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Prediction of unprecedented biological shifts in the global ocean

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Abstract

Impermanence is an ecological principle[1] involving changes that can sometimes occur non-linearly as Abrupt Community Shifts (ACSs) to transform ecosystem states and the goods and services they provide[2]. Here, we present a model based on niche theory[3] to explain and predict ACSs at the global scale. We test our model using 14 multi-decadal time series of marine metazoans from zooplankton to fish, spanning all latitudes and the shelf to the open ocean. Predicted and observed fluctuations correspond, with both identifying ACSs at the end of the 1980s[4-7] and 1990s[5,8]. We show that these ACSs coincide with changes in climate that alter local thermal regimes, which in turn interact with the thermal niche of species to trigger long-term and sometimes abrupt shifts at the community level. A large-scale ACS is predicted after 2014 - unprecedented in magnitude and extent - coinciding with a strong El Niño event and major shifts in Northern Hemisphere climate. Our results underline the sensitivity of the Arctic Ocean, where unprecedented melting may reorganize biological communities[5,9] and suggest an increase in the size and consequences of ACS events in a warming world.

Main text

The processes that cause long-term changes and Abrupt Community Shifts (ACSs) in ecosystems are poorly understood despite decades of research[2,4,10-12]. We define an ACS as a stepwise shift in community structure[12], a definition that does not necessarily imply the existence of stable states[2,10], which are rarely observed in pelagic ecosystems[10,12-14]. Such ACSs correspond to rapid and major alterations in species composition[15], which alter biodiversity with consequences for ecosystem services. Here, we apply a framework based on the MacroEcological Theory on the Arrangement of Life (METAL; Methods and Supplementary Table 1 for a list of acronyms)[12,16-18]. METAL integrates key ecological concepts (e.g. the ecological niche *sensu* Hutchinson) into a unique and coherent scheme that unifies space and time patterns at both species and community levels and enables quantifiable predictions. METAL has been used to explain responses of species and communities to climate change and the large-scale arrangement of biodiversity[12,16-18].

We applied the METAL-based model to investigate long-term community changes and ACSs in pelagic marine metazoans in the global ocean from 1960 to 2015. In each geographical cell of a gridded ocean, we built pseudo-communities from a pool of pseudo-species, i.e. simulated species characterised by unique thermal niches ranging from stenotherms (species with narrow temperature tolerance) to eurytherms (adapted to extreme temperature variations) and from psychrophiles (adapted to cold temperatures) to thermophiles (adapted to warm temperatures)[12]. Pseudo-communities were built from pseudo-species adapted to temperature fluctuations in a given region. We therefore focused on climate-induced changes that originate from fluctuations in the thermal regime and not from shifts induced by other environmental parameters[19] (e.g. nutrients, salinity, oxygen) or anthropogenic pressures (e.g. fishing, eutrophication and pollution)[2]. It is now a key principle in ecology that thermal tolerance is species-specific[3] and the strong influence of temperature on species through their thermal niche has been observed for a variety of ecosystems and taxonomic groups[17,20,21]. The novelty in this present analysis is our conceptual incorporation of the niche into a model that allows us to explore the influence of temperature at the community level in the context of climate-induced changes, including ACSs.

We first tested if our model's predictions of long-term changes in pseudo-communities agreed with independent observations from 14 multi-decadal series (Supplementary Figure 1; Supplementary Tables 2-3). These records included measurements of zooplankton (11 ecosystems), decapods (1 ecosystem), and/or fish (4 ecosystems) spanning tropical (Hawaii) to polar regions (Southern Ocean), coastal (e.g. Adriatic and San Francisco Bay) to deep/open oceans (Pacific, Atlantic and Southern Oceans) and seas (Adriatic, Ligurian, North and Baltic Seas). For each observed community we performed a standardised Principal Components Analysis (PCA) on a matrix of years by biological variables (e.g. species abundance, biomass, or size fraction) and retained the first two Principal Components to investigate their long-term changes (Obs-PC1-PC2s). In each system, 10,000 PCAs were also performed on 10,000 pseudo-communities, each resulting from different simulated pseudo-species associations. From these, we retained 10,000 pairs of predicted changes (Pred-PC1-PC2s)[12]. We provide an illustrative case-example of the skill of our model for the North Sea (Figure 1). Here, the first obs-PC shows a pronounced change at the end of the 1980s for 43% of taxa, and our simulated first PC also exhibits the same pattern for 71% of the pseudo-species; both PCs were highly correlated (Figure 1a-b,e-f; $r=0.83$,$p=0.01$,$n=50$).

