Climate change alters fish community size-structure, requiring adaptive policy targets

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Abstract
Size-based indicators are used worldwide in research that supports the management of commercially exploited wild fish populations, because of their responsiveness to fishing pressure. Observational and experimental data, however, have highlighted the deeply rooted links between fish size and environmental conditions that can drive additional, interannual changes in these indicators. Here, we have used biogeochemical and mechanistic niche modelling of commercially exploited demersal fish species to project time series to the end of the 21st century for one such indicator, the large fish indicator (LFI), under global CO2 emissions scenarios. Our modelling results, validated against survey data, suggest that the LFI's previously proposed policy target may be unachievable under future climate change. In turn, our results help to identify what may be achievable policy targets for demersal fish communities experiencing climate change. While fisheries modelling has grown as a science, climate change modelling is seldom used specifically to address policy aims. Studies such as this one can, however, enable a more sustainable exploitation of marine food resources under changes unmanageable by fisheries control. Indeed, such studies can be used to aid resilient policy target setting by taking into account climate-driven effects on fish community size-structure.

Keywords
climate change, fisheries, indicator, ocean acidification, policy, size-spectrum
Large fish tend to occur high in food webs and to fluctuate in a more predictable manner than smaller fish, being most valued in, and more vulnerable to, commercial exploitation (Engelhard, Lynam, García-Carreras, Dolder, & Mackinson, 2015; Greenstreet et al., 2010). Large fish therefore represent a key attribute of a healthy marine ecosystem (Greenstreet et al., 2010). Consequently, metrics reflecting the size distribution of wild fish are often used to assess the state of fisheries in support of fisheries management around the world (Shin, Rochet, Jennings, Field, & Gislason, 2005; hereafter, "size-based indicators"). For example, in the United States of America, average fish length has been monitored for over four decades and is used in ecosystem assessments of the Northeast Large Marine Ecosystem and West Hawaii (EAP, 2012, PIFSC, 2016). In Canada, the size-structure of wild fish populations is monitored as part of ecosystem status reports in Newfoundland and the Beaufort Sea (Niemi et al., 2012; Templeman, 2010). In Europe, the proportion of large demersal fish in wild communities is used in the monitoring of the environmental status of exploited demersal fish communities as part of the Marine Strategy Framework Directive (MSFD, EC, 2017).

Meanwhile, climate change is unfolding across the world’s oceans, causing complex ecosystem-level changes (Beniston et al., 2007; IPCC, 2013; Queirós, Huebert, et al., 2016). These effects will particularly impact ecological indicators such as those used in fisheries assessments and in the monitoring of the environmental status of world’s seas (McQuatters-Gollop, 2012). Indeed, evidence from climate change research predicts that resulting warmer oceans will lead to smaller individuals in taxa of commercial interest, such as fish and shellfish, in several regions of the world (Forster & Hirst, 2012; Shackell, Frank, Fisher, Petrie, & Leggett, 2010). This trend has already been observed in Europe and Australia (Audzijonyte et al., 2016; Baudron, Needle, Rijsdorp, & Tara Marshall, 2014), and it can be exacerbated by fishing pressure (Canales, Law, Wiff, & Blanchard, 2015). This is because long-term size-selective fishing practices can exert an evolutionary pressure towards reduced growth and increased reproductive investment in wild populations (Audzijonyte et al., 2016). In addition to warming, ocean acidification can drive reduced growth and increased mortality in fish among complex effects on ecosystems (Queirós, Huebert, et al., 2016), and together, these stressors may reduce wild fish captures regionally (Fernandes et al., 2017). So while fisheries management relies on the response of fished communities to regulated fishing pressure, the effects of environmental change, compounded by evolutionary responses of wild populations, may lead to unexpected changes in fish size-structure (Audzijonyte et al., 2016). It is therefore a reasonable expectation that assessing the performance of size-based indicators under climate change and other regionally meaningful environmental pressures should precede their operationalization within fisheries policies. Without such an assessment, associated policy indicator targets may be overambitious, introducing inadequate standards against which the environmental status of marine food resources is regulated, in turn imposing unfair limitations on the activities of those whose livelihoods depend on wild fisheries.

