Spatial and body-size dependent response of marine pelagic communities to projected global climate change

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Abstract

Temperature, oxygen, and food availability directly affect marine life. Climate models project a global warming of the ocean's surface (~+3 °C), a de-oxygenation of the ocean's interior (~−3%) and a decrease in total marine net primary production (~−8%) under the 'business as usual' climate change scenario (RCP8.5). We estimated the effects of these changes on biological communities using a coupled biogeochemical (PISCES) – ecosystems (APECOSM) model forced by the physical outputs of the last generation of the IPSL-CM Earth System Model. The APECOSM model is a size-structured bio-energetic model that simulates the 3D dynamical distributions of three interactive pelagic communities (epipelagic, mesopelagic, and migratory) under the effects of multiple environmental factors. The PISCES-APECOSM model ran from 1850 to 2100 under historical forcing followed by RCP8.5. Our RCP8.5 simulation highlights significant changes in the spatial distribution, biomass, and maximum body-size of the simulated pelagic communities. Biomass and maximum body-size increase at high latitude over the course of the century, reflecting the capacity of marine organisms to respond to new suitable environment. At low- and midlatitude, biomass and maximum body-size strongly decrease. In those regions, large organisms cannot maintain their high metabolic needs because of limited and declining food availability. This resource reduction enhances the competition and modifies the biomass distribution among and within the three communities: the proportion of small organisms increases in the three communities and the migrant community that initially comprised a higher proportion of small organisms is favored. The greater resilience of small body-size organisms resides in their capacity to fulfill their metabolic needs under reduced energy supply and is further favored by the release of predation pressure due to the decline of large organisms. These results suggest that small body-size organisms might be more resilient to climate change than large ones.

Keywords: biogeochemical model, body-size of organisms, climate change, climate scenario, high trophic level model, pelagic communities, trophic transfer

Introduction

The functioning of marine ecosystems is projected to change over the 21st century as a result of anthropogenic climate change (e.g. Cheung et al., 2009, 2011; Blanchard et al., 2012). Studies examining both historical observations and climate model projections over the 21st century agree on a future basin-wide warming of several degrees and an increased ocean stratification (Walsh & Chapman, 2001; Bindoff et al., 2007; Capotondi et al., 2012; Bopp et al., 2013) that, in turn, may reduce subsurface dissolved oxygen concentration and net primary production (Keeling et al., 2010; Bopp et al., 2013). All

these changes are likely to alter the physiology (Fabry et al., 2008; Somero, 2012) and modify the spatial distribution (e.g. Parmesan & Yohe, 2003; Root et al., 2003; Parmesan, 2006; Poloczanska et al., 2013) of marine organisms, for example by restricting the habitat and reducing the resources available for higher trophic levels (Jones et al., 2014; Dueri et al., 2014).

One of the most widely documented ecological consequences of climate change is the geographic range shift of marine species (e.g. Parmesan & Yohe, 2003; Root et al., 2003; Parmesan, 2006; Poloczanska et al., 2013). In response to environmental changes, like temperature increase, species are shifting and extending their habitat poleward to stay in their preferred temperature range (Cheung et al., 2013; Poloczanska et al., 2013). In addi-

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tion, there is some evidence that marine ecosystems might experience a reduction in organisms' size and an overall biomass decrease due to climate change (Daufresne *et al.*, 2009; Jones *et al.*, 2014). However, these studies rely mostly on empirical or statistical relationships that do not include the mechanisms underlying species shift or body-size changes and thus might not represent accurately past or future variations. As a matter of fact, mechanistic analysis and projections of climate change effects on marine ecosystems are still largely to be explored.

Projecting physical and biogeochemical impacts on high trophic levels (HTL) is challenging because it requires the consideration of a large number of intrinsic (e.g. physiology, behavior and life history traits) and extrinsic (e.g. interactions between species-specific population dynamics and environmental modifications) factors and processes (Cheung *et al.*, 2010; Stock *et al.*, 2011; Blanchard *et al.*, 2012). Existing methods to forecast HTL shifts due to climate change are mostly limited to Ecological Niche Modeling (ENM), also known as species distribution modeling, habitat suitability modeling, or climate envelope modeling. ENM considers the statistical relationships between species occurrences and a set of known environmental variables used to determine species distribution (Peterson, 2003). However, most ENMs are limited to the predictive modeling of single species, neglecting biotic interactions with other species. In addition, they rely on the strong assumptions that statistical relationships will not change in the future (Araújo *et al.*, 2005). Size-based methods are a suitable alternative to species centered approaches as they describe the energy flux and production at a particular body-size, without the need of an explicit description of particular species. Size-structured models consider that body-size is the most important structuring variable of the ecosystem for both trophic interactions and metabolic rates. They capture trophic interactions and represent the propagation of perturbations along the trophic chain (Maury *et al.*, 2007a; Blanchard *et al.*, 2012). They can also include an explicit representation of HTL physiological functions for some species, providing mechanistic insights to explain the effect of climate change on marine communities (Dueri *et al.*, 2014).

In this article, we use the size-structured ecosystem model APECOSM (Maury, 2010) to study the multi-stressors effects of climate change on generic pelagic communities that interact together. We analyze and disentangle the mechanisms responsible for their potential future changes in distribution and dynamics.

Materials and methods

Models

We use the coupled PISCES-APECOSM model, which is simulating marine biogeochemistry with PISCES (Aumont *et al.*,

2003; Aumont & Bopp, 2006), and three open ocean pelagic communities (OOPCs) – epipelagic, mesopelagic, and migratory communities – with APECOSM (Maury, 2010; Maury *et al.*, in prep.). In the present study, small organisms (from 0.1 cm to approximately 2 cm) in APECOSM feed on the low trophic levels (LTL) simulated in PISCES, but there is no feedback from APECOSM to PISCES. More details about the model are provided in the supplementary material.

