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Overfishing species on the move may burden seafood provision in the low-latitude Atlantic Ocean

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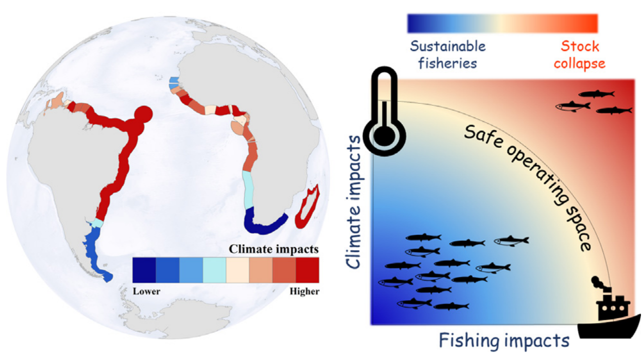
HIGHLIGHTS

- Shifting distributions of commercial marine species may threaten food security.
- Few studies have previously focused on the Central and Southern Atlantic Ocean.
- Climate impacts on pelagic fish mainly affect low-latitude regions.
- The spatial co-occurrence of climate and fishing stressors threaten pelagic fish.
- Redistributing/lowering fishing pressure may enhance resilience to climate change.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate and fisheries interact, often synergistically, and may challenge marine ecosystem functioning and management, along with seafood provision. Here, we spatially combine highly resolved assessments of climate-driven changes in optimal environmental conditions (i.e., optimal habitats) for the pelagic fish community with available industrial fishery data to identify highly impacted inshore areas in the Central and Southern Atlantic Ocean. Overall, optimal habitat availability remained stable or decreased over recent decades for most commercial, small and medium size pelagic species, particularly in low-latitude regions. We also find a worrying overlap of these areas with fishing hotspots. Nations near the Equator (particularly along the African coast) have been doubly impacted by climate and industrial fisheries, with ultimate consequences on fish stocks and ecosystems as a whole. Management and conservation actions are urgently required to prevent species depletions and ensure seafood provisioning in these highly impacted, and often socioeconomically constrained areas. These actions may include redistributing fishing pressure and reducing it in local areas where climate forcing is particularly high, balancing resource exploitation and the conservation of marine life-supporting services in the face of climate change.

1. Introduction

At a time when the world is anticipating unprecedented human population growth and demand for natural resources, climate-driven changes in marine ecosystems may threaten seafood provisioning and, hence, livelihoods and food security for billions of people (García-Molinos et al., 2016; Lenoir et al., 2020; Pecl et al., 2017). Understanding how marine ecosystems and associated provisioning services respond to climate change has been recognized as a major societal challenge (Boyce et al., 2020; Lotze et al., 2019; Pecl et al., 2017), and is underpinning the need for management and conservation actions contributing to the sustainability of key socio-economic activities, while safeguarding the integrity of life-

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supporting marine systems (FAO, 2020; Pecl et al., 2017; Pinsky et al., 2018; Ramírez et al., 2021, 2017).

The oceans are listed among the most impacted of Earth's biomes, and are showing rates of environmental changes similar to past events that resulted in increasing extinction rates or ecosystem collapses (Burrows et al., 2011; Halpern et al., 2015, 2007). Climate change is impacting the oceans at multiple levels (from genes to communities; Scheffers et al., 2016) and in different ways (from species physiological to demographic responses; Poloczanska et al., 2016, 2013). The potential shifts in species' geographic distributions are widely recognized as one of the most alarming consequences (Burrows et al., 2011; Lenoir et al., 2020; Maureaud et al., 2021; Pinsky et al., 2020). Besides the ecological effects that may threaten the integrity of marine ecosystems (Poloczanska et al., 2016), climate-driven shifts in species' distributions may pose socioeconomic challenges through their impacts on fisheries and seafood provision (Mendenhall, 2020; Ojea et al., 2020; Pecl et al., 2017; Ramos Martins et al., 2021). Indeed, commercially valuable marine species are shifting their distributions and it is expected that 23% to 35% of global exclusive economic zones (EEZs) will have new transboundary stocks by the end of this century (Ojea et al., 2020; Palacios-Abrantes et al., 2022; Pinsky et al., 2018). Species redistribution are reshaping the patterns of catch potential between regions and fishing sectors (Cheung et al., 2010; Palacios-Abrantes et al., 2022), and may lead to increasing impacts on marine resources and substantial geopolitical conflict (Boyce et al., 2020; Mendenhall, 2020; Pecl et al., 2017; Pinsky et al., 2018).