Aspirationally, ecosystem-based management (Pikitch et al., 2004) assumes that ecological (state) indicators respond in a predictable manner to managed pressures such as fishing effort and that this relationship is stronger than the relationship between a given indicator and other unregulated pressures (Jennings, 2005). In practice, ecological indicators often behave differently from theoretical expectations due to the influence of external environmental drivers; this has been observed for size-based metrics, even in heavily exploited systems (Blanchard et al., 2010). Yet, climate change is seldom considered a manageable pressure within the policies regulating marine resources worldwide (e.g. the European MSFD, EC, 2008). As a consequence, the setting of targets for policies affecting fisheries management is often carried out without an assessment of how climate change affects the indicators we use to monitor resources (Adams, Jennings, & Reuman, 2017). Policy assessment cycles (e.g. 6 years for the MSFD, Lynam et al., 2016) represent potential opportunities to accommodate adaptive target setting in line with climate change within marine policies regulating fisheries. Modelling approaches can be used to support this process, providing a sound scientific basis with which to assess dependencies between the status of exploited marine ecosystems and environmental conditions, including present and future climate change (Fernandes et al., 2015; Lynam et al., 2016; Queirós, Huebert, et al., 2016; Rossberg et al., 2017). Here, we explore the potential to use modelling to inform climate-adaptive target setting for community-level size-based indicators, focusing explicitly on the North Sea demersal fish community and the large fish indicator (LFI) as an example.

The LFI expresses the proportion of the biomass of a surveyed fish community that is above a given size threshold, the latter typically determined based on the understanding of the historical size-structure of a community and past fishing pressure (Greenstreet et al., 2010). The LFI has been in use by OSPAR as
a fish community ecological quality objective for the north-east Atlantic region since 2010 (OSPAR, 2017) and has also been considered for the Baltic and Mediterranean Seas. This indicator has also been chosen by some European coastal member states to monitor the environmental status of demersal fish communities within the implementation of the Marine Strategy Framework Directive. The European Commission Decision (EC, 2017) explicitly states that threshold values for indicator assessments should accommodate the dynamic nature of marine ecosystems and that targets for recovery of deteriorated ecosystems should reflect prevailing climatic conditions rather than specific states in the past. But this aim has not yet been put into practice. In parallel, recent work has suggested that pressures to generate temporary and spatial trends of the LFI in some areas of the North Sea (Marshall et al., 2016; Stamoulis & Torreele, 2016). In this study, we used advanced process-based modelling as a means to investigate how climate change-related stressors may impact upon the historically dominant fish species that have driven change in the North Sea LFI (Greenstreet et al., 2010). Using mechanistic niche models parameterized for each of the seven species that make up the majority of demersal fish in International Bottom Trawl Survey catches in the North Sea (Greenstreet et al., 2010), we estimated changes in the size-structure of the North Sea demersal fish community that could result from ocean warming and acidification (Fernandes et al., 2013), and how these may impact upon the LFI in this community. Environmental changes were simulated using biogeochemical models under two global greenhouse gas emissions scenarios, representing the range of possible futures for the region during the 21st century (IPCC, 2013). We therefore tested whether setting of fixed targets is a realistic aim for policies regulating fisheries, such as the MSFD through its use of the LFI. We address this question considering time series for the LFI to the end of the 21st century which we constructed based on model simulations. We compared model-based estimates with the existing survey-based estimate time series (International Bottom Trawl Survey, IBTS) to assess the skill of our models in reproducing the hereto observed spatial and temporal variability of the LFI.

2 | METHODS AND MATERIALS

We used three different biogeochemical models to estimate the environmental conditions (temperature, salinity, pH, currents and oxygen) and primary production of the North Sea over the period 1983–2099. They were used to provide robustness to our estimates, as different models have different skill for particular ecosystem dynamic attributes, and their outputs can be seen to depend on specific initialization and parameterization conditions (Jones & Cheung, 2014). Simulations were produced under two scenarios of global greenhouse gas emissions (low: RCP2.6 and high: RCP8.5), representing the range of actions on climate change during the 21st century, as defined in the 5th Special Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2013). We used these simulations to drive the size-spectrum dynamic bioclimatic envelope model (SS-DBEM) (Fernandes et al., 2013), an advanced mechanistic niche model, to project possible changes in biogeography, biomass and size-spectrum of fish species. This model considers how species physiology, growth, population dynamics and dispersal potential respond to temperature, oxygen, salinity, depth, pH and primary production; how each species is able to compete for basal resources within the simulated species assemblage; and the effect of food and temperature on the size-structure of individual populations (Supporting Information, Fernandes et al., 2013; Queirós et al., 2015). We modelled seven species which together typically make up the majority of demersal fish caught within the community surveyed by the IBTS in the North Sea (Greenstreet et al., 2010): cod (Gadus morhua, Gadidae), haddock (Melanogrammus aeglefinus, Gadidae), saithe (Pollachius virens, Gadidae), whiting (Merlangius merlangus, Gadidae), plaice (Pleuronectes platessa, Pleuronectidae), common sole (Solea solea, Soleidae) and Norway pout (Trisopterus esmarkii, Gadidae). This list included those species which have been identified as key drivers of the temporal trend of the North Sea LFI (Stamoulis & Torreele, 2016). The SS-DBEM captures long-term shifts in species biomass distribution well, and these model outputs are considered to be more reliable than modelled absolute biomass values (Fernandes et al., 2013). We accommodated this aspect using a modified formulation for the LFI (“LFI’”, see Supporting Information). LFI’ time series were then calculated based on SS-DBEM simulations (1983-2099) under the two emissions scenarios and each biogeochemical model (Supporting Information). Simulated estimates were aggregated across the five (spatial) ecological subdivisions considered relevant for the assessment of demersal fish community indicators in the North Sea (Figure 1, ICES, 2015).

