

## Solutions for ecosystem-level protection of ocean systems under climate change

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### Abstract :

The Paris Conference of Parties (COP21) agreement renewed momentum for action against climate change, creating the space for solutions for conservation of the ocean addressing two of its largest threats: climate change and ocean acidification (CCOA). Recent arguments that ocean policies disregard a mature conservation research field and that protected areas cannot address climate change may be oversimplistic at this time when dynamic solutions for the management of changing oceans are needed. We propose a novel approach, based on spatial meta-analysis of climate impact models, to improve the positioning of marine protected areas to limit CCOA impacts. We do this by estimating the vulnerability of ocean ecosystems to CCOA in a spatially explicit manner and then co-mapping human activities such as the placement of renewable energy developments and the distribution of marine protected areas. We test this approach in the NE Atlantic considering also how CCOA impacts the base of the food web which supports protected species, an aspect often neglected in conservation studies. We found that, in this case, current regional conservation plans protect areas with low ecosystem-level vulnerability to CCOA, but disregard how species may redistribute to new, suitable and productive habitats. Under current plans, these areas remain open to commercial extraction and other uses. Here, and worldwide, ocean conservation strategies under CCOA must recognize the long-term importance of

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these habitat refuges, and studies such as this one are needed to identify them. Protecting these areas creates adaptive, climate-ready and ecosystem-level policy options for conservation, suitable for changing oceans.

**Keywords** : climate change, conservation, COP21, ecosystem model, habitat, marine spatial planning, ocean, ocean acidification, species distribution, warming

50 The perspective that ocean conservation cannot be used to limit the overwhelming pressures that  
51 climate change and ocean acidification (CCOA) exert on marine systems (Nagelkerken &  
52 Connell, 2015) is still often held (Hilborn, 2015). In parallel, research efforts to improve the  
53 effectiveness of marine conservation under climate change have rapidly increased in recent years  
54 (Côté & Darling, 2010, Levy & Ban, 2013, Maxwell *et al.*, 2015). However, studies addressing  
55 the ecosystem-level impacts of CCOA, in the context of the multiple human uses of the ocean  
56 within which conservation takes place, are still largely absent. Solutions for ocean conservation  
57 are now needed when many ecosystem components are simultaneously and indirectly affected by  
58 long-term CCOA and other human activities, driving declines across large numbers of species at  
59 the same time (Audzijonyte *et al.*, 2016, Griffith *et al.*, 2012, Hobday & Pecl, 2014). Crucially,  
60 how can we plan for foodweb changes that would affect many protected (and unprotected)  
61 species, such as regional reduction in plankton productivity driven by CCOA (Nagelkerken &  
62 Connell, 2015)? Complex, ecosystem-level changes caused by CCOA may continue to occur  
63 across the foodweb, no matter how limited commercial extraction is inside marine reserves.

64 Many governments (including the USA, UK, Chile and New Zealand) are betting on the closure  
65 of vast areas of the ocean to fisheries to meet the need to reduce overfishing, and increase the  
66 sustainability of marine food resources. Some agree that this reduction in local stressors such as  
67 fisheries can also, in some cases, improve resistance to climate stressors (Carilli *et al.*, 2010).

68 These efforts have thus been welcomed, but do they unwittingly offer false hope? Beyond the  
69 need to secure larger areas of the ocean against commercial extraction, conservation strategies  
70 must embrace novel climate change research, which reveals that curbing CCOA impacts on  
71 marine foodwebs may require more comprehensive aims. Alongside human activities such as  
72 fisheries (Campbell *et al.*, 2014); nutrient loading (Wakelin *et al.*, 2015); aquaculture  
73 (UKMMAS, 2010); and energy production (Rourke *et al.*, 2010); CCOA impacts marine species  
74 both directly by altering life history processes and vital rates, as well as indirectly, through  
75 changes in the distribution of suitable habitat and food availability (i.e. primary production,  
76 Audzijonyte *et al.*, 2016, Blanchard *et al.*, 2012, Cheung *et al.*, 2011). Consequently, solutions  
77 for conservation that protect against CCOA cannot focus solely on the protection of declining  
78 species. Consideration must be given to how CCOA impacts processes affecting population  
79 sustainability locally but, equally, to the relationships between these processes and habitat  
80 characteristics, which are also be impacted by CCOA.

81 A growing body of theory and mechanistic evidence has demonstrated that the responses of  
82 populations to stressors such as CCOA not only depend on the gradient of change experienced,  
83 but also on how that gradient relates to the range of variability that populations have experienced  
84 historically for each of these variables (Peck *et al.*, 2009, Somero, 2010). A prerequisite for the  
85 local populations to persist in the short-term, failure of which negates the possibility for long-  
86 term adaptation to occur (Somero, 2010), is acquiring sufficient food from the environment to  
87 support energetically costly stress response pathways (Queirós *et al.*, 2015b, Thomsen *et al.*,  
88 2013). Sufficient food uptake therefore allows the option to allocate energy where needed, i.e. to  
89 respond to stress in addition to fueling population dynamic processes such as growth and  
90 reproduction (Calosi *et al.*, 2013, Gaylord *et al.*, 2015, Pörtner & Farrell, 2008). Food

91 availability can therefore dictate whether or not a given organism is able to withstand  
92 environmental changes such as ocean acidification, and deserves attention in conservation  
93 planning. A greater focus of conservation research in considering impacts on primary  
94 productivity, alongside those on multiple species, should thus yield more effective conservation  
95 aims in light of ecosystem-level impacts of CCOA: 1) because it would ensure that food  
96 resources are available to organisms in communities experiencing environmental change through  
97 CCOA; and 2) because protecting areas of the ocean that make important contributions to  
98 primary and secondary production have positive outcomes to other human uses of the ocean  
99 (Brown *et al.*, 2010).

