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Prediction of unprecedented biological shifts in the global ocean

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31 **Abstract**

32 **Impermanence is an ecological principle¹ involving changes that can sometimes occur non-linearly**
33 **as Abrupt Community Shifts (ACSs) to transform ecosystem states and the goods and services they**
34 **provide². Here, we present a model based on niche theory³ to explain and predict ACSs at the global**
35 **scale. We test our model using 14 multi-decadal time series of marine metazoans from zooplankton**
36 **to fish, spanning all latitudes and the shelf to the open ocean. Predicted and observed fluctuations**
37 **correspond, with both identifying ACSs at the end of the 1980s⁴⁻⁷ and 1990s^{5,8}. We show that these**
38 **ACSs coincide with changes in climate that alter local thermal regimes, which in turn interact with**
39 **the thermal niche of species to trigger long-term and sometimes abrupt shifts at the community**
40 **level. A large-scale ACS is predicted after 2014 - unprecedented in magnitude and extent - coinciding**
41 **with a strong El Niño event and major shifts in Northern Hemisphere climate. Our results underline**
42 **the sensitivity of the Arctic Ocean, where unprecedented melting may reorganize biological**
43 **communities^{5,9} and suggest an increase in the size and consequences of ACS events in a warming**
44 **world.**

45

46 **Main text**

47 The processes that cause long-term changes and Abrupt Community Shifts (ACSs) in ecosystems are
48 poorly understood despite decades of research^{2,4,10-12}. We define an ACS as a stepwise shift in
49 community structure¹², a definition that does not necessarily imply the existence of stable states^{2,10},
50 which are rarely observed in pelagic ecosystems^{10,12-14}. Such ACSs correspond to rapid and major
51 alterations in species composition¹⁵, which alter biodiversity with consequences for ecosystem
52 services. Here, we apply a framework based on the MacroEcological Theory on the Arrangement of
53 Life (METAL; Methods and Supplementary Table 1 for a list of acronyms)^{12,16-18}. METAL integrates key
54 ecological concepts (e.g. the ecological niche *sensu* Hutchinson) into a unique and coherent scheme
55 that unifies space and time patterns at both species and community levels and enables quantifiable
56 predictions. METAL has been used to explain responses of species and communities to climate change
57 and the large-scale arrangement of biodiversity^{12,16-18}.

58

59 We applied the METAL-based model to investigate long-term community changes and ACSs in pelagic
60 marine metazoans in the global ocean from 1960 to 2015. In each geographical cell of a gridded ocean,
61 we built pseudo-communities from a pool of pseudo-species, i.e. simulated species characterised by
62 unique thermal niches ranging from stenotherms (species with narrow temperature tolerance) to
63 eurytherms (adapted to extreme temperature variations) and from psychrophiles (adapted to cold
64 temperatures) to thermophiles (adapted to warm temperatures)¹². Pseudo-communities were built

65 from pseudo-species adapted to temperature fluctuations in a given region. We therefore focused on
66 climate-induced changes that originate from fluctuations in the thermal regime and not from shifts
67 induced by other environmental parameters¹⁹ (e.g. nutrients, salinity, oxygen) or anthropogenic
68 pressures (e.g. fishing, eutrophication and pollution)². It is now a key principle in ecology that thermal
69 tolerance is species-specific³ and the strong influence of temperature on species through their thermal
70 niche has been observed for a variety of ecosystems and taxonomic groups^{17,20,21}. The novelty in this
71 present analysis is our conceptual incorporation of the niche into a model that allows us to explore the
72 influence of temperature at the community level in the context of climate-induced changes, including
73 ACSs.

74

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

90

91 When all 14 ecoregions are considered (Fig. 2a-n), 89% (25) of all first two observed eigenvalues are
92 significant (Supplementary Table 4). The observed and predicted community changes are highly
93 correlated for every ecoregion, except for the highly dynamic and heterogeneous²² Western Pacific
94 Transition Zone where only the two late-1980s and -1990s substantial shifts were predicted (Figure 2;
95 Supplementary Note 1 and Table 5). Note that long-term changes shown in the figure are the examples
96 showing the highest correlations between an observed and a predicted PC. As it might be expected,
97 some observed PCs were weakly correlated with predicted PCs (Supplementary Table 5), which could
98 be because i) some species may not react to temperature when their thermal optimum coincides with
99 the mean local thermal regime^{12,23}, or ii) some species may be more sensitive to other forcing (e.g.

