

1 **i) Solutions for ecosystem-level protection of ocean systems under climate change**

2 **ii) Climate-ready ocean conservation**

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24 planning; ocean; ocean acidification; species distribution; warming.

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26 **Abstract**

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

46

47

48 **Introduction**

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

63 Many governments (including the USA, UK, Chile and New Zealand) are betting on the closure
64 of vast areas of the ocean to fisheries to meet the need to reduce overfishing, and increase the
65 sustainability of marine food resources. Some agree that this reduction in local stressors such as
66 fisheries can also, in some cases, improve resistance to climate stressors (Carilli *et al.*, 2010).
67 These efforts have thus been welcomed, but do they unwittingly offer false hope? Beyond the
68 need to secure larger areas of the ocean against commercial extraction, conservation strategies

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

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

92 planning. A greater focus of conservation research in considering impacts on primary
93 productivity, alongside those on multiple species, should thus yield more effective conservation
94 aims in light of ecosystem-level impacts of CCOA: 1) because it would ensure that food
95 resources are available to organisms in communities experiencing environmental change through
96 CCOA; and 2) because protecting areas of the ocean that make important contributions to
97 primary and secondary production have positive outcomes to other human uses of the ocean
98 (Brown *et al.*, 2010).

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

109 New technological approaches to data collection and analysis can support dynamic ocean
110 management (Lewison *et al.*, 2015, Maxwell *et al.*, 2015). Yet, ocean observations alone have
111 limited value in the long-term forecasting of systems when conditions are expected to depart
112 considerably from those observed historically due to the long-term impacts of climate change
113 (Barnsley, 2007, Payne *et al.*, 2015). Conversely, the combined use of models that simulate
114 multiple levels of the ocean foodweb resolved in time and space can be used to explore: 1) how

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

130 Here, we overcome these shortcomings using a novel approach to extract common patterns in
131 long-term projections from a large ensemble of ecosystem models forced with climate change
132 and, where possible, ocean acidification, taking into account additional human activities. Using
133 global change scenarios and a range of modeling projections for the middle of the 21st century,
134 we present an analysis focused on the NE Atlantic continental shelf that identifies areas where
135 consensus exists across models regarding the occurrence of large and directional change of
136 ecosystem components (hereafter, “hotspots of change”). The large model ensemble analyzed
137 here covered as many ecosystem components and trophic levels as possible from 54 distinct
138 models. Various global scenarios of change in CO₂ emissions, as defined by the

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

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

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

186 *Materials and methods*

187 *Input data*

188 All model projections analyzed were produced or made available within the EU research project
189 VECTORS (Vectors of Change in Oceans and Seas Marine Life, Impact on Economic Sectors,
190 FP7/2007-2013), during which a large number of projections were produced to assess the impacts
191 of pressures of change on specific components of marine ecosystems (Teal *et al.*, 2013).
192 Modelling outputs were scoped to include any level of the foodweb and relevant ecosystem
193 processes within the domain of the NE Atlantic Continental Shelf. Each dataset had to comprise
194 two comparable states of the ecosystem; i.e. a baseline and an effect state that could be used to
195 quantify change. Typically, the data structure included projections for a “present” and a “future”
196 time slice (5-10 yrs each) for each given model, simulated under a given scenario of future
197 change, e.g. a specific IPCC special report emissions scenario (IPCC, 2007). Each dataset
198 included spatial arrays of mean and standard deviation for each variable, for each time slice. We
199 gathered 63 outputs, originating from 54 distinct models, which are summarized in Table SI
200 (supporting information). Detailed descriptions of each model can be found in references within
201 it.

202 Modelled data on “jellyfish” were not available in this study, reflecting the limited sampling and
203 understanding of this group of organisms that currently exists. However, jellyfish play an
204 important role in coastal and shelf seas impacted by climate change, diverting carbon from higher
205 trophic levels (Robinson & Graham, 2013) and should be considered in similar studies in the
206 future.