When all 14 ecoregions are considered (Fig. 2a-n), 89% (25) of all first two observed eigenvalues are significant (Supplementary Table 4). The observed and predicted community changes are highly correlated for every ecoregion, except for the highly dynamic and heterogeneous[22] Western Pacific Transition Zone where only the two late-1980s and -1990s substantial shifts were predicted (Figure 2; Supplementary Note 1 and Table 5). Note that long-term changes shown in the figure are the examples showing the highest correlations between an observed and a predicted PC. As it might be expected, some observed PCs were weakly correlated with predicted PCs (Supplementary Table 5), which could be because i) some species may not react to temperature when their thermal optimum coincides with the mean local thermal regime[12,23], or ii) some species may be more sensitive to other forcing (e.g.

anthropogenic pressure, other ecological factors, biotic interactions or local complex circulation patterns)[5,19,22,24]. Such differences in response may explain why the climatic signal identified by the PCAs was sometimes associated with PC1 and at other times with PC2. Therefore, to consider the full complexity of the signal, we used the first 2 predicted PCs (mean Pred-PC1-2, averaged over 10,000 simulated PCs; Figure 2a-n) and applied a regression (Methods) that explained 50.4% ($r=0.71, p<0.01, n=567$,Fig. 2o) of the total variance of all observed long-term changes in the 14 ecoregions (red Obs-PCs; Figure 2a-n). Since predicted communities are independent of the observed communities, correlations of observed and predicted PCs are higher than we expected. This suggests that our framework captures the main drivers of changing communities.

To verify that these results were not due to chance, we also examined correlations between observations and null models generated for each system and composed of random time series both with and without autocorrelation (Methods). Simulated Pred-PC1-PC2s from these null models exhibited a pronounced variability in each system, far exceeding that originating from METAL (Supplementary Figure 2 *versus* Figure 2a-n). All mean correlations were smaller than those expected from METAL, with the exception of the HOT time series. When all PCs were combined together (Fig. 2o-p), the correlations based on METAL were substantially higher than could be explained by chance (Figure 2p). The small range in METAL/observation correlations (Fig. 2p, red bar) in comparison to null models (Fig. 2p, green and blue) indicates that results are stable, regardless of the selected pseudo-species. This suggests that inclusion of all species might not be necessary to assess a community's state. This is fortuitous because most monitoring programmes sample only a small part of a community (Supplementary Table 3).

Next, we tested the capability of our framework to reveal large-scale community changes, including ACSs, by combining results from all 14 ecoregions (Figure 3). To extract the overall biological variability, we performed 'global' PCAs on the first two Pred-PCs extracted from (i) simulated (METAL and the null model based on autocorrelated time series) and (ii) observed communities for the 14 systems (14 systems x 2 PCs =28 variables for each PCA). Therefore, we used all of the first two observed and predicted PCs for this analysis, which represents the full set of interactions within the observed and predicted PCs (Supplementary Table 6). We chose the period 1960-2007 because it had less than 50% missing data per year in each time series (Supplementary Figure 3). We performed this procedure in two ways: (i) a single 'global' PCA based on the average of 10,000 PC1-PC2s for each system to calculate the correlation between observations and predictions from METAL, and (ii) 10,000 'global' PCAs to compare the variability of long-term changes from METAL and the null model. The first global PC originating from observed communities was highly correlated ($r=0.87$) with the first global PC derived from the mean of 10,000 theoretical communities (Figure 3a). Predicted and observed PC2s and PC3s were also significantly correlated, although at a lower level (Figure 3b-c). METAL predictions had smaller variability than predictions based on the null model (Figure 3a-c, green *versus* blue curves).

We verified the representativity of these time series with respect to the global ocean. While our 14 initial sites or ecoregions span a range of water depths from 31 to 5492m, many are close to the coastline and so our results could be biased towards shallow marine environments (Supplementary Table 3). To address this possibility, we analysed observations in 5 additional regions of the North Atlantic where we had spatially and temporally consistent data from nearshore and offshore and from shallow to deep waters (Supplementary Note 1). This analysis confirmed the validity of our framework in open oceanic domains (Supplementary Note 1) even if no data were available to us from the centre of oceanic basins nor from the South Pacific, South Atlantic or Indian Oceans (Supplementary Note 1).

We then tested METAL predictions of abrupt shifts. Using pooled data from the 14 initial sites, we identified ACSs using an Abrupt Shift Detection (ASD) algorithm on 10,000 global PC1-PC3s (Methods). The algorithm detected a significant shift *circa* 1987 in our North Sea example for both predicted and observed first PCs (Figure 1c-d). For global PCs, the first two observed and predicted PCs showed significant ACSs at the end of the 1980s and 1990s respectively (Figure 3d-e). Predicted ACSs (blue curves) occurred one year before observed ACSs (red curves), possibly reflecting inertia related to species' life cycles[16]. This analysis shows that the most frequent (but not necessarily the most intense) shift in the ecoregions coincided with the well-documented events of the late 1980s (Figure 3a,d)[4,6,7]. Although they were not significant, we detected acceleration phases on both third predicted and observed PCs (Figure 3c,f). The well documented 1976/77 ACS[15] was not significant when all systems were considered (Fig. 3), probably because our observations did not include many areas where this shift occurred (Figure 2k, Supplementary Note 1). No significant trends were observed in global PCs based on autocorrelated time series (Figure 3d-f, green curves). These results suggest that our model can predict a substantial part of long-term community change, including ACSs.