The biogeochemical model PISCES. The Pelagic Interaction Scheme for Carbon and Ecosystem Studies (PISCES) is a Nutrient-Phytoplankton-Zooplankton-Detritus model (Aumont *et al.*, 2003; Aumont & Bopp, 2006). It explicitly simulates the cycle of five nutrients (nitrate, ammonium, iron, silicate, and phosphate), as well as two types of phytoplankton (nano-phytoplankton and diatoms), two sizes of zooplankton (micro- and meso-zooplankton), two sizes of detritus (small and large particulate organic carbon) and dissolved organic carbon. Diatoms differ from nanophytoplankton by their need for Si, and higher half saturation constants for N, P, and Fe. Micro-zooplankton differs from meso-zooplankton because micro-zooplankton feed on both nanophytoplankton and diatoms whereas meso-zooplankton can also feed on micro-zooplankton. Small particles differ from large particles because of their vertical sinking speed (3 m d^{-1} vs. 50–200 m d^{-1} for large particles). Dissolution, growth, and uptake rates are temperature dependant.

As the currency of PISCES variables is expressed in moles (usually of carbon), all biomass values have been multiplied by the mean biomass free energy, i.e. 474.6 kJ Cmol^{-1}, to be converted into energy content of biomass and be compatible with APECOSM (Kooijman, 2000; Maury *et al.*, 2007a).

The ecosystem model APECOSM. The Apex Predators ECO-System Model (APECOSM) represents the flow of energy through the ecosystem with a size-resolved structure in both 3D-space and time (Maury *et al.*, 2007a; Maury, 2010). The model is based on ecological and physiological processes and mass conservation principles. It rests on the DEB theory (Kooijman, 2009) for its bio-energetic components. It simulates explicitly size-based opportunistic trophic interactions, predator's competition for food, allocation of energy to growth and reproduction, somatic and maturity maintenance, and predatory, starvation, as well as other natural mortality sources. All the physiological rates are temperature-dependent. Both passive and active movements are taken into account (Faugeras & Maury, 2007). The model outputs the dynamic size-spectrum of marine ecosystems in term of energy content per organism's weight class as well as many other size-dependent diagnostic variables such as organisms' functional response, growth rate, egg production, and mortalities. In our configuration, the model includes 20 size-classes for each of the three generic pelagic communities considered, which are ranging from 1 mm to 2 m length with an enhanced resolution in small-size classes (see supplementary material Tables S1 and S2).

The three OOPCs are not taxonomically resolved, and they are defined on the basis of their habitat-driven vertical behavior constrained by light, temperature, food, and oxygen

(Maury, 2010). Predation controls energy fluxes through the ecosystem. The 3D fields of primary (flagellates and diatoms) and secondary (micro-zooplankton and meso-zooplankton) production as well as particulate organic carbon simulated by the biogeochemical model PISCES (Aumont *et al.*, 2003; Aumont & Bopp, 2006) fuel the entire size-spectra of the OO-PCs. A few adaptations from the original model were made. The epipelagic community is mostly located above the thermocline, in the first 200 m depth. This community includes visual predators and filter feeders. Although they are not explicitly simulated in the model, this last group is taken into account by using specific ingestion rates. We assume that individuals in the euphotic layer can reach satiety with three times less food than individuals below the euphotic layer during the day, while at night they all behave similarly. The mesopelagic community is found in deep waters, most of the time at depth below 200 m. It is assumed to feed day and night (Maury *et al.*, in prep.). The migratory community performs diurnal vertical migration (Maury, 2010). The migratory community feeds at night in the upper ocean and dives at dawn to several hundred of meters where it continues to feed. At high latitudes, when days are continuous, this community is assumed to perform desynchronized vertical movements (i.e. independently of the daytime and not all at once), whereas in winter it is assumed to still perform diel vertical migrations like in spring or autumn (Cottier *et al.*, 2006). Because of its diurnal vertical migrations, the migratory community experiences strong temperature and food changes that may limit growth and reproduction of these organisms (McLaren, 1963; Loose & Dawidowicz, 1994). To reflect these conditions and reduce computing time, physiological functions are averaged for the day and for the night. The simulated biomass are in the range of values reported in empirical studies (Maury *et al.*, in prep.; Maury, 2010).

Experimental design

PISCES is part of the Nucleus for European Modeling of the Ocean (NEMO) framework. We use the ORCA2 global configuration (Madec, 2008), i.e. we run PISCES-APECOSM at the global scale. Our model has a mean horizontal resolution of about $2° \times 2°\cos\Phi$ (where Φ is the latitude) with an enhanced resolution of 0.5° at the equator. It has 31 vertical levels with decreasing resolution with depth, from 10 m intervals over the first 150 m to 500 m intervals from 2250 m depth to the bottom.

In this study, we use an 'offline' version of PISCES-APECOSM, i.e. PISCES-APECOSM is forced by the outputs of the ocean dynamical simulation. The ocean forcing set was computed using the IPSL-CM5A-LR Earth System Model (Institut Pierre Simon Laplace Coupled Model 5th generation Low Resolution). The IPSL-CM5 is a global earth system model that comprises physical atmosphere-land-ocean-sea ice models with a representation of the carbon cycle, stratospheric chemistry, and tropospheric chemistry with aerosols (Dufresne *et al.*, 2013). The IPSL-CM5 model has been developed as part of the recent effort of the Coupled Model Intercomparison Project 5 (CMIP5) for the Intergovernmental Panel on Climate Change's 5th Assessment Report (IPCC AR5).