Climate impacts on species distributions are further aggravated by human activities such as fisheries (Berkeley et al., 2004; Coll et al., 2020; García-Molinos et al., 2016; Ottersen et al., 2006; Ramírez et al., 2021). Fishing pressure has increased over the last decades, with recent assessments showing that ca. 60% and 34% of fish stocks worldwide are completely exploited and overexploited, respectively (FAO, 2020; Rousseau et al., 2019). This high fishing pressure has been suggested to speed up the climate-driven displacement of marine species distribution through resource depletion and population crashes at the trailing edge (Lenoir et al., 2020). However, fisheries constitute an important socioeconomic sector that provides a major source of food for humanity and supply employment and economic benefits to those engaged in the activity (Pinello et al., 2017). Therefore, there is a necessary shift towards sustainable fisheries that requires finding a balance between exploitation of natural resources to ensure human well-being and the conservation of marine life-supporting services in the face of climate change (i.e. "Doughnut" fisheries; Ramírez et al., 2021; Raworth, 2017; see also FAO, 2020; O'Neill et al., 2018).

The Safe Operating Space (SOS) has recently been proposed as a suitable and achievable framework to contribute to the conservation and sustainable use of marine living resources and essential provisioning services, including fisheries, in the face of climate change (Ramírez et al., 2021). A central element of SOS application to fisheries is that critical climate levels for environmental collapse can be lowered locally by fishing pressure, thus increasing the risk of commercial stocks collapse. Redistributing and reducing fishing pressure in areas where climate forcing is particularly high can contribute to maintain marine ecosystems within a SOS, by alleviating pressure on, and enhancing resilience of key species, communities and associated ecosystem services (including provisioning, but also regulating, supporting and cultural services).

Unfortunately, the effective implementation of SOS for fisheries has been hampered by the lack of spatially-explicit assessments of the spatial congruence between fishing and climate impacts (O'Neill et al., 2018; Ramírez et al., 2021, 2017). This represents a major challenge for the vast and remote oceans, where biological observations and integrated measures on the spatial distribution of these impacts are difficult to obtain at required spatial and temporal resolutions to identify those highly impacted areas where fisheries should be more strongly monitored and regulated (Maureaud et al., 2021). Long-term satellite-based remote-sensing applications now provide a means for investigating climate-driving changes in optimal environmental habitat availabilities, likely driving marine species distribution shifts, at an unprecedented extent and spatial resolution. This is particularly true for the marine realm, where organisms apparently track climate-driven shifts in environmental conditions more closely than terrestrial species (Lenoir et al., 2020; Pinsky et al., 2019, 2013). Previous research that evaluated marine species distributional shifts mostly focused on responses to changing temperatures (Burrows et al., 2011; García-Molinos et al., 2016; Lenoir et al., 2020; Morley et al., 2018). However, it is unlikely that all species will shift their ranges towards higher latitudes in response to isothermal shifts because of additional biological and environmental processes (Coll et al., 2020; Fuchs et al., 2020; Ramos Martins et al., 2021; Rivadeneira and Fernández, 2005). There is a growing appreciation for the role of the multiple environmental factors beyond thermal conditions that may shape patterns of marine biodiversity in general and commercially relevant species in particular (Ojea et al., 2020; Ramos Martins et al., 2021; Rilov et al., 2019; Woodin et al., 2013).

In this study, we aim to identify highly impacted areas in the Central and Southern Atlantic Ocean (including seven Large Marine Ecosystems -LME- and 27 associated EEZs), where the combined impact of climate and human fisheries may threaten the small and medium size pelagic community (Fig. 1). We focussed on these species because of their key role in pelagic food webs and their high commercial value (Cury et al., 2000; Pauly et al., 2020; Pikitch et al., 2014; see also Table S1). Thus, we first integrate multiple predictors, such as depth, sea surface temperature (SST), salinity (SSS), and net primary productivity (NPP) to perform spatially-explicit assessments of climate-driven changes in optimal environmental habitats (hereafter optimal habitat) that are likely to drive distribution shifts of 20 main commercial species (Fig. S1). We then combine these assessments with the most spatially-explicit information on industrial fishery data to identify highly impacted areas where climate-driven changes in optimal habitat availability and fishing pressure overlap spatially. Management and conservation actions aimed at enhancing ecosystems' resilience to climate change by redistributing and reducing fishing pressure in these "doubly" and highly impacted areas (i.e., our SOS framework) can potentially contribute to the present and future environmental status of marine ecosystems and the sustainable exploitation of marine resources (Coll et al., 2016, 2012; Ramírez et al., 2021).