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

109

110 To verify that these results were not due to chance, we also examined correlations between
111 observations and null models generated for each system and composed of random time series both
112 with and without autocorrelation (Methods). Simulated Pred-PC1-PC2s from these null models
113 exhibited a pronounced variability in each system, far exceeding that originating from METAL
114 (Supplementary Figure 2 *versus* Figure 2a-n). All mean correlations were smaller than those expected
115 from METAL, with the exception of the HOT time series. When all PCs were combined together (Fig.
116 2o-p), the correlations based on METAL were substantially higher than could be explained by chance
117 (Figure 2p). The small range in METAL/observation correlations (Fig. 2p, red bar) in comparison to null
118 models (Fig. 2p, green and blue) indicates that results are stable, regardless of the selected pseudo-
119 species. This suggests that inclusion of all species might not be necessary to assess a community's
120 state. This is fortuitous because most monitoring programmes sample only a small part of a community
121 (Supplementary Table 3).

122

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

135 from the mean of 10,000 theoretical communities (Figure 3a). Predicted and observed PC2s and PC3s
136 were also significantly correlated, although at a lower level (Figure 3b-c). METAL predictions had
137 smaller variability than predictions based on the null model (Figure 3a-c, green *versus* blue curves).

138

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

147

148 We then tested METAL predictions of abrupt shifts. Using pooled data from the 14 initial sites, we
149 identified ACSs using an Abrupt Shift Detection (ASD) algorithm on 10,000 global PC1-PC3s (Methods).
150 The algorithm detected a significant shift *circa* 1987 in our North Sea example for both predicted and
151 observed first PCs (Figure 1c-d). For global PCs, the first two observed and predicted PCs showed
152 significant ACSs at the end of the 1980s and 1990s respectively (Figure 3d-e). Predicted ACSs (blue
153 curves) occurred one year before observed ACSs (red curves), possibly reflecting inertia related to
154 species' life cycles¹⁶. This analysis shows that the most frequent (but not necessarily the most intense)
155 shift in the ecoregions coincided with the well-documented events of the late 1980s (Figure 3a,d)^{4,6,7}.
156 Although they were not significant, we detected acceleration phases on both third predicted and
157 observed PCs (Figure 3c,f). The well documented 1976/77 ACS¹⁵ was not significant when all systems
158 were considered (Fig. 3), probably because our observations did not include many areas where this
159 shift occurred (Figure 2k, Supplementary Note 1). No significant trends were observed in global PCs
160 based on autocorrelated time series (Figure 3d-f, green curves). These results suggest that our model
161 can predict a substantial part of long-term community change, including ACSs.

162

163 We then used our ASD algorithm to predict ACSs in space and time by applying it to the whole ocean
164 for the period 1960-2015 and covering areas and years not monitored. For this analysis, we did not use
165 any PCA but applied our algorithm to pseudo-species and retained only ACSs when they involved half
166 or more pseudo-species for a given location and year. Our analysis suggests that ACSs may occur every
167 year, but only in a limited part of the ocean (~2.8%), involving on average an area of ~10 million km²
168 of ocean per year (Figure 4a and Supplementary Figure 4). Some periods had geographically limited
169 ACSs (e.g. 0.89 million km² for 1984-1987) whereas others showed more extensive shifts (e.g. 50.5

170 million km² for 2012-2015). Widespread predicted ACSs were always observed after El Niño events
171 (e.g. weak El Niño episode of 1977-1978 and very strong episodes of 1997-1998 and 2015-2016) but
172 not all El Niño events led to widespread ACS predictions (e.g. very strong episodes of 1982-1983; Figure
173 4a). The late-1980s ACS, so frequently found in areas where monitoring took place^{4-6,8,11,12}, was not
174 predicted on a global scale. Despite similar strength in the two strong El Niño events 1997-1998 and
175 2015-2016, the spatial extent of the predicted ACSs was very different, the recent one being more
176 widespread (50 million km² *circa* 2014 *versus* 29 million km² *circa* 1999). The mean magnitude of ACSs
177 increased substantially after the mid-2000s with a peak *circa* 2012 (Figure 4b). When both spatial
178 extent (number of geographical cells) and magnitude were combined, an unprecedented shift (5 and
179 3 times the average extent and magnitude, respectively) occurred after 2010 with a maximum ~2014
180 (Figure 4c). Our null model (Figure 3d-f) showed that such an ACS at the end of the time series is
181 unlikely to be an artifact as is sometimes reported with other techniques⁴ (Methods).