We then used our ASD algorithm to predict ACSs in space and time by applying it to the whole ocean for the period 1960-2015 and covering areas and years not monitored. For this analysis, we did not use any PCA but applied our algorithm to pseudo-species and retained only ACSs when they involved half or more pseudo-species for a given location and year. Our analysis suggests that ACSs may occur every year, but only in a limited part of the ocean (~2.8%), involving on average an area of ~10 million km^2 of ocean per year (Figure 4a and Supplementary Figure 4). Some periods had geographically limited ACSs (e.g. 0.89 million km^2 for 1984-1987) whereas others showed more extensive shifts (e.g. 50.5

million km² for 2012-2015). Widespread predicted ACSs were always observed after El Niño events (e.g. weak El Niño episode of 1977-1978 and very strong episodes of 1997-1998 and 2015-2016) but not all El Niño events led to widespread ACS predictions (e.g. very strong episodes of 1982-1983; Figure 4a). The late-1980s ACS, so frequently found in areas where monitoring took place[4-6,8,11,12], was not predicted on a global scale. Despite similar strength in the two strong El Niño events 1997-1998 and 2015-2016, the spatial extent of the predicted ACSs was very different, the recent one being more widespread (50 million km² *circa* 2014 *versus* 29 million km² *circa* 1999). The mean magnitude of ACSs increased substantially after the mid-2000s with a peak *circa* 2012 (Figure 4b). When both spatial extent (number of geographical cells) and magnitude were combined, an unprecedented shift (5 and 3 times the average extent and magnitude, respectively) occurred after 2010 with a maximum ~2014 (Figure 4c). Our null model (Figure 3d-f) showed that such an ACS at the end of the time series is unlikely to be an artifact as is sometimes reported with other techniques[4] (Methods).

The next question was whether the predicted ACSs could be associated to climate. We investigated these relationships using six climate parameters measured at a global scale: annual Sea Level Pressure (SLP), meridional and zonal winds, wind intensity, cloudiness, and Sea Surface Temperature (SST) (Methods). Using maps of ACSs and climatic shifts calculated for each year (Supplementary Figures 4-5), we found significant correlations (Supplementary Table 7) between the spatial extent of both predicted and observed ACSs from 1960 to 2015 with annual SLP ($r=0.69, p_{ACF}<0.01, n=53$), atmospheric circulation (wind intensity and direction) variables ($r=0.54\text{-}0.57, p_{ACF}<0.01, n=53$) and, as expected, with annual SST ($r=0.97, p_{ACF}<0.01, n=53$). No significant correlation was found with cloudiness. These results identify a strong link between the spatial extent of predicted ACSs and shifts in atmospheric circulation and SST.

We subsequently calculated predicted shifts on a global scale, focusing on 5 time periods: 1975-1979, 1985-1989 and 1995-1999 because these include previously documented ACS[4-8,11,15], 2005-2009 as an example of a relatively stable period; and 2010-2014 because of its exceptional nature (Figure 5). The predicted 2014-2015 ACS, clearly evident by visual inspection (Supplementary Figure 4), is much more intense and widespread than previous shifts (Figures 4-5), encompassing meteo-oceanic warm anomalies in the Northwest Atlantic, Northeast Pacific Ocean and many areas of the Arctic Ocean and the central North-Atlantic cold blob[9,25-27](Figure 5). Although changes in the North Atlantic and Pacific Oceans resulted in part from changes in atmospheric and oceanic circulation and its influence on regional thermal regimes, changes in the Arctic resulted mainly from abrupt shifts in annual SST (Figure 5e,j, Supplementary Figure 6).

Our framework provides a theoretical explanation for long-term biological changes and ACSs. Each species responds individually, depending upon the interaction between its thermal niche and fluctuations in the thermal environment[12], with cumulative responses leading to ecosystem shifts. The close correspondence between shifts in predicted and observed communities supports our framework and provides a useful basis for predicting climate/temperature-induced ACS at the community scale. However, large unexpected events such as the collapse or explosive growth of some populations (black-swan events[28]) may not be predicted by our approach.

Our ability to resolve the spatial extent of oceanic community shifts is severely constrained by a paucity and unrepresentative coverage of observations. Most marine communities, in particular marine metazoans, are hidden from earth observation tools and adequate monitoring coverage for the entire ocean is logistically unlikely. Our framework could therefore be meshed with existing monitoring programmes to provide a macroscopic tool for identifying regions likely to develop ACSs and to help anticipate biological perturbations that could affect production of ecosystem goods and services[27]. For example, our framework has predicted an ACS of unprecedented scale in 2014-2015 that may have substantial ecological consequences[25,27] across the Northern Hemisphere, including in the Arctic where current changes such as sea-ice melting are accelerating[9]. Finally, our study alerts us to the potential for a growing size and consequence of future ACS events as the world warms in response to rapidly increasing concentrations of atmospheric greenhouse gases. Even though it will remain difficult to predict ACSs, both because of model uncertainties and the fact that some event types will remain unpredictable[29,30], the ability to forecast putative ACS events is an important development in our understanding of climate change biology.

