Prediction of unprecedented biological shifts in the global ocean

G. Beaugrand, A. Conversi, A. Atkinson, J. Cloern, S. Chiba, S. Fonda-Umani, R. R. Kirby, C. H. Greene, E. Goberville, S. A. Otto, et al.

Prediction of unprecedented biological shifts in the global ocean

G. Beaugrand[1,2*], A. Conversi[3,4], A. Atkinson[5], J. Cloern[6], S. Chiba[7], S. Fonda-Umani[8], R.R. Kirby[9], C.H. Greene[10], E. Goberville[11], S.A. Otto[12], P.C. Reid[2,4], L. Stemmann[13], M. Edwards[2,4]

* Corresponding author: gregory.beaugrand@cnrs.fr

[1] Centre National de la Recherche Scientifique, Laboratoire d'Océanologie et de Géosciences' UMR LOG CNRS 8187, Station Marine, Université des Sciences et Technologies de Lille 1 - Lille 1 BP 80, 62930 Wimereux, France
[2] Marine Biological Association, the Continuous Plankton Recorder (CPR) survey, The Laboratory, Citadel Hill, The Hoe, Plymouth PL1 2PB, UK
[3] ISMAR–Marine Sciences Institute in La Spezia, CNR–National Research Council of Italy, Forte Santa Teresa, Loc. Pozzuolo, 19032, Lerici, SP, Italy
[4] School of Biological & Marine Sciences, University of Plymouth, Plymouth, PL4 8AA, UK
[5] Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL13DH, UK
[6] USGS MS496 345 Middlefield Rd., Menlo Park, CA, 94025, USA
[7] RCGC, JAMSTEC, 3173-25 Showa-machi, Kanazawa-ku, Yokohama, 236-0001 Japan
[8] Department of Life Sciences, University of Trieste, v. Giorgieri, 10, 34127 Trieste, Italy
[9] The Secchi Disk Foundation, Kiln Cottage, Gnaton, Yealmpton, PI8 2HU, UK
[10] Ocean Resources and Ecosystems Program, Cornell University, Ithaca, NY 14853-1504, USA
[11] Muséum National d'Histoire Naturelle, UMR 7208 BOREA, Sorbonne Université, CNRS, UCN, UA, IRD, Paris, France
[12] Institute of Marine Ecosystem and Fishery Science (IMF), Center for Earth System Research and Sustainability, University of Hamburg, 22767 Hamburg, Germany
[13] Sorbonne Université, Institut de la Mer de Villefranche, CNRS, UMR 7093, Laboratoire d'Océanographie de Villefranche, F-06230, Villefranche/mer, France

31 **Abstract**

32 **Impermanence is an ecological principle[1] 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 **provide[2]. Here, we present a model based on niche theory[3] 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 1980s[4-7] 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 structure[12], 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 composition[15], 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 parameters[19] (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-specific[3] 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 heterogeneous[22] 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 cycles[16]. 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 ACS[15] 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 techniques[4] (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 environment[12], 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 events[28]) 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 services[27]. 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 accelerating[9]. 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

238

239

255

256 **Literature cited**

257

258 1   Boero, F. et al. From biodiversity and ecosystem functioning to the roots of ecological

259 complexity. Ecological Complexity 1, 101-109 (2004).

260 2   Scheffer, M. Critical transitions in nature and society. (Princeton University Press, 2009).

261 3   Hutchinson, G. E. An introduction to population ecology. (Yale University Press, 1978).

262 4   Reid, P. C. et al. Global impacts of the 1980s regime shift. Global Change Biology 22, 682-703,

263 doi:10.1111/gcb.13106 (2016).

264 5   Greene, C. H., Pershing, A. J., Cronin, T. M. & Ceci, N. Arctic climate change and its impacts on

265 the ecology of the North Atlantic. Ecology 89, S24-S38 (2008).