2. Material and methods

Data analyses and GIS procedures were conducted in R version 3.6.2 (R Core Team, 2021), whereas mapping designs and displays were performed with ArcGIS 10.5 (ESRI, Redland, USA).

2.1. Data mining

Optimal ranges for key environmental features (i.e., depth, SST, SSS, and NPP) likely driving the distribution of selected species were taken from AquaMaps. AquaMaps is an approach to generate model-based, large-scale predictions of natural occurrence of marine species. Models are constructed from estimates of the environmental tolerance of a given species to depth, SST, SSS, NPP, dissolved bottom oxygen and sea-ice concentration. Environmental tolerances are provided by a trapezoidal-shaped response curve that assumes that the probability that a species is present is uniformly highest where mean environmental conditions fall within the "preferred parameter range" of the species (see details in Ready et al., 2010). To explore changes in the availability and distribution of optimal habitats for target pelagic species, we exclusively considered environmental values within species-specific preferred ranges of depth, SST, SSS, and NPP provided by AquaMaps (Table S2).

To produce our spatially-explicit assessments of optimal habitats, we took the depth information from the ETOPO1 Global Relief Model (NOAA, https://www.ngdc.noaa.gov/mgg/global/). Spatial-temporal information on ocean temperature was taken by averaging annually the NOAA Optimum interpolation (OI) SST (°C) V2 (1° horizontal resolutions; sourced at https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.html; accessed on September 2018). SSS (PSU) and NPP ($mol{\cdot}m^{-3}$) were sourced from the Global Ocean Physics and Biogeochemistry Reanalyses (GLOBAL_REANALYSIS_PHY_001_030–0.083° horizontal resolution- and GLOBAL_REANALYSIS_BIO_001_029–0.25° horizontal resolution- for SSS