PISCES-APECOSM is forced using monthly physical fields over the historical period (1850–2005) and for future projections (2006–2100). The historical simulation started from preindustrial conditions (year 1850) with atmospheric CO_2 concentration set at 284.7 ppm. Future projections followed the Radiative Concentration Pathway 8.5 (RCP8.5) labeled according to the peak value of radiative forcing (W m^{-2}) in 2100 (Moss *et al.*, 2010). In RCP8.5, the radiative forcing steadily increases until 2100 due to high greenhouse gas emissions and the absence of climate mitigation (Riahi *et al.*, 2011).

We ran a control simulation from 1850 to 2100 in which CO_2 was kept constant at its preindustrial value. In this simulation, we checked that the output fields were steady (no drift) over the simulation period. PISCES-APECOSM was spun up for 600 years prior to the control and climate (i.e. historical and future projections) simulations.

Analysis performed on model output

In this section, we describe the calculations performed on model output fields and used further in the result and discussion sections. Note that the biomass of LTL always refers to the sum of both total plankton (nanophytoplankton, diatoms, micro- and meso-zooplankton) and total particulate organic matter (small and large detritus) simulated by PISCES, while the HTL biomass corresponds to the total pelagic biomass (i.e. the sum overall size classes and the three communities) simulated by APECOSM. The HTL community biomass refers to the biomass summed up on all size classes in the specified community.

Although the model outputs monthly fields, all analysis presented in this article were performed on yearly means. To convert the distribution function of energy content of the HTL size spectrum (in J kg^{-1} m^{-3}) into HTL biomass (in Cmol m^{-3}), the energy density in each community was divided by the value of biomass free energy, i.e. 474.6 kJ Cmol^{-1} (Kooijman, 2000; Maury *et al.*, 2007a).

Cut-off frequency or maximum body-size. In a system's frequency response, the cut-off frequency is the critical frequency after which the energy flowing through the system begins to be significantly reduced. By analogy, we define the cut-off frequency of the size-spectrum as the body length at which the biomass density ratio between two successive size classes is less than 1/10. This value was determined empirically to provide an accurate indicator of the size at which the slope of the size-spectrum decreases markedly. To avoid potential biases resulting from the size-spectra variability, the cut-off frequency was determined on a 20 years averaged time frame for present (1985–2005) and future (2080–2100) conditions in each spatial cell and for each pelagic community.

Latitudinal shift. The latitudinal shift was calculated following the method described in Cheung *et al.* (2013). The mean latitude of the biomass was determined as:

$$LC = \frac{\sum_{i=1}^{n}(\text{Lat}_i \times \text{Dbio}_i)}{\sum_{i=1}^{n}\text{Dbio}_i}$$

where Lat_i is the latitude of the center of the spatial cell i, Dbio_i is the predicted biomass density in the cell i (corrected
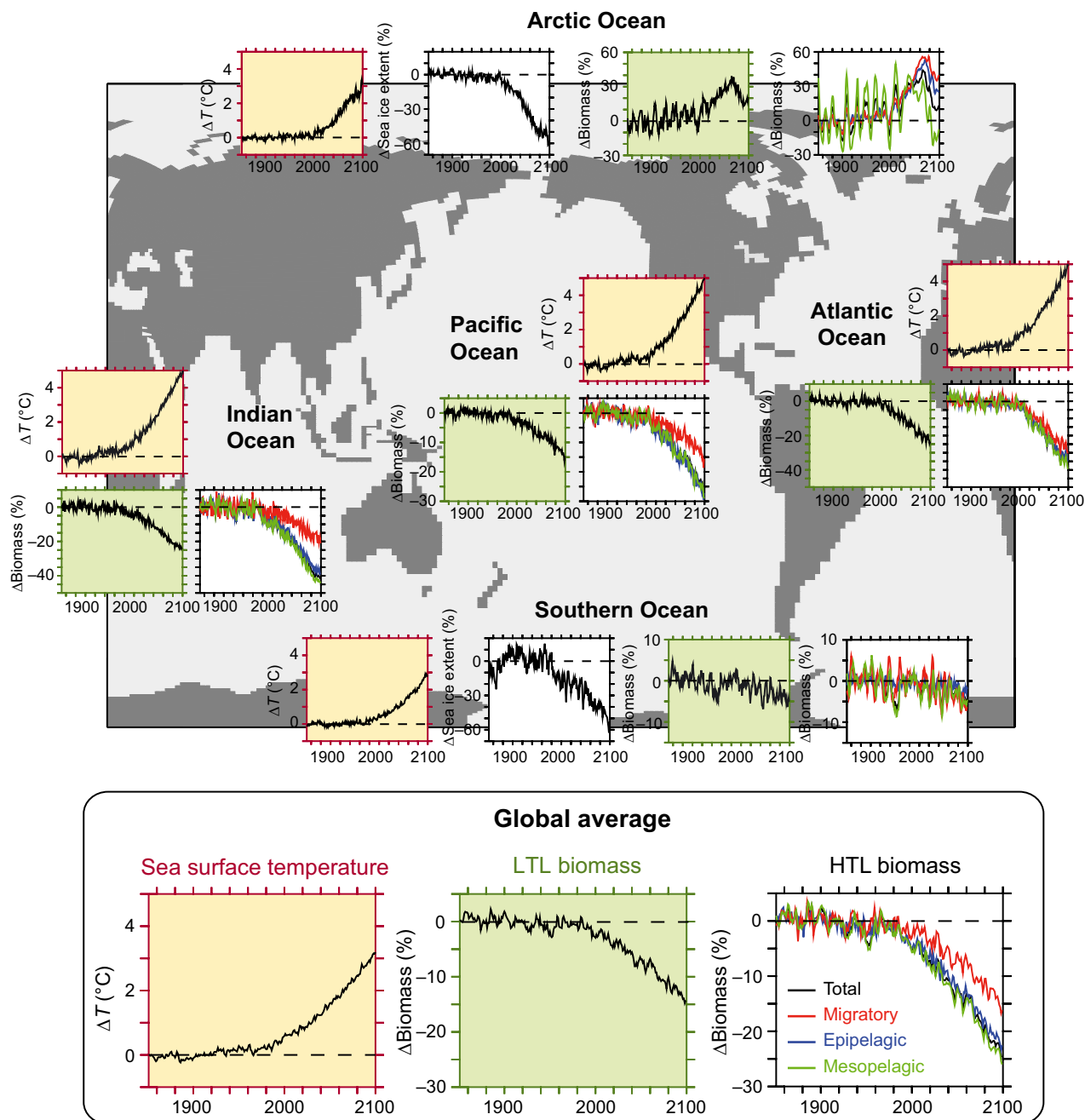
Fig. 1 Worldwide and basin-wide anomalies of Sea Surface Temperature (yellow panel), Low Trophic Level (LTL) biomass (green panel), and High Trophic Level (HTL) biomass concentrations of the pelagic generic communities (white panel). The change in sea-ice extent is shown in the Arctic and Southern Oceans (white panel, black curve).