100 Changes in system productivity, in plankton communities and other groups at the base of the  
101 foodweb, associated with CCOA (Nagelkerken & Connell, 2015) have seldom been considered  
102 in conservation research, perhaps because of the challenges of collecting and integrating these  
103 data to answer management questions. Nonetheless, to adequately inform policy, conservation  
104 science must broaden to include ecosystem-level vulnerability, e.g. to recommend areas for  
105 protection where species could be able to remain in (or locate to) suitable habitat, and thrive  
106 productively. We argue that, to this end, habitat modeling (Gormley *et al.*, 2013) and similar  
107 approaches can be powerful tools to integrate novel CCOA knowledge, which are underused in  
108 conservation research and policy advice. We exemplify here the potential benefits of more  
109 comprehensively using these tools in ocean conservation.

110 New technological approaches to data collection and analysis can support dynamic ocean  
111 management (Lewison *et al.*, 2015, Maxwell *et al.*, 2015). Yet, ocean observations alone have  
112 limited value in the long-term forecasting of systems when conditions are expected to depart  
113 considerably from those observed historically due to the long-term impacts of climate change

114 (Barnsley, 2007, Payne *et al.*, 2015). Conversely, the combined use of models that simulate  
115 multiple levels of the ocean foodweb resolved in time and space can be used to explore: 1) how  
116 levels of CCOA not yet observed could in the long-run impact marine life and the distribution of  
117 productivity that supports it (Queirós *et al.*, 2015b); and 2) whether ocean conservation and  
118 exploitation strategies may be optimized to address environmental stressors and their future  
119 effects (Jones & Cheung, 2014, Levin *et al.*, 2009, Sumaila *et al.*, 2015). However, the  
120 application of such models in conservation research is often narrowly focused. For example, the  
121 effects of changes in sea temperature are often examined in isolation (Molinos *et al.*, 2015)  
122 despite evidence that ocean acidification is a co-occurring global stressor and can strongly  
123 modify species vulnerability to thermal stress (Kroeker *et al.*, 2013, Nagelkerken & Connell,  
124 2015). Furthermore, vulnerability of local species to CCOA can be exacerbated by human uses  
125 of the marine environment (Carilli *et al.*, 2010, Planque *et al.*, 2010) but a holistic view of their  
126 combined impacts is rarely considered by conservation studies. Finally, focus is frequently placed  
127 on single or small subsets of species or ecosystem properties (e.g. Gormley *et al.*, 2013), although  
128 the current management paradigm in the United States and in Europe requires decisions to be  
129 weighed based on their impacts on whole ecosystems and not just based on single human  
130 activities or ecosystem components (EC, 2008, EU, 2014, NOC, 2013, Rice, 2013).

131 Here, we overcome these shortcomings using a novel approach to extract common patterns in  
132 long-term projections from a large ensemble of ecosystem models forced with climate change  
133 and, where possible, ocean acidification, taking into account additional human activities. Using  
134 global change scenarios and a range of modeling projections for the middle of the 21<sup>st</sup> century,  
135 we present an analysis focused on the NE Atlantic continental shelf that identifies areas where  
136 consensus exists across models regarding the occurrence of large and directional change of  
137 ecosystem components (hereafter, “hotspots of change”). The large model ensemble analyzed

138 here covered as many ecosystem components and trophic levels as possible from 54 distinct  
139 models. Various global scenarios of change in CO<sub>2</sub> emissions, as defined by the  
140 Intergovernmental Panel on Climate Change at the time of the study (IPCC, 2007), allowed  
141 changes in ocean temperature, oxygen, pH and productivity to be simulated. Changes in riverine  
142 nutrient loadings were also considered based on assumptions of human use consistent with the  
143 IPCC's representative concentration pathways (Langmead *et al.*, 2007). Similarly to others  
144 (Hobday & Pecl, 2014), we propose that hotspots of change pinpoint long-term ecosystem-level  
145 CCOA vulnerabilities in this region and should receive special consideration in conservation  
146 plans. Alongside other individually threatened or declining habitats or species, response to  
147 CCOA requires that priority should be given to: i) protect areas where ecosystem-level change  
148 will be significant and positive (i.e. increasing with time) and thus where productivity will  
149 remain high; ii) protect areas where the ecosystem will not change significantly due to CCOA;  
150 and iii) shifting (the often limited) resources for conservation away from areas where negative,  
151 CCOA-driven changes are expected to occur and/or where productivity is expected to decrease,  
152 because limiting commercial extraction in those areas may not increase the sustainability of local  
153 populations. We suggest that making these distinctions may initiate a new stage for conservation  
154 research-policy dialogue that, in addition to traditional goals, responds dynamically to limit ocean  
155 impacts of CCOA.

156 By considering a diversity of models and potential trajectories of environmental change, we  
157 aimed to provide a balanced view of possible futures for the NE Atlantic shelf driven by CCOA.  
158 To best address inherent variation among model setups, we used a novel spatial approach to a  
159 well-established statistical technique (random effects meta-analysis, Borenstein *et al.*, 2011).  
160 Specifically, we estimated changes over time driven by CCOA at the ecosystem-level, by  
161 constructing meta-analysis models which, at each point in space, quantified the agreement in the

162 changes measured across the populations of various species and ecosystem components, as  
163 measured by each individual model. This approach circumvents the difficulty of summarizing  
164 ecosystem-level information from the aggregate estimates of a large number of models which, in  
165 our opinion, has hindered the integrated use of model-derived estimates in conservation advice to  
166 policy. Furthermore, we statistically quantify the uncertainty of the overall model analysis, by  
167 providing an easily understandable measure of confidence to our findings (significance testing)  
168 which is especially useful in informing policy. Accordingly, significant change measured at the  
169 ecosystem-level in each point in space indicates the presence of hotspots of change, reflecting  
170 uniformity in the response(s) of the assessed ecosystem component(s) to environmental variation  
171 in the various independent models analyzed, and lending confidence to the results. We compare  
172 the estimated distribution of hotspots of change with projected spatial planning actions in the  
173 region, focusing on areas currently (or foreseen to be) designated for conservation and offshore  
174 energy developments (windfarms). The approach combines a large amount of ecosystem-level  
175 information into one analysis to answer straightforward questions relevant to develop climate-  
176 ready conservation policies: which areas will, in the long term, not change due to CCOA, or  
177 support positive change (i.e. higher productivity) for marine species and habitats? This study is  
178 the first attempt to identify areas of high ecosystem-level vulnerability to CCOA through the use  
179 of a spatially explicit meta-analysis of a model ensemble. Our results highlight future challenges  
180 for marine conservation policy in areas experiencing multiple human pressures as well as  
181 undergoing rapid climate-driven change. The co-mapping of hotspots of ecosystem-level  
182 vulnerability to CCOA and human uses can help pave the way for effective and well informed  
183 marine spatial planning. We did not consider the potentially additional impact of present and  
184 future fishing on the assessed ecosystem components given that our primary aim was to address

185 CCOA driven impacts as the background against which other human actions on the marine  
186 environment, including conservation, could be investigated.