266 6   Conversi, A. et al. The Mediterranean Sea regime shift at the end of the 1980s, and intriguing

267 parallelisms with other European basins. PLOS one 5, 1-15 (2010).

268 7   Beaugrand, G. et al. Synchronous marine pelagic regime shifts in the Northern Hemisphere.

269 Philosophical Tansactions of the Royal Society B: Biological Sciences 370, 20130272,

270 doi:10.1098/rstb.2013.0272 (2015).

271 8   Luczak, C., Beaugrand, G., Jaffré, M. & Lenoir, S. Climate change impact on Balearic Shearwater

272 through a trophic cascade. Biology Letters 7, 702-705 (2011).

273 9   Arctic Council. Arctic Resilience Report., (Stockholm Environment Institute and Stockholm
274 Resilience Centre, Stockholm, 2016).

275 10   Conversi, A. et al. A holistic view of marine regime shifts. Philosophical Transations of the Royal
276 Society B 370, 20130279, doi:10.1098/rstb.2013.0279 (2015).

277 11   Möllmann, C. & Diekmann, R. Marine ecosystem regime shifts induced by climate and
278 overfishing: A review for the Northern hemisphere. Advances in Ecological Research 47, 303-347
279 (2012).

280 12   Beaugrand, G. Theoretical basis for predicting climate-induced abrupt shifts in the oceans.
281 Philosophical Tansactions of the Royal Society B: Biological Sciences 370 20130264,
282 doi:10.1098/rstb.2013.0264 (2015).

283 13   Mac Nally, R., Albano, C. & Fleishman, E. A scrutiny of the evidence for pressure-induced state
284 shifts in estuarine and nearshore ecosystems. Austral Ecology 39, 898-906 (2014).

285 14   Di Lorenzo, E. & Ohman, M. D. A double-integration hypothesis to explain ocean ecosystem
286 response to climate forcing. Proceedings of the National Academy of Sciences of the United States of
287 America 110, 2496-2499, doi:10.1073/pnas.1218022110 (2013).

288 15   Hare, S. R. & Mantua, N. J. Empirical evidence for North Pacific regime shifts in 1977 and 1989.
289 Progress in Oceanography 47, 103-145 (2000).

290 16   Beaugrand, G., Goberville, E., Luczak, C. & Kirby, R. R. Marine biological shifts and climate.
291 Proceedings of the Royal Society B: Biological Sciences 281, 20133350, doi:10.1098/rspb.2013.3350
292 (2014).

293 17   Beaugrand, G., Edwards, M., Raybaud, V., Goberville, E. & Kirby, R. R. Future vulnerability of
294 marine biodiversity compared with contemporary and past changes. Nature Climate Change 5, 695-
295 701, doi:10.1038/NCLIMATE2650 (2015).

296 18   Beaugrand, G. Marine biodiversity, climatic variability and global change., (Routledge, 2015).

297 19   Cloern, J. E. & Jassby, A. D. Drivers of change in estuarine-coastal ecosystems: discoveries from
298 four decades of study in San Francisco Bay. Reviews of Geophysics 50, rg4001,
299 doi:10.1029/2012RG000397 (2012).

300 20   Sunday, J. M., Bates, A. E. & Dulvy, N. K. Global analysis of thermal tolerance and latitude in
301 ecthoterms. Proceedings of the Royal Society B 278, 1823-1830 (2011).

302 21   Stuart-Smith, R. D., Edgar, G. J., Barrett, N. S., Kininmonth, S. J. & Bates, A. E. Thermal biases
303 and vulnerability to warming in the world's marine fauna. Nature 528, 88-92 (2015).

304 22   Di Lorenzo, E. et al. Synthesis of Pacific Ocean climate and ecosystems dynamics.
305 Oceanography 26, 68-81 (2014).

306 23   Beaugrand, G. & Kirby, R. R. Quasi-deterministic responses of marine species to climate
307 change. Climate Research 69, 117-128, doi:10.3354/cr01398 (2016).