182

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

193

194 We subsequently calculated predicted shifts on a global scale, focusing on 5 time periods: 1975-1979,
195 1985-1989 and 1995-1999 because these include previously documented ACS^{4-8,11,15}, 2005-2009 as an
196 example of a relatively stable period; and 2010-2014 because of its exceptional nature (Figure 5). The
197 predicted 2014-2015 ACS, clearly evident by visual inspection (Supplementary Figure 4), is much more
198 intense and widespread than previous shifts (Figures 4-5), encompassing meteo-oceanic warm
199 anomalies in the Northwest Atlantic, Northeast Pacific Ocean and many areas of the Arctic Ocean and
200 the central North-Atlantic cold blob^{9,25-27}(Figure 5). Although changes in the North Atlantic and Pacific
201 Oceans resulted in part from changes in atmospheric and oceanic circulation and its influence on
202 regional thermal regimes, changes in the Arctic resulted mainly from abrupt shifts in annual SST (Figure
203 5e,j, Supplementary Figure 6).

204

205 Our framework provides a theoretical explanation for long-term biological changes and ACSs. Each
206 species responds individually, depending upon the interaction between its thermal niche and
207 fluctuations in the thermal environment¹², with cumulative responses leading to ecosystem shifts. The
208 close correspondence between shifts in predicted and observed communities supports our framework
209 and provides a useful basis for predicting climate/temperature-induced ACS at the community scale.
210 However, large unexpected events such as the collapse or explosive growth of some populations
211 (black-swan events²⁸) may not be predicted by our approach.

212

213 Our ability to resolve the spatial extent of oceanic community shifts is severely constrained by a paucity
214 and unrepresentative coverage of observations. Most marine communities, in particular marine
215 metazoans, are hidden from earth observation tools and adequate monitoring coverage for the entire
216 ocean is logistically unlikely. Our framework could therefore be meshed with existing monitoring
217 programmes to provide a macroscopic tool for identifying regions likely to develop ACSs and to help
218 anticipate biological perturbations that could affect production of ecosystem goods and services²⁷. For
219 example, our framework has predicted an ACS of unprecedented scale in 2014-2015 that may have
220 substantial ecological consequences^{25,27} across the Northern Hemisphere, including in the Arctic where
221 current changes such as sea-ice melting are accelerating⁹. Finally, our study alerts us to the potential
222 for a growing size and consequence of future ACS events as the world warms in response to rapidly
223 increasing concentrations of atmospheric greenhouse gases. Even though it will remain difficult to
224 predict ACSs, both because of model uncertainties and the fact that some event types will remain
225 unpredictable^{29,30}, the ability to forecast putative ACS events is an important development in our
226 understanding of climate change biology.

227

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238

239

240 **Author contributions**

241 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.
242 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.,
243 M.E. and all other co-authors discussed the results and contributed to the paper writing.

244

245 **Additional information**

246 The authors declare no competing financial interests. Supplementary information
247 accompanies this paper at www.nature.com. Reprints and
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251

