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Projecting contributions of marine protected areas to rebuild fish stocks under climate change

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No-take marine protected areas (No-take MPAs) are considered as a major tool for conserving marine biodiversity and ecosystem services. No-take MPAs can also contribute to climate adaptation for exploited fish stocks. Meanwhile, many fish stocks in the world are overfished and management institutions are developing plans to rebuild them. Understanding the potential effects of no-take MPAs on fish stocks under climate change can help develop strategies for climate-resilient stock rebuilding. Here, using a linked climate-fish-fishing model, we undertake simulation experiments to examine the effects of no-take MPAs on biomass and potential catches of 231 exploited fish and invertebrate species in eight marine ecoregions in the Northeast Atlantic under climate change. The simulations include different levels of fishing, no-take MPAs coverage, atmospheric global warming levels, and account for the expected displacement of fishing to the area around the no-take MPAs. Average individual stock biomass is projected to decrease by 5–15% per degree Celsius atmospheric warming. Having 30% of the distribution of over-exploited fish stocks under no-take MPAs together with conservation-focused fisheries management of these stocks are projected to offset the negative impacts on their biomass under 2.6–2.9 °C global warming. Meanwhile, potential catches increase when a portion of the over-exploited fish stocks is protected from fishing as higher biomass in the no-take MPAs spills-over to the surrounding areas. Our findings highlight that no-take MPAs, combined with reducing fishing intensity, can help rebuild over-exploited fish biomass and benefit their dependent fisheries in the Northeast Atlantic under projected climate change in the 21st century.

Climate change is negatively impacting many marine fish stocks and fisheries ("fish stock" refers generically to both fishes and invertebrates)[1–3]. Human-induced climate change and carbon dioxide emissions are altering ocean conditions that include slow-onset and rapid changes[4]. These ocean changes, for example, include warming, loss of oxygen, acidification, sea level rise, and increase in intensity and frequency of marine heatwaves[5]. Consequently, climate change is causing shifts in the distribution of marine species, the timing of biological events and the structure and function of ecosystems[2,6,7]. Overall, fisheries yield has so far been negatively impacted by climate change with some positive impacts for some stocks and regions[3]. Meanwhile, considerable numbers of fish stocks in the world are over-exploited[8,9]. Some fish stocks and regions are in better shape than others. For example, in European waters and the Mediterranean Sea, there is a strong north-south gradient, with over 60% of the stocks exploited sustainably with biomass levels that are above the targets for maximum sustainable yield (MSY) in the Barents Sea and Norwegian Sea[10] or over 70% in the Northeast Atlantic region[8]. In contrast, biomass of less than 20–40% of stocks in the Mediterranean Sea and the Black Sea are above such targets[8,10].

Rebuilding fish stocks is considered a main conservation and fisheries management objective[11–13]. There are many ecological, social and economic benefits of rebuilding fish stocks. Rebuilding of over-exploited species is a formal requirement of fisheries-related law and policies in some countries and regions[10,14,15]. For example, the Common Fisheries Policies of the European Union calls for rebuilding all commercially used fish stocks above levels that are capable of producing the MSY as its explicit objective[16]. Measures to rebuild fish stocks include effective reduction in fishing level and setting up spatial and temporal closures[12]. Previous meta-analysis of

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MPAs shows that effectively implemented no-take MPAs are more effective in rebuilding fish biomass than those that allowed fishing[17].

Intensifying climate change is impacting the potential to rebuild over-exploited fish stock to targeted sustainable levels[18,19]. Negative impacts of climate change on growth, reproduction and survivorship of marine species reduce their scope for biomass rebuilding. A study that simulated global fish stocks under climate change projects that 10% and 25% of the world's marine ecoregions showed no sign of biomass rebuilding relative to their current levels under global atmospheric warmings of 1.5 and 2.6 °C, respectively[19] when fishing is managed at MSY level. The study also projected that a more conservation-focused fishing reduction plan instead of one that is aimed for catch maximization is needed to rebuild fish stocks under climate change. At the same time, area-based management (e.g., MPA) are considered as tools for marine conservation and their effectiveness for achieving climate-ready fisheries have been explored[20,21].

When effective, no-take MPAs (i.e., areas of the ocean closed to fishing) can have multiple biological benefits such as increasing population biomass, diversity, and individual sizes within the no-take MPAs[22]. No-take MPAs can help rebuild over-exploited fish stocks and benefits often extend beyond the no-take MPAs boundary through population 'spill-over' which can benefit biodiversity and fisheries[23]. The potential social and ecological benefits of no-take MPAs have been explored using modeling studies[24], although the social-ecological trade-offs of MPAs in reality are likely to be more intense and complex[25,26]. Thus, as climate change re-shapes marine ecosystems worldwide, well established no-take MPAs could prove to be even more critical as adaptation tools[27]. In contrast, species and ecosystems in no-take MPAs are protected from human disturbance while over-exploitation may select for more resilient species - a hypothesis called the "Protection Paradox"[28]. Understanding the extent to which no-take MPAs can rebuild biomass under climate change within the no-take MPAs borders and its surrounding waters is still limited. Such knowledge is useful to develop climate-resilient rebuilding plans as well as support potential implementation of new no-take MPAs to achieve sustainable development targets.

Here, building on previous studies that focus on rebuilding fish biomass through reduction in fishing effort[10,19], this study uses a linked climate-fish-fishing model to explore the effects of having no-take MPAs in addition to fishing effort management would further contribute to achieving biomass rebuilding targets under climate change. We undertake simulation experiments to examine the effects of no-take MPAs on biomass and potential catches of 231 exploited fish and invertebrate species in eight marine ecoregions in the Northeast Atlantic (739 species-ecoregion stock units) under climate change. The simulations include different levels of fishing, no-take MPAs coverage, atmospheric global warming levels, and account for the expected displacement of fishing to the area around the no-take MPAs. The model does not account for trophic interactions between species. We hypothesize that (1) no-take MPAs contribute positively to increasing biomass of fish stocks under climate change, (2) larger no-take MPAs coverage combined with stronger conservation-focused fisheries management are more effective in rebuilding stock biomass under expected climate change than scenarios with smaller no-take MPAs coverage and/or higher exploitation levels, and (3) no-take MPAs contribute to improving catches of fish stocks in surrounding waters under climate change.

