

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

**ii) Climate-ready ocean conservation**

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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 over-simplistic 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 re-distribute 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 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.

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

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

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

levels of CCOA not yet observed could in the long-run impact marine life and the distribution of productivity that supports it (Queirós *et al.*, 2015b); and 2) whether ocean conservation and exploitation strategies may be optimized to address environmental stressors and their future effects (Jones & Cheung, 2014, Levin *et al.*, 2009, Sumaila *et al.*, 2015). However, the application of such models in conservation research is often narrowly focused. For example, the effects of changes in sea temperature are often examined in isolation (Molinos *et al.*, 2015) despite evidence that ocean acidification is a co-occurring global stressor and can strongly modify species vulnerability to thermal stress (Kroeker *et al.*, 2013, Nagelkerken & Connell, 2015). Furthermore, vulnerability of local species to CCOA can be exacerbated by human uses of the marine environment (Carilli *et al.*, 2010, Planque *et al.*, 2010) but a holistic view of their combined impacts is rarely considered by conservation studies. Finally, focus is frequently placed on single or small subsets of species or ecosystem properties (e.g. Gormley *et al.*, 2013), although the current management paradigm in the United States and in Europe requires decisions to be weighed based on their impacts on whole ecosystems and not just based on single human activities or ecosystem components (EC, 2008, EU, 2014, NOC, 2013, Rice, 2013). Here, we overcome these shortcomings using a novel approach to extract common patterns in long-term projections from a large ensemble of ecosystem models forced with climate change and, where possible, ocean acidification, taking into account additional human activities. Using global change scenarios and a range of modeling projections for the middle of the 21<sup>st</sup> century, we present an analysis focused on the NE Atlantic continental shelf that identifies areas where consensus exists across models regarding the occurrence of large and directional change of ecosystem components (hereafter, “hotspots of change”). The large model ensemble analyzed here covered as many ecosystem components and trophic levels as possible from 54 distinct models. Various global scenarios of change in CO<sub>2</sub> emissions, as defined by the

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

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

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

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

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

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

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

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

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

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

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

## **Results**

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

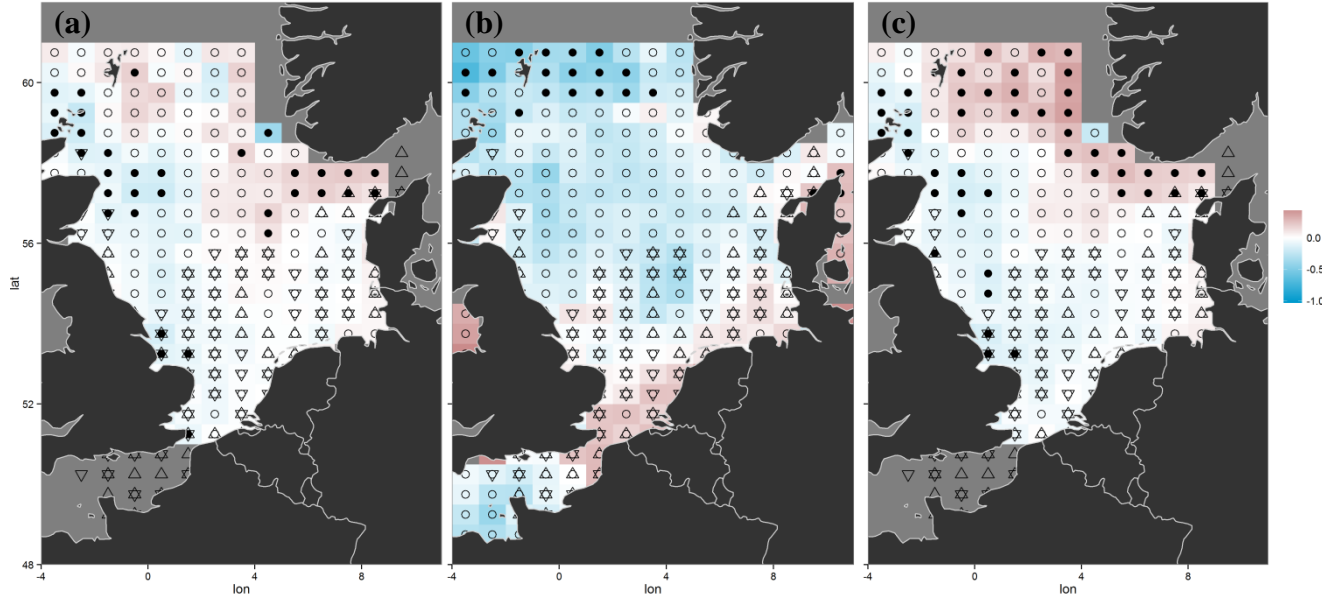
could also impact these species negatively, through decreased supply of oxygen (Whitney *et al.*, 2007), nutrient and larval dispersal. However, potential negative effects of seasonal stratification leading to decreased habitat suitability would have been considered by 38% of the fish projections analyzed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

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

When all datasets were pooled (63 projection sets from 54 models, Fig. 1c), hotspots of change 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 21<sup>st</sup> 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.