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Author contributions

G.B. conceived the study; G.B., A.C., A.A., E.G., J.C., S.C. and all co-authors compiled the data and G.B. analysed the data. G.B. wrote the (initial draft) paper. G.B., A.C., A.A., P.C.R., E.G., J.C., R.R.K., S.O., S.C., M.E. and all other co-authors discussed the results and contributed to the paper writing.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper at www.nature.com. Reprints and permissions information are available online at www.nature.com/reprints.

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Data availability

The authors declare that data supporting the findings of this study are available from the corresponding author upon request.

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Figure legends

Figure 1 | Long-term biological changes and abrupt community shifts (ACSs) for both the observed community and a simulated pseudo-community in the North Sea. a-b. Long-term changes of the first principal components (PCs) and in biological variables related to them (i.e. absolute values of the normalized eigenvector ≥0.6; blue): (**a**) observed species and (**b**) simulated pseudo-species. The first PC, reflecting major changes in community structure, is in black for observed taxa (**a**,**e**) and red (**b**,**e**) for simulated pseudo-species. Taxa related to the observed first PC included *Calanus finmarchicus* (negative relationship, -), *C. helgolandicus* (positive relationship, +), *Candacia armata* (+), *Centropages typicus* (+), *Corycaeus* spp. (+), and *Oithona* spp. (-). Ten pseudo-species were related to the simulated first PC. The grey band shows the timing of the ACS revealed in panels **c**-**d**. **c**-**d**. Detection of ACSs for the first PC based on (**c**) the observed community and (**d**) the simulated pseudo-community. The dashed red horizontal line indicates the threshold of 3 used throughout this study. **e**-**f**. Measured (black) and simulated (red) first PCs (**e**) and their relationships (**f**). This ecosystem, and most biological systems considered in this study (except HOT, Southern Ocean and San Francisco Bay; see Methods) were also analysed in detail by Beaugrand[12] and Beaugrand and colleagues[7], respectively.

Figure 2 | Predicted (grey) and observed (red) long-term community changes for 14 systems. Principal components were standardised between -1 and 1. Pred-PC: 10,000 Principal Components (grey) based on 10,000 simulated communities. Obs-PC: Principal Component based on observed communities (red). **a**. North Sea (Pred-PC1s and Obs-PC1), **b**. Baltic Sea (Pred-PC1s and Obs-PC1), **c**. Adriatic Sea (Pred-PC1s and Obs-PC1), **d**. Ligurian Sea (Pred-PC2s and Obs-PC1), **e**. Northwest Atlantic, southern area (Pred-PC1s and Obs-PC2), **f**. Northwest Atlantic, northern area (Pred-PC1s and Obs-PC1), **g**. West Pacific Transition zone (Pred-PC1s and Obs-PC1), **h**. Oyashio (Pred-PC1s and Obs-PC1), **i**. CALCOFI (Pred-PC1s and Obs-PC1), **j**. San Francisco Bay (Pred-PC1s and Obs-PC1), **k**. East Pacific region (Pred-PC1s and Obs-PC1), **l**. West Pacific region (Pred-PC1s and Obs-PC2), **m**. HOT (Pred-PC1s and Obs-PC2), **n**. Antarctic Peninsula area (Pred-PC1s and Obs-PC2). **a-n.** r_m are the mean linear correlations between the mean of 10,000 predicted and the observed community PC. Biological variables considered at each site are indicated by **D** (benthic decapods), **Z** (zooplankton), and **F** (Fish). Biological variables are indicated in the Methods. x|y: x is the number of pseudo-species used in METAL and y is the number of time periods (1 indicates the annual value). The total number of variables used in METAL model is the product of x and y. For California Current (total zooplankton biomass) and Hawaii (zooplankton size fractions), we chose arbitrarily pseudo-communities composed of 30 pseudo-species. **o.** Long-term community shifts predicted from a regression on principal components, using the first two Pred-PCs from the 14 systems (averaged from the 10,000 first 2 PCs) and observed community shifts as in panels **a-n**. **p.** Histograms of the 10,000 correlations between selected Obs-PCs and predictions based on the first 2 Pred-PCs from (i) the null model based on random time series (grey), (ii) randomly generated time series with an order-1 autocorrelation ≥ 0.5 (blue), and (iii) the METAL theory (red).

Figure 3 | Comparisons of observed (red) and predicted (blue and green; 10,000 simulations) community shifts, all ecoregions combined. Model predictions are in blue and predictions from a null model with autocorrelation in green. (**a**) First PC (30.72% of the total variance): predicted and observed community changes. (**b**) Second PC (21.46%): predicted and measured community changes. (**c**) Third PC (15.47%): predicted and observed community changes. Index of abruptness of predicted and observed community changes: (**d**) First PC. (**e**) Second PC. (**f**) Third PC. Correlation (r), probability of significance without (p) and with (p_{ACF}) correction for temporal autocorrelation, and degree of freedom (n) are indicated in panels **a**, **b** and **c** and correspond to the correlation calculated between observations and METAL predictions when all local PCs are averaged. In **d-f**, the wide blue (METAL) and green (null model) curves correspond to the medians of 10,000 simulations and the lower and upper part, are the 5th and 95th percentiles, respectively. The first three axes of the PCA performed on observed data were significant using a statistical test based on a broken-stick distribution (Methods).