Results

We found that the simulated biomass of the studied fish stocks in the Northeast Atlantic Ocean was related significantly and negatively to global atmospheric warming ($p < 0.05$, Fig. 1). Summing biomass across all stocks, the projected rate of change in total biomass relative to the level at MSY is -8% °C^{-1} of global mean atmospheric warming (Fig. 1A), although this is considered a theoretical estimate as the model does not account for factors such as species interactions and evolutionary responses. Under the 'overfishing' scenario where $F/F_{MSY} = 1.5$, the rate of change in biomass reduces to around -4% °C^{-1}. When we analyzed each fish stock individually, the majority (84%) of the stocks were projected to decrease in biomass significantly ($p < 0.05$) with 9% showing significant increases under increasing levels of global warming (Fig. 1B). The median rate of change in biomass across the stocks was projected to be −5.4% °C^{-1} relative to the biomass at MSY (i.e., $F/F_{MSY} = 1$). The drop in simulated biomass around global warming level of 1.5 °C under SSP1-2.6 scenario is because of time lag of changes in oceanographic variables relative to changes in greenhouse gases concentration and the resulting atmospheric warming (Fig. 1A).

Our results show that larger no-take MPAs coverage was projected to contribute positively to biomass rebuilding under climate change (Fig. 2, Table S4–5). We analyzed the simulation outputs for the different no-take MPAs, fishing and climate scenarios using mixed-effect models and compared the performance across these models (see Method). Model 4 that considered the interactions between fishing and global warming levels was estimated to have the lowest AIC (Table S2) and thus we presented the results from this model here. Larger no-take MPAs coverage was related to a larger increase in biomass (Fig. 2A, B). For example, a 15% area as no-take MPAs scenario is projected to increase biomass by an average of 2.5% relative to the baseline scenario of having 5% no-take MPAs scenario and without climate change (Fig. 2A). Protecting 30% of the Northeast Pacific Ocean from fishing almost doubled the positive effects on stock biomass relative to the 15% MPAs scenario. Moreover, reducing fishing by 25% from the level at MSY would increase biomass by an average of 29.2%. However, a 1 °C increase in global warming level relative to pre-industrial levels would reduce biomass by 12.6% at that level of fishing. Interestingly, relative biomass of fish stocks was projected to decrease more under scenarios of lower fishing intensity, suggesting the possibility of "protection paradox". Our sensitivity analysis shows that alternative sets of locations of no-take MPAs did not have significant effect ($p > 0.05$) on the projected changes in biomass.

At the individual fish stock level, the studied stocks were projected to increase, on average, by 3.4% per one tenth of their geographic range being protected from fishing (Fig. 2B). As the stock's spatial distributions vary, the proportion of their geographic ranges that were protected from fishing under a no-take MPAs scenario differed from one stock to another (Fig. 3). We undertook the statistical analysis of the model outputs again by using the proportion of geographic range that were protected from fishing for each stock instead of the total no-take MPAs area (See Method). Based on the estimates from the mixed effects models (Fig. 2B), protecting 30% of the stock's range size from fishing was estimated to increase stock biomass in the Northeast Atlantic region by 10.2 ± 0.6% while protecting the same proportion of the region without consideration of the stock's biogeography was estimated to increase stock biomass by 5.4 ± 0.4% only.

We projected that large no-take MPAs (or a network of no-take MPAs covering a broad region) combined with a more conservative fishing target are projected to rebuild stock biomass under expected climate change. Expanding the no-take MPAs coverage from 5% to 30% of the total area would increase the average biomass of the fish stocks by around 5% relative to B_{MSY} (Fig. 2A). Managing fishing at $F/F_{MSY} = 0.75$ would increase stock biomass by 30%. Meanwhile, a recent study suggests that, under current global policies and actions (as documented by Nov 2022), projected greenhouse gas emissions in the 21st century would lead to a global warming of 2.6–2.9 °C relative to pre-industrial levels[29]. Our model projects that if fishing target is 25% lower than F_{MSY}, biomass is projected to increase by 29% while 30% coverage of no-take MPAs would further increase the biomass by 5.4% relative to the baseline (5% no-take MPAs coverage with GWL = 0 °C). However, global warming would lower such biomass increase by 31–39% under a global warming of 2.6–2.9 °C (calculated from the effects of global warming of −12.6 ± 0.7% °C^{-1}) (Fig. 2A). Thus, biomass increases projected from more conservative fishing levels and larger no-take MPAs coverage would almost compensate for the projected decrease in biomass due to climate change expected from the current mitigation actions and policies. On the other hand, potential catches were also projected to decrease under this specific example (Fig. 2C, D).

No-take MPAs contribute to increasing catch potential of over-exploited fish stocks but have negative effects on catches in under- to fully-exploitation scenarios (Fig. 2C, D). The linear mixed effect model that

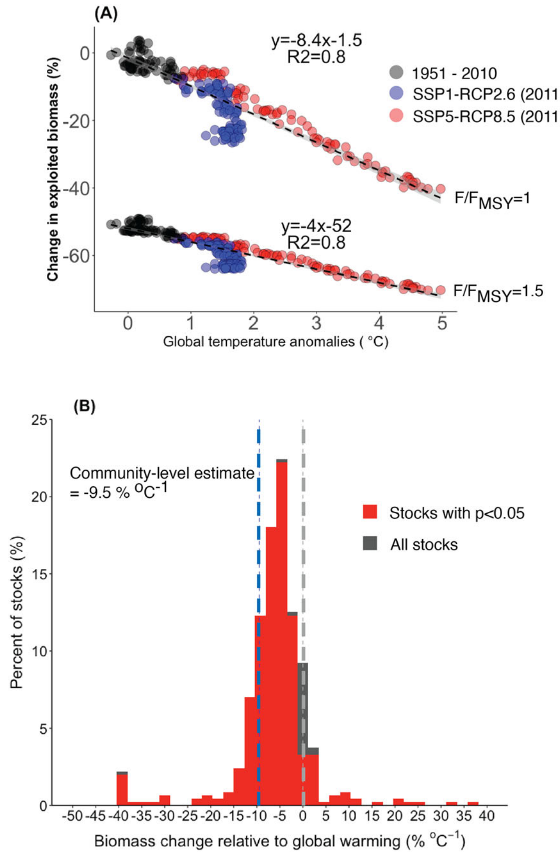

Fig. 1 | Estimated changes in biomass in the Northeast Atlantic marine ecoregions relative to global warming levels. **A** Projected changes in total exploited biomass across all stocks at global warming levels for the periods 1951–2010 (black dots) and 2011–2100 under SSP1-RCP2.6 (blue dots) and SSP5-RCP8.5 (red dots) climate change scenarios simulated by the Earth system model and two fisheries scenarios ($F/F_{MSY} = 1$ and $F/F_{MSY} = 1.5$) and the 5% no-take MPAs coverage scenario. The shading around the dashed line represents the 95% confident intervals of the linear regression (dark dashed line) between changes in exploited biomass (y) and biomass change (x). **B** Proportion of stocks at different rates of biomass change relative to global warming levels estimated from a linear regression between biomass and global warming levels for each stock [all stocks: gray bars, stocks with significant ($p < 0.05$) relation between biomass and global warming levels: red bars]. The community-level average change in biomass relative to global warming levels (red dashed line) was estimated from a linear mixed effect model with different stocks being a random effect (blue dashed line). Gray dash line provides a reference that indicates change in biomass = 0%.