## Discussion

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

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

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

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

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

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

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

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

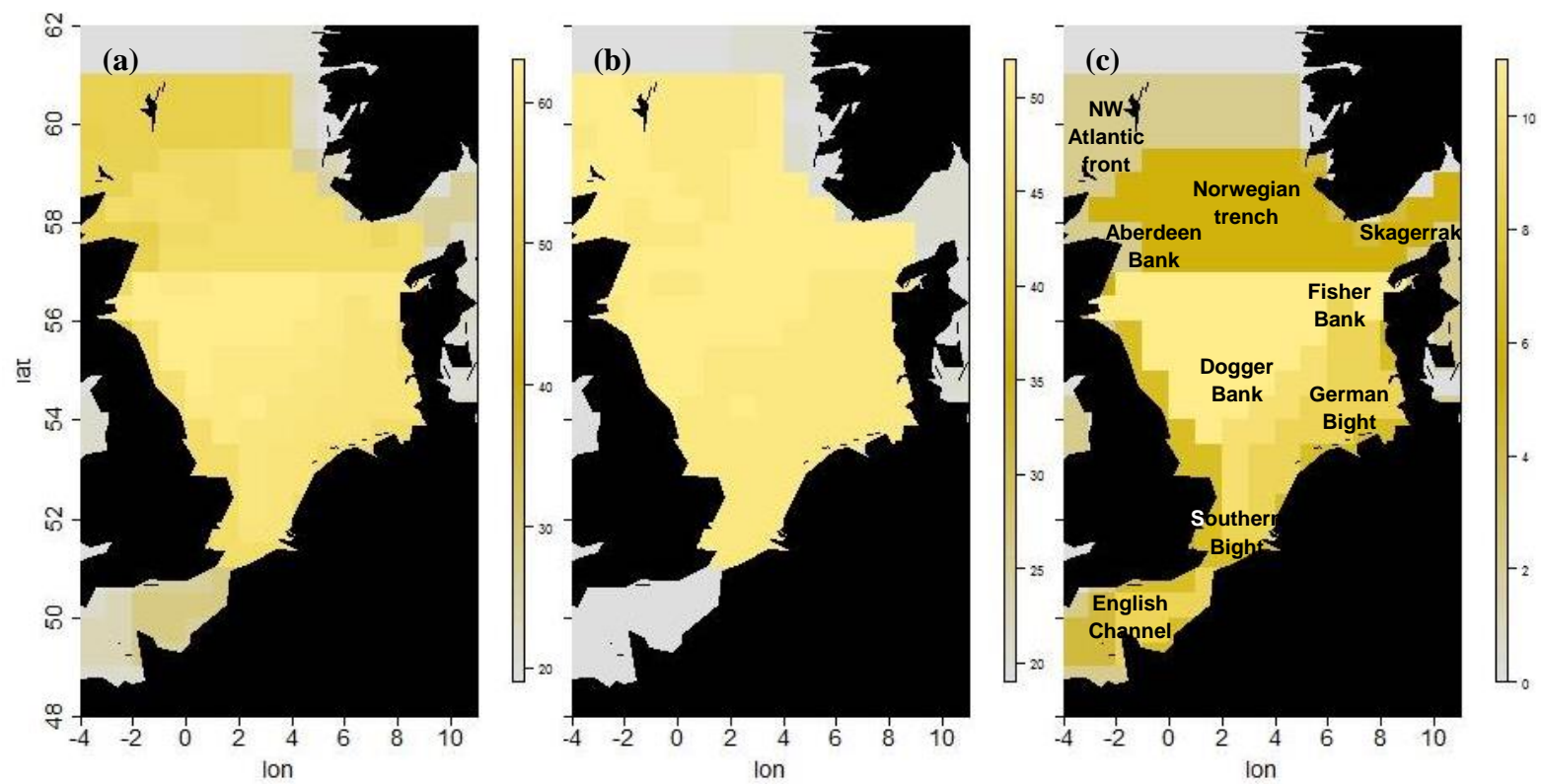
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Gadus morhua</i>	Cod	ML	Yes	No
HT	Fish SDM	F	A2 and B1	baseline: 2000 - 2009 effect: 2040 - 2049	Size-class mean relative local abundance	<i>Gadus morhua</i>	Cod	L	Yes	No
HT	Fish SDM	F	A2 and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

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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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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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