by the area of the grid cell), and n is the total number of cells. Then, the shift rate was calculated as:

$$\text{latitude shift rate} = 2\pi R \frac{\Delta \text{LC}}{360 \times \Delta t}$$

where $\Delta \text{LC} = \text{LC}_f - \text{LC}_p$, with the subscript p and f, respectively, referring to present (1985–2005) and future (2080–2100) period, Δt is the time interval between these two periods, and R is the Earth radius.

The mean latitude and shift rate were calculated in the Northern and Southern hemisphere, for each size class and for each pelagic community (Figure S1). The averaged global shift rates reported in Section 'Reorganization of pelagic communities in response to climate change' were calculated for each community by first averaging over space and then over size classes.

Trophic transfer. We evaluated the response of trophic transfer to climate change in a synthetic way. For that purpose, we
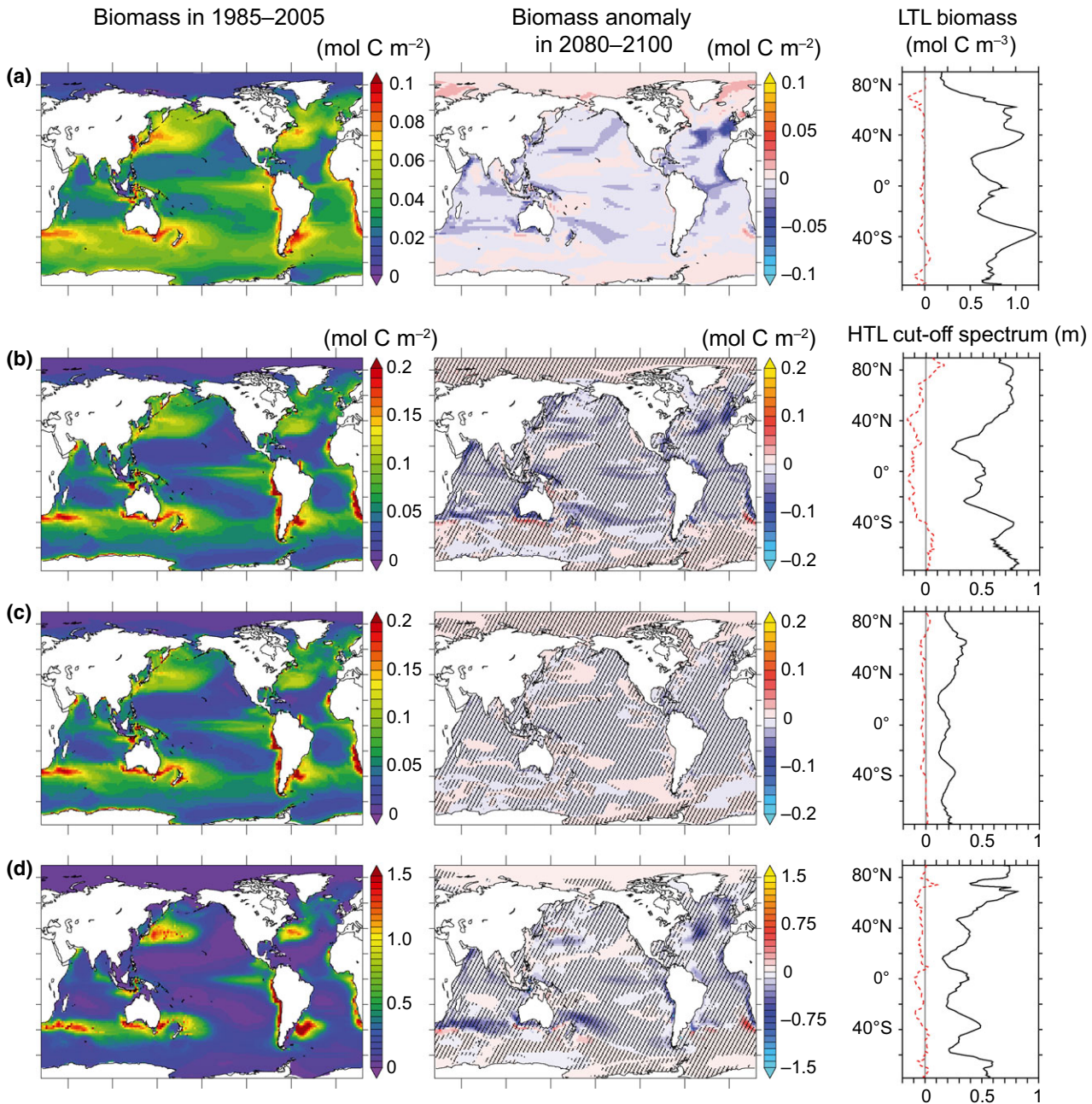
Fig. 2 Present (1985–2005) concentrations and future (2080–2100 compared to 1985–2005) changes in biomass and cut-off frequency (maximum body-size) in (a) LTL, (b) Epipelagic community, (c) Migratory community, and (d) Mesopelagic community. The LTL total biomass is integrated over all depth and the HTL biomass over all depth and size classes. The hatched area in the central panels corresponds to regions with similar trends in both biomass and maximum organisms' body-size. The right column represents the present (black line) latitudinal distribution and future (2080–2100 referred to 1985–2005) changes (red dashed line) of LTL biomass and cut-off frequency.