Figure 4 | Predicted long-term variation of Abrupt Community Shifts (ACSs) in the global ocean. **(a)** spatial extent, **(b)** magnitude and **(c)** spatial extent and magnitude of ACS. Curves in red are order-1 moving average of predicted values (blue bars) (Methods). Thin-dashed, thin-solid and thick red arrows identify weak, moderate, and strong El Niño events, 'E' = super El-Niño events. Thin and thick blue arrows identify moderate and strong La Niña events.

Figure 5 | Predicted Abrupt Community Shifts (ACSs; a-e) and climatic shifts (f-j) during the period 1960-2015 with a focus on the years 1975-1979 (a and f), 1985-1989 (b and g), 1995-1999 (c and h), 2005-2009 (d and i) and 2010-2014 (e and j). Colour bars show the percentage of individual time series having a significant shift (threshold>3). For ACSs, 50% means that half the pseudo-species exhibited a significant shift for a given pseudo-community. For climatic shifts, 50% means that half the climate parameters (3 of 6 parameters) had a significant shift. White areas are regions with no shift. When the percentage of shifts is >0, the percentage is indicated by a colour: yellow and red for low and high percentage, respectively. The six climatic parameters are: annual Sea Level Pressure (SLP), meridional wind, zonal wind, wind intensity, cloudiness and annual sea surface temperature (SST). The spatial extent of ACSs increases when the climatic shifts are more widespread. Individual maps of all predicted ACSs and observed climatic shifts are displayed in Supplementary Figures 4-5. Black arrow: direction and intensity of mean annual wind (1960-2015). Black line: isobar based on mean annual SLP (1960-2015).

Methods section

Materials

Sea surface Temperature

Annual SSTs originated from the dataset ERSST_v3 (1960-2015). The dataset is derived from a reanalysis based on the most recently available International Comprehensive Ocean-Atmosphere Data Set (ICOADS). Improved statistical methods have been applied to produce a stable monthly reconstruction, on a 2° x 2° spatial grid, based on sparse data[31]. Data were interpolated on a global grid of 1° latitude x 1° longitude.

Sea Level Pressure, wind and cloudiness

Sea Level Pressure (SLP), cloudiness and both the meridional (V) and the zonal (U) components of the wind were extracted from the National Center for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) Reanalysis project[32]. NCEP uses a climate model that is initialised with observations originating from a variety of sources (e.g. ships, planes and satellite observations). The spatial grid (2.5° latitude x 2.5° longitude) of annual average SLP and U and V wind data were constructed for the period 1960-2015. Wind intensity was calculated from U and V wind. Data were interpolated on a global grid of 1° latitude x 1° longitude for the period 1960-2015.

Observed biological data

We used a summary of long-term community shifts (i.e. the first 2 principal components after applying a Principal Components Analysis, PCA) in 14 regions located in three oceans (the Atlantic, the Pacific and the Southern Oceans) and four Longhurst biomes[33] (Polar, Westerlies, Trade-Winds, and Coastal biomes). The first 11 regions have been analysed by standardised PCA in Beaugrand and colleagues[7], the 12th has been analysed in Cloern and colleagues using the same technique[34] and both the 13th and 14th time series were added to the present study, following the same procedure. Supplementary Note 2 summarized the main characteristics of the 14 selected regions (see also Supplementary Figure 1 and Supplementary Table 2 for more details).

Models and numerical procedures

Overview of the METAL theory

We applied a framework based on the MacroEcological Theory on the Arrangement of Life (METAL)[12,16-18,35,36], a theory that explains how marine pelagic metazoans are arranged in the sea and how changing environmental conditions alter biological arrangements in space and time at different organisational levels (e.g. species, community, ecosystem), allowing precise predictions to be tested. METAL proposes that biodiversity is to a large extent influenced by climate and the environment. This influence mainly takes place through the interactions between the species ecological niche (*sensu* Hutchinson[37]) and both climatic and environmental changes. This interaction determines in large part the arrangement of life in the oceans at different organisational levels from the species to the ecosystem level and from small to large ecosystems[18]. More information on the METAL theory is available in Supplementary Note 3.

Generation of pseudo-species and pseudo-communities

To construct long-term changes in pseudo-community in each geographical cell of the global ocean, we used here the model described in Beaugrand[12] and Beaugrand and colleagues[17]; this model only uses one environmental parameter: temperature. We create pseudo-species, each having a unique Gaussian thermal niche with distinct degrees of eurythermy and thermophily[16,17,38] (Supplementary Figure 7, step 1). The response curve of the abundance E of a pseudo-species s in a given site i and time j to change in SSTs was modelled by the following function[17,39]:

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

With $E_{i,j,s}$ the expected abundance of a pseudo-species s at location i and time j; c_s the maximum value of abundance for species s fixed to one; $x_{i,j}$ the value of SST at location i and time j; u_s the thermal optimum and t_s the thermal amplitude for species s. The thermal tolerance is an estimation of the breadth (or thermal amplitude) of the species thermal niche[39].