expressed potential catches as a function of F/F_{MSY}, global warming level, coverage of no-take MPAs and a categorical variable that classified a stock as over-exploited if $F/F_{MSY} > 1$ (Model 5*) was estimated to have the lowest AIC compared to other models (Table S3, see Method) and thus results from Model 5* were presented here. For over-exploited fish stocks ($F/F_{MSY} = 1.5$), our model projected that no-take MPAs coverage of 15% and 30% in the Northeast Atlantic Ocean would result in an increase in catch potential by 6 and 10% respectively (Fig. 2C). Meanwhile, intensifying climate change was projected to reduce catch potential by 6 to 8% °C^{-1} of global warming (or 15 to 25% under 2.6 to 2.9 °C warming relative to pre-industrial levels). In contrast, if the fish stocks were already managed sustainably ($F/F_{MSY} = 1$), protected areas were projected to reduce catch potential by 3 to 5% under the 15 and 30% no-take MPAs scenarios because of the decrease in area open to fishing under the larger MPAs scenario. Projected catch potential was more sensitive to climate change when stock biomass is higher (under lower fishing and larger MPAs scenarios) (Fig. 2).

The projected changes in stock biomass were driven by the relationships between ocean conditions and global warming levels (Fig. 4). The ocean variables that affect biomass and biogeography of marine species, as represented in the climate-fish-fisheries model, have significant relationships with warming levels ($p < 0.05$). Specifically, previous analysis showed that projections from DBEM are driven by sea water temperature, followed by net primary production and oxygen[30]. Increases in global warming levels raised sea water temperature (Fig. 4A, B) and reduced oxygen concentration (Fig. 4C, D) and net primary production (Fig. 4E). For primary production, we found a bifurcation of the relationship with warming levels at around 2 °C relative to pre-industrial levels that is associated with the increasingly diverging pathways between SSP1-2.6 and SSP5-8.5 projected at around the 2030 s period (Fig. 4F).

Discussion

Our scenario and modeling analyses support the three hypotheses posed in this manuscript. Firstly, no-take MPAs contribute positively to rebuilding biomass of over-exploited fish stocks in the Northeast Atlantic region under climate change. Secondly, larger no-take MPAs cover combined with conservation-focused fisheries management can rebuild over-exploited stock biomass to target levels while compensating for the negative impacts of climate change on these species. Thirdly, no-take MPAs would increase potential catches of over-exploited stocks under climate change. Thus no-take MPAs should be considered an important component of a portfolio of intervention to rebuild over-exploited fish stocks, restore seafood production potential and adapt to climate change impacts on marine species and fisheries.

Exploited fish stocks and the dependent fisheries in the Northeast Atlantic are being threatened by climate change and overfishing[10,31]. Intensifying climate change is driving ocean warming and oxygen losses in the region. Warming and decreasing oxygen level are projected to reduce the metabolic scope of marine fishes and invertebrates through increasing their metabolic rates (and the associated demand for oxygen) and, consequently, reducing the available aerobic scope for growth, reproduction and other related activities[32,33]. Meanwhile, net primary production that supplies energy to the food web where the studied species inhabit was projected to decrease. The combination of reduced metabolic scope and decrease in potential energy supply through the food web led to the projected decrease in biomass and catch potential under climate change. In addition, although there are some improvement in the status of fish stocks in the Northeast Atlantic[34], many are still considered over-exploited, the expected climate change under the current documented mitigation policies and global actions substantially increase the likelihood of local extinctions of these stocks and reduce the viability of the fisheries targeting these species.

No-take MPAs are projected to contribute to rebuilding over-exploited fish stocks and benefit their fisheries under climate change even if regional fishing efforts remain unchanged. Biomass was projected to be higher within no-take MPAs than the surrounding areas despite the stocks being impacted by climate change. Thus, no-take MPAs could serve as a “fish bank” or refuge to conserve fish stocks under climate change and to help repopulate its surrounding areas as greenhouse gas emissions are being mitigated[35]. Meanwhile, fishing around the no-take MPAs also benefited from the ‘spill-over’ of biomass from the no-take MPAs as our model redistributed fishing effort displaced from the no-take MPAs to its surrounding areas. Such fisheries responses to and benefits from no-take MPAs, which have been empirically observed in many regions[36–38], could help fisheries adapt to the negative impacts of climate change on catch potential. When fish stocks are rebuilt and sustainably managed ($F/F_{MSY} < 1$), no-take MPAs continue to contribute to higher stock biomass.

Designing and implementing no-take MPAs as part of the climate-resilient biomass rebuilding plan should account for possible trade-offs and negative consequences associated with no-take MPAs on local seafood available, livelihood and culture[39,40]. As indicated from our projections, no-take MPAs could reduce potential catches if fish stocks are already well-managed. Also, no-take MPAs may limit specific local communities from accessing their fishing grounds or fish stocks while others may have increased access because of the biomass spill-over from the no-take MPAs.