207 *Meta-analyses of model projections*

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

216 “Dataset” hereafter refers to the mean, standard deviation and number of observations for each
217 model output detailed in Table SI ($n = 63$), for a given domain cell. “Change” was initially
218 calculated using Hedge’s g (Hedges, 1981), the unbiased standardized mean difference estimator,
219 under a fixed effects model structure. This metric considers the mean, standard deviation and the
220 number of observations in each of the slices (usually temporal slices, supporting information
221 Table SI for time span covered in each case). The calculation of individual effect-sizes (i.e. per
222 model, per domain cell) was conventionalized across analyses so that positive change indicated
223 an increase of the given variable in the future in relation to present, in that specific cell of the
224 domain, and vice-versa. For example, positive Hedge’s g for primary productivity indicated that
225 this process was higher in the future, in a specific cell of the domain. We then estimated the
226 effects across datasets (i.e. the summary-effects) per domain cell, considering that in this case we
227 expected not one, but a family of possible effect-sizes, given the diversity of datasets considered.
228 This attribute of the data justified the use of a random-effects meta-analysis model. Accordingly,
229 the variance of the effect-size for each dataset was re-calculated as the sum of: i) the variance of
230 Hedge’s g within each dataset, for each cell (as before); and ii) the variance between datasets, for

231 that cell. The latter (τ^2) was estimated using the DerSimonian-Laird method (DerSimonian &
232 Laird, 1986). The variances of the summary-effects were then used to calculate confidence
233 intervals for the summary-effects in each cell, and hence to test their departure from zero, under a
234 normal distribution. Statistically significant departure from zero for summary-effects was
235 therefore considered to be indicative of significant change. The analysis was carried out across all
236 the datasets together (n=63) and, in this case, significant change indicated ecosystem-level
237 vulnerability. Additionally, two subgroup analyses were undertaken, separately: one considering
238 fish (or high trophic level) datasets (n=52); and one considering lower trophic level datasets
239 (n=11, Table SI). The spatial coverage of datasets can be found in supporting information
240 figure.S1. Preliminary analyses indicated that the number of datasets influenced the estimate of
241 variance between datasets (τ^2). As the latter is used to estimate confidence intervals for summary-
242 effects, all analyzes including fish datasets excluded domain edge areas (grey, Fig.S1b) where the
243 number of available datasets was contrastingly lower.

244 The reasoning to investigate summary-effects within subsets of meta-analysis datasets has been
245 discussed at length elsewhere, and is beyond the scope of this study (Lyons *et al.*, 2015). Study
246 selection for meta-analysis should be made transparently and a priori, guided by the research
247 question investigated, as done here. This study aimed to provide a balanced view of long-term,
248 ecosystem-level dynamics in the NE Atlantic Shelf. Accordingly, all modelling outputs available
249 to the authors at the time of the analysis, were used. However, the influence of individual datasets
250 on summary-effects could be expected to vary, due to the context dependency of individual
251 modelling results (Jones *et al.*, 2013). Two precautions were implemented in meta-analysis
252 protocols to address this matter. Specifically, meta-analysis is not a vote counting procedure, in
253 that not all datasets count equally. When a summary-effect was calculated (across datasets), more

254 confidence was given to variables for which the mean over the time period analyzed varied less
255 within and between datasets. Larger weight was also given to estimates calculated over a larger
256 number of observations (or larger model sampling), because they are assumed to provide a wider
257 coverage of the dynamics of the process simulated. These two considerations thus reduce the
258 influence of information derived from poorly constrained models, or less comprehensive datasets,
259 on summary-effects.