assessed the transfer of energy from low to high trophic levels in each pelagic community, by representing the change in HTL as a function of the changes in LTL (Figure S2). The response can be split into four categories of trophic propagation: amplification, attenuation, bottom-up control, and top down control as defined in Chust *et al.* (2014). All categories have both a negative and a positive phase.

Results

In response to increasing atmospheric CO_2 concentration under the RCP8.5 business as usual scenario, simulated global ocean surface temperature warms by 3.2 °C, LTL biomass drops by 15%, both leading to a
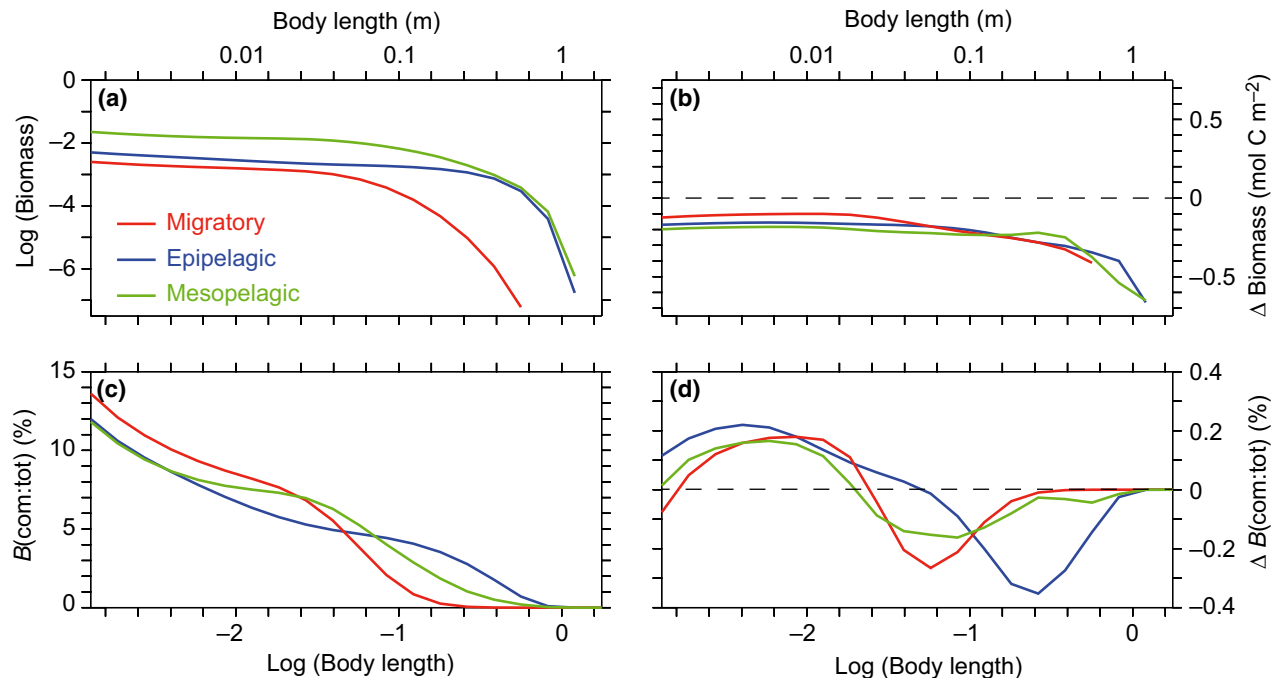
Fig. 3 HTL biomass variations along the size spectrum. (a) Present global average of the global size-spectrum for the three communities. (b) Relative changes of the distribution of biomass along the size-spectrum for the three communities. (c) Proportion of biomass (B) in a given size-class for the considered community (com) with respect to total (tot) biomass. (d) Future change in the proportion of biomass in a given size-class for the considered community with respect to total biomass.

decrease of 25% in HTL biomass by the end of the century (Fig. 1). At high latitude, temperature increases by 3 °C and sea-ice extent decreases by 60%. While both LTL and HTL biomasses increase in the Arctic Ocean (+12% at the end of the century), they both slightly decrease with the same amplitude in the Southern Ocean (−5% at the end of the century). In contrast, LTL and HTL biomasses strongly decrease in the Atlantic, Pacific, and Indian Oceans with a stronger drop in HTL biomass than in LTL biomass (respectively −33% and −19% at the end of the century averaged over the three oceans). In these oceanic basins, the temperature increases by 4.5 °C in average.