308   24   Mollmann, C. et al. Reorganization of a large marine ecosystem due to atmospheric and
309   anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. . Global Change Biology
310   15, 1377-1393 (2009).

311   25   Bond, N. A., Cronin, M. F., Freeland, H. & Mantua, N. Causes and impacts of the 2014 warm
312   anomaly in the NE Pacific. Geophysical Research Letters 42, 3414-3420, doi:10.1002/2015/GL063306
313   (2015).

314   26   Duchez, A. et al. Drivers of exceptionally cold North Atlantic Ocean temperatures and their link
315   to the 2015 European heat wave. Environmental Research Letters 11, 074004, doi:10.1088/1748-
316   9326/11/7/074004 (2016).

317   27   Greene, C. H. North America's iconic marine species at risk due to unprecedented ocean
318   warming. Oceanography 29, 14-17 (2016).

319   28   Aarssen, L. W. High productivity in grassland ecosystems: effected by species diversity or
320   productive species? Oikos 80, 183-184 (1997).

321   29   Boettiger, C. & Hastings, A. Early warning signals and the prosecutor's fallacy. Proceedings of
322   the Royal Society B 279, 4734-4739 (2012).

323   30   Schindler, D. & Hillborn, R. Prediction, precaution and policy under climate change. Science
324   347, 953-954 (2015).

325   31   Smith, T. M., Reynolds, R. W., Peterson, T. C. & Lawrimore, J. Improvements to NOAA's
326   Historical Merged Land-Ocean Surface Temperature Analysis (1880-2006). Journal of Climate 21, 2283-
327   2296 (2008).

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 Beaugrand[12] and Beaugrand and colleagues[7], 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 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).

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 Beaugrand[12].
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 variation[41], the measure of the autocorrelation[42], or the quantification of
497 the multi-scale variance along time series[43]. 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 colleagues[43]. 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 **Z** a time series, **Z**=[z_i] was standardised as follows:
505
506
$$x_i = \frac{z_i - \min(z)}{\max(z) - \min(z)} \qquad (2)$$

507
508 The amplitude vector **A^p**=[a^p_i] was subsequently calculated as the first p difference between a
509 value of **X**=[x_i] at year t+p and year t, with $1 \leq p \leq 5$:
510
511
$$a^p = \left| x_{t+p} - x_t \right| \qquad (3)$$

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 **M^p**=[m^p_i] 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
$$m^p_i = \frac{a^p_i}{\frac{1}{n-p-1} \sum_{j=1, i \neq j}^{n-p} a^p_j} \qquad (4)$$

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 **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 performed[7] 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 procedure[34]. We
541 tested the significance of the first two axes (eigenvalues) by using a broken-stick distribution[44]
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 Beaugrand[12]; 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 kept[45]. 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 autocorrelation[46]. 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 Components[47] 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 distribution[44]. 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).

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.

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).

Predictions of Abrupt Community Shifts

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 kept [45]. 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).

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]:

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

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).

Literature cited

32   Kalnay, E. et al. The NCEP/NCAR 40-year reanalysis project. Bulletin of the American meteorology society 77, 437-470 (1996).

33   Longhurst, A. Ecological geography of the Sea. (Academic Press, 1998).

34   Cloern, J. E. et al. Biological communities in San Francisco Bay track large-scale climate forcing over the North Pacific. Geophysical Research Letters 37, L21602, doi:10.1029/2010GL044774 (2010).

35   Beaugrand, G. & Kirby, R. R. How do marine species respond to climate change? Theories and observations. Annual Review of Marine Sciences 10, 169–197, doi:10.1146/121916-063304 (2018).

36   Beaugrand, G., Luczak, C., Goberville, E. & Kirby, R. R. Marine biodiversity and the chessboard of life Plos One 13, e0194006, doi:https://doi.org/10.1371/journal.pone.0194006 (2018).