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

268 *Co-mapping of spatial planning actions*

269 The spatial planning actions considered in this analysis are the construction of windfarms and the
270 delimitation of marine protected areas. The NE Atlantic Continental Shelf is shared between
271 several countries' exclusive economic zones (EEZ), and each country is responsible for marine
272 planning within it. The scenarios presented here do not necessarily reflect actual plans or legally
273 authorized decisions, but are based on ongoing discussions in the countries. Future projections
274 for the distribution of windfarms and marine protected areas ("MPAs") were estimated based on
275 Bartelings *et al.* (2013), Schulze *et al.* (2012) and on Delavenne (2012). The latter was

276 specifically used to support the definition of conservation areas and windfarms in the Eastern
277 English Channel (to include the French EEZ). Nature conservation areas were defined here
278 including the Natura 2000 areas for the British, French, Dutch, Danish, and German EEZ,
279 designated under the EU's Habitats and Birds Directives. OSPAR (2013) was used to verify the
280 projected distribution of protected areas. To project the expansion of windfarms by the middle of
281 the 21st century, given a political scenario favoring green energy, all the planned, pre-planned and
282 search areas of the French, UK German, Dutch and Danish planned windfarms were included. In
283 the Eastern English Channel, only the 12-, 6-, and 3-mile restricted coastal zones were considered
284 to be restrictive to fishing activities (in the present and in the short-term future), and only those
285 were implemented as marine protected areas in the projections. These data were aggregated at
286 the ICES statistical rectangle resolution, to match the meta-analyses datasets. This aggregation
287 considered only whether either of these actions was projected for each domain cell, and not the
288 actual area of each cell expected to be covered by each action. Consideration of cell fractions was
289 not possible given the need to aggregate projections produced by the different models under
290 different gridding systems. The projected future distributions of windfarms and conservation
291 areas were then overlaid onto spatial domains illustrating the results of each of the meta-analyses
292 results (Fig. 1a-c) to highlight potential conflict areas.

293 We were not able to include fishing pressure in our analysis though recent work has demonstrated
294 that the impacts of climate on marine species may be impacted by extent to which communities
295 are exploited through fisheries (Blanchard *et al.*, 2012). Future expansions of this work should
296 therefore consider such information.