A large number of pseudo-species was created with u_s varying between -1.8°C and 40°C by 0.1°C increments and t_s varying between 1.1°C and 10°C by increments of 0.05°C. This represented a total of 39,218 potential species. However, to consider niche vacancy[38], we randomly selected half of this number[17]. At the end of the procedure, the global pool of pseudo-species was equal to 19,609; pseudo-species were randomly chosen to create local pseudo-communities (Supplementary Figure 7, step 1) so long as they could withstand the local temperature (annual SST) regime (Supplementary Figure 7, steps 1-3).

In each geographical cell, a pseudo-community was composed of a given number of pseudo-species (see the map in Supplementary Figure 7). A similar biodiversity map generated by the procedure can also be seen in Beaugrand and colleagues (their figure 1a)[17]. Each pseudo-species has an index of abundance varying between 0 and 1 (Supplementary Figure 7, step 4). The expected abundance of such pseudo-species was determined by linear interpolation from the pseudo-species' thermal niche and monthly SSTs in a given geographical cell from 1960 to 2015 (Supplementary Figure 7, step 4). The procedure has been evaluated in detail for the North Sea by Beaugrand[12].

A summary of the state of the community is subsequently made by Principal Components Analysis (PCA), using the first two principal components (Supplementary Figure 7, step 5). More details on this analysis are presented in subsequent sections.

Detection of Abrupt Community Shifts

Many methods have been proposed[40,41]. Shift detection can be accomplished by the use of the coefficient of variation[41], the measure of the autocorrelation[42], or the quantification of the multi-scale variance along time series[43]. Here, we calculated an index of abruptness to identify in a simple way Abrupt Community Shifts (ACSs). Our abrupt shift detection algorithm was a simplified version of the methodology developed in Beaugrand and colleagues[43]. This index was developed because (i) it does not require stable states in contrast to other algorithms, (ii) it identifies a shift by evaluating the variability of the time series and (iii) it can be applied in the intensive research of ACSs on a global scale. For a given time series, we first calculated the order-1-5 difference of a time series where observations were standardised between 0 and 1. Be **Z** a time series, **Z**=[z_i] was standardised as follows:

$$x_i = \frac{z_i - \min(z)}{\max(z) - \min(z)} \quad (2)$$

The amplitude vector **A**^{p}=[a^{p}_{i}] was subsequently calculated as the first p difference between a value of **X**=[x_i] at year t+p and year t, with 1≤p≤5:

$$a^{p} = \left| x_{t+p} - x_{t} \right| \quad (3)$$

After transformation, the time series has a length of n-p. This transformation enables the time series to become stationary (i.e. constant mean, variance and autocorrelation structure), an important assumption for many statistical tests. The magnitude vector **M**^{p}=[m^{p}_{i}] was subsequently calculated by making the ratio of the amplitude of change a on the average amplitude of the time series:

$$m_i^{p} = \frac{a_i^{p}}{\frac{1}{n-p-1}\sum_{j=1, i\neq j}^{n-p} a_j^{p}} \quad (4)$$

The denominator can reach values up to 1; therefore, for a constant numerator, the smaller the denominator the higher the values of **M**. On 100 simulated time series of 10,001 points, 95% of the 10,000 first differences ranged between 2.29 and 2.37. To be conservative, we selected a detection threshold of 3. Any values above 3 were considered to be indicative of an abrupt shift. We also used an order-1 symmetrical moving average prior to the application of the abrupt shift detection algorithm to diminish the influence of white noise in biological time series. Test of the procedure can be found in Supplementary Note 4 (see also Supplementary Figures 8-13).

Relationships between observed and predicted long-term community shifts

To test whether the METAL model was able to reproduce well long-term community shifts (including Abrupt Community Shifts or ACSs), we compared METAL predictions of long-term pseudo-community shifts with observed community shifts in 14 oceanic regions (Supplementary Figure 14). We applied a standardised PCA on a table years x biological variables and used the first 2 principal components to characterise biological changes in each of the 14 regions for which we had data. For 12 of those regions, the standardised Principal Components Analyses (standardised PCAs) were already performed[7] and we applied a similar procedure for the two others: (i) HOT station and (ii) Antarctic Peninsula area. Note that the standardised PCA for San Francisco Bay was updated to 2013 using the same procedure[34]. We tested the significance of the first two axes (eigenvalues) by using a broken-stick distribution[44] (Supplementary Table 7).