252 **Data availability**

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

255

256 **Literature cited**

257

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328

329 **Figure legends**

330 **Figure 1 | Long-term biological changes and abrupt community shifts (ACSs) for both the observed**
331 **community and a simulated pseudo-community in the North Sea. a-b.** Long-term changes of the first
332 principal components (PCs) and in biological variables related to them (i.e. absolute values of the
333 normalized eigenvector ≥ 0.6 ; blue): (a) observed species and (b) simulated pseudo-species. The first
334 PC, reflecting major changes in community structure, is in black for observed taxa (a,e) and red (b,e)
335 for simulated pseudo-species. Taxa related to the observed first PC included *Calanus finmarchicus*
336 (negative relationship, -), *C. helgolandicus* (positive relationship, +), *Candacia armata* (+), *Centropages*
337 *typicus* (+), *Corycaeus* spp. (+), and *Oithona* spp. (-). Ten pseudo-species were related to the simulated
338 first PC. The grey band shows the timing of the ACS revealed in panels c-d. c-d. Detection of ACSs for
339 the first PC based on (c) the observed community and (d) the simulated pseudo-community. The
340 dashed red horizontal line indicates the threshold of 3 used throughout this study. e-f. Measured
341 (black) and simulated (red) first PCs (e) and their relationships (f). This ecosystem, and most biological

342 systems considered in this study (except HOT, Southern Ocean and San Francisco Bay; see Methods)
343 were also analysed in detail by Beaugrand¹² and Beaugrand and colleagues⁷, respectively.

344 **Figure 2 | Predicted (grey) and observed (red) long-term community changes for 14 systems.**

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

366

367 **Figure 3 | Comparisons of observed (red) and predicted (blue and green; 10,000 simulations)**

368 **community shifts, all ecoregions combined.** Model predictions are in blue and predictions from a null
369 model with autocorrelation in green. **(a)** First PC (30.72% of the total variance): predicted and observed
370 community changes. **(b)** Second PC (21.46%): predicted and measured community changes. **(c)** Third
371 PC (15.47%): predicted and observed community changes. Index of abruptness of predicted and
372 observed community changes: **(d)** First PC. **(e)** Second PC. **(f)** Third PC. Correlation (r), probability of
373 significance without (p) and with (p_{ACF}) correction for temporal autocorrelation, and degree of freedom
374 (n) are indicated in panels **a**, **b** and **c** and correspond to the correlation calculated between
375 observations and METAL predictions when all local PCs are averaged. In **d-f**, the wide blue (METAL)

376 and green (null model) curves correspond to the medians of 10,000 simulations and the lower and
377 upper part, are the 5th and 95th percentiles, respectively. The first three axes of the PCA performed on
378 observed data were significant using a statistical test based on a broken-stick distribution (Methods).

379

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

385

386 **Figure 5 | Predicted Abrupt Community Shifts (ACSs; a-e) and climatic shifts (f-j) during the period**
387 **1960-2015 with a focus on the years 1975-1979 (a and f), 1985-1989 (b and g), 1995-1999 (c and h),**
388 **2005-2009 (d and i) and 2010-2014 (e and j).** Colour bars show the percentage of individual time series
389 having a significant shift (threshold>3). For ACSs, 50% means that half the pseudo-species exhibited a
390 significant shift for a given pseudo-community. For climatic shifts, 50% means that half the climate
391 parameters (3 of 6 parameters) had a significant shift. White areas are regions with no shift. When the
392 percentage of shifts is >0, the percentage is indicated by a colour: yellow and red for low and high
393 percentage, respectively. The six climatic parameters are: annual Sea Level Pressure (SLP), meridional
394 wind, zonal wind, wind intensity, cloudiness and annual sea surface temperature (SST). The spatial
395 extent of ACSs increases when the climatic shifts are more widespread. Individual maps of all predicted
396 ACSs and observed climatic shifts are displayed in Supplementary Figures 4-5. Black arrow: direction
397 and intensity of mean annual wind (1960-2015). Black line: isobar based on mean annual SLP (1960-
398 2015).

399

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 data³¹. 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 project³². 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 biomes³³ (Polar, Westerlies, Trade-Winds, and Coastal biomes). The first 11 regions have been analysed by standardised PCA in Beaugrand and colleagues⁷, the 12th has been analysed in Cloern and colleagues using the same technique³⁴ 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

438

439

440 Overview of the METAL theory

441

442 We applied a framework based on the MacroEcological Theory on the Arrangement of Life
443 (METAL)^{12,16-18,35,36}, a theory that explains how marine pelagic metazoans are arranged in the
444 sea and how changing environmental conditions alter biological arrangements in space and
445 time at different organisational levels (e.g. species, community, ecosystem), allowing precise
446 predictions to be tested. METAL proposes that biodiversity is to a large extent influenced by
447 climate and the environment. This influence mainly takes place through the interactions
448 between the species ecological niche (*sensu* Hutchinson³⁷) and both climatic and
449 environmental changes. This interaction determines in large part the arrangement of life in
450 the oceans at different organisational levels from the species to the ecosystem level and from
451 small to large ecosystems¹⁸. More information on the METAL theory is available in
452 Supplementary Note 3.