## 187 ***Materials and methods***

### 188 *Input data*

189 All model projections analyzed were produced or made available within the EU research project  
190 VECTORS (Vectors of Change in Oceans and Seas Marine Life, Impact on Economic Sectors,  
191 FP7/2007-2013), during which a large number of projections were produced to assess the impacts  
192 of pressures of change on specific components of marine ecosystems (Teal *et al.*, 2013).

193 Modelling outputs were scoped to include any level of the foodweb and relevant ecosystem  
194 processes within the domain of the NE Atlantic Continental Shelf. Each dataset had to comprise  
195 two comparable states of the ecosystem; i.e. a baseline and an effect state that could be used to  
196 quantify change. Typically, the data structure included projections for a “present” and a “future”  
197 time slice (5-10 yrs each) for each given model, simulated under a given scenario of future  
198 change, e.g. a specific IPCC special report emissions scenario (IPCC, 2007). Each dataset  
199 included spatial arrays of mean and standard deviation for each variable, for each time slice. We  
200 gathered 63 outputs, originating from 54 distinct models, which are summarized in Table SI  
201 (supporting information). Detailed descriptions of each model can be found in references within  
202 it.

203 Modelled data on “jellyfish” were not available in this study, reflecting the limited sampling and  
204 understanding of this group of organisms that currently exists. However, jellyfish play an  
205 important role in coastal and shelf seas impacted by climate change, diverting carbon from higher

206 trophic levels (Robinson & Graham, 2013) and should be considered in similar studies in the  
207 future.

### 208 *Meta-analyses of model projections*

209 Because the different models used here had different resolutions and gridding systems,  
210 aggregation to a coarser, common grid was required. Accordingly, all model outputs considered  
211 were aggregated across 164 standard statistical rectangles ( $1.0^\circ \times 0.5^\circ$  lon x lat) used by the  
212 International Council for the Exploration of the Sea (ICES). One separate meta-analysis model  
213 for each cell of the NE Atlantic Continental Shelf domain was then calculated across datasets,  
214 following the procedures documented in Borenstein *et al.* (2011), which provides a  
215 comprehensive synthesis of methodologies, strengths and caveats. The following procedure was  
216 employed, per domain cell.

217 “Dataset” hereafter refers to the mean, standard deviation and number of observations for each  
218 model output detailed in Table SI (n = 63), for a given domain cell. “Change” was initially  
219 calculated using Hedge’s g (Hedges, 1981), the unbiased standardized mean difference estimator,  
220 under a fixed effects model structure. This metric considers the mean, standard deviation and the  
221 number of observations in each of the slices (usually temporal slices, supporting information  
222 Table SI for time span covered in each case). The calculation of individual effect-sizes (i.e. per  
223 model, per domain cell) was conventionalized across analyses so that positive change indicated  
224 an increase of the given variable in the future in relation to present, in that specific cell of the  
225 domain, and vice-versa. For example, positive Hedge’s g for primary productivity indicated that  
226 this process was higher in the future, in a specific cell of the domain. We then estimated the  
227 effects across datasets (i.e. the summary-effects) per domain cell, considering that in this case we

228 expected not one, but a family of possible effect-sizes, given the diversity of datasets considered.  
229 This attribute of the data justified the use of a random-effects meta-analysis model. Accordingly,  
230 the variance of the effect-size for each dataset was re-calculated as the sum of: i) the variance of  
231 Hedge's  $g$  within each dataset, for each cell (as before); and ii) the variance between datasets, for  
232 that cell. The latter ( $\tau^2$ ) was estimated using the DerSimonian-Laird method (DerSimonian &  
233 Laird, 1986). The variances of the summary-effects were then used to calculate confidence  
234 intervals for the summary-effects in each cell, and hence to test their departure from zero, under a  
235 normal distribution. Statistically significant departure from zero for summary-effects was  
236 therefore considered to be indicative of significant change. The analysis was carried out across all  
237 the datasets together ( $n=63$ ) and, in this case, significant change indicated ecosystem-level  
238 vulnerability. Additionally, two subgroup analyses were undertaken, separately: one considering  
239 fish (or high trophic level) datasets ( $n=52$ ); and one considering lower trophic level datasets  
240 ( $n=11$ , Table SI). The spatial coverage of datasets can be found in supporting information  
241 figure.S1. Preliminary analyses indicated that the number of datasets influenced the estimate of  
242 variance between datasets ( $\tau^2$ ). As the latter is used to estimate confidence intervals for summary-  
243 effects, all analyzes including fish datasets excluded domain edge areas (grey, Fig.S1b) where the  
244 number of available datasets was contrastingly lower.

245 The reasoning to investigate summary-effects within subsets of meta-analysis datasets has been  
246 discussed at length elsewhere, and is beyond the scope of this study (Lyons *et al.*, 2015). Study  
247 selection for meta-analysis should be made transparently and a priori, guided by the research  
248 question investigated, as done here. This study aimed to provide a balanced view of long-term,  
249 ecosystem-level dynamics in the NE Atlantic Shelf. Accordingly, all modelling outputs available  
250 to the authors at the time of the analysis, were used. However, the influence of individual datasets

251 on summary-effects could be expected to vary, due to the context dependency of individual  
252 modelling results (Jones *et al.*, 2013). Two precautions were implemented in meta-analysis  
253 protocols to address this matter. Specifically, meta-analysis is not a vote counting procedure, in  
254 that not all datasets count equally. When a summary-effect was calculated (across datasets), more  
255 confidence was given to variables for which the mean over the time period analyzed varied less  
256 within and between datasets. Larger weight was also given to estimates calculated over a larger  
257 number of observations (or larger model sampling), because they are assumed to provide a wider  
258 coverage of the dynamics of the process simulated. These two considerations thus reduce the  
259 influence of information derived from poorly constrained models, or less comprehensive datasets,  
260 on summary-effects.