37   Hutchinson, G. E. Concluding remarks. Cold Spring Harbor Symposium Quantitative Biology 22, 415-427 (1957).

38   Beaugrand, G., Rombouts, I. & Kirby, R. R. Towards an understanding of the pattern of biodiversity in the oceans. Global Ecology and Biogeography 22, 440–449 (2013).

39   Ter Braak, C. J. F. Unimodal models to relate species to environment. (DLO-Agricultural Mathematics Group, 1996).

40   Rodionov, S. A sequential algorithm for testing climate regime shifts. Geophysical Research Letters 31, L09204, doi:10.1029/2004GL019448 (2004).

41   Carpenter, S. R. & Brock, W. A. Rising variance: a leading indicator of ecological transition. Ecology Letters 9, 311-318 (2006).

42   Carpenter, S. R. et al. Early Warnings of Regime Shifts: A Whole-Ecosystem Experiment. Science 332, 1079-1082 (2011).

43   Beaugrand, G., Edwards, M., Brander, K., Luczak, C. & Ibañez, F. Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. Ecology Letters 11, 1157-1168 (2008).

44   Frontier, S. Etude de la décroissance des valeurs propres dans une analyse en composantes principales: comparaison avec le modèle du bâton brisé. Journal of Experimental Marine Biology and Ecology 25, 67-75 (1976).

45   Ibanez, F. & Dauvin, J.-C. Shape analysis of temporal ecological processes: long-term changes in English Channel macrobenthic communities. Coenoses 13, 115-129 (1998).

745 46   Pyper, B. J. & Peterman, R. M. Comparison of methods to account for autocorrelation analyses
746 of fish data. Canadian Journal of Fisheries and Aquatic Sciences 55, 2127-2140 (1998).

747 47   Legendre, P. & Legendre, L. Numerical Ecology. 2 edn, (Elsevier Science B.V., 1998).

748 48   Goberville, E., Beaugrand, G. & Edwards, M. Synchronous response of marine plankton
749 ecosystems to climate in the Northeast Atlantic and the North Sea. Journal of Marine Systems,
750 doi:10.1016/j.jmarsys.2013.05.008 (2013).

751 49   Beaugrand, G. & Ibañez, F. Spatial dependence of pelagic diversity in the North Atlantic Ocean.
752 Marine Ecology Progress Series 232, 197-211 (2002).

Literature cited

1   Boero, F. *et al.* From biodiversity and ecosystem functioning to the roots of ecological complexity. *Ecological Complexity* **1**, 101-109 (2004).

2   Scheffer, M. *Critical transitions in nature and society*. (Princeton University Press, 2009).

3   Hutchinson, G. E. *An introduction to population ecology*. (Yale University Press, 1978).

4   Reid, P. C. *et al.* Global impacts of the 1980s regime shift. *Global Change Biology* **22**, 682-703, doi:10.1111/gcb.13106 (2016).

5   Greene, C. H., Pershing, A. J., Cronin, T. M. & Ceci, N. Arctic climate change and its impacts on the ecology of the North Atlantic. *Ecology* **89**, S24-S38 (2008).

6   Conversi, A. *et al.* The Mediterranean Sea regime shift at the end of the 1980s, and intriguing parallelisms with other European basins. *PLOS one* **5**, 1-15 (2010).

7   Beaugrand, G. *et al.* Synchronous marine pelagic regime shifts in the Northern Hemisphere. *Philosophical Tansactions of the Royal Society B: Biological Sciences* **370**, 20130272, doi:10.1098/rstb.2013.0272 (2015).

8   Luczak, C., Beaugrand, G., Jaffré, M. & Lenoir, S. Climate change impact on Balearic Shearwater through a trophic cascade. *Biology Letters* **7**, 702-705 (2011).

9   Arctic Council. Arctic Resilience Report., (Stockholm Environment Institute and Stockholm Resilience Centre, Stockholm, 2016).

10   Conversi, A. *et al.* A holistic view of marine regime shifts. *Philosophical Transations of the Royal Society B* **370**, 20130279, doi:10.1098/rstb.2013.0279 (2015).