453

454 Generation of pseudo-species and pseudo-communities

455

456 To construct long-term changes in pseudo-community in each geographical cell of the global
457 ocean, we used here the model described in Beaugrand¹² and Beaugrand and colleagues¹⁷;
458 this model only uses one environmental parameter: temperature. We create pseudo-species,
459 each having a unique Gaussian thermal niche with distinct degrees of eurythermy and
460 thermophily^{16,17,38} (Supplementary Figure 7, step 1). The response curve of the abundance E
461 of a pseudo-species s in a given site i and time j to change in SSTs was modelled by the
462 following function^{17,39}:

463

$$464 \quad E_{i,j,s} = c_s e^{-\left(\frac{(x_{i,j} - u_s)^2}{2t_s^2}\right)} \quad (1)$$

465

466 With $E_{i,j,s}$ the expected abundance of a pseudo-species s at location i and time j ; c_s the
467 maximum value of abundance for species s fixed to one; $x_{i,j}$ the value of SST at location i and
468 time j ; u_s the thermal optimum and t_s the thermal amplitude for species s . The thermal
469 tolerance is an estimation of the breadth (or thermal amplitude) of the species thermal
470 niche³⁹.

471

472 A large number of pseudo-species was created with u_s varying between -1.8°C and 40°C by
473 0.1°C increments and t_s varying between 1.1°C and 10°C by increments of 0.05°C . This
474 represented a total of 39,218 potential species. However, to consider niche vacancy³⁸, we
475 randomly selected half of this number¹⁷. At the end of the procedure, the global pool of
476 pseudo-species was equal to 19,609; pseudo-species were randomly chosen to create local
477 pseudo-communities (Supplementary Figure 7, step 1) so long as they could withstand the
478 local temperature (annual SST) regime (Supplementary Figure 7, steps 1-3).

479

480 In each geographical cell, a pseudo-community was composed of a given number of pseudo-
 481 species (see the map in Supplementary Figure 7). A similar biodiversity map generated by the
 482 procedure can also be seen in Beaugrand and colleagues (their figure 1a)¹⁷. Each pseudo-
 483 species has an index of abundance varying between 0 and 1 (Supplementary Figure 7, step 4).
 484 The expected abundance of such pseudo-species was determined by linear interpolation from
 485 the pseudo-species' thermal niche and monthly SSTs in a given geographical cell from 1960 to
 486 2015 (Supplementary Figure 7, step 4). The procedure has been evaluated in detail for the
 487 North Sea by Beaugrand¹².

488
 489 A summary of the state of the community is subsequently made by Principal Components
 490 Analysis (PCA), using the first two principal components (Supplementary Figure 7, step 5).
 491 More details on this analysis are presented in subsequent sections.

492 493 **Detection of Abrupt Community Shifts**

494
 495 Many methods have been proposed^{40,41}. Shift detection can be accomplished by the use of
 496 the coefficient of variation⁴¹, the measure of the autocorrelation⁴², or the quantification of
 497 the multi-scale variance along time series⁴³. Here, we calculated an index of abruptness to
 498 identify in a simple way Abrupt Community Shifts (ACSs). Our abrupt shift detection algorithm
 499 was a simplified version of the methodology developed in Beaugrand and colleagues⁴³. This
 500 index was developed because (i) it does not require stable states in contrast to other
 501 algorithms, (ii) it identifies a shift by evaluating the variability of the time series and (iii) it can
 502 be applied in the intensive research of ACSs on a global scale. For a given time series, we first
 503 calculated the order-1-5 difference of a time series where observations were standardised
 504 between 0 and 1. Be \mathbf{Z} a time series, $\mathbf{Z}=[z_i]$ was standardised as follows:

$$505$$

$$506 \quad x_i = \frac{z_i - \min(z)}{\max(z) - \min(z)} \quad (2)$$

507
 508 The amplitude vector $\mathbf{A}^p=[a_i^p]$ was subsequently calculated as the first p difference between a
 509 value of $\mathbf{X}=[x_i]$ at year $t+p$ and year t , with $1 \leq p \leq 5$:

$$510$$

$$511 \quad a^p = |x_{t+p} - x_t| \quad (3)$$

512
 513 After transformation, the time series has a length of $n-p$. This transformation enables the time
 514 series to become stationary (i.e. constant mean, variance and autocorrelation structure), an
 515 important assumption for many statistical tests. The magnitude vector $\mathbf{M}^p=[m_i^p]$ was
 516 subsequently calculated by making the ratio of the amplitude of change a on the average
 517 amplitude of the time series:

$$518$$

$$519 \quad m_i^p = \frac{a_i^p}{\frac{1}{n-p-1} \sum_{j=1, i \neq j}^{n-p} a_j^p} \quad (4)$$

520
 521 The denominator can reach values up to 1; therefore, for a constant numerator, the smaller
 522 the denominator the higher the values of \mathbf{M} . On 100 simulated time series of 10,001 points,

523 95% of the 10,000 first differences ranged between 2.29 and 2.37. To be conservative, we
524 selected a detection threshold of 3. Any values above 3 were considered to be indicative of an
525 abrupt shift. We also used an order-1 symmetrical moving average prior to the application of
526 the abrupt shift detection algorithm to diminish the influence of white noise in biological time
527 series. Test of the procedure can be found in Supplementary Note 4 (see also Supplementary
528 Figures 8-13).

529

530 **Relationships between observed and predicted long-term community shifts**

531

532 To test whether the METAL model was able to reproduce well long-term community shifts
533 (including Abrupt Community Shifts or ACSs), we compared METAL predictions of long-term
534 pseudo-community shifts with observed community shifts in 14 oceanic regions
535 (Supplementary Figure 14). We applied a standardised PCA on a table years x biological
536 variables and used the first 2 principal components to characterise biological changes in each
537 of the 14 regions for which we had data. For 12 of those regions, the standardised Principal
538 Components Analyses (standardised PCAs) were already performed⁷ and we applied a similar
539 procedure for the two others: (i) HOT station and (ii) Antarctic Peninsula area. Note that the
540 standardised PCA for San Francisco Bay was updated to 2013 using the same procedure³⁴. We
541 tested the significance of the first two axes (eigenvalues) by using a broken-stick distribution⁴⁴
542 (Supplementary Table 7).

543

544 We calculated long-term pseudo-community shifts in each of the 14 regions by applying the
545 procedure described in Beaugrand¹²; we produced a pool of pseudo-species that were able to
546 colonise each of the 14 regions so long as they could withstand annual changes in SSTs
547 (Supplementary Figure 7; see the section “Generation of pseudo-species and pseudo-
548 communities”). The generation of the pseudo-species was made using Equation (1) for the
549 period 1960-2015. Many pseudo-species were produced. However, only pseudo-species with
550 an annual relative (i.e. expressed as percentage) abundance > 0.005 and a presence > 6% for
551 all years of the time period were kept⁴⁵. As more pseudo-species were generated than
552 observed biological variables involved in the calculations of the summary of each observed
553 community shifts, we chose randomly, for each region, a number of pseudo-species that
554 corresponded to the number of biological variables (Supplementary Table 3 and
555 Supplementary Figure 14). For example in the Pacific Rim, we selected a number of pseudo-
556 species that corresponded to the number of biological variables used to perform the PCA.
557 However, when total zooplankton biomass (CalCOFI) or size fractions (HOT) were used, we
558 arbitrarily chose 30 pseudo-species and also chose two 2-month periods instead of a single 4-
559 month period for the Southern Ocean. For CalCOFI and HOT, the selection of this number of
560 pseudo-species did not affect significantly the results above 5 pseudo-species. For the
561 Southern Ocean, the selection of two 2-month periods instead of one 4-month period reduced
562 the variability of the different trajectories but did not strongly affect our conclusions. We
563 repeated the selection of the pseudo-species 10,000 times and recalculated each time the first
564 two principal components on pseudo-species (Supplementary Figure 14). Therefore, 10,000
565 PCAs were performed for each of the 14 regions. When the number of pseudo-species was
566 high in a given system, variability in the METAL predictions was low.