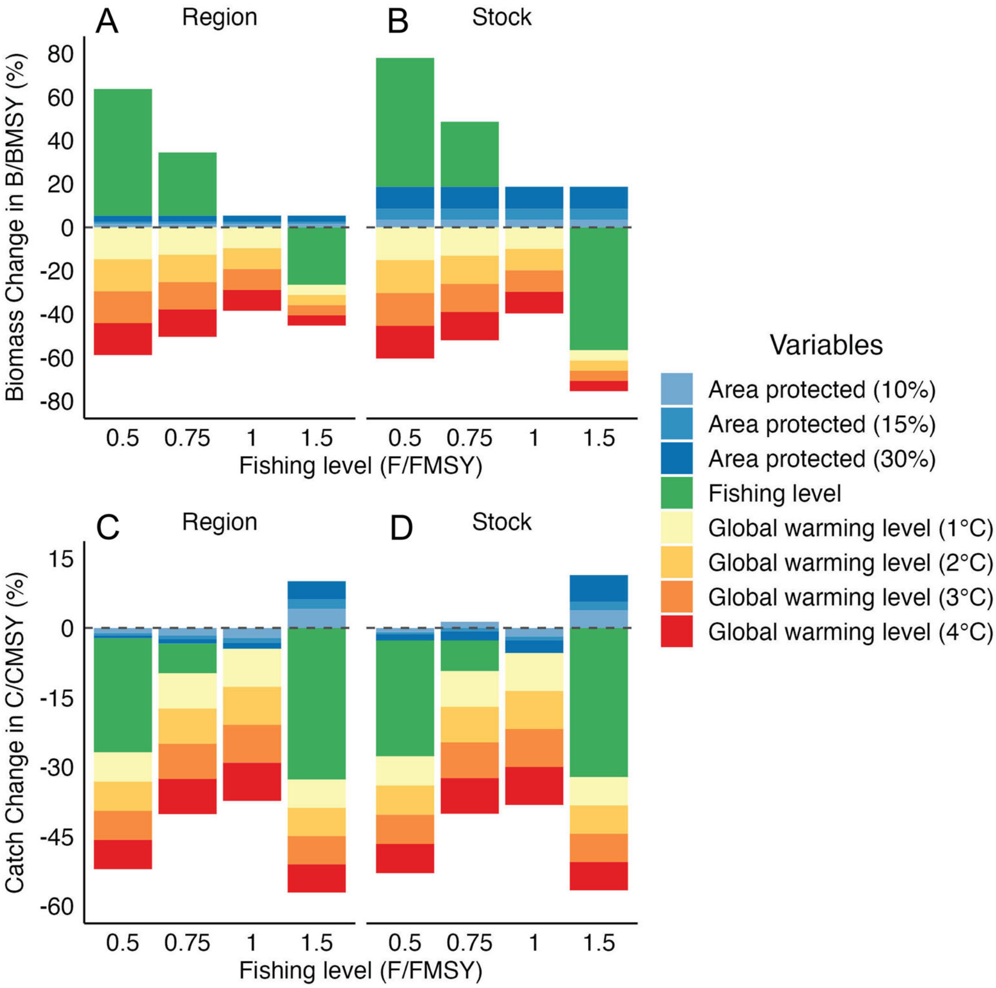

Fig. 2 | Projected relative contribution of scenarios of no-take marine protected areas coverage, fishing levels and climate change to changes in biomass and catch potential. The cumulative positive and negative effects on changes in (**A**, **B**) biomass relative to the level at maximum sustainable yield (B/B_{MSY}, y-axis) and (**C**, **D**) catch potential relative to maximum sustainable yield (C/C_{MSY}) from fishing (green bars), no-take MPAs (blue bars) and climate change (represented by global warming levels, warm color bars) across different fishing level scenarios (x-axis). The relative changes in biomass and catch potential as a result of the different factors represented by the bars are cumulative. The effects of the factors were estimated from the mixed-effect model by region (**A**, **C**) and stock (**B**, **D**) (see Method).

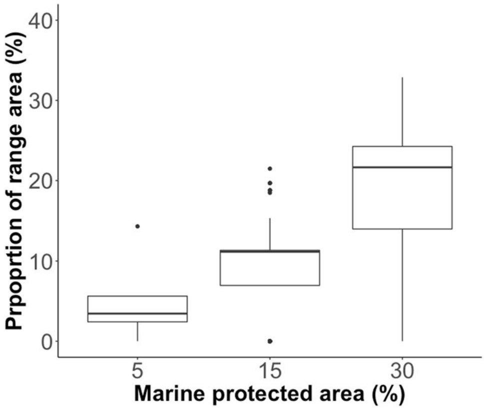

Fig. 3 | Relationship between no-take marine protected area scenarios and the proportion of the range area of the studied fish and invertebrates' stocks falling within the protected area under each no-take marine protected area scenarios. The black dots are the extremes of the whisker (values exceeding 1.5 times the interquartile range), the vertical lines represent the maximum and lower ranges, the upper and lower ends of the box indicate the interquartile range while the line within the box indicates the median.

Moreover, our analysis assumes re-location of fishing effort displaced by the no-take MPAs, potentially increasing fishing costs. Future studies could consider modeling the economics of fishing and the effects on fishing effort under climate change and no-take MPAs scenarios. While theoretically, no-take MPAs contributes positively to biomass rebuilding under climate change, its effectiveness supporting sustainable development in practice is conditioned on other measures such as equitable consideration, engagement, and participation of different stakeholders in MPAs design and implementation[41,42].

We found evidence of the 'protection paradox' for biomass rebuilding under climate change[28]. As stock biomass is rebuilding beyond the level required to achieve MSY, fisheries benefits from the 'spill-over' effects of no-take MPAs are projected to decrease because of density-dependent compensatory effects on population growth. Moreover, we projected that under-exploited fish stocks would be more sensitive to climate change. Over-exploitation reduces body size of the fish stocks. Individuals with smaller body size relative to their maximum size have larger metabolic scope in many cases[43,44]. Larger species also generally have higher sensitivity to warming[45,46]. Thus, as over-exploited fish stocks are being rebuilt, our findings suggest a potential transition from having co-benefits of no-take MPAs to achieve conservation and fisheries objectives under climate