For a given oceanic basin, biomass anomalies of the three pelagic communities display the same trend, although they do not vary at the same rate (Fig. 1). In general, the migratory community is less affected by climate change than the epipelagic community, which in turn is less affected than the mesopelagic community (global average of −11%, −23%, and −26% at the end of the century, respectively). The sign of biomass changes is constant over time except in the Arctic Ocean, where biomass increases to reach a maximum in the 2070s and then decreases. In this basin, the biomass of the migratory community increases the most, while, in contrast, the mesopelagic biomass returns to

the historical level at the end of the century. In the Arctic Ocean and at low and midlatitude, the proportion of biomass in the migratory community with respect to the total biomass always increases, while it is always reduced for the mesopelagic community (Figure S3). Unlike other basins, the three pelagic communities have the same temporal trend in the Southern Ocean (Fig. 1) and they vary at about the same rates (Figure S3). These differences between the Southern Ocean and other basins may result from the strong spatial heterogeneities of the temporal changes in this region (Fig. 2). For this reason, we focus our study on the Arctic Ocean for the high latitude response.

At the global scale, climate change leads to a reduction in the maximum body-size of pelagic communities. By the end of the century, the maximum body-size of HTL organisms is expected to shrink by 9–10.5% depending on the community (Fig. 2). The migratory community displays the smallest changes in size with a shrinking of 1.3 cm in 2080–2100 compared to 1985–2005; the mesopelagic community experiences a reduction of 2.1 cm length; and the epipelagic community is the most affected with a decrease of 5.0 cm of its mean maximum body-size (Fig. 2). In average, the migratory community has a smaller cut-off size and includes a higher proportion of small-size organisms than the
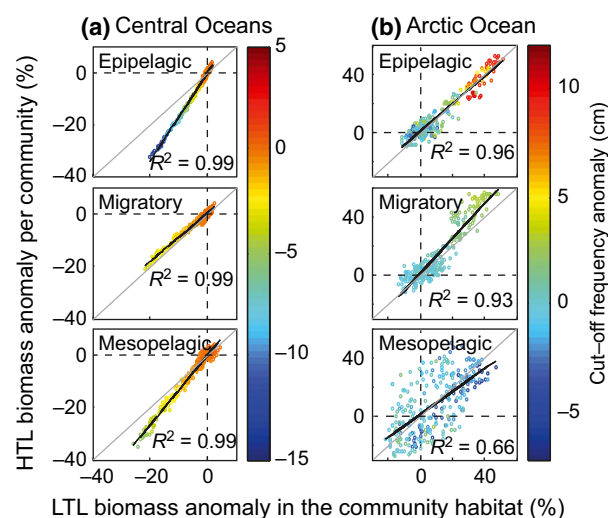
Fig. 4 Transfer of biomass anomalies from low to high trophic level in the epipelagic community in relationship with cut-off frequency anomalies (color dots) for the (a) Central and (b) Arctic Oceans. The Central Oceans refers to the Pacific, Atlantic, and Indian Oceans. We grouped these three oceans as one because they display similar trend in change (Fig. 1). The gray dashed line represents the proportional 1 : 1. The changes of biomass were averaged over depth, space, and size classes. The correlation between the LTL and HTL biomass anomalies is reported on the figure. The correlation between LTL and size anomalies, and HTL and size anomalies are reported in Table S2. Refer to Figure S2 for schematic interpretation.

other two communities (Figs 1 and 3c). On the other hand, the epipelagic community has the largest averaged cut-off size and includes a smaller and larger proportion respectively of small- and large-size organisms than the other two communities (Figs 1 and 3c).

In the future, the HTL biomass is projected to decrease in all size classes and in all communities (Fig. 3b). However, the biomass of small HTL organisms (<1 cm length) decreases three times more slowly than the biomass of larger HTL organisms (>10 cm

length): at the end of the century the former is reduced by 12%, while the latter decreases by 36%. This leads to an increase in the proportion of small size organisms – with respect to total – and a decrease in large-size organisms – with respect to total (Fig. 3d).

At the global scale, changes in body-size, LTL, and HTL biomasses are all intimately correlated (Figs 2 and 4; Table S2). Broadly, the changes in body-size and in LTL and HTL biomass have the same trends: both are reduced at low- and midlatitude while they increase across the Arctic Ocean (Fig. 2). The relationship between the change in body-size, LTL and HTL biomass is much stronger at low- and midlatitude than at high latitude for the three pelagic communities (Fig. 4; Table S2). The migratory community displays the smallest changes in both size and biomass (Figs 1 and 2). In addition, the trophic transfer from low to high trophic levels in this community is proportional to changes in LTL biomass at low- and midlatitude, whereas it is negatively amplified in the other two communities (Fig. 4). In the Arctic Ocean, the trophic transfer is positively amplified in the migratory community, while it is proportional in the epipelagic community and attenuated in the mesopelagic community.

The physiological functions of the pelagic communities are modified with climate change (Table 1). By the end of the century, the functions contributing to increase HTL biomass and body-size (i.e. the egg production) are reduced as well as the growth rate that is transferring biomass from small to large sizes, while the functions contributing to reduce HTL biomass and body-size (i.e. the predatory and natural mortalities) increase. There is an exception for the growth and reproduction of the migratory community that increase (Table 1) while the migratory biomass decreases (Figs 1–2). Except for the predatory mortality, the amplitude of physiological functions is stronger in the mesopelagic community than in the epipelagic or migratory community. In the Central Oceans, all physiological functions are well correlated with biomass

Table 1 Percentage of change in physiological functions between 2080–2100 and 1985–2005 normalized to the 1850–1950 period for the Central and Arctic Oceans in each pelagic community. GR, Growth; PM, Predatory Mortality; NM, Natural Mortality; FR, functional Response; EP, Egg Production. The values are spatially integrated and corrected for grid cell area