11   Möllmann, C. & Diekmann, R. Marine ecosystem regime shifts induced by climate and overfishing: A review for the Northern hemisphere. *Advances in Ecological Research* **47**, 303-347 (2012).

12   Beaugrand, G. Theoretical basis for predicting climate-induced abrupt shifts in the oceans. *Philosophical Tansactions of the Royal Society B: Biological Sciences* **370** 20130264, doi:10.1098/rstb.2013.0264 (2015).

13   Mac Nally, R., Albano, C. & Fleishman, E. A scrutiny of the evidence for pressure-induced state shifts in estuarine and nearshore ecosystems. *Austral Ecology* **39**, 898-906 (2014).

14   Di Lorenzo, E. & Ohman, M. D. A double-integration hypothesis to explain ocean ecosystem response to climate forcing. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 2496-2499, doi:10.1073/pnas.1218022110 (2013).

15   Hare, S. R. & Mantua, N. J. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* **47**, 103-145 (2000).

16   Beaugrand, G., Goberville, E., Luczak, C. & Kirby, R. R. Marine biological shifts and climate. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20133350, doi:10.1098/rspb.2013.3350 (2014).

17   Beaugrand, G., Edwards, M., Raybaud, V., Goberville, E. & Kirby, R. R. Future vulnerability of marine biodiversity compared with contemporary and past changes. *Nature Climate Change* **5**, 695-701, doi:10.1038/NCLIMATE2650 (2015).

18   Beaugrand, G. *Marine biodiversity, climatic variability and global change.*, (Routledge, 2015).

19   Cloern, J. E. & Jassby, A. D. Drivers of change in estuarine-coastal ecosystems: discoveries from four decades of study in San Francisco Bay. *Reviews of Geophysics* **50**, rg4001, doi:10.1029/2012RG000397 (2012).

20   Sunday, J. M., Bates, A. E. & Dulvy, N. K. Global analysis of thermal tolerance and latitude in ecthoterms. *Proceedings of the Royal Society B* **278**, 1823-1830 (2011).

21   Stuart-Smith, R. D., Edgar, G. J., Barrett, N. S., Kininmonth, S. J. & Bates, A. E. Thermal biases and vulnerability to warming in the world's marine fauna. *Nature* **528**, 88-92 (2015).

22   Di Lorenzo, E. *et al.* Synthesis of Pacific Ocean climate and ecosystems dynamics. *Oceanography* **26**, 68-81 (2014).

23   Beaugrand, G. & Kirby, R. R. Quasi-deterministic responses of marine species to climate change. *Climate Research* **69**, 117-128, doi:10.3354/cr01398 (2016).