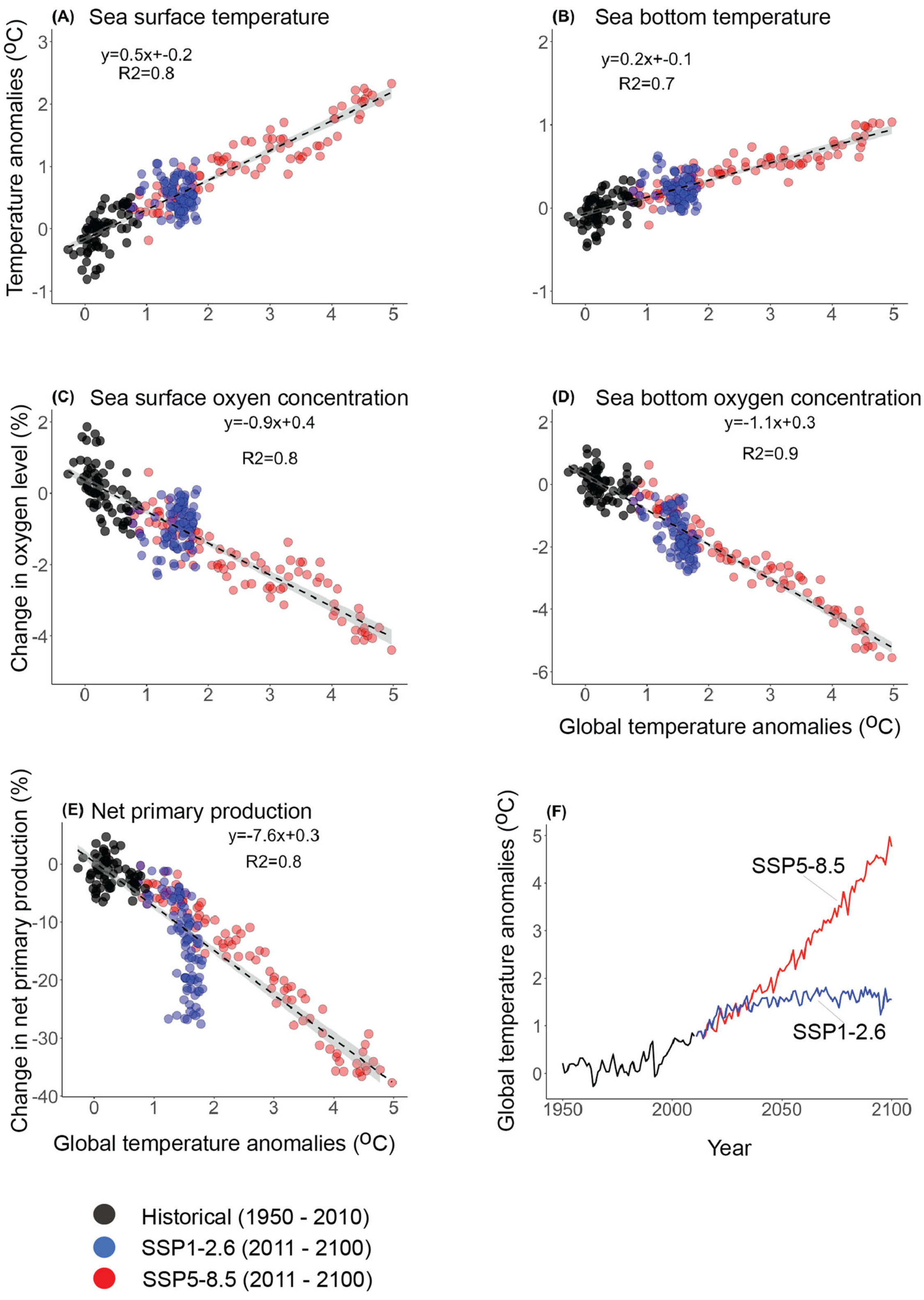

Fig. 4 | Relationship between projected ocean variables in the Northeast Atlantic ocean (FAO Area 27), global mean surface warming and greenhouse gas emissions scenarios. Global mean atmospheric surface temperature relative to pre-industrial levels is significantly ($p < 0.05$) related to regional (**A**) sea surface temperature, (**B**) sea bottom temperature, (**C**) sea surface oxygen, (**D**) sea bottom oxygen and (**E**) net primary production. Ocean variables are expressed relative to 1950–1969. Projections of ocean variables included historical period (1950–2010) (black dots and line) and projected scenarios under SSP1-2.6 (blue dots and line) and SSP5-8.5 (red dots and line) (**F**). Dashed lines represent the linear regressions (equations of the models are annotated) between the ocean variables and global mean surface temperature and the shaded area are the 95% confidence limits.

change, to having trade-offs between objectives for fisheries, climate adaptation and conservation for biodiversity. On the other hand, no-take MPAs can serve as insurance against uncertainties in climate impacts including those from extreme events such as marine heatwaves as well as protection of critical habitats such as seagrass beds, kelp forests and coral reefs. These uncertainties are not explicitly evaluated in our model and should be further explored as extreme events become more frequent and intense.

In this study no-take MPAs were randomly established within the study site. Such randomization invariably influenced the result as it determined what region was closed to fishing. By randomizing, our protection scenarios consisted of smaller no-take MPAs with large edge-to-area ratios, which could overestimate the number of surrounding cells, and thus the "spillover effect"; however, most no-take MPAs are smaller in size, suggesting our estimates are likely more realistic than forcing large, clumped MPAs (mean MPAs area in FAO zone 27 was 653 km^2). On the other hand, the average area of patches of non-take MPAs pixels that were adjacent to each other increased with higher MPAs coverage. Also, alternative random allocations of no-take MPAs pixels do not have significant effects on projected biomass rebuilding under different MPAs coverage scenarios. In reality, the establishment of a no-take MPAs should follow a rigorous approach including not only scientific considerations (e.g., ecological targets) but also stakeholder engagement. We found that the effects of no-take MPAs were strongly related to the proportion of each species' geographic range that is under protection. Thus, it is expected that alternative no-take MPAs designs and its coverage on species' range would alter no-take MPAs effectiveness in rebuilding fish stocks under climate change. While our model projected changes in biogeography of the studied species that affected stock biomass, we did not analyze specifically the interactions of range shifts and the effects of no-take MPAs on biomass rebuilding. Also, the model did not consider inter-specific interactions or evolutionary responses of the populations under climate change and fishing. Trophic interactions may lead to more complex responses of fish stocks to no-take MPAs, such as trophic cascades[47], and evidence of such effects on biomass rebuilding in protected areas are mixed[48]. Also, no-take MPAs may increase genetic diversity that enhances the adaptive capacity of fish stocks to climate change while these MPAs may also select for traits such as dispersal ability that affects the biomass in and their spill-over from the no-take zone[49]. Future studies can examine the specific effects of range shifts under climate change and explore how different no-take MPAs coverage, potential "network" designs and their connectivity may be affected by such shifts. The analysis presented here can also be repeated using other models with explicit representation of trophic interactions[50] and evolutionary responses[51].

We make the important assumption that all the MPAs are effective no-take zones, and that outside of the MPAs (and fisheries in general) are well managed, rules are enforced, and they are effectively designed. However, most MPAs established in the Northeast Atlantic allow different levels of fishing and that effective MPAs governance is case-dependent[17]. Allowing fishing in the MPAs would inevitably reduce the level of stock biomass from the projections presented here and reduce the effectiveness of these MPAs in achieving rebuilding targets under climate change. Although the MPAs target under the Kunming-Montreal Global Biodiversity Framework does not stipulate no-take zone, our study shows that lower fishing level with larger coverage of no-take MPAs help achieve biomass rebuilding targets under climate change. Moreover, although the overarching policy target is to eliminate overfishing, fisheries management and rebuilding plans in the Northeast Atlantic are not fully effective because of the shortcomings of the implementation tactics particularly under the challenges of changing climate[52,53]. The complexity of transboundary coordination within and beyond national jurisdictions add further challenges to effective marine spatial management and planning. Thus, in practice, achieving rebuilding targets under climate change effectively as shown in our projections would be conditioned on having no-take MPAs and good governance and management within and outside of the MPAs.