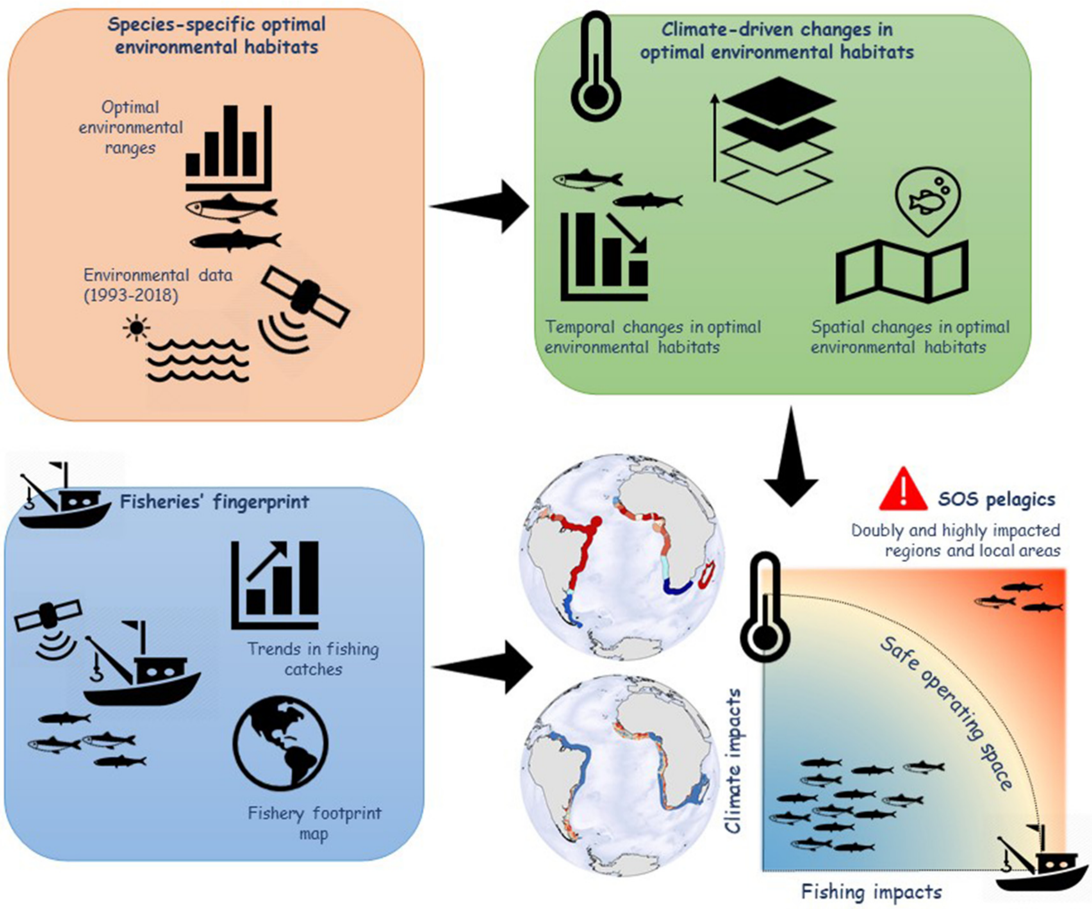

Fig. 1. Workflow and work concept. Spatially-explicit assessments of changes in optimal habitat availabilities for main commercial species within the small and medium size pelagic functional groups were combined with available data on industrial fishing catches and spatial fingerprint to identify local to regional "doubly" and highly impacted marine areas. Redistributing and reducing fishing pressure in these areas may help to reach the balance between resource exploitation and the conservation of marine life-supporting services in the face of climate change (i.e., Safe Operating Space -SOS- framework).

and NPP, respectively; sourced at EU Copernicus Monitoring Environment Marine Service; https://marine.copernicus.eu/). Environmental time series were restricted to the 1993–2018 period; the minimum time period for which information on SST, SSS and NPP is available.

We obtained spatially-explicit estimates of fishing effort from Global Fishing Watch -GFW- (http://globalfishingwatch.org/; accessed on August 2018). GFW is a global repository of fishing activity where automatic identification system (AIS) data are processed to discern fishing pressure by main fishing gears (Kroodsma et al., 2018). Our analyses focused on 2012–2016 GFW data for those fishing gears targeting small and medium size pelagic fish species (i.e., a combination of trawlers and purse seiners). The fishing gears considered may target additional species besides the ones on which the current study focuses on. However, selected species contributed the most to total catches within the small and medium size pelagic functional groups (Fig. S1). Long-term trends in fishing catches for the small and medium size pelagic fish species included in the analyses were obtained from the Sea Around Us project -SAU-, (http://www.seaaroundus.org/; accessed on July 2020). SAU is the only data source with long-term (1951–2016), spatially explicit (i.e., at the LME and EEZ levels), and global estimates of fishing catches (Pauly et al., 2020). Here, we selected fishing catches from 1993 onwards to match the time period of environmental data.

2.2. Spatial-temporal trends in optimal habitat availability

Based on depth profiles and long-term, spatially-explicit data on SST, SSS, and NPP, we evaluated how areas encompassing preferred parameter ranges for selected species (i.e., optimal habitats) varied temporally and spatially within LMEs and EEZs. First, we estimated the total area of species-specific optimal habitats yearly within LMEs and EEZs; i.e., the spatial intersect between areas encompassing optimal ranges of depth, SST, SSS, and NPP expressed in km^2 (Table S3). As a proxy to changes in optimal habitat availability, we evaluated trends in the extent (km^2) of optimal habitats along the 1993–2018 period through linear regressions with Gaussian distributions, and using the slopes (and significances; α-value) as estimates for the magnitudes of observed changes (Figs. 2 to 4).

We quantified the persistence of the species' optimal habitats on a per-pixel/cell basis by counting how many years (for the 1993–2018 period) each pixel was identified as optimal in terms of SST, SSS, and NPP. Thereby, we obtained a spatially-explicit proxy for climate-driven environmental effects on the distribution of species' optimal habitats. Depth was not considered here as it was assumed to be constant throughout the study period. Spatial outputs for each feature ranged from 0 (all years categorized as sub-optimal; i.e., permanently sub-optimal conditions) to 26 (all years categorized as optimal; permanently optimal conditions).

We used an equally weighted combination of feature-specific outputs (i.e., SST, SSS, and NPP outputs) as a proxy to the overall persistence of optimal environmental conditions for target species (Fig. S2). The resulting outputs encompassed marine areas with minimum values indicating a higher persistence of sub-optimal conditions, and maximum values denoting areas with a higher persistence of optimal conditions (Figs. S3 and S4). Here, we considered that optimal ranges of SST, SSS and NPP equally contribute to species distribution. However, our approach can be revisited, updated and refined by incorporating information on the relative weight these multiple drivers might have in shaping species-specific distributions.