	Central Oceans			Arctic Ocean		
	Epipelagic	Migratory	Mesopelagic	Epipelagic	Migratory	Mesopelagic
GR	−8.2	4.2	−9.7	−0.3	28.0	−39.0
PM	19.1	13.5	2.0	31.8	22.9	1.4
NM	14.4	16.0	22.0	1.8	25.0	70.8
FR	−11.3	−11.6	−20.4	−6.3	−6.0	−35.6
EP	−8.2	4.5	−9.7	−0.3	28.4	−39.0

changes, except for predatory mortality of the mesopelagic community (see Table S2). On the contrary, in the Arctic Ocean, only the predatory mortality is well correlated with changes in the mesopelagic community biomass. In the Arctic Ocean, although both LTL and HTL biomasses increase in response to climate change, none of the communities are correlated with the functional response. At these latitudes, the change in epipelagic and migratory biomass is correlated with the variations of LTL biomass, maximum body-size, growth, egg production, and predatory mortality (Table S2). Only the migratory biomass changes display a significant trend with natural mortality.

Discussion

The PISCES-APECOSM model allows us to evaluate the response of marine ecosystems to changes of temperature, currents, oxygen, and primary production resulting from climate change. In agreement with observations and previous climate modeling studies, we report profound modifications of the ecosystem structure, such as biomass decrease, geographical shift, and shrinking of community-level body-sizes. In addition, we report changes of biomass distribution among pelagic communities and an amplification of the biomass decrease though the trophic chain.

Reorganization of pelagic communities in response to climate change

In agreement with observations and previous climate modeling studies, our simulations reveal a decrease in LTL and HTL biomass everywhere except in the Arctic, suggesting that the environmental suitability for marine life will decrease in low latitude regions while it will increase at higher latitudes in the future. Based on the evolution of the biomass per communities (see Section 'Latitudinal shift'), we calculated that the biomass of pelagic communities would shift poleward at a mean median rate of 21.7–31.7 km per decade between 1985–2005 and 2080–2100. Consistently, observations show that marine species have shifted poleward at a median rate of 30.6 ± 5.2 km per decade between 1960 and 2009 (Poloczanska et al., 2013) and models project species displacement to cooler water at a median rate of 27.5–36.4 km per decade between 2000 and 2050 (Cheung et al., 2013). This geographical shift reflects the capacity of organisms to track suitable environments, but might alter the ecosystem structure and functioning as the displacement of marine organisms creates new competition for habitat and resources.

The strong response of modeled pelagic communities to climate change emphasizes the dependency of marine ecosystems to changes occurring in their environment. The most illustrative example probably occurs in the Arctic Ocean where ocean warming and sea ice retreat open up new habitats and allow LTL and HTL biomass to develop. But seawater warming and ice melting also increase stratification, reducing the supply of nutrients to surface waters. Nutrients will ultimately become limiting and drive a reduction in primary production (Vancoppenolle et al., 2013). This, in turn, diminishes the flux of organic matter exported to the mesopelagic zone. The reduction in the exported flux limits the availability of resources to the mesopelagic community and increases its mortality by starvation (Table 1), leading to a strong reduction in mesopelagic biomass and maximum body-size (Figs 1, 2, and 4). On the other hand, the epipelagic and migratory communities are not as strongly affected than the mesopelagic community, because they have access to more resources as they can feed in surface water and do not rely on settling matter (Maury, 2010). This suggests a strong dependency of the pelagic communities to available resources at the base of the food chain and highlights the necessity to include several environmental factors in ecosystem model projections.

The maximum body-size of marine communities is projected to shrink with ocean warming. Shrinking of maximum body-size in response to ocean warming is theoretically expected and has been observed in natural environment (Daufresne et al., 2009; Gardner et al., 2011; Forster et al., 2012), and reported in modeling studies (Cheung et al., 2013; Jones et al., 2014). It has been proposed that shift in species, spatial changes, increase in young age (i.e. small size) classes, and higher oxygen demand and reduction in oxygen content both resulting from warming may lead to body-size shrinking (Daufresne et al., 2009; Cheung et al., 2013). In agreement, our results show an increased proportion of small sized organisms (Fig. 3) that may reduce average marine organisms body-size (Daufresne et al., 2009). In addition, our simulation reveals that the reduction in LTL biomass resulting from climate change is the major factor leading to shrinking body-size. Indeed, when food availability decreases, organisms reduce growth but have to maintain basic maintenance expenses (Maury et al., 2007b). Furthermore, warming increases metabolic rates (Pörtner & Knust, 2007) and in return organisms need more resources to meet their physiological needs (Daufresne et al., 2009; Sheridan & Bickford, 2011). This temperature-driven increase in metabolic dissipation leads to a net decrease in biomass at the community level (Maury et al., 2007b). The decrease in LTL biomass propagates to small preys and from small preys to large predators that cannot fulfill their metabolic needs and

decline (Fig. 3b and d), thus reducing the maximum body-size of marine communities (Fig. 2). This decline of large size organisms leads to a reduction in predation pressure, which limits the decrease in small body-size organisms who can still balance their physiological needs (Figure S4). This suggests that small organisms might be more resilient to climate change that large organisms.

Trophic transfer

The three marine pelagic communities display bottom-up control of energy transfer along the trophic pyramid with climate change (Fig. 4). This confirms the importance of resource availability for the sustainability of HTL biomass and body size. However, the three pelagic communities respond with different strength to climate change. The epipelagic and mesopelagic communities are not as efficient as the migratory community to transfer energy from low to high trophic levels (Fig. 4).