In some cases, the implementation of no-take MPAs can displace fishing effort, often leading to overfishing in surrounding waters while also impacting the efficiency of the no-take MPAs[54]. Our study captures such an effect by allocating a proportion of fishing to surrounding areas. However, in reality, it is possible that such effort is not proportionally distributed around the no-take MPAs but rather localized in some areas, or not re-distributed at all. In terms of modeling, we used a mechanistic species distribution model (the DBEM) to project future species distributions. Despite this being a common tool in biogeography, these types of models do not include species interactions, potential evolutionary adaptation, and are subjected to the original data from which the model distribution was made[55]. We only explored a limited number of climate, fishing, and no-take MPAs scenarios. These scenarios represent the subset of possible societal pathways for the future. Future studies could examine the existing no-take MPAs around the world, as well as alternative MPAs plans. Models that incorporate different mechanisms in which fishing effort is re-allocated around a no-take MPAs could help illuminate how social and economic factors related to fishing may affect the contribution of no-take MPAs to fish stock rebuilding under climate change, and vice versa. Nevertheless, a recent study used the DBEM to simulate changes in fish biomass with and without no-take MPAs and concluded that the simulations without no-take MPAs would result in fish biomass lower than those with no-take MPAs[27]. Also, when fish stocks are under-exploited ($F/F_{MSY} < 1$), no-take MPAs was projected to result in a reduction in catch while biomass was projected to increase. In contrast, under the over-exploited scenario ($F/F_{MSY} > 1$), no-take MPAs is projected to increase both catch and biomass. Such results indicated that the positive effect of no-take MPAs was not endogenous in the model, but were resulted from the interactions of fishing, climate change and the responses of fish stocks to these drivers.

Conclusion

The United Nations' Convention on Biological Diversity has set a target of "effective conservation and management of at least 30% of the world's lands, inland waters, coastal areas and oceans."[56] The countries bordering the marine ecoregions in the Northeast Atlantic included in this study, amongst many others in the world, have pledged to achieve such a target. Our findings show that no-take MPAs, combined with reducing fishing intensity, would help rebuild over-exploited fish biomass and benefit their dependent fisheries in the Northeast Atlantic under projected climate change in the 21st century. No-take MPAs should be a part of the portfolio of measures in developing climate-resilient stock rebuilding plans and achieving regional and global biodiversity targets.

Method

Fish and invertebrates stocks in the Northeast Atlantic

We included 739 exploited fish and invertebrates stocks (hereafter referred collectively as fish stocks) in the Northeast Atlantic ocean. Stock is defined here in the fisheries context, which is a fish or invertebrate species that is exploited in a spatial area unit. Following previous studies on assessing the current status of fish stocks[9] and projecting their future under climate change and fishing scenarios[19], we used marine ecoregions[57] to delineate the spatial area unit. We focused on species that were exploited in eight marine ecoregions in the Northeast Atlantic (Fig. 5). Specifically, stocks are defined as species occurring in a marine ecoregion with estimated catches. This includes 231 species (202 fishes and 29 invertebrates) with estimated catches between 2000 - 2019 in the Sea Around Us catch database[58] (www.seaaroundus.org, Table S1). Although uncertainties exist in the spatial allocation and reconstruction of catches in the Sea Around Us data[59], such uncertainties would only affect the identification of a stock and would not affect the projected relative changes in biomass and catch under climate change.

Climate-fish-fisheries model

We projected changes in biomass and potential catches of exploited species using a linked climate-fish-fisheries model called dynamic bioclimate envelope model (DBEM). The structure of DBEM is described in Cheung et al[19,55]. In brief, the model has a horizontal spatial resolution of 0.5°