261 It is noteworthy that in following this aim of including all available datasets in this analysis, we  
262 included data on the phenology of plankton species (supporting information Table SI), because  
263 these are important indicators of ecosystem dynamics, particularly in coastal systems (Zhang *et*  
264 *al.*, 2015). However, changes in these processes (i.e. changes in the timing of primary  
265 productivity and *Phaeocystis* sp. peaks across years) may be difficult to interpret within the  
266 present statistical framework. Since North Sea phytoplankton blooms have been predicted to  
267 occur earlier (not later) by the middle of the century, we decided a priori to treat this direction of  
268 change as "negative" (Friocourt *et al.*, 2012).

#### 269 *Co-mapping of spatial planning actions*

270 The spatial planning actions considered in this analysis are the construction of windfarms and the  
271 delimitation of marine protected areas. The NE Atlantic Continental Shelf is shared between  
272 several countries' exclusive economic zones (EEZ), and each country is responsible for marine

273 planning within it. The scenarios presented here do not necessarily reflect actual plans or legally  
274 authorized decisions, but are based on ongoing discussions in the countries. Future projections  
275 for the distribution of windfarms and marine protected areas (“MPAs”) were estimated based on  
276 Bartelings *et al.* (2013), Schulze *et al.* (2012) and on Delavenne (2012). The latter was  
277 specifically used to support the definition of conservation areas and windfarms in the Eastern  
278 English Channel (to include the French EEZ). Nature conservation areas were defined here  
279 including the Natura 2000 areas for the British, French, Dutch, Danish, and German EEZ,  
280 designated under the EU’s Habitats and Birds Directives. OSPAR (2013) was used to verify the  
281 projected distribution of protected areas. To project the expansion of windfarms by the middle of  
282 the 21<sup>st</sup> century, given a political scenario favoring green energy, all the planned, pre-planned and  
283 search areas of the French, UK German, Dutch and Danish planned windfarms were included. In  
284 the Eastern English Channel, only the 12-, 6-, and 3-mile restricted coastal zones were considered  
285 to be restrictive to fishing activities (in the present and in the short-term future), and only those  
286 were implemented as marine protected areas in the projections. These data were aggregated at  
287 the ICES statistical rectangle resolution, to match the meta-analyses datasets. This aggregation  
288 considered only whether either of these actions was projected for each domain cell, and not the  
289 actual area of each cell expected to be covered by each action. Consideration of cell fractions was  
290 not possible given the need to aggregate projections produced by the different models under  
291 different gridding systems. The projected future distributions of windfarms and conservation  
292 areas were then overlaid onto spatial domains illustrating the results of each of the meta-analyses  
293 results (Fig. 1a-c) to highlight potential conflict areas.

294 We were not able to include fishing pressure in our analysis though recent work has demonstrated  
295 that the impacts of climate on marine species may be impacted by extent to which communities

296 are exploited through fisheries (Blanchard *et al.*, 2012). Future expansions of this work should  
297 therefore consider such information.

## 298 ***Results***

### 299 *Ecosystem-level vulnerability to climate change and ocean acidification of the NE Atlantic shelf*

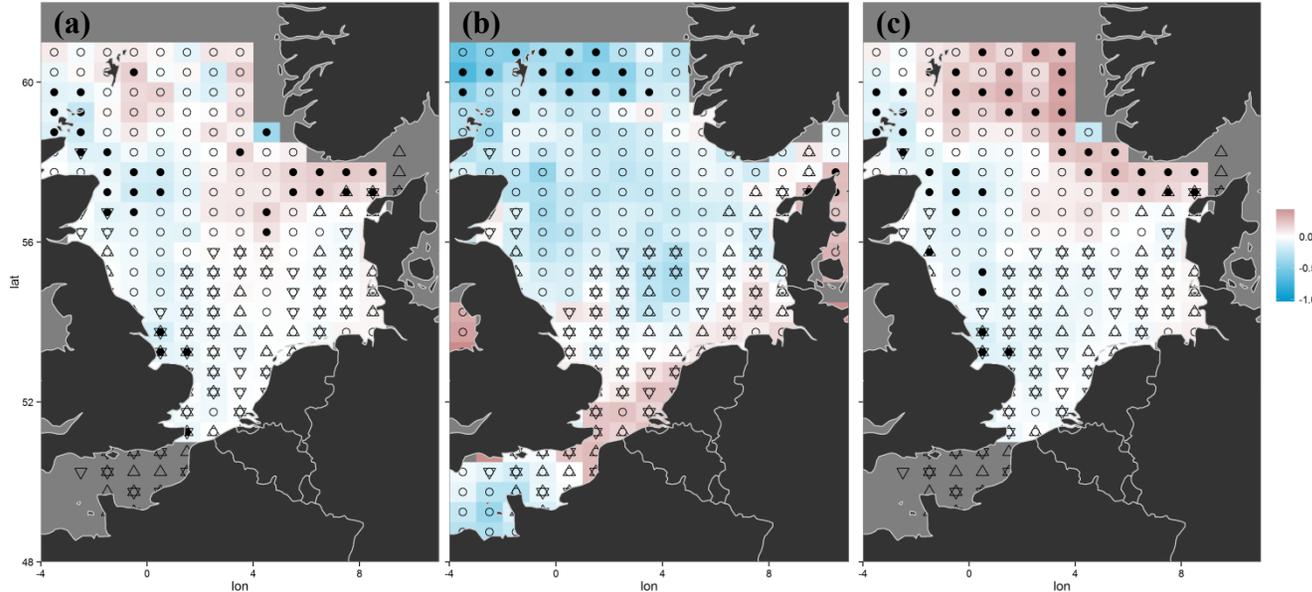
300 Our analysis shows that areas currently (or that are planned to be) designated for conservation in  
301 the NE Atlantic shelf predominantly cover regions that do not exhibit ecosystem-level  
302 vulnerability to CCOA (on average, more than 90% of protected areas, Figure 1, open circles  
303 overlaid by upright triangles). Conversely, areas projected to be most vulnerable to CCOA-driven  
304 ecosystem-level change (black dots, Fig. 1) are largely unprotected, and yet may come to  
305 represent important areas of high productivity in the future (both at the base of the food web and  
306 for demersal fish; black dots over pink, Fig.1). Hotspots of negative change estimated based on  
307 projections for fish (n=52 models) occurred along the E and NE coast of the UK (Fig.1a and  
308 Table SI) and illustrate loss of suitable habitat or lower productivity as a result of CCOA. The  
309 proportion of these areas under (or foreseen for) conservation is low (21%) and the majority of  
310 these will also host windfarms, according to ongoing dialogue in the respective countries (see  
311 methods; Fig.1a, inverted triangles and black dots overlaid on blue). Hotspots of positive change  
312 – areas where fish are projected to re-distribute to – occurred in the NE region of our study, near  
313 the Norwegian coast (Fig.1a, black dots overlaid on pink, Fig.S1c). Less than a tenth of those  
314 areas are currently under (or foreseen for) conservation and half of these coincide with areas that  
315 will in the future host windfarms (Fig.1a, upright and inverted triangles and black dots overlaid  
316 on pink). The potential displacement of fish species to the deeper NE areas of the North Sea shelf  
317 identified here is consistent with a movement towards areas of the seabed that remain suitable