We then compared the simulated time series with corresponding indicator estimates derived from regional survey data from the International Bottom Trawl Survey (quarter 1, Heessen, 1996), considering the same species and geographical spread. This comparison was used to determine the skill of the simulations in reproducing hereto observed trends in community size-structure. We focused on the 1983–2014 period to include the early 1980s, when North Sea fisheries were still deemed sustainable and thus the standard against which fish community biomass in the region is usually considered (Greenstreet et al., 2010). Skill was considered to be significant when the model-based indicator estimates could significantly predict the corresponding annual survey-based estimates, as investigated using ordinary least-squares regression (detailed in Supporting Information). Survey-based estimates of the LFI (original formulation) and the LFI’ were also compared to determine the likeness of the two metrics and thus determine how our study, and future uses of SS-DBEM modelling, may help discern future trends for the LFI. Finally, we analysed the SS-DBEM-based LFI’ time series, from present time to the end of the 21st century, under the two different emissions scenarios, and compared these results to the LFI’s previously suggested policy target (Greenstreet et al., 2010). This methodology is further detailed as Supporting Information.
3 | RESULTS AND DISCUSSION

3.1 | Size-based modelling as a means to support climate-adaptive fisheries management

The adapted LFI formulation used to accommodate modelling outputs ("LFI’, see Supporting Information), focused on seven key species expressed more than 80% of the variability of the North Sea LFI (all species) when both formulations were compared using the survey data ($\rho_{\text{Pearson}} = 0.82, p < .01$, Figure 2). The LFI’, is thus a good proxy to explore possible futures for the LFI using model simulations, suggesting that in this case, modelling can be used to explore the suitability of policy targets for this size-based indicator across different scenarios of climate change. It is likely that this should be the case for many other size-based indicators across the world, given how ubiquitous size-spectrum-based models have become (Blanchard, Heneghan, Everett, Trebilco, & Richardson, 2017), including the one we used (SS-DBEM). Size-based models could therefore become a useful support to ecosystem assessment and fisheries management where size-based indicators are already used, such as in the United States and Europe, and support their uptake in other regions of the globe. These and other ecosystem models based on mechanistic understanding (Nielsen et al., 2018) are also likely to be useful in data-poor areas. For example, in Bangladesh, oceanographic surveys have only recently started but size-spectrum models and SS-DBEM have been applied to provide a first-order, mechanistic assessment of the impacts of future climate change on fisheries, in support of fisheries management (Fernandes et al., 2015). Size-based modelling and associated indicators have also been used in the context of managing fisheries within a mosaic of other uses of the marine environment, towards climate-adaptive conservation and marine spatial planning (Queirós, Huebert, et al., 2016). In spite of the uncertainties associated with projecting the impacts of climate change on fish populations (Payne et al., 2015), it is clear that size-based models have a potentially important role to play in supporting the management of wild stocks under a changing climate through ecological indicator assessment.