We calculated long-term pseudo-community shifts in each of the 14 regions by applying the procedure described in Beaugrand[12]; we produced a pool of pseudo-species that were able to colonise each of the 14 regions so long as they could withstand annual changes in SSTs (Supplementary Figure 7; see the section "Generation of pseudo-species and pseudo-communities"). The generation of the pseudo-species was made using Equation (1) for the period 1960-2015. Many pseudo-species were produced. However, only pseudo-species with an annual relative (i.e. expressed as percentage) abundance > 0.005 and a presence > 6% for all years of the time period were kept[45]. As more pseudo-species were generated than observed biological variables involved in the calculations of the summary of each observed community shifts, we chose randomly, for each region, a number of pseudo-species that corresponded to the number of biological variables (Supplementary Table 3 and Supplementary Figure 14). For example in the Pacific Rim, we selected a number of pseudo-species that corresponded to the number of biological variables used to perform the PCA. However, when total zooplankton biomass (CalCOFI) or size fractions (HOT) were used, we arbitrarily chose 30 pseudo-species and also chose two 2-month periods instead of a single 4-month period for the Southern Ocean. For CalCOFI and HOT, the selection of this number of pseudo-species did not affect significantly the results above 5 pseudo-species. For the Southern Ocean, the selection of two 2-month periods instead of one 4-month period reduced the variability of the different trajectories but did not strongly affect our conclusions. We repeated the selection of the pseudo-species 10,000 times and recalculated each time the first two principal components on pseudo-species (Supplementary Figure 14). Therefore, 10,000 PCAs were performed for each of the 14 regions. When the number of pseudo-species was high in a given system, variability in the METAL predictions was low.

We subsequently compared the first two observed and predicted Principal Components (PCs) of the 14 regions; Obs-PC for PCs from the PCA based on observed community and Pred-PC for PCs from the PCAs based on pseudo-communities (PC1 and PC2 for first and second principal components, respectively). This comparison was made in 3 different ways (Supplementary Figure 14).

First, we calculated the linear correlation coefficients between each Obs-PC and the average of the 10000 Pred-PCs (Supplementary Table 4); when the average was calculated, probabilities were calculated with and without adjusting the degree of freedom to correct for temporal autocorrelation[46]. Based on the correlation coefficients, we represented the best relationships between one of the two Obs-PCs and Pred-PCs for the 14 systems (Figure 2).

Second, we performed a regression on Principal Components[47] between the Obs-PC selected in Figure 2a-n and the first two corresponding Pred-PCs (averaged for the 10000 simulations) for the 14 systems. Those analyses were performed because they better integrate the complexity of the temporal signal of predictive PCs and removes any bias related to the selection of a given Pred-PC. A scatterplot was then performed between observed and modelled Obs-PCs of all systems and a linear correlation coefficient was calculated (Figure 2o). We also repeated the procedure for every simulation (10000) to examine the variability of the correlations between observed and predicted PCs (Figure 2p, red bars).

Third, we calculated two 'global' standardised PCAs: the first, on the matrix that combined the first 2 Obs-PCs obtained from each PCA applied on observed communities; the second, on the matrix that resulted from the combination of the first 2 Pred-PCs obtained from PCAs applied on simulated pseudo-communities (after averaging the 10,000 simulations). Prior to these analyses, we estimated the number of missing data from 1950 to 2014 to select a time period for which years had less than 50% of missing data (period 1960-2007; Supplementary Figure 3). This threshold of 50% was chosen to have a maximum of years in the analyses with an alteration towards the beginning and the end of the selected time period as low as possible. We examined the relationships between the first 3 global Obs-PCs and Pred-PCs. We tested the significance of the first three axes by using a broken-stick distribution[44]. Normalised eigenvectors (i.e. correlations between long-term changes in the value of each variable with the first three principal components) are in Supplementary Table 5. This analysis focused on the different long-term and more abrupt patterns that were observed in the 14 systems. We also repeated the procedure for every simulation (10000) to examine the variability of the first 3 predicted global PCs (Figure 3a-c; curves in blue) and its influence on the detection of ACSs (Figure 3d-f; curves in blue). We applied our abrupt shift detection algorithm to identify ACSs in the three global Obs-PCs and Pred-PCs. For this analysis, we used an order-3 weighted difference in all analyses after having applied an order-1 symmetrical moving average (see Equation 4 with p=3). This procedure was chosen to remove the effects of episodic events and to concentrate on ACSs that may have persistent effects.

Null models

We designed two null models to examine whether our METAL predictions fit better the observations than those obtained randomly (with and without temporal autocorrelation; Supplementary Figure 14). The first null model generated a number of random time series for each station corresponding to the species richness simulated by METAL, with a length corresponding to the time period covered in each sampling site (Figure 2) and a length corresponding to the time period chosen to perform 'global' PCAs (Figure 3). The second null model generated the same number of time series but using random time series with an order-1 temporal autocorrelation ≥ 0.5 as many of our observed and METAL-simulated time series were autocorrelated. We analysed those data using the same procedures applied to analyse METAL-simulated data (see the previous section) and to examine the relationships with observed biological data (Supplementary Figure 14). We only represented expected biological changes based on the null model using randomly generated time series with an order-1 autocorrelation ≥ 0.5 as the null model based on random time series gave similar results. The average correlation between expected and observed changes was reported for each site (Supplementary Figure 2).

Subsequently, we calculated regression on PCs (the first two PCs for each system) using the same procedure as above for every expected Pred-PCs (therefore 10000 times). We performed this analysis for both random time series and randomly generated time series with an autocorrelation ≥ 0.5. A histogram of all correlations (random time series and randomly generated time series) was performed and compared with correlations based on the METAL model (Figure 2p). Green: correlations between Pred-PCs based on random time series and Obs-PCs; Blue: correlations between Pred-PCs based on randomly generated time series with an order-1 autocorrelation ≥ 0.5 and Obs-PCs; Red: correlations between Pred-PCs based on the METAL model and Obs-PCs.