297 ***Results***

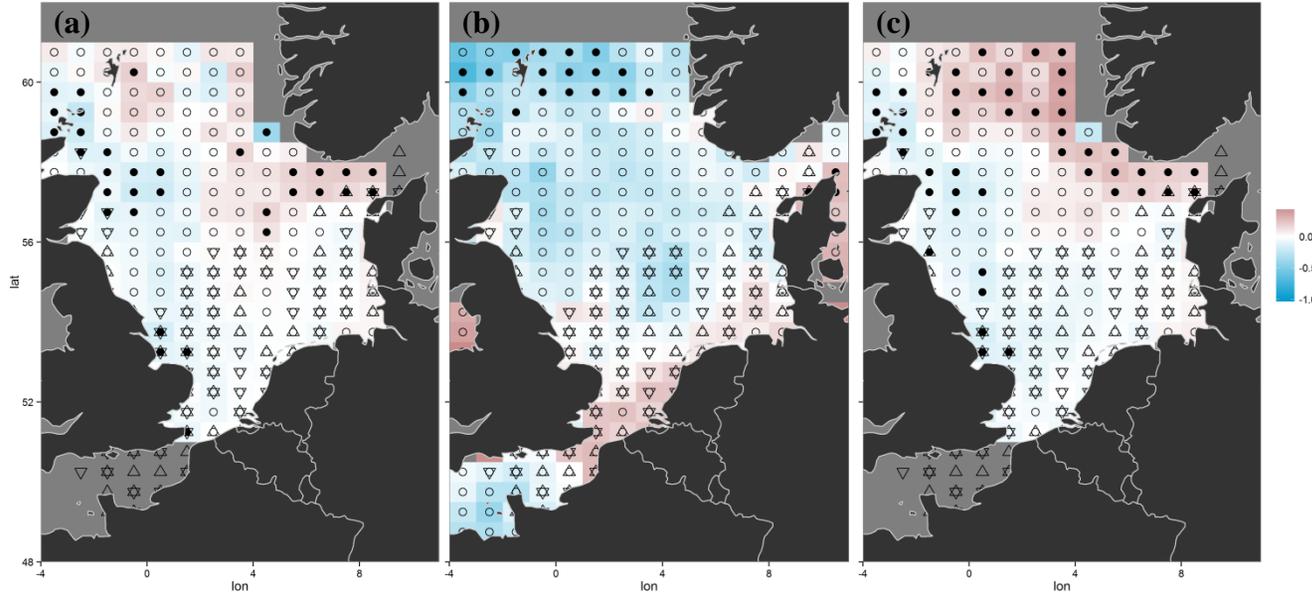
299 Our analysis shows that areas currently (or that are planned to be) designated for conservation in
300 the NE Atlantic shelf predominantly cover regions that do not exhibit ecosystem-level
301 vulnerability to CCOA (on average, more than 90% of protected areas, Figure 1, open circles
302 overlaid by upright triangles). Conversely, areas projected to be most vulnerable to CCOA-driven
303 ecosystem-level change (black dots, Fig. 1) are largely unprotected, and yet may come to
304 represent important areas of high productivity in the future (both at the base of the food web and
305 for demersal fish; black dots over pink, Fig.1). Hotspots of negative change estimated based on
306 projections for fish (n=52 models) occurred along the E and NE coast of the UK (Fig.1a and
307 Table SI) and illustrate loss of suitable habitat or lower productivity as a result of CCOA. The
308 proportion of these areas under (or foreseen for) conservation is low (21%) and the majority of
309 these will also host windfarms, according to ongoing dialogue in the respective countries (see
310 methods; Fig.1a, inverted triangles and black dots overlaid on blue). Hotspots of positive change
311 – areas where fish are projected to re-distribute to – occurred in the NE region of our study, near
312 the Norwegian coast (Fig.1a, black dots overlaid on pink, Fig.S1c). Less than a tenth of those
313 areas are currently under (or foreseen for) conservation and half of these coincide with areas that
314 will in the future host windfarms (Fig.1a, upright and inverted triangles and black dots overlaid
315 on pink). The potential displacement of fish species to the deeper NE areas of the North Sea shelf
316 identified here is consistent with a movement towards areas of the seabed that remain suitable
317 habitat given current projections of future warming trend for the area. The warming trend will be
318 less pronounced in these deeper, seasonally-stratified areas (Dulvy *et al.*, 2008, Holt *et al.*, 2012),
319 representing potential habitat refuges for the majority fish species we analyzed, which are benthic
320 or demersal (supporting information Table SI). Increased seasonal stratification in these areas

321 could also impact these species negatively, through decreased supply of oxygen (Whitney *et al.*,
322 2007), nutrient and larval dispersal. However, potential negative effects of seasonal stratification
323 leading to decreased habitat suitability would have been considered by 38% of the fish
324 projections analyzed here (supporting information Table SI, see also Cheung *et al.*, 2011,
325 Fernandes *et al.*, 2013).

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

342 When all datasets were pooled (63 projection sets from 54 models, Fig. 1c), hotspots of change
343 largely reflected projected changes where the responses of lower and higher trophic levels

344 converged, indicating ecosystem-level vulnerability (e.g. NW of the domain in Fig.1a-c). We also
345 found that conservation efforts currently focus on areas which will not exhibit significant
346 ecosystem-level CCOA change by the mid of the 21st century. In parallel, only 15% of areas
347 where the ecosystem will respond significantly and positively to CCOA are currently under (or
348 foreseen for) protection in the NE Atlantic shelf, and half of those that are will also host
349 windfarms. This indicates that areas potentially responding positively to CCOA are open to other
350 types of pressures, such as fisheries.