3.2 | The LFI as a community-level indicator of fishing pressure

The calculation of the LFI’ gives equal weight to all species in the community and to each spatial cell (Supporting Information). In
contrast, the calculation of the LFI is more heavily influenced by the distribution of species accounting for the greatest proportion of the biomass and by the grid cells showing the greatest proportion of biomass for each year (Supporting Information). Spatial-temporal variations of community composition and size-structure expressed by the LFI are therefore likely better captured by the model when the LFI’ is calculated using those species that are most common in the community (dominant) and those occurring most of the time (those in our seven species list, including cod and plaice, Stamoulis & Torreele, 2016). This may explain why a lower correlation between the two formulations was found when data for all the species in the survey were considered (LFI cf. LFI’, \( \rho_{\text{Pearson}} = 0.75, p < .01, \) Figure 2) rather than just the dominant seven (LFI cf. LFI’,, Supporting Information). As the majority of the seven species used in our analyses are among the larger bodied demersal fish species surveyed in the North Sea community, the absolute value of the LFI’, is higher than the corresponding LFI (Figure 2), despite the similar temporal trends. The LFI’, is therefore a somewhat optimistic proxy for the LFI, and this aspect should be taken into consideration in future studies.

Figure 2 highlights that, despite showing signs of recovery, the size-structure of North Sea fish has, within the period of analysis, remained well below the size ranges found in the 1980s, as previously noted (Engelhard et al., 2015; Stamoulis & Torreele, 2016). Specifically, the LFI remained below the previously proposed LFI target of 0.3 (Greenstreet et al., 2010) throughout the vast majority of the available IBTS data time series (Figure 2). Some authors have attributed these changes to overall reductions in North Sea fishing effort as a result of European fishing policies, whilst others have argued that, in some areas of the North Sea, the observed changes in the fish community size-structure have been driven by environmental and ecological processes (Engelhard et al., 2015; Greenstreet et al., 2010; Marshall et al., 2016; Stamoulis & Torreele, 2016). Although slight differences in methodology may partially explain this contrast, differences in the outcome of these analyses of the same data raise the question of whether we fully understand the responsiveness of the LFI to fishing pressure at present, and particularly, its recovery time under reduced fishing effort. These are essential criteria of robust ecological indicators (Queirós, Strong, et al., 2016). Furthermore, while past LFI declines may have been driven largely by fishing (Engelhard et al., 2015; Greenstreet et al., 2010), the size-structure of the North Sea demersal fish community may now reflect the effects of natural mortality more than in the past, due to the reduction in fishing pressure.

Reductions in fishing effort are not expected to trigger fast recovery in fish community size-structure, taking at least one generation to become fully apparent within fish populations (Shin et al., 2005). Other, less well-understood processes, such as Allee effects (Gascoigne & Lipcius, 2004) and even “fisheries induced evolution” (FIE) may have contributed to a slow recovery of the LFI in the North Sea in the period analysed. FIE has been reported in various areas around the globe (e.g. Haarr, Sainte-Marie, Comeau, Tremblay, & Rochette, 2018) and is manifested through smaller body sizes and increased reproductive investment within populations, which occur as evolutionary responses to long-term size-selective fishing pressure (Audzijonyte et al., 2016). Although FIE has not been reported unambiguously in the North Sea (Audzijonyte et al., 2016), it may be exacerbating the negative effects of regional ocean warming on fish body sizes (Baudron et al., 2014), thus contributing to the observed slow recovery of fish size-structure to pre-exploitation levels. Such uncertainty in pressure-state relationships has been recognized as a wider challenge in the use of community-level indicators around the globe, including size-based metrics as well as those focusing on other community-level traits (e.g. mean trophic level, Adams et al., 2017). The causes of temporal trends in community-level indicator time series can thus be ambiguous, resulting from complex, multivariate environmental phenomena that can affect fish communities alongside fishing pressure and climate change (Adams et al., 2017; Shin et al., 2005). These aspects constitute challenges to the practical application of the LFI in support of fisheries management and indeed to that of any community-level ecological indicator (Branch et al., 2010).

Given pre-existing, detailed analyses of the observed North Sea LFI trend (Engelhard et al., 2015; Marshall et al., 2016; Stamoulis & Torreele, 2016), we focus now on the future of the LFI in the North Sea and its previously proposed target, under long-term climate change.

### 3.3 Setting a future policy target for the North Sea LFI under climate change

The skill of our simulations in projecting the trend of the equivalent data-based metric (LFI’,,) varied across the North Sea regions, depending on which biogeochemical model we used (Tables S1 and S2). The size-spectrum-based model we used to project LFI’, reproduced survey data trends with the best skill when using ERSEM to generate the biogeochemical fields (Supporting Information). Nevertheless, we estimated the LFI’, time series using the combined estimates from the three biogeochemical models (Figure 3) because the three are well established and in this way provide a more robust perspective of possible futures for the North Sea LFI (Jones & Cheung, 2014). None of our simulations projected the IBTS data-based LFI’, with skill in the Kattegat-Skagerrak region (Figure 1, Tables S1 and S2), suggesting that different, regionally specific model set-ups are probably required, instead of the set-ups we implemented, some of which are known to have greater skill in the shelf of the United Kingdom (Butenschön et al., 2015; Fernandes et al., 2013). We therefore focus our subsequent analyses on the remaining four regions of the North Sea (Figure 1).