318 habitat given current projections of future warming trend for the area. The warming trend will be  
319 less pronounced in these deeper, seasonally-stratified areas (Dulvy *et al.*, 2008, Holt *et al.*, 2012),  
320 representing potential habitat refuges for the majority fish species we analyzed, which are benthic  
321 or demersal (supporting information Table SI). Increased seasonal stratification in these areas  
322 could also impact these species negatively, through decreased supply of oxygen (Whitney *et al.*,  
323 2007), nutrient and larval dispersal. However, potential negative effects of seasonal stratification  
324 leading to decreased habitat suitability would have been considered by 38% of the fish  
325 projections analyzed here (supporting information Table SI, see also Cheung *et al.*, 2011,  
326 Fernandes *et al.*, 2013).

327 Significant negative changes across the base of the foodweb (n=11 model projections; Table SI)  
328 were found in the NW part of the NE Atlantic shelf (Fig. 1b), and none of these areas are  
329 currently under (or foreseen for) conservation. The co-occurrence of negative hotspots for fish  
330 and lower trophic level models north of Aberdeen Bank and the North Atlantic Front of the North  
331 Sea (Fig. 1a and b, and Fig. S1c) suggest strong foodweb connection in this area, which is  
332 supported by empirical evidence (Cubillos-Moreno *et al.*, *in prep*). Positive change, reflecting  
333 increases in both nutrients and productivity at the base of the foodweb was only significant in one  
334 site in the Skagerrak, hosting both protected areas and windfarms (Fig. 1b). Most other positive  
335 changes at the base of the foodweb occurred in coastal areas in the southern North Sea (German  
336 Bight and eastern English Channel), although this was not sufficiently consistent across modeling  
337 projections, or large enough, to be statistically significant. However, 38% of the fish models  
338 considered here are forced by primary production simulations, so potential increases in primary  
339 production would be captured in Fig. 1a. Present (and planned) conservation in the NE Atlantic  
340 seems to encompass primarily areas where no significant change is projected with regard to

341 climate or nutrient loading of coastal areas, the majority of which will also host windfarms  
342 (Fig.1b, upright and inverted triangles overlaid).

343 When all datasets were pooled (63 projection sets from 54 models, Fig. 1c), hotspots of change  
344 largely reflected projected changes where the responses of lower and higher trophic levels  
345 converged, indicating ecosystem-level vulnerability (e.g. NW of the domain in Fig.1a-c). We also  
346 found that conservation efforts currently focus on areas which will not exhibit significant  
347 ecosystem-level CCOA change by the mid of the 21<sup>st</sup> century. In parallel, only 15% of areas  
348 where the ecosystem will respond significantly and positively to CCOA are currently under (or  
349 foreseen for) protection in the NE Atlantic shelf, and half of those that are will also host  
350 windfarms. This indicates that areas potentially responding positively to CCOA are open to other  
351 types of pressures, such as fisheries.



352

353 **Figure 1:** Ecosystem-level vulnerability to CCOA by 2050 calculated across three model ensembles. Color shading indicates positive  
 354 (pink) or negative (blue) change across analyzed model projections. Black dots indicate hotspots of change: areas where there was  
 355 consensus in the direction and magnitude of change over time across models for fish (a), lower trophic levels (b) and all ecosystem  
 356 components (c). The future distribution of conservation areas (black upright triangles) and windfarms (inverted black triangles) is  
 357 superimposed. Open circles superimposed on color indicate areas where there was no consistency across models and/or changes were  
 358 small in individual datasets. Gray cells omit areas with low number of datasets (c and a) and those not covered by the models analyzed  
 359 (a, b and c). We argue that areas where consensus exists across models on the occurrence of large and positive change of ecosystem  
 360 components driven by CCOA (marked by pink color overlaid by black dots) should be considered as conservation priorities.

