defined as the species accounting for >5% of the total abundance. We used time series of the proportion of juveniles (young-of-the-year individuals) to test the population age-structure shift hypothesis. Each year, young-of-the-year individuals were identified by analysis of size-class frequencies. Finally, we used the yearly mean size of young-of-the-year individuals of the most abundant species to test the size-at-age shift hypothesis. We only considered the most abundant species having high juvenile numbers (i.e., on average >50 young-of-the-year individuals per year) to test the population age-structure shift hypothesis and the size-at-age shift hypothesis. For all time series, values were calculated for biological (i.e., not calendar) years fitted on the biological cycle of cyprinids. This enabled comparison of similar year class individual among sites (22, 34). Times series are provided in Table S3.

Brown trout populations. We used data that were collected yearly over 15 years from 3 French streams. The sites experienced a significant increase in water temperature during the 1985–2005 period (Table S2, Mann–Kendall trend tests, $n = 21$ for each test, P values ranging from 2.6×10^{-6} to 1.7×10^{-2}). Each site consisted of a stream section of 140–200 m closed by upstream and downstream nets. Trout were sampled by using 2-pass removal electrofishing, and each individual was measured and weighed before being released. For each sample, young-of-the-year individuals were identified by analysis of size-class frequencies. We used the time series of yearly mean individual size in the 3 populations to test the population body size shift hypothesis. The population age-structure shift hypothesis was tested by using the yearly proportions of young-of-the-year fish. Times series are provided in Table S4.

Herring and sprat populations. We used fishery data provided by the International Council for the Exploration of the Sea (ICES; available online at www.ices.dk/reports/ACFM/2005/WGBFAS/directory.asp). Data consisted of time se-

ries of yearly total catch in numbers and mean weight in the catch for different age classes (1 y old to >8 y old) over 31 years in the Baltic Sea. Sprat data were available for the whole Baltic Sea except the Kattegat area (i.e., for ICES subdivisions 22–32). Herring data were available for the whole Baltic Sea except zones located to the east of ≈15°05′00″ E (i.e., for ICES subdivisions 25–32 and Gulf of Riga). Baltic Sea surface temperature during the sampling period increased significantly (36) (Table S2). We used yearly mean weights to test the population body size shift hypothesis. Mean weights were calculated as the ratio of total biomass to total catch per year. Total biomasses were estimated as the product of weights-at-age and catches in numbers per age, summed over all ages. The population age-structure shift hypothesis was tested by using the yearly proportions of fish <3 years old. Time series of weight-at-age were used to test the size-at-age shift hypothesis.

Published data. To test the species shift hypothesis, we used observed changes in fish community structure in the North Sea under global warming (17). The study was based on the North Sea IBTS (International Bottom Trawl Survey) fishery data from DATRAS (Database of Trawl Surveys) and were provided by the ICES to the authors.

Experimental Data. Experimental data were obtained by sampling female adults of the copepod *Pseudocalanus* sp., bacteria, and phytoplankton communities in indoor mesocosms that simulated early spring (February–April) environmental conditions in the Kiel Bight (Baltic Sea) under different climatic scenarios (15, 16). Eight mesocosms were exposed to 4 temperature regimes (i.e., 2 mesocosms per chamber). The reference regime (+0 °C) corresponded to the 1993–2002 average temperature regime observed in the Kiel Bight, whereas the +2, +4, and +6 °C regimes corresponded to different levels of warming. Percentage of the natural light intensity above cloud cover (Io) was controlled to simulate different cloud cover and underwater light attenuation. Phytoplankton was sampled at 16%, 64%, and 32% Io (2005, 2006, and 2007 experiments). *Pseudocalanus* sp. and bacteria were only sampled at 64% and 16% Io, respectively.

Bacteria communities. Data were collected in the +0 and +6 °C mesocosms during the 2005 experiment (37). Bacteria were sampled on average 1.33 times a week in the reference mesocosms and on average 1.5 times a week in the +6 °C mesocosms. For each sample, mean cell volume of the community was derived from length and width cell measurements. Measurements were assessed by means of a new Porton grid—G12 after DAPI staining in an epifluorescence microscope by vision. We used mean cell volume in the different mesocosms to test the community body size shift hypothesis. Times series are provided in Table S5.

Pseudocalanus sp. individuals. Female adults of *Pseudocalanus* sp. were sampled and individually measured at the end of the 2006 experiment. The size-at-age shift hypothesis was tested by using mean length of individuals in the different mesocosms. Copepods are particularly suitable for testing this hypothesis because they do not increase in length after having molted to the adult stage. Times series are provided in Table S6.

Published data. We used a study dealing with changes in size structure of phytoplankton communities in Kiel mesocosms (16) to test the community body size hypothesis and the species shift hypothesis.

Statistical Analysis. Hypotheses were tested with the time series data by using a weighted metaanalysis (38). The "effect sizes" in the metaanalysis were S statistics from Mann–Kendall trend tests (39) (see Fig. S1, SI Text, and Table S7 and S8). Variances of S were corrected for temporal autocorrelation when they occurred (40). Mean temporal trends were considered significant if their 95% confidence intervals did not contain 0 (38). To test whether fishery pressure on herring and sprat populations can influence the response of organisms to warming (population body size shift, population age-structure shift, and size-at-age shift hypotheses), we defined a categorical variable that discriminated marine vs. freshwater populations. Fishery effect was evaluated by checking for significant between-group heterogeneity (Qb) in the effect size (38).

For experimental data, we used LME models (41) to evaluate the effect of temperature on the dependent variables (see Fig. S1, SI Text, and Table S7 and Table S8). This allowed the potential differences in variance among mesocosms to be considered when evaluating the coefficients of the models and their confidence intervals. All statistical analyses were performed by using R (42).

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