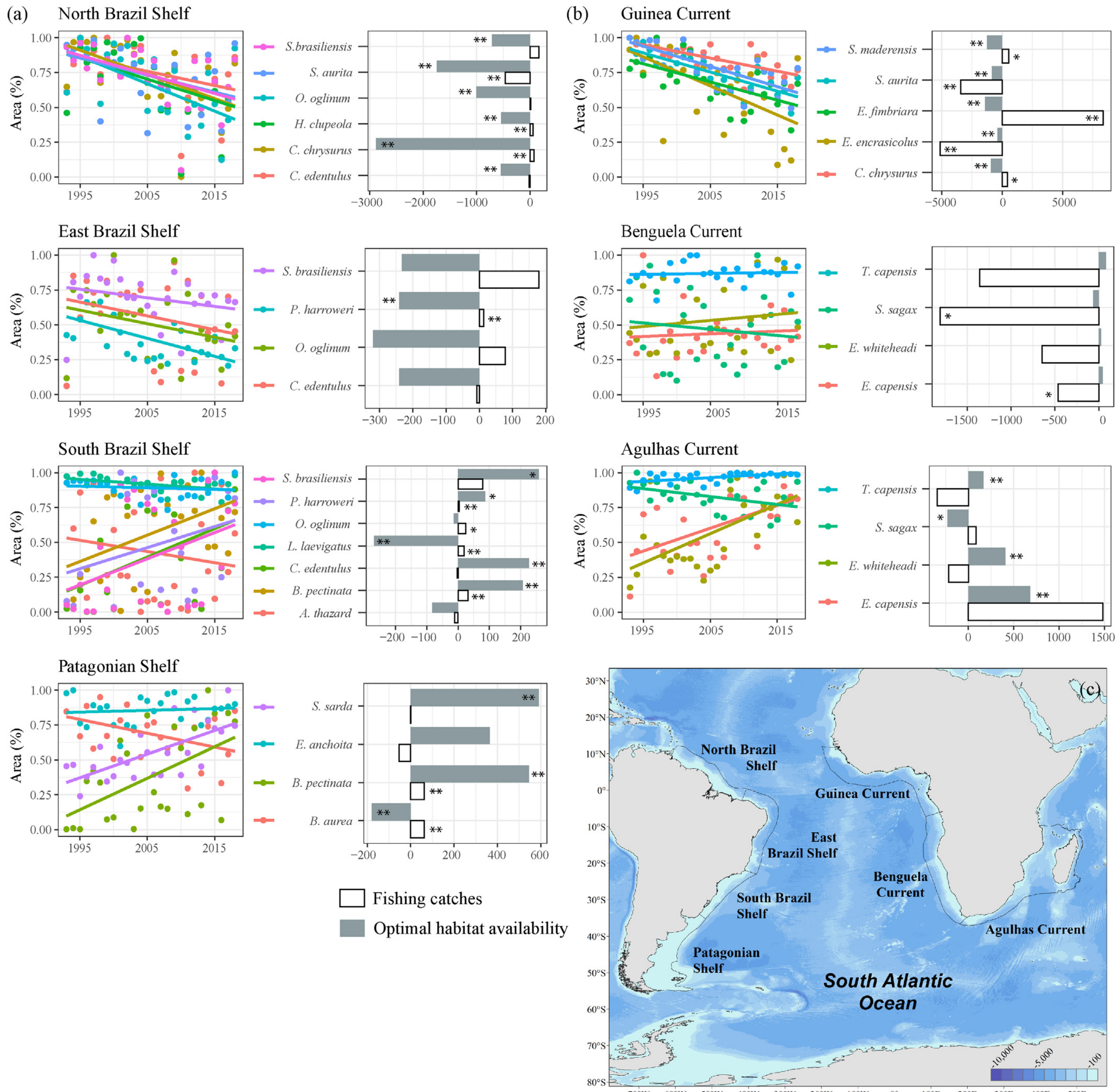

Fig. 2. Long term (1993–2018) trends in the availability of marine areas encompassing optimal ranges of depth, SST, SSS and NPP (i.e., optimal habitat availability) for main species occurring at the (a) South American and (b) African Large Marine Ecosystems (LME). The geographic distribution of LMEs is shown in (c). For representation purpose, and to make comparable the long-term trends in optimal habitat availabilities for all species, the scatterplots represent the area of optimal habitats in % respect maximum recorded surface per species. Bar plots represent the slopes (magnitude) and significances (asterisks; *: *p*-values < 0.1; **: *p*-value < 0.05) for the linear regressions on the long-term trends in the absolute values of optimal habitat availabilities (grey) and total catches by fisheries (white; data from Sea Around Us for the 1993–2016 time period).

As a proxy to the overall persistence of optimal environmental conditions for all species within LMEs, we calculated a combination of species-specific products weighted by species' relative contributions to total catches per LME (based on data from SAU, Fig. 5). These cumulative changes were roughly similar when considering an equally-weighted combination of species-specific products (Fig. S5).