361 **Discussion**

362 This study suggests that conservation policies in the NE Atlantic shelf are, by and large, not  
363 focused on areas where species and habitats are expected to be sharply impacted by CCOA,  
364 as analyzed here. Specifically, we found a low degree of overlap between identified negative  
365 hotspots of change, for both high and low trophic levels, and the current and planned  
366 positioning of MPAs. Whilst this is clearly a positive outcome, our analysis also highlights  
367 that areas which may become important for many species and for primary productivity by the  
368 middle of the 21<sup>st</sup> century are currently not protected and thus open to other types of  
369 pressures, such as commercial extraction and energy exploration. In this area, and worldwide,  
370 not protecting areas into which species could re-distribute as the location of suitable habitat is  
371 modified by CCOA, could have important adverse consequences for natural populations of  
372 fish and other mobile fauna (Cheung *et al.*, 2011, Raab *et al.*, 2013). Conversely, protecting  
373 from commercial extraction areas where significant adverse, long-term and climate-driven  
374 change could occur (e.g. by loss of suitable habitat) may be perceived as serving little  
375 purpose given what we know about CCOA (Nagelkerken & Connell, 2015). Reduction of  
376 manageable pressures such as fisheries to improve the ability of some species to better  
377 withstand environmental stressors has been endorsed by some (Carilli *et al.*, 2010). However,  
378 focusing on changes on pressures alone may not be sufficient to protect multiple species  
379 assemblages experiencing multiple stressors like CCOA. Recent empirical evidence and  
380 advances in physiological theory and modelling indicate that co-occurrence of stressors such  
381 as CCOA, and intrinsic differences among species will influence responses (Gaylord *et al.*,  
382 2015, Griffith *et al.*, 2012, Kroeker *et al.*, 2013, Kroeker *et al.*, 2010, Nagelkerken &  
383 Connell, 2015, Pörtner & Farrell, 2008). Environmental change beyond individual tolerance  
384 thresholds for each stressor result in individual-level trade-offs in the allocation of energy  
385 between stress response pathways and processes supporting population dynamics and

386 dispersal (Calosi *et al.*, 2013, Parker *et al.*, 2013, Queirós *et al.*, 2015b). These, in turn,  
387 determine short- and medium-term plasticity of populations within communities, and long-  
388 term adaptive potential, the understanding of which is still limited (Calosi *et al.*, 2013,  
389 Morley *et al.*, 2009, Queirós *et al.*, 2015b). This is because the majority of the knowledge  
390 base is still comprised of studies on single generations of individual species, responding to  
391 single stressors, which often neglect also how inter-specific interactions may impact on the  
392 development of adaptive strategies within populations (Queirós *et al.*, 2015b, Riebesell &  
393 Gattuso, 2015). From first principles, the uptake of sufficient energetic resources from the  
394 environment (i.e. food) to support the higher metabolic costs endured during environmental  
395 change is a fundamental part of local survival of individual species in the short- and medium-  
396 term, before adaptation can take place (Melzner *et al.*, 2011, Queirós *et al.*, 2015b, Thomsen  
397 *et al.*, 2013). Assessing changes in primary productivity and other elements at the base of the  
398 foodweb, such as nutrient availability, as proxies for food availability could therefore be  
399 important. Ensuring high food availability could be seen as an insurance policy for the  
400 conservation of multiple-species assemblages in a multi-stressor future ocean. The relative  
401 value of considering the base of the foodweb under climate change has only seldom been  
402 discussed in conservation studies (e.g. Brown *et al.*, 2010). A solid theoretical and empirical  
403 evidence base now supports the perspective that projecting species distributions to support  
404 MPA design in the face of CCOA requires consideration of these changes at the base of the  
405 foodweb too, as done here.

406 Our findings for the NE Atlantic shelf suggest that CCOA, as considered here, will create  
407 distinct areas where lower and upper trophic levels respond differently to this change. The  
408 joint consideration of upper and lower trophic levels in MPA design and adaptation in this  
409 region, and potentially in others, may thus require extending the focus of conservation to  
410 areas other than those which may be of more obvious relevance to the (generally high trophic

411 level) species protected. Similarly, the statistical approach used here led to the identification  
412 of ecosystem-level hotspots of change which were not immediately predictable from the  
413 analyses focused on specific levels of the foodweb. Whole ecosystem conservation may too  
414 require the allocation of resources to areas other than those immediately obvious from a focus  
415 on the sensitivities of single species, or ecosystem components. Here, and potentially in other  
416 ocean areas, a re-evaluation of which ecosystem components will be most important to  
417 conserve, and which of those are protected under current spatial plans in the face of CCOA,  
418 may therefore be needed. Climate change and ocean acidification are rapidly shifting the  
419 conservation goal posts through unprecedented and widespread change in marine ecosystems  
420 (Pörtner *et al.*, 2014, Riebesell & Gattuso, 2015). We argue that experimental research and  
421 modelling tools that integrate this knowledge, similar to those presented here, and by others,  
422 can support needed innovation in marine conservation research, and contribute to the  
423 development of solutions that address these challenges (cf. Hilborn, 2015, Lubchenco &  
424 Grorud-Colvert, 2015).

425 Enforcing conservation requires the allocation of limited resources at the national and  
426 international level, and influences economic sectors such as fisheries, shipping, tourism and  
427 energy production (Christie *et al.*, 2014). Providing adequate advice to conservation policy  
428 under these circumstances therefore requires a better understanding of climate change and  
429 ocean acidification impacts in a multi-species and multi-use context. Meeting this aim  
430 requires the use of tools which consider these multiple elements simultaneously. The  
431 combined use of estimates from different types of models undertaken here provides a holistic  
432 view of ecosystems where the impacts of conservation, management, and global change  
433 scenarios can be explored (Hollowed *et al.*, 2013, Queirós *et al.*, 2015a). Use of these models  
434 to inform advice for policy has, however, been hindered by uncertainty associated with  
435 climate modeling projections, but the research community has begun addressing this issue

436 (Cheung *et al.*, 2016, Payne *et al.*, 2015). It is worth highlighting that the majority of models  
437 available, including some of those used here, does not yet consider the specific impacts of  
438 more recently recognized pressures such as OA and the increased use of the ocean for  
439 renewable energy developments. For instance, the full life-cycle analysis (construction,  
440 operation, and decommissioning) of potential ocean impacts of windfarms is unquantified  
441 and remains a critical gap in knowledge to be filled (Papathanasopoulou *et al.*, 2015). We  
442 found that the small proportion of areas we identified as responding positively to CCOA  
443 which are already considered for protection under current spatial plans were frequently co-  
444 located in the vicinity of existing (or planned) windfarms. A rapid need to decarbonize the  
445 global economy alongside as of yet limited knowledge of the impacts of windfarms on the  
446 physical properties of ocean (Cazenave *et al.*, 2016) suggest that this too is a an area of  
447 marine conservation research requiring fast development. In parallel, large emphasis has  
448 already been placed on developing models to help project the impacts of CCOA and coastal  
449 development on ocean ecosystems (Holt *et al.*, 2012, Jørgensen *et al.*, 2012, Queirós *et al.*,  
450 2015b). Integrated analyses of multiple human uses of the marine environment and CCOA in  
451 a multi-species context, as presented here, are crucial to develop ecosystem-based  
452 management solutions for the oceans, of which conservation is just one part.