351

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

360 *Discussion*

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

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

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

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

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

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

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

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

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704 **Supporting information**

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

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

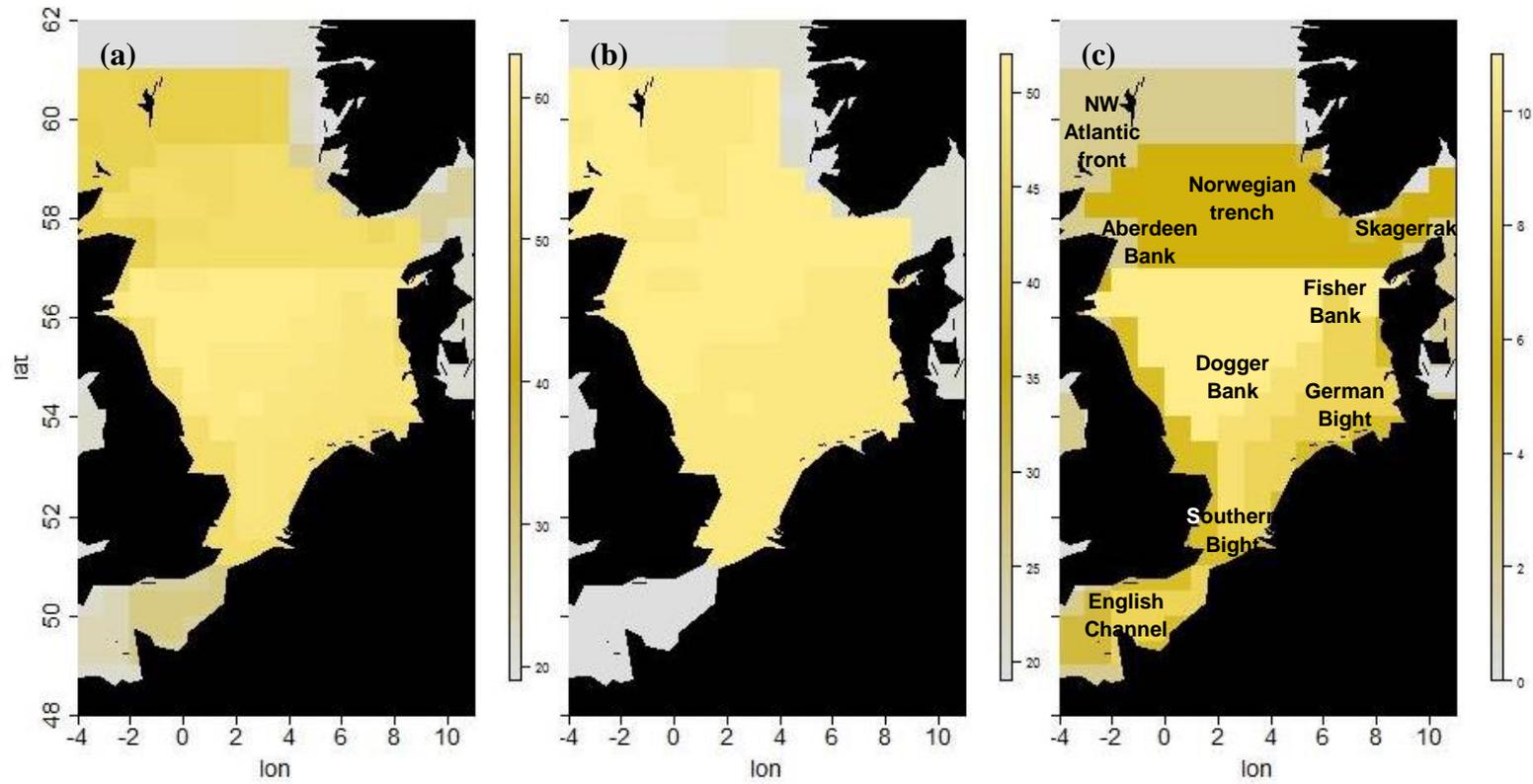
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Gadus morhua</i>	Cod	ML	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Gadus morhua</i>	Cod	L	Yes	No
HT	Fish SDM	F	A2 and 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 ₃	NA	NA	NA	Yes	Yes

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724 **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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