2.3. The overlapping impact of fisheries

Using species-specific, long-term (1993–2016) data on total catches from SAU we evaluated trends in fish catches for target species within LMEs and EEZs. To this aim, we conducted linear regressions with Gaussian distribution and considered the slopes (and significance) as estimates for the magnitudes of observed changes (Figs. 2 to 4).

We also overlapped our proxy of climate impacts on species' optimal habitat distributions (i.e., the persistence of optimal habitats) with spatially-explicit information on the combined fishing pressure by trawlers and purse seiners (data from GFW). Previously, we summed daily fishing records to spatially explicit annual totals for the 2012–2016 period. Then, we averaged the entire time series to obtain an overview of the spatial distribution of fishing pressure, which allowed us to highlight those marine areas that fisheries have particularly impacted over recent years. We then

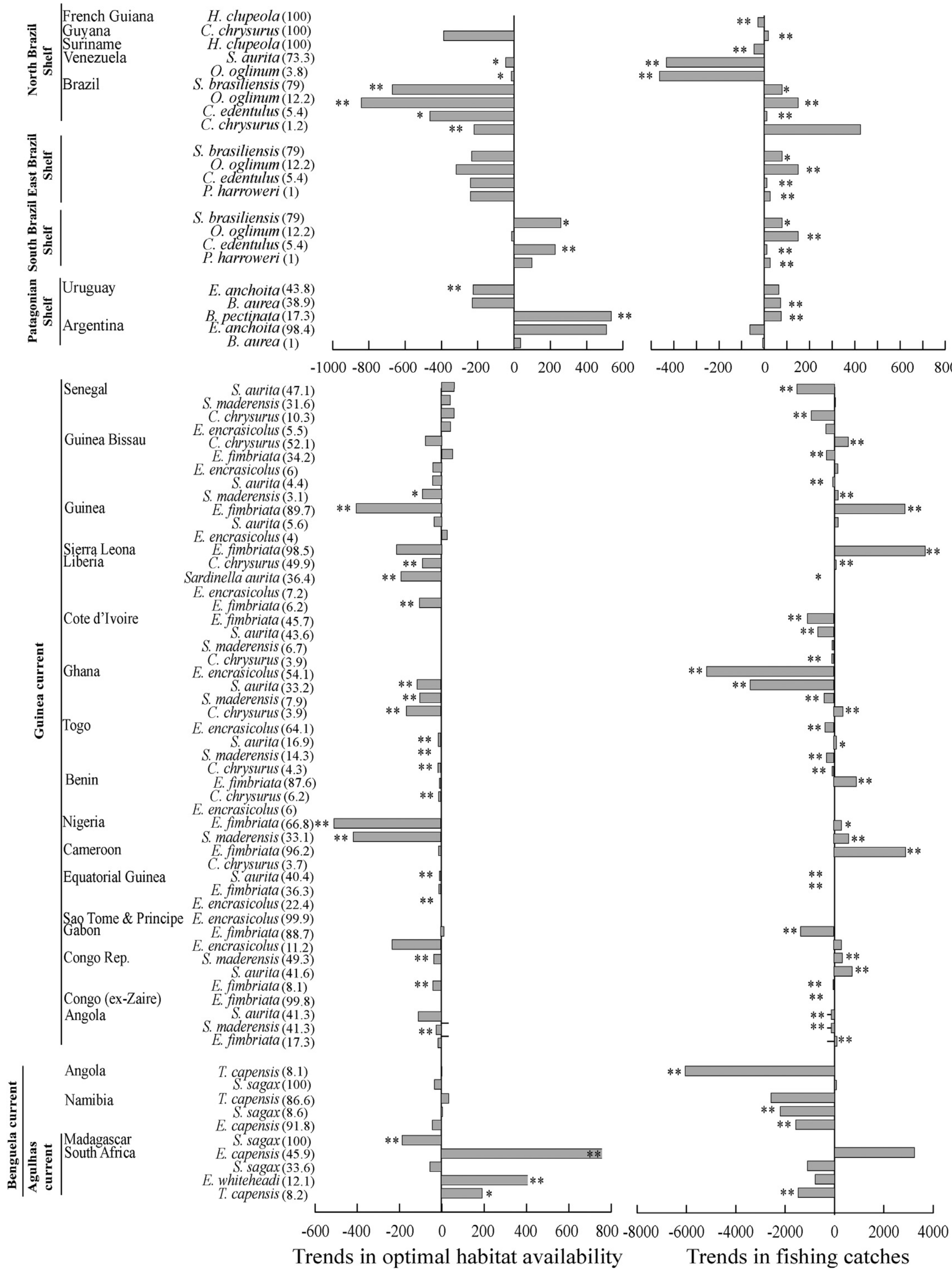

Fig. 3. Long-term (1993–2018) trends in optimal habitat availability and fish catches (data from Sea Around Us for the 1993–2016 time period) per main species and EEZ (sorted by their relative contributions to total catches of small and medium size pelagic fish, % in brackets). We represent the trends (slopes of the linear regressions) and significances (asterisks; *: p-values <0.1; **: p-value <0.05). For simplification, we exclusively represent small and medium size pelagic fish species with relative contributions to total catches ≥1%.