453 The new Sustainable Development Goals put forward by the United Nations are a clear call  
454 to “take urgent action to combat climate change and its impacts” and to “conserve and  
455 sustainably use the oceans”: it is urgent that the conservation research community considers  
456 these aims together. This approach could become part of a climate-ready solution for marine  
457 conservation that improves marine spatial planning in the face of CCOA, by helping to  
458 identify marine areas with ecosystem-level vulnerability; by identifying areas where  
459 ecosystem-level CCOA impacts may not be significant in the long term (Côté & Darling,  
460 2010); and identifying problematic areas, where hotspots of positive change associated with

461 CCOA coincide with manageable human uses of the ocean. Expansion of the temporal  
462 elements of this approach could support the development of more adaptive conservation  
463 solutions. The goal is clear: 10% of marine areas to be protected by 2020 (Lubchenco &  
464 Grorud-Colvert, 2015). Let these areas also best insure against climate change and ocean  
465 acidification.

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476

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705 **Supporting information**

706 **Table SI:** Datasets used in model ensemble. “HT” – high trophic level. “LT” – low trophic level. “SDM” – species distribution model.

707 The specific model configurations used are indicated (A-F) and refer to: A) Size-spectrum-Dynamic bioclimate envelope model using  
708 environmental forcing from the coupled hydrodynamic-biogeochemical model NEMO-MEDUSA 2.0 (Fernandes *et al.*, 2013, IPCC, 2007, Yool  
709 *et al.*, 2013); B) Dynamic bioclimate envelope model using environmental forcing from the coupled hydrodynamic-biogeochemical model  
710 WCRP-CMIP3 - GFDL-ESM 2.1 (Cheung *et al.*, 2011, Dunne *et al.*, 2010, IPCC, 2007, Jones *et al.*, 2013); C) Species specific life-history  
711 stage-structured models using environmental forcing from the coupled hydrodynamic-biogeochemical model DMI-BSHcmod - ERGOM (Maar  
712 *et al.*, 2013, Maar *et al.*, 2011, Møller *et al.*, 2012, Philippart *et al.*, 2007); D) Coupled hydrodynamic-biogeochemical model Delf-3D using  
713 modules FLOW and DELWAQ(BLOOM/GEM) and environmental forcing from RACMO 2.1(Blauw *et al.*, 2009, Friocourt *et al.*, 2012, IPCC,  
714 2007, Lesser *et al.*, 2004, Van Meijgaard *et al.*, 2008); E) Coupled hydrodynamic-biogeochemical model POLCOMS – ERSEM (Butenschön *et*  
715 *al.*, 2015, Butenschön & Kay, 2013, Holt *et al.*, 2009, IPCC, 2007); F) Size-class mechanistic species distribution model based on General  
716 Additive Modelling, using coupled hydrodynamic-biogeochemical model POLCOMS-ERSEM (Butenschön *et al.*, 2015, Butenschön & Kay,  
717 2013, IPCC, 2007, Teal *et al.*, 2013). “CC”: climate change. “CCOA”: climate change and ocean acidification.

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Foodweb level	Model type	Configuration	Scenario	Slices	Variable	Species	Common name	Size	Model considers CC	Model considers CCOA
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Lepidorhombus boscii</i>	Fourspotted megrim	NA	Yes	Yes
HT	Fish SDM	B	A2	baseline: 1981 - 2000 effect: 2041 - 2060	Abundance	<i>Pollachius virens</i>	Saithe	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Brosme brosme</i>	Tusk	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Culpea harrengus</i>	Atlantic herring	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Cyclopterus lumpus</i>	Lumpsucker	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Dicentrarchus labrax</i>	European seabass	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Engraulis encrasicolus</i>	European anchovy	NA	Yes	Yes
HT	Fish SDM	B	A2	baseline: 1981 - 2000 effect: 2041 - 2060	Abundance	<i>Gadus morhua</i>	Cod	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Gadus morhua</i>	Cod	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Glyptocephalus cynoglossus</i>	Righteye flounder/Witch	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Katsuwonus pelamis</i>	Skipjack tuna	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Lepidorhombus whiffiagonis</i>	Megrim	NA	Yes	Yes

HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Merlangius merlangus</i>	Whiting	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Merluccius merluccius</i>	European hake	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Microchirus variegatus</i>	Thickback sole	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Micromesistius poutassou</i>	Blue whiting	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Molva molva</i>	Ling	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Pollachius pollachius</i>	Pollack	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Scomber scombrus</i>	Atlantic mackerel	NA	Yes	Yes
HT	Fish SDM	A	A1b	baseline: 2001 -2010 effect: 2050-2059	Abundance	<i>Squalus acanthia</i>	Spiny dogfish	NA	Yes	Yes
LT	Copepod SDM	C	+ 2° C	baseline: 2005 effect:2005 + 2°C	Abundance	<i>Calanus helgolandicus</i> (two quarters)	NA	NA	Yes	No
LT	Copepod SDM	C	+ 2° C	baseline: 2005 effect:2005 + 2°C	Abundance:	<i>Calanus finmarchicus</i> (two quarters)	NA	NA	Yes	No
LT	Coupled biogeochemical model	D	A1b	baseline: 1984 - 2003 effect: 2031 - 2050	Chl a biomass	NA	NA	NA	Yes	No
LT	Coupled biogeochemical model	D	A1b	baseline: 1984 - 2003 effect: 2031 - 2050	Chla phenology (peak)	NA	NA	NA	Yes	No
LT	Coupled biogeochemical model	E	A2	baseline: 2000 - 2009 effect: 2040 - 2049	Commnity Production	NA	NA	NA	Yes	Yes