804   24   Mollmann, C. *et al.* Reorganization of a large marine ecosystem due to atmospheric and
805   anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. . *Global*
806   *Change Biology* **15**, 1377-1393 (2009).
807   25   Bond, N. A., Cronin, M. F., Freeland, H. & Mantua, N. Causes and impacts of the 2014 warm
808   anomaly in the NE Pacific. *Geophysical Research Letters* **42**, 3414-3420,
809   doi:10.1002/2015/GL063306 (2015).
810   26   Duchez, A. *et al.* Drivers of exceptionally cold North Atlantic Ocean temperatures and their
811   link to the 2015 European heat wave. *Environmental Research Letters* **11**, 074004,
812   doi:10.1088/1748-9326/11/7/074004 (2016).
813   27   Greene, C. H. North America's iconic marine species at risk due to unprecedented ocean
814   warming. *Oceanography* **29**, 14-17 (2016).
815   28   Aarssen, L. W. High productivity in grassland ecosystems: effected by species diversity or
816   productive species? *Oikos* **80**, 183-184 (1997).
817   29   Boettiger, C. & Hastings, A. Early warning signals and the prosecutor's fallacy. *Proceedings of*
818   *the Royal Society B* **279**, 4734-4739 (2012).
819   30   Schindler, D. & Hillborn, R. Prediction, precaution and policy under climate change. *Science*
820   **347**, 953-954 (2015).
821   31   Smith, T. M., Reynolds, R. W., Peterson, T. C. & Lawrimore, J. Improvements to NOAA's
822   Historical Merged Land-Ocean Surface Temperature Analysis (1880-2006). *Journal of Climate*
823   **21**, 2283-2296 (2008).
824   32   Kalnay, E. *et al.* The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American*
825   *meteorology society* **77**, 437-470 (1996).
826   33   Longhurst, A. *Ecological geography of the Sea*. (Academic Press, 1998).
827   34   Cloern, J. E. *et al.* Biological communities in San Francisco Bay track large-scale climate
828   forcing over the North Pacific. *Geophysical Research Letters* **37**, L21602,
829   doi:10.1029/2010GL044774 (2010).
830   35   Beaugrand, G. & Kirby, R. R. How do marine species respond to climate change? Theories and
831   observations. *Annual Review of Marine Sciences* **10**, 169–197, doi:10.1146/121916-063304
832   (2018).
833   36   Beaugrand, G., Luczak, C., Goberville, E. & Kirby, R. R. Marine biodiversity and the chessboard
834   of life *Plos One* **13**, e0194006, doi:https://doi.org/10.1371/journal.pone.0194006 (2018).
835   37   Hutchinson, G. E. Concluding remarks. *Cold Spring Harbor Symposium Quantitative Biology*
836   **22**, 415-427 (1957).
837   38   Beaugrand, G., Rombouts, I. & Kirby, R. R. Towards an understanding of the pattern of
838   biodiversity in the oceans. *Global Ecology and Biogeography* **22**, 440–449 (2013).
839   39   Ter Braak, C. J. F. *Unimodal models to relate species to environment*. (DLO-Agricultural
840   Mathematics Group, 1996).
841   40   Rodionov, S. A sequential algorithm for testing climate regime shifts. *Geophysical Research*
842   *Letters* **31**, L09204, doi:10.1029/2004GL019448 (2004).
843   41   Carpenter, S. R. & Brock, W. A. Rising variance: a leading indicator of ecological transition.
844   *Ecology Letters* **9**, 311-318 (2006).
845   42   Carpenter, S. R. *et al.* Early Warnings of Regime Shifts: A Whole-Ecosystem Experiment.
846   *Science* **332**, 1079-1082 (2011).
847   43   Beaugrand, G., Edwards, M., Brander, K., Luczak, C. & Ibañez, F. Causes and projections of
848   abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecology Letters* **11**, 1157-1168
849   (2008).
850   44   Frontier, S. Etude de la décroissance des valeurs propres dans une analyse en composantes
851   principales: comparaison avec le modèle du bâton brisé. *Journal of Experimental Marine*
852   *Biology and Ecology* **25**, 67-75 (1976).
853   45   Ibanez, F. & Dauvin, J.-C. Shape analysis of temporal ecological processes: long-term changes
854   in English Channel macrobenthic communities. *Coenoses* **13**, 115-129 (1998).

855   46   Pyper, B. J. & Peterman, R. M. Comparison of methods to account for autocorrelation
856   analyses of fish data. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 2127-2140
857   (1998).
858   47   Legendre, P. & Legendre, L. *Numerical Ecology*. 2 edn, (Elsevier Science B.V., 1998).
859   48   Goberville, E., Beaugrand, G. & Edwards, M. Synchronous response of marine plankton
860   ecosystems to climate in the Northeast Atlantic and the North Sea. *Journal of Marine*
861   *Systems*, doi:10.1016/j.jmarsys.2013.05.008 (2013).
862   49   Beaugrand, G. & Ibañez, F. Spatial dependence of pelagic diversity in the North Atlantic
863   Ocean. *Marine Ecology Progress Series* **232**, 197-211 (2002).

864