estimated the cumulative impact of our proxies for climate effects and fishing pressure by multiplying both layers. Here, we interpret the cumulative impact as the spatial overlap between climate-driven environmental changes and fishing pressure. By multiplying both layers, we exclusively considered those marine areas where both impacts co-occur spatially (i.e., excluding those areas that were exclusively impacted either by climate forcing or fishing pressure). The spatial output ranged from 0 (i.e., no fishing and climate impacts) to maximum values depicting those areas impacted the most by both stressors. Marine areas with an overlying climate and fishing impact effect were subsequently categorized according to quartiles (Q1 to Q4), covering the magnitude of the cumulative effect within different LMEs. Therefore, areas within the Q4 can be interpreted as those marine systems that are impacted the most by both climate change and fishing pressure (Fig. 5).

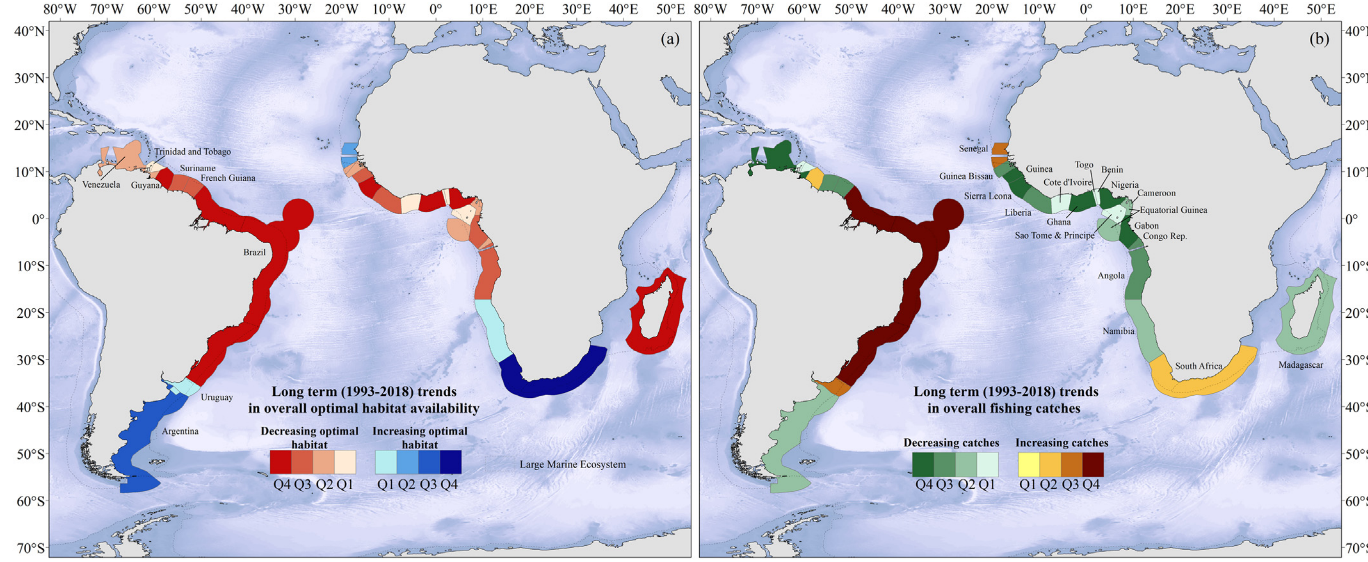

Fig. 4. Long term trends (slopes of the linear regressions) in (a) the EEZ-specific overall availability (absolute area in km^2) of marine areas encompassing optimal ranges of depth, SST, SSS and NPP for all target species (i.e., average for species-specific optimal habitat availabilities; 1993–2018 period); (b) total catches from fisheries at EEZs (data from Sea Around Us -www.seaaroundus.org-; 1993–2016 period). EEZs have been categorized in quartiles according to increasing or decreasing optimal habitat availability and fishing catches.