Considering the five sets of seven species simulations, which span across two emissions scenarios and the three biogeochemical models, our analysis of the calibrated LFI’, (Figure S1, Tables S1 and S2) suggests that the North Sea demersal fish community will be negatively influenced through climate-driven change (Figure 3). That is, in the majority of cases we studied, the proportion of large fish in the community continues to decrease in the community...
(and most individual species) as climate change unfolds in the region (Figure 3, Figure S2). Under the lower emissions scenario we considered (AR5 RCP 2.6, IPCC, 2013, Figure 3a), the decline in the size-structure of the 7 key species is less pronounced, being most evident in projections that used the higher emission scenario (AR5 RCP 8.5, IPCC, 2013, Figure 3b). In this case, the LFI may decrease by as much as 60% in the NW North Sea, by the end of the century and relative to the 1980s, despite the potential overestimation of the LFI, relative to the traditional LFI (Figure 2). With large fish being an indicator of the health of exploited communities (Engelhard et al., 2015), our analysis suggests that the effects of ocean warming and acidification, alongside other associated environmental changes, can place sufficient pressure on fish size-structure to create the need to revise size-based community-level indicator targets as climate change unfolds. Modelling studies such as this one can be used to explore what may be more realistic targets for the LFI (Blanchard et al., 2014). Given the known tight dependency between fish size and environmental conditions (Forster, Hirst, & Atkinson, 2012), similar analyses may be required in the general use of size-based indicators in fisheries management under future climate change.

Considering our results, it is still reasonable to expect that the management of fishing effort (through the MSFD, the European fisheries policy and similar policies around the world) can drive community size-structure towards an LFI target? The LFI reflects the size-structure of surveyed populations, and large fish will decline more rapidly with fishing effort than smaller ones (Jennings & Kaiser, 1998). Yet, the SS-DBEM configuration we used here to generate LFI, projections did not consider fishing effort as a component of fish mortality rates. Rather, mortality rates in the models were primarily linked to natural mortality, and how it is affected by climate change. Under the assumption that survey data in itself reflects both natural and fishing mortality, despite potential observational or catch error (Fraser, Greenstreet, & Piet, 2007; Stamoulis & Torreele, 2016), it is reasonable to assume that our projections calibrated with IBTS data, to a degree, may reflect the effect of fishing mortality on the modelled fish community (Figure S1). However, it is noteworthy that we found stronger relationships between survey-based and modelling-based indicator estimates in the northern North Sea (Tables S1 and S2), where it has been argued that the main drivers of observed changes in the LFI were environmental factors (including ocean warming), and not fishing effort (Marshall et al., 2016; Stamoulis & Torreele, 2016). Conversely, in the southern North Sea, where fishing has been highlighted as the main driver of the LFI (Engelhard et al., 2015; Stamoulis & Torreele, 2016), our model and data relationships were found to be worse (Figure S1, Tables S1 and S2). Considering the LFI, simulations forced using ERSEM for the NW and NE of the North Sea, our simulations with the best skill (Tables S1 and S2), it seems that interannual variations of the LFI due to the seven selected species are driven by as much as 60% by environmental change (as simulated). The remaining variation is driven by other pressures and processes not explicitly represented in our models, which potentially include fishing effort (and associated evolutionary-based life-history changes, Audzijonyte et al., 2016). Given the progression of the LFI, illustrated in Figure 3, it is therefore likely that a North Sea LFI target based in the early 1980s (i.e. 0.3, or 30%, Greenstreet et al., 2010) will not be an achievable aim in the long term. Recent modelling studies (Marshall et al., 2016) and an observed increasing trend towards smaller fish in the North Sea as a result of ocean warming...
(Baudron et al., 2014) support the expectation. Given the current understanding of wild populations’ responses to climate-driven pressures and fishing, our analysis thus suggests that a target for these communities lower than 0.3 (or a smaller size threshold than 40 cm) will be a more meaningful aim in the long-term for the LFI in the region, under climate change. This target likely needs to be spatially explicit, given the very different changes in demersal fish size-structure we project across the North Sea regions (Figure 3). The contrasting results we found across the tested emissions scenarios (Figure 3a, b) suggest that this target would likely also depend on the degree of climate change experienced by the North Sea over time and its effects on wild fish populations. International, political and scientific conventions discussing and agreeing on the degree to which actions will be taken globally to curb greenhouse gas emissions, such as the Paris Agreement, will therefore play a key role in determining the size-structure of wild fish communities in this and other regions of the world’s oceans. Whatever the target chosen, our analysis strongly supports the view that size-based indicator targets set within policies regulating fishing effort should be adaptive and consider the deeply rooted physiological link between individual fish size and environmental conditions (Forster et al., 2012).