Previous studies suggest that the total biomass of the ecosystem is proportional to primary production (Benoît & Rochet, 2004; Shin & Cury, 2004; Ware & Thomson, 2005). For example, Woodworth-Jefcoats *et al.* (2013) evaluated that changes in large HTL abundance would be on the same order of magnitude as changes in large phytoplankton abundance under 21st century climate projection. On the contrary, we show that a trophic amplification for the epipelagic and mesopelagic communities at low- and midlatitude is a possibility. This discrepancy could result from substantial differences between the two approaches: organisms maintenance is not represented in the model of Woodworth-Jefcoats *et al.* (2013) so that the increase in energy dissipation with increasing temperature and the associated decrease in biomass (Maury *et al.*, 2007b) might be underestimated, whereas it is explicitly simulated in our model. The simulation of maintenance implies that organisms first allocate the energy provided by food ingestion to fulfill their maintenance needs and then use the remaining energy to grow. Without explicit representation of maintenance, organisms grow continuously and proportionally to the food ingested. With explicit representation of maintenance, organisms can survive without growing thus reducing the transfer of energy through the trophic chain.

The migratory community presents a transfer of energy through the trophic chain as efficient under climate change as it was during the historical period. The migratory community is advantaged in comparison to the other two communities because it feeds everywhere (i.e. in the epipelagic and mesopelagic zones) and all

the time (i.e. night and day) and avoids too much dissipation by staying in deep cold waters during the day. In addition, when feeding in the surface water at night, the migratory benefits from the energy accumulated by the epipelagic community who fed during the day. This result highlights the importance to represent several communities and explicitly consider trophic interactions and food competition between them. Furthermore, the migratory community is composed of a higher proportion of small individuals that can sustain an optimum growth despite the decrease in resources availability (Figure S4). Consequently, the current body-size composition and the feeding strategy of a marine community might determine its resilience to climate change. Thus, organisms exhibiting diel vertical migrations are more likely to accommodate to climate change.

Bias and limitations

Our study required a number of assumptions and simplifications to represent and project long-term changes in the complex biological and earth systems, and is thus subject to several sources of uncertainty. For example, there are uncertainties associated with projections of climate and ocean conditions. Because of the coarse spatial resolution, meso-scale physical processes influencing primary production (Lévy, 2008) are not represented in our simulations. This may induce an error on the estimation of phytoplankton production that might be transferred along the trophic chain. In addition, there are simplifications in the ecosystem model. For example, a mechanistic representation of the interactions between the effects of temperature, oxygen, and acidification on marine organisms metabolism needs to be implemented in the model for future work.

One limitation of our approach is the use of a single Earth System Model (IPSL-CM5-LR) with a single climate scenario (RCP8.5). Indeed, there are four plausible climate scenarios (Moss *et al.*, 2010) that have been proposed in the last IPCC assessment report and for a given scenario models project a large range of responses for net primary production (NPP) over the next century (Bopp *et al.*, 2013). Under the RCP8.5 scenario, models project a NPP decrease between −2% and −16% at the end of the century. Since LTL biomass, which is related to NPP, constrains the HTL biomass, the variations of NPP projections would certainly lead to a wide range of HTL biomass projections. However, all models agree on the sign of the global change in NPP (Bopp *et al.*, 2013) and despite differences between the physical or biogeochemical fields from

various models and scenarios, Vancoppenolle *et al.* (2013) reported similar trends in the Arctic Ocean for NPP over the next century. This suggests that the use of several models and scenarios would only affect the magnitude of the HTL biomass change in our results. Nevertheless, future studies should include outputs from several earth system models and climate scenarios to better assess model uncertainties on HTL biomass and body-size.

To finish, we did not investigate the potential effects of interactions between climate change and other human stressors such as fishing, habitat destruction, and pollution on the pelagic community response. These factors might have synergistic effects and are likely to further exacerbate the response of pelagic communities to climate change. For example, Blanchard *et al.* (2012) compared the effects of climate change and overfishing on coastal ecosystems. They showed that ecosystems were much more negatively impacted when overfishing was superimposed on climate change than with climate change alone. In addition, large-bodied species fish assemblage (e.g. *Lophius piscatorius* and *Raja Clavata*) has declined in abundance and body-size over the XXth century in the western English Channel, consistent with seawater warming and fishing in this region (Genner *et al.*, 2010).

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Shift rate of epipelagic (a–b), migrant (c–d) and mesopelagic (e–f) communities in 2080–2100 referred to 1985–2005. Positive rates are directed toward higher latitudes. The conversion between size class number and length of organisms is listed in Table S1.

Figure S2. Schematic representation of the various modes of propagation of the climate change signal from low to high trophic level. Adapted from (Chust *et al.*, 2014). See method section for details.

Figure S3. Proportion of biomass (B) in a community (com) referenced to total (tot) biomass for present (1985–2005) and future (2080–2100) conditions. The percentage indicates the difference in proportion between present and future conditions.

Figure S4. Changes in growth as a function of changes in biomass for the (a, c) epipelagic (blue) and (b, d) migratory (red) communities. Growth and biomass anomalies are averaged (a, b) over the body-size range 0–2 cm (cross) and (c, d) over the whole size spectrum (circle). The data are spatially integrated and corrected for grid cell area.

Table S1. Conversion table between size class number and centered size class length.

Table S2. Correlation coefficients between the temporal anomalies of biomass and cut-off frequency, and the temporal anomalies of biomass and physiological functions. CF, Cut-off Frequency; FR, Functional Response; GR, Growth; EP, Egg Production; PM, Predatory Mortality; NM, Natural Mortality. Insignificant correlations are reported in dark orange.