567

568 We subsequently compared the first two observed and predicted Principal Components (PCs)
569 of the 14 regions; Obs-PC for PCs from the PCA based on observed community and Pred-PC

570 for PCs from the PCAs based on pseudo-communities (PC1 and PC2 for first and second
571 principal components, respectively). This comparison was made in 3 different ways
572 (Supplementary Figure 14).

573
574 First, we calculated the linear correlation coefficients between each Obs-PC and the average
575 of the 10000 Pred-PCs (Supplementary Table 4); when the average was calculated,
576 probabilities were calculated with and without adjusting the degree of freedom to correct for
577 temporal autocorrelation⁴⁶. Based on the correlation coefficients, we represented the best
578 relationships between one of the two Obs-PCs and Pred-PCs for the 14 systems (Figure 2).

579
580 Second, we performed a regression on Principal Components⁴⁷ between the Obs-PC selected
581 in Figure 2a-n and the first two corresponding Pred-PCs (averaged for the 10000 simulations)
582 for the 14 systems. Those analyses were performed because they better integrate the
583 complexity of the temporal signal of predictive PCs and removes any bias related to the
584 selection of a given Pred-PC. A scatterplot was then performed between observed and
585 modelled Obs-PCs of all systems and a linear correlation coefficient was calculated (Figure 2o).
586 We also repeated the procedure for every simulation (10000) to examine the variability of the
587 correlations between observed and predicted PCs (Figure 2p, red bars).

588
589 Third, we calculated two 'global' standardised PCAs: the first, on the matrix that combined the
590 first 2 Obs-PCs obtained from each PCA applied on observed communities; the second, on the
591 matrix that resulted from the combination of the first 2 Pred-PCs obtained from PCAs applied
592 on simulated pseudo-communities (after averaging the 10,000 simulations). Prior to these
593 analyses, we estimated the number of missing data from 1950 to 2014 to select a time period
594 for which years had less than 50% of missing data (period 1960-2007; Supplementary Figure
595 3). This threshold of 50% was chosen to have a maximum of years in the analyses with an
596 alteration towards the beginning and the end of the selected time period as low as possible.
597 We examined the relationships between the first 3 global Obs-PCs and Pred-PCs. We tested
598 the significance of the first three axes by using a broken-stick distribution⁴⁴. Normalised
599 eigenvectors (i.e. correlations between long-term changes in the value of each variable with
600 the first three principal components) are in Supplementary Table 5. This analysis focused on
601 the different long-term and more abrupt patterns that were observed in the 14 systems. We
602 also repeated the procedure for every simulation (10000) to examine the variability of the first
603 3 predicted global PCs (Figure 3a-c; curves in blue) and its influence on the detection of ACSs
604 (Figure 3d-f; curves in blue). We applied our abrupt shift detection algorithm to identify ACSs
605 in the three global Obs-PCs and Pred-PCs. For this analysis, we used an order-3 weighted
606 difference in all analyses after having applied an order-1 symmetrical moving average (see
607 Equation 4 with $p=3$). This procedure was chosen to remove the effects of episodic events and
608 to concentrate on ACSs that may have persistent effects.

609 610 **Null models**

611
612 We designed two null models to examine whether our METAL predictions fit better the
613 observations than those obtained randomly (with and without temporal autocorrelation;
614 Supplementary Figure 14). The first null model generated a number of random time series for
615 each station corresponding to the species richness simulated by METAL, with a length
616 corresponding to the time period covered in each sampling site (Figure 2) and a length

617 corresponding to the time period chosen to perform 'global' PCAs (Figure 3). The second null
618 model generated the same number of time series but using random time series with an order-
619 1 temporal autocorrelation ≥ 0.5 as many of our observed and METAL-simulated time series
620 were autocorrelated. We analysed those data using the same procedures applied to analyse
621 METAL-simulated data (see the previous section) and to examine the relationships with
622 observed biological data (Supplementary Figure 14). We only represented expected biological
623 changes based on the null model using randomly generated time series with an order-1
624 autocorrelation ≥ 0.5 as the null model based on random time series gave similar results. The
625 average correlation between expected and observed changes was reported for each site
626 (Supplementary Figure 2).