The parallel effects of environmental and fishing pressures on community-level size-based indicators have been detected in many of the world’s marine ecosystems beyond the North Sea, including the Bering, Southern Catalan, Irish, Adriatic and Baltic Seas, Guinea and the Eastern Scotian shelf (Blanchard et al., 2010). In countries such as Australia, fisheries management organizations have also recognized that climate change will pose significant challenges to the life histories of exploited populations, which will require monitoring (Caputi et al., 2014a,b). Studies such as the present one should precede the operationalization of fish size-based indicators, because they can support the identification of adaptive, ecologically meaningful management targets as a changing climate starts to manifest itself in wild, fished populations.

3.4 | New fish in the North Sea

Growth, and ultimately size, are modified by how close a population occurs relative to its optimal temperature range, decreasing outside of it (i.e. scope for growth, Clark, Sandblom, & Jutfelt, 2013; Pörtner & Farrell, 2008). So while raising temperatures in the North Sea appear to be driving down the size of its dominant species (Baudron et al., 2014), and although this may continue into the future (Figure 3), the North Sea fish community will not likely continue to be dominated by the same species into the end of the 21st century. Several studies have found that warm-affiliated species continue to move north into the North Sea as the region warms, with cold water fish species retreating, into deeper, cooler areas (Dulvy et al., 2008; Hiddink & Ter Hofstede, 2008; van Walraven et al., 2017).

Ocean acidification and warming are expected to drive further ecosystem-level effects in the North Sea in the coming decades (Queirós, Huebert, et al., 2016). Over time, these changes may markedly modify the size-structure of local communities through changes in life histories, and through the relationship between the thermal affinity of species present and regional climate, in the North Sea as in other regions of the world’s oceans (EAP, 2012). Finally, vulnerable species will potentially be regionally replaced by more tolerant ones. The precise effect of these changes is difficult to predict, but it further complicates the effect of climate on autochthonous communities, re-organizing food webs and species interactions. Together, these processes challenge the perspective that reduction of fishing effort alone can revert the size-structure of fish communities to a pre-exploitation state. A growing body of evidence demonstrates that environmental change, as driven by climate, must be seen as an integral part of target setting for ecological indicators in support an ecosystem approach to fisheries management. Without this consideration, target setting is likely inadequate.

ACKNOWLEDGEMENTS

This study stemmed from funding under the European Union’s 7th Framework Programme, “The Ocean of Tomorrow” Theme, as part of project: Development of innovative Tools for understanding Marine biodiversity and assessing good Environmental Status project, DEVOTES, [308392]. AMQ further acknowledges funding support from the Marine Ecosystems Research Programme (UK Natural Environment Research Council and the UK Department for the Environment, Food and Rural Affairs, DEFRA, [NE/L003279/1]). CPL acknowledges funding support from DEFRA Projects From Physics to Fisheries (“Fizzyfish” [MF1228]) and “Appraisal of indicators of Good Environmental Status” (BX020). JAF further acknowledges funding through the Gipuzkoa Talent Fellowships programme, by the Gipuzkoa Provincial Council, Spain; and co-financing by the Basque Government (Department Deputy of Agriculture, Fishing, and Food Policy), Spain. Momme Butenschön, Andrew Yool and Thomas L. Frölicher are thanked for allowing us the use of their biogeochemical simulations, from models ERSEM, MEDUSA and ESM2 Mb, respectively. Henn Ojaveer, Jason Link and Ian Perry are thanked for advice on governmental fisheries reports. Prof Paul Hart and two anonymous reviewers are thanked for helpful comments during peer review.

CONFLICTS OF INTEREST

None.

AUTHORSHIP

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