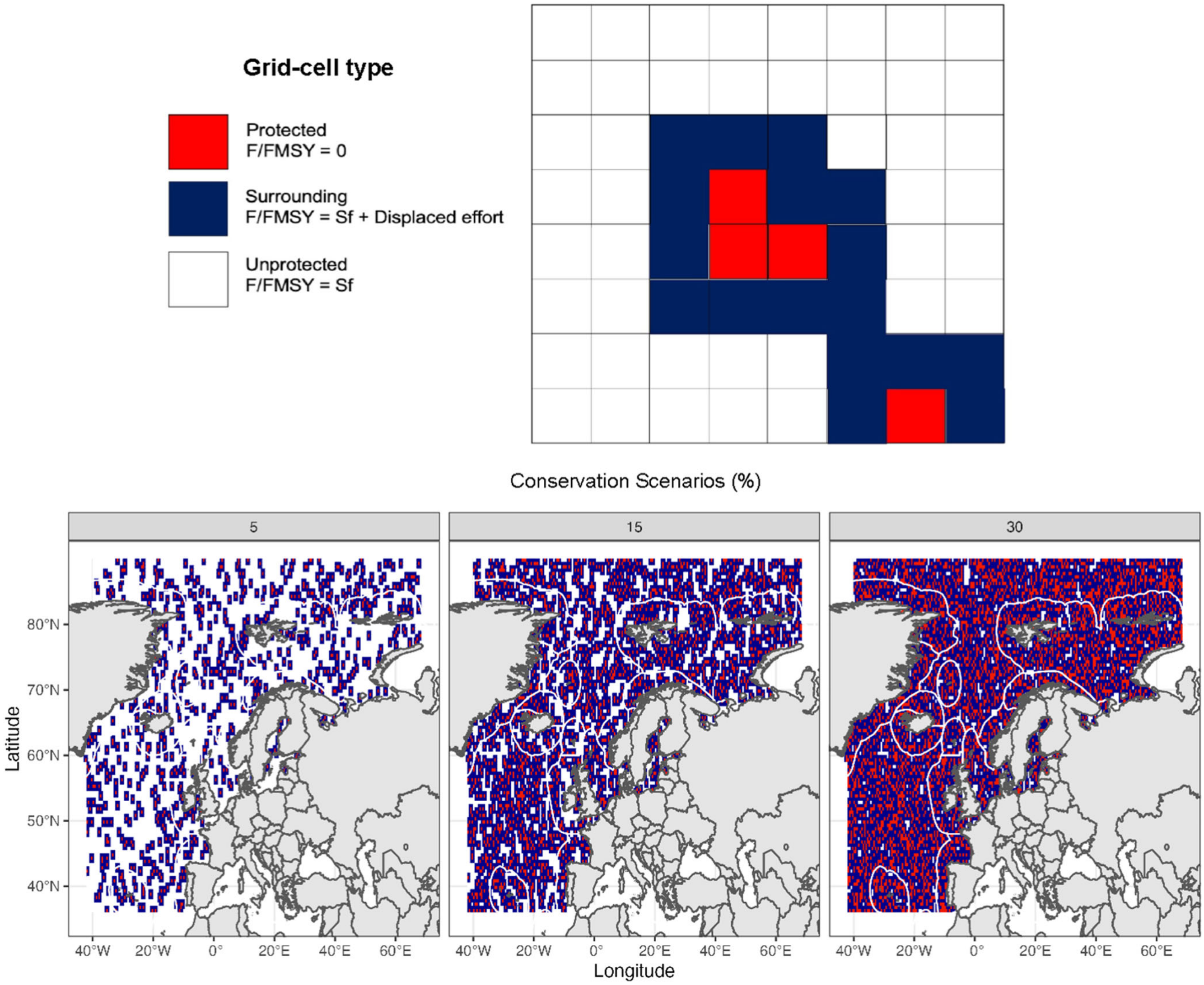

Fig. 5 | Map of no-take marine protected area scenarios and marine ecoregions within the United Nations' Food and Agriculture Organization's major fishing area 27 - Northeast Atlantic. Red shows protected cells, blue shows surrounding waters. The boundary of marine ecoregions is delineated by white lines.

latitude x 0.5° longitude for the sea surface and bottom, and simulates annual average abundance and catches of each modeled species. DBEM uses spatially explicit outputs from coupled atmospheric-ocean biogeochemical models, including temperature, oxygen level, salinity, surface advection, sea ice extent and net primary production. Sea bottom and surface temperature, oxygen and salinity are used for demersal and pelagic species, respectively. These outputs are then used to calculate an index of habitat suitability for each species in each spatial cell. Other information used to calculate habitat suitability includes bathymetry and specific habitats (coral reef, continental shelf, shelf slope, and seamounts). Changes in carrying capacity in each cell is assumed to be a function of the estimated habitat suitability, and net primary production in each cell.

The model simulates the net changes in abundance in each spatial cell based on logistic population growth, fishing mortality, and movement and dispersal of adults and larvae modeled through advection–diffusion–reaction equations. Specifically, pelagic larval dispersal is dependent on ocean current (simulated by the Earth system models) and pelagic larval duration estimated from an empirical equation. Dispersal of adults is dependent on spatial gradients of density relative to the carrying capacity (dependent on environmental habitat suitability) and species' mobility (e.g., large pelagic fishes have high movement rate while sessile species have negligible movement rate).

DBEM then calculates biomass from abundance using a characteristic weight representing the average mass of an individual in the cell. The model simulates how changes in temperature and oxygen content would affect the growth of the individual using a submodel derived from a generalized von Bertalanffy growth function. DBEM has a spin-up period of 100 years using the climatological average oceanographic conditions from 1951 to 2000, thereby allowing the species to reach equilibrium before it is perturbed with oceanographic changes. Previous studies have found strong correlation between catch data and DBEM projections from marine regions[55,60]. Although DBEM can account for the potential effects of ocean acidification (changes in pH) on growth, reproduction and survivorship[61,62], we did not include ocean acidification in this study because of its large variation of effects on exploited marine species.

In our model, fishing intensity was assumed in the fisheries scenarios, represented by fishing mortality rates (F) relative to the F required to achieve MSY (i.e., F/F_{MSY}). As the fish model assumes logistic population growth, following the derivation from a simple surplus production model, FMSY is approximately equal to half of the intrinsic growth rate of each species[63].

Climate and fishing scenarios and analysis

DBEM was forced with projections from the Geophysical Fluid Dynamics Laboratory (GFDL)-ESM4[64]. The variables that we extracted from the Earth

Table 1 | Summary of the climate change, conservation and fishing scenarios

Scenario	Number of scenarios	Differences between scenarios	Variable for each scenario	Values for each scenario
Climate Change	2	Radiative forcings	Global mean atmospheric surface warming (°C)	2.6 (low emission), 8.5 (high emission)
Conservation	3	Protection cover	Percentage of grids protected (%)	5, 15, 30
Fishing	4	Fishing effort	F/F_{MSY}	0.5, 0.75, 1.0, 1.5

system model simulation include global mean surface atmospheric temperature, sea surface and bottom temperature, dissolved oxygen concentration and salinity, vertically integrated total net primary production, sea ice extent, and surface advection.

Projections followed two contrasting scenarios—shared socioeconomic pathway (SSP) 1—representative concentration pathway (RCP) 2.6 (SSP1-2.6) and SSP5-8.5[65,66]. The SSP1-2.6 and SSP5-8.5 represent a “strong mitigation” low-emissions pathway and a “no mitigation” high-emissions pathway, respectively. The simulation time frame is from 1950 to 2100. The Earth system model projections consider 1950 to 2010 as a historical period that diverges into the two climate change scenarios from 2011 to 2100.

We re-expressed the simulated changes in ocean conditions and fish stocks under the SSPs according to the respectively projected global atmospheric warming levels. Different Earth system models and their versions vary in their projected intensity of climate change[67]. One commonly-used option to account for such variabilities in projections, especially for impacts and risk assessments, is to express response variables relative to global mean atmospheric warming level instead of time frame[67]. In this study, the simulated annual response variables from the climate-fish-fisheries model were related to the global mean atmospheric warming levels at the respective year and SSP. Such approaches to analyze projected climate impacts on fish stocks and fisheries have been used in previous studies[19,30,68]. We included four fishing scenarios and three no-take marine protected area scenarios. The F/F_{MSY} scenarios included 0.5, 0.75, 1 and 1.5, with 1 being at MSY level, and 1.5 at over-exploited level (Table 1). We implemented the fishing scenarios across the simulation time frame (1950 – 2100). Thus, these are idealized fishing scenarios intended for theoretical explorations of the effects of no-MPAs under climate change.

No-take marine protected areas scenarios and analysis

No-take marine protected area scenarios were expressed as the area of the Northeast Atlantic Ocean with no fishing (5%, 15% and 30% of the modeled ocean area). The analysis was limited to the Food and Agricultural Organization of the United Nations (FAO) major fishing zone 27-Atlantic Northeast (https://www.fao.org/fishery/en/area/27). The region was gridded into 0.5° latitude x 0.5° longitude grid cells. We identified the specific grid cells to be protected from fishing using the statistical software R. The 5% protection scenario includes the proportion of cells within FAO area 27 that are currently occupied by MPAs (by calculating the spatial coverage of protected areas relative to the total area of FAO zone 27 following the world database of protected areas[69]). The computed area (5.5% of the total area of the FAO area) is different from the actual designated area of the MPAs because of the coarser grid resolution of our model relative to the size of the MPA. The larger no-take MPAs coverage scenarios were then built on the smaller ones by progressively adding protected areas through randomly designating locations to be no-take MPAs from the 5, to 15 and 30% protection scenarios. Thus, the 5 and 15% scenarios are subsets of the 30% scenario. The average sizes of no-take MPAs patches (i.e., group of neighboring pixels that were assigned as MPAs) were $1246 \pm 1056\ \mathrm{km}^2$ (standard deviation, $n = 614$ patches), $1555 \pm 1364\ \mathrm{km}^2$ ($n = 1379$ patches) and $1646 \pm 1510\ \mathrm{km}^2$ ($n = 2571$ patches) for the 5, 15 and 30% scenarios, respectively.