LT	Coupled biogeochemical model	D	A1b	baseline: 1984 - 2003 effect: 2031 - 2050	Net primary production	NA	NA	NA	Yes	No
LT	Coupled biogeochemical model	D	A1b	baseline: 1984 - 2003 effect: 2031 - 2050	Phaeocystis sp biomass	NA	NA	NA	Yes	No
LT	Coupled biogeochemical model	D	A1b	baseline: 1984 - 2003 effect: 2031 - 2050	Phaeocystis sp phenology (peak)	NA	NA	NA	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Culpea harrengus</i>	Atlantic herring	S	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Eutrigla gurnardus</i>	Grey gurnard	S	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Eutrigla gurnardus</i>	Grey gurnard	M	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Eutrigla gurnardus</i>	Grey gurnard	L	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Gadus morhua</i>	Cod	S	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Gadus morhua</i>	Cod	MS	Yes	No

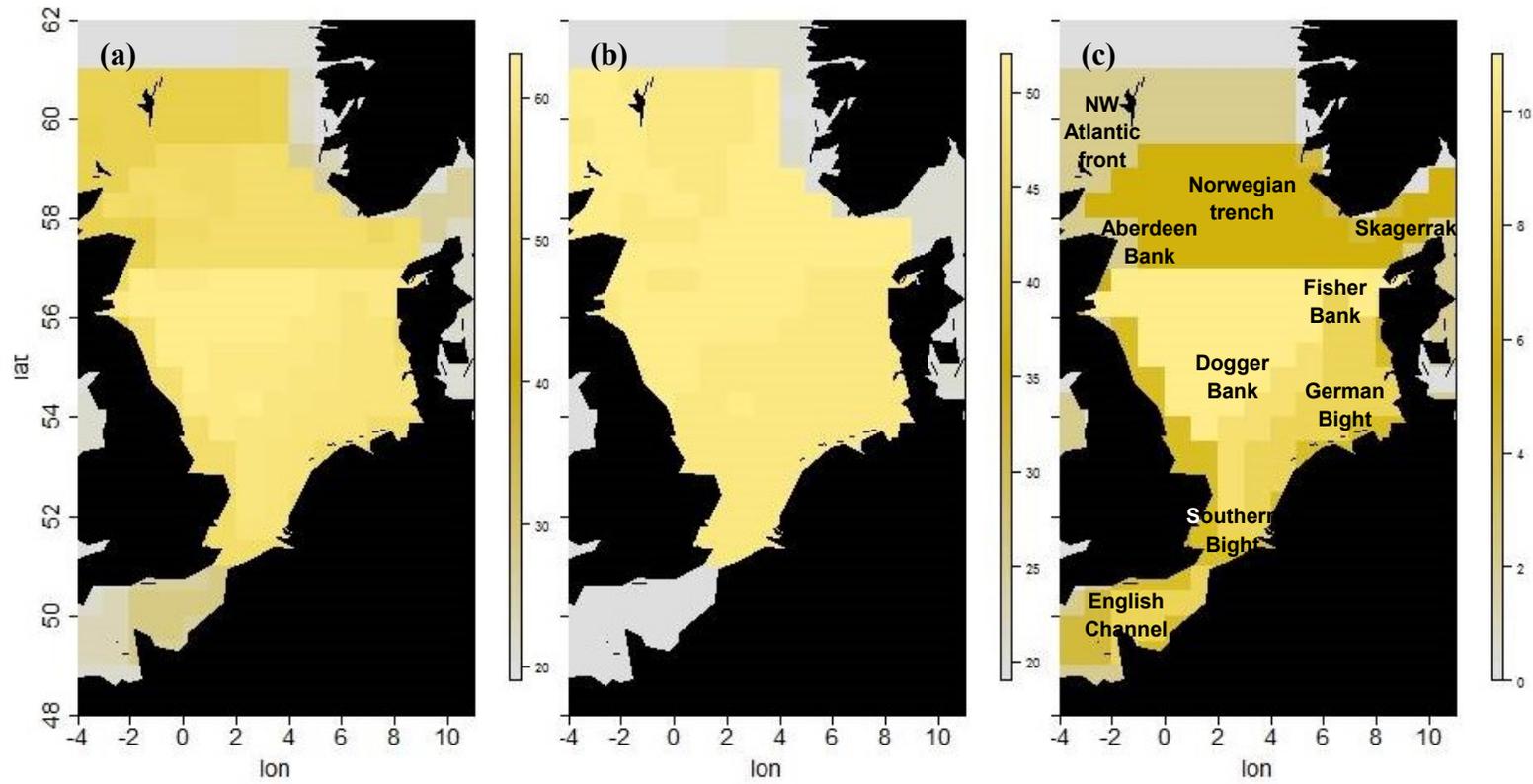
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Gadus morhua</i>	Cod	ML	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Gadus morhua</i>	Cod	L	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Melanogrammus aeglefinus</i>	Haddock	S	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Melanogrammus aeglefinus</i>	Haddock	M	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Melanogrammus aeglefinus</i>	Haddock	L	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Merlangius merlangus</i>	Whiting	S	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Merlangius merlangus</i>	Whiting	M	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Merlangius merlangus</i>	Whiting	L	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Sprattus sprattus</i>	European sprat	S	Yes	No

HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Trisopterus esmarkii</i>	Norway pout	S	Yes	No
LT	Coupled biogeochemical model	E	A2	baseline: 2000 - 2009 effect: 2040 - 2049	Surface NO <sub>3</sub>	NA	NA	NA	Yes	Yes

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725 **Figure. S1.** The number of datasets in overall (a), fish (b) and lower trophic levels analyzes in each area (b), indicated by the color scales.

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