We calculated 'global' PCAs based on the 10000 Pred-PCs originating from Pred-PCs based on randomly generated time series with an order-1 autocorrelation ≥ 0.5; 10000 global PCAs were thereby calculated to examine the variability of the first 3 'global' PCs (Figure 3a-c; green). We also applied the Abrupt Shift Detection algorithm on each global PC (1-3 global PCs) and represented the 5th, 50th (median) and 95th percentiles (Figure 3d-f; green).

Predictions of Abrupt Community Shifts

After testing our theoretical framework and abrupt shift detection algorithm against field observations, we estimated theoretically ACSs from 1960 to 2015 in all areas of the oceans. Here also, only pseudo-species with an annual relative (i.e. expressed as percentage) abundance > 0.005 and a presence >6% for all years of the time period were kept [45]. In each geographical cell of the oceans, we estimated ACSs for all pseudo-species composing a pseudo-community. To estimate ACSs, we used an order-3 weighted difference after having applied an order-1 symmetrical moving average (see Equation 4 with p=3), as above. Then, we represented for each tested time period from 1960-1963 (mean year 1961.5) to 2012-2015 (mean year 2013.5) the amount of species that exhibit ACSs out of the pseudo-species composing the pseudo-community (Supplementary Figure 4). Data of mean sea level pressure and mean wind circulation were superimposed on maps for the corresponding time period. Because the number of maps was large (see Supplementary Figure 4 for all maps), we chose 5 time periods: (i) 1975-1979, 1985-1989 and 1995-1999 because these include already documented ACSs[4,7,8,15,48], (ii) 2005-2009 because it is an example of a relatively calm period and (iii) the last period 2010-2014 (Figure 5). To pool different mean year of shift (e.g. 1976.5 as an average of period 1975-1978) within those time periods (e.g. 1975-1979), we calculated the highest percentage of pseudo-species' shift in each geographical cell (e.g. 1975.5, 1976.5, 1977.5, 1978.5, 1979.5).

Observations of abrupt climatic shifts

We applied the same procedure to identify abrupt climatic shifts from 1960 to 2015. We also applied an order-3 weighted difference after having applied an order-1 symmetrical moving average (see Equation 4 with p=3). The abrupt shift detection algorithm was performed on annual sea level pressure, meridional (U) and zonal (V) wind, wind intensity, cloudiness and SST. We then added the number of significant shifts observed in each geographical cell from 1960-1963 to 2012-2015 (Supplementary Figure 5). To examine the potential relationships between predicted ACSs and climatic shifts, we applied the same procedure as above for the same time periods: 1975-1979, 1985-1989, 1995-1999, 2005-2009 and 2010-2014 (Figure 4d-f). Abrupt climatic shifts were mapped for the period 2010-2014 for each climatic variable (2010-2014) in an attempt to understand the exceptional nature of the time period identified by our theoretical framework (Supplementary Figure 6).

Long-term changes in spatial extent and magnitude of abrupt shifts

For each year, we estimated the spatial extent, the magnitude, and both combined, of ACSs (Figure 5).

Estimation of spatial extent of ACSs

For each geographical cell that had a percentage of pseudo-species that shifted significantly above 50% in a given pseudo-community, geographical distances in a geographical cell were calculated as follows [49]:

$$d(i,j)=6377.221 \text{ x } h_{i,j} \qquad (5)$$

With $d_{i,j}$ being the geographical distance between point i and j, the constant the Earth radius and $h_{i,j}$ computed as follows[49]:

$$h_{i,j} = ar\cos\left(\sin\varphi_i \sin\varphi_j + \cos\varphi_i \cos\varphi_j \cos g\right) \qquad (6)$$

With φ_i the latitude (in radians) at point i, φ_j the latitude (in radians) at point j and g the difference in longitude between i and j. The area was subsequently calculated by multiplying the zonal and meridional distance of the cell. Finally, we added all areas to obtain the spatial extent concerned by ACSs (Figure 4a). The same type of calculation was applied for each climatic variable that shifted significantly. This procedure allowed us to calculate the correlation (and its probability of significance p_{ACF}; ACF means autocorrelation function) between long-term changes in spatial extent of significant ACSs and the spatial extent of climatic shift (threshold of 3) for each variable taken individually (Supplementary Table 6).

Estimation of the magnitude of ACSs

We also estimated the magnitude of ACSs for each year of the time period (1960-2015) by averaging the index of abruptness for each geographical cell for which more than 50% of pseudo-species shifted significantly (threshold of 3; Figure 4b).

Estimation of both magnitude and spatial extent

The last index was calculated by summing the magnitude of all ACSs characterised by at least 50% of pseudo-species' shifts inside a pseudo-community. This index takes into consideration both the magnitude of the shift and the number of geographical cells concerned by an ACS (Figure 4c).

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