3. Results

According to our findings, trends in optimal habitat availability contrast between species, LMEs, and EEZs (Table S3 and Figs. 2 to 4). Overall, optimal habitat availability remained stable or decreased for most small and medium size pelagic species throughout our study area. However, we found a latitudinal gradient whereby low-latitude regions (e.g., Guinea Current and North Brazil Shelf LME, and associated EEZs) are most affected by decreasing availability of optimal habitats. Contrastingly, species' optimal habitat availability in poleward regions (e.g., Patagonian Shelf or South Brazil Shelf LMEs) remains roughly stable, or even increases, throughout the last decades (with a few exceptions, see Figs. 2 to 4).

Historical trends (based on SAU data) reveal that fishing catches have decreased through the study period for most areas, with few exceptions (e.g. Brazil and South Africa, Figs. 2 to 4; decreasing trends in fish catches are reported for 22 out of 27 EEZs). Finer-scale analyses on the distribution of fishing pressure (based on GFW data) indicate that fishing activities are heterogeneously distributed spatially and concentrated mainly in particular areas within the Patagonian Shelf or the Guinea and Benguela Currents (Fig. 5).

By combining our fine-scale analyses on optimal habitats and fishing pressure distribution, we identified "doubly" and highly impacted marine areas. In these areas, persistently suboptimal (hereafter refereed as suboptimal) environmental conditions (i.e., environmental conditions were categorized as suboptimal persistently over the 1993–2018 period) overlap with an intense fishing pressure (see Fig. 5 and Figs. S2 to S4).

We show that these "doubly impacted" marine areas are unevenly distributed in the Central and South Atlantic LMEs as a result of the heterogeneous distribution of suboptimal marine areas and fishing pressure (Fig. 5). Overall, in the North and East Brazil Shelfs, doubly impacted marine areas are nearly absent, except a relatively small area in the central, coastal region of the North Brazil Shelf. In contrast, large marine areas within the South Brazil and the Patagonian Shelfs are identified as environmentally suboptimal and subjected to an intense and combined fishing pressure by trawlers and purse-seiners. The highest impacted areas largely occur along the coast of the South Brazil Shelf and the continental shelf-break of the Patagonian Shelf. On the eastern side of the Central and South Atlantic Basin, doubly impacted areas are distributed along with coastal areas of the Central and North Benguela, and in three main regions of the Guinea Current (South, Central, and West).

4. Discussion

4.1. Following climate-driven environmental shifts

Available information on climate-driven distribution shifts for marine species is mainly biased towards the Northern hemisphere (Comte et al., 2020; Lenoir et al., 2020; Morato et al., 2020; Pinsky et al., 2020). In this study, we provide spatially-explicit assessments of changing optimal habitat availabilities likely driving shifting distributions for main pelagic species in the ecologically relevant Central and Southern Atlantic Ocean. Naturally, other ecological, biological, and physical variables may play an additional role in delimiting species' fundamental niches and, hence, may affect species' distribution. Our approach is not limited to the environmental tolerances provided by AquaMaps, and can be updated to use any set of drivers of change.

A proper understanding of the determinants of current and historical distributional range shifts of species is necessary to improve the prediction of future trajectories under different climate scenarios (Heller and Zavaleta, 2009; Rilov et al., 2019). It should be noted that projecting specific future distributions were beyond the scope of this study. Forecasting distributions of species on the move has a risk of failure without considering (i) the complex processes reflecting the interaction and nonlinear dynamic of multiple environmental and human derived factors; and (ii) how the organisms (even individuals within populations) may respond to the novel, non-analogous environmental conditions presented by climate change through several physiological (e.g., thermal tolerance), ecological (e.g., predatory interactions) and evolutionary processes (e.g., adaptation / acclimatation) (Rilov et al., 2019; Woodin et al., 2013; and references therein). Rather, the value of this first step lies in using past observations to demonstrate that fishing in areas where climate change impacts have resulted in reduced suitable habitat is likely to be detrimental, not only to fished stocks but to the states of the underlying ecosystems as a whole; i.e., the SOS framework. This framework may highlight important considerations for present fisheries adaptive management by regulating and/or redistributing fisheries to ameliorate pressure in those areas where environmental conditions are changing at the fastest rates.

Trends in optimal habitat availability differed spatially, with low-latitude regions being the most affected by decreasing availability of optimal habitats over recent decades. This concurs with general global trends reported on the uneven distribution of environmental change effects in