627

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

637

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

643

644 **Predictions of Abrupt Community Shifts**

645

646 After testing our theoretical framework and abrupt shift detection algorithm against field
647 observations, we estimated theoretically ACSs from 1960 to 2015 in all areas of the oceans.
648 Here also, only pseudo-species with an annual relative (i.e. expressed as percentage)
649 abundance > 0.005 and a presence $>6\%$ for all years of the time period were kept⁴⁵. In each
650 geographical cell of the oceans, we estimated ACSs for all pseudo-species composing a
651 pseudo-community. To estimate ACSs, we used an order-3 weighted difference after having
652 applied an order-1 symmetrical moving average (see Equation 4 with $p=3$), as above. Then, we
653 represented for each tested time period from 1960-1963 (mean year 1961.5) to 2012-2015
654 (mean year 2013.5) the amount of species that exhibit ACSs out of the pseudo-species
655 composing the pseudo-community (Supplementary Figure 4). Data of mean sea level pressure
656 and mean wind circulation were superimposed on maps for the corresponding time period.
657 Because the number of maps was large (see Supplementary Figure 4 for all maps), we chose
658 5 time periods: (i) 1975-1979, 1985-1989 and 1995-1999 because these include already
659 documented ACSs^{4,7,8,15,48}, (ii) 2005-2009 because it is an example of a relatively calm period
660 and (iii) the last period 2010-2014 (Figure 5). To pool different mean year of shift (e.g. 1976.5
661 as an average of period 1975-1978) within those time periods (e.g. 1975-1979), we calculated
662 the highest percentage of pseudo-species' shift in each geographical cell (e.g. 1975.5, 1976.5,
663 1977.5, 1978.5, 1979.5).

664

665 **Observations of abrupt climatic shifts**

666

667 We applied the same procedure to identify abrupt climatic shifts from 1960 to 2015. We also
668 applied an order-3 weighted difference after having applied an order-1 symmetrical moving
669 average (see Equation 4 with $p=3$). The abrupt shift detection algorithm was performed on
670 annual sea level pressure, meridional (U) and zonal (V) wind, wind intensity, cloudiness and
671 SST. We then added the number of significant shifts observed in each geographical cell from
672 1960-1963 to 2012-2015 (Supplementary Figure 5). To examine the potential relationships
673 between predicted ACSs and climatic shifts, we applied the same procedure as above for the
674 same time periods: 1975-1979, 1985-1989, 1995-1999, 2005-2009 and 2010-2014 (Figure 4d-
675 f). Abrupt climatic shifts were mapped for the period 2010-2014 for each climatic variable
676 (2010-2014) in an attempt to understand the exceptional nature of the time period identified
677 by our theoretical framework (Supplementary Figure 6).

678

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

680

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

683

684 **Estimation of spatial extent of ACSs**

685

686 For each geographical cell that had a percentage of pseudo-species that shifted significantly
687 above 50% in a given pseudo-community, geographical distances in a geographical cell were
688 calculated as follows⁴⁹:

689

$$690 \quad d(i,j)=6377.221 \times h_{i,j} \quad (5)$$

691 With $d_{i,j}$ being the geographical distance between point i and j , the constant the Earth radius
692 and $h_{i,j}$ computed as follows⁴⁹:

$$693 \quad h_{i,j} = ar \cos \left(\sin \varphi_i \sin \varphi_j + \cos \varphi_i \cos \varphi_j \cos g \right) \quad (6)$$

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

702

703 **Estimation of the magnitude of ACSs**

704

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

708

709 **Estimation of both magnitude and spatial extent**

710

711 The last index was calculated by summing the magnitude of all ACSs characterised by at least
712 50% of pseudo-species' shifts inside a pseudo-community. This index takes into consideration
713 both the magnitude of the shift and the number of geographical cells concerned by an ACS
714 (Figure 4c).

715

716

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