Under each MPAs scenario, we reallocated fishing mortality from the protected area grid cell to the immediate surrounding grid cells, simulating the redistribution of fishing effort that often occurs when an area is closed to fishing (Fig. 5). To do this, we assigned which grid cells were protected and classified cells immediately surrounding them as *surrounding*, all other grid cells were classified as *unprotected* [27]. Fishing mortality was then proportionally redistributed from protected cell to surrounding cells (*prop*), with *prop* defined as:

$$prop = 1 + 1/\mathit{total\ number\ of\ grid\ cells\ surrounding\ an\ MPA}$$

For example, if there are 4 cells surrounding a protected cell, then *prop* $= 1.25$, if there are 2 surrounding cells then $prop = 1.5$.

Based on the computed *prop*, we re-estimated fishing mortality (f_{mort}) (i.e., reallocate fishing effort) in the surrounding cells as:

$$\hat{f}_{mort} = f_{mort} * prop$$

where $\hat{f}_{mort}$ is the fishing mortality adjusted for the ‘spill-over’ of fishing effort from the protected grid cell. If the cell is not protected nor surrounding a protected grid cell then $\hat{f}_{mort} = f_{mort}$, that is, fishing mortality will not be adjusted for the no-take MPAs effects.

Statistical analysis

We analyzed the relative contributions of no-take MPAs, fishing intensity and climate change on stock biomass and potential catches in the Northeast Atlantic region. Firstly, we analyzed the relationship between the simulated changes in biomass of the studied fish stocks, individually and aggregated across the stocks in the Northeast Atlantic region, relative to the projected global atmospheric warming levels. Secondly, we analyzed the mean responses of the biomass across the studied stocks in the Northeast Atlantic region under the various no-take MPAs, fishing and climate change scenarios using linear mixed effect models (‘lme4’ package of *R*). Here, the fixed effects were the area protected from fishing (no-take MPAs = 5%, 15% and 30%, as a factor), F/F_{MSY} (0.5, 0.75, 1, 1.5, as a factor) and global atmospheric warming levels (GWL, as a continuous variable). We set $F/F_{MSY} = 1$ (i.e., fishing at maximum sustainable rate) as the base factor in the models. To minimize the confounding effects of the algorithm that reallocated fishing effort of no-take MPAs to its surrounding area, we analyzed the effects of no-take MPAs relative to the 5% no-take MPAs scenario instead of a 0% no-take MPAs scenario. The different fish stocks were considered as random effects (1|stock). We used a multi-model approach to compare the following model structure:

Model 1: Biomass~factor(F/F_{MSY}) + (1|stock)
Model 2: Biomass~factor(F/F_{MSY}) + factor(MPA) + (1|stock)
Model 3: Biomass~factor(F/F_{MSY})+ factor(MPA) + GWL + (1|stock)
Model 4: Biomass~factor(F/F_{MSY})*GWL+factor(MPA) + GWL + (1|stock)

We tested the interactions between fishing and global warming level because preliminary exploration of the data indicated stocks’ sensitivity to climate change may vary at different stock sizes in the Northeast Atlantic region. We computed and compared the Akaike Information Criteria (AIC) of the models using the outputs from the climate-fish-fisheries models across all the scenarios and the ‘*AIC*’ function in *R*. We selected the model with the lowest AIC.

We also apply the same set of model structures to examine the effects of the variables and factors on catch potential. For catch, we expected that over-exploited fish stocks have lower biomass production, and no-take MPAs may have different effects on the catch of these fish stocks compared to those that are under- or fully- exploited (i.e., fishing mortality below or at MSY level). Thus, we added a model structure with a term that represented whether the stock is subjected to over-exploitation or not (i.e., fish stocks were considered being over-exploited if $F/F_{MSY} > 1$). This over-exploited term was included as a factor that interacted with MPAs.

Model 5*: Catch~factor(F/F_{MSY})*GWL+factor(MPA)*factor(over-exploited) + GWL + (1|stock)

We repeated the analysis of the linear mixed effects models by changing the MPA factor from the area protected in the Northeast Atlantic (factor) to the area of the geographic range of each stock that was protected from fishing (continuous variable). In this study, we randomly assigned spatial cells as protected areas. Thus, the no-take MPAs scenarios were not designed for optimizing biomass or catch potential, or other ecological, social or economic objectives. We therefore undertook a *post-hoc* by calculating the proportions of distribution of the fish stocks that were within the designated no-take MPAs under each scenario and testing the effects of such proportions on the projected changes in biomass and catch. The results of such additional analysis would help understand how alternative no-take MPAs designs that protect different proportions of the stocks may contribute to biomass rebuilding under climate change.

Based on the outcomes of selected models, we can identify the relative contribution of each factor and variable, and their combinations, to changes in biomass and catch potential. Biomass and catch potential changes were expressed relative to the estimated biomass or catch at F = FMSY (i.e., dividing the estimated effects of each variable or factor by the intercept of the model).

Sensitivity analysis

We ran a sensitivity analysis by repeating the selection locations three times for each of the three no-take MPAs scenarios with F/F_{MSY} set to 1 under SSP RCP8.5. We applied these alternative sets of locations to a subset of species ($N = 10$) that broadly represent different ecology (pelagic and demersal, coastal and oceanic), life history characteristics (small-bodied/fast-growing and large-bodied/lowered growing) and taxonomy (crustaceans, molluscs, finfish and elasmobranchs) (Table S1). We ran an additional mixed effect model and examined the effects of the no-take MPAs locations (locations) on biomass:

Model (sensitivity analysis): Biomass ~ factor(MPA) + GWL + factor(locations)+(1|stock)

This study does not require ethical approval from the Research Ethic Board.

Data availability

Data are available at: https://doi.org/10.5061/dryad.gf1vhhmtb.

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Authors contributions

W.W.L.C and J.P-A conceived and designed the study. All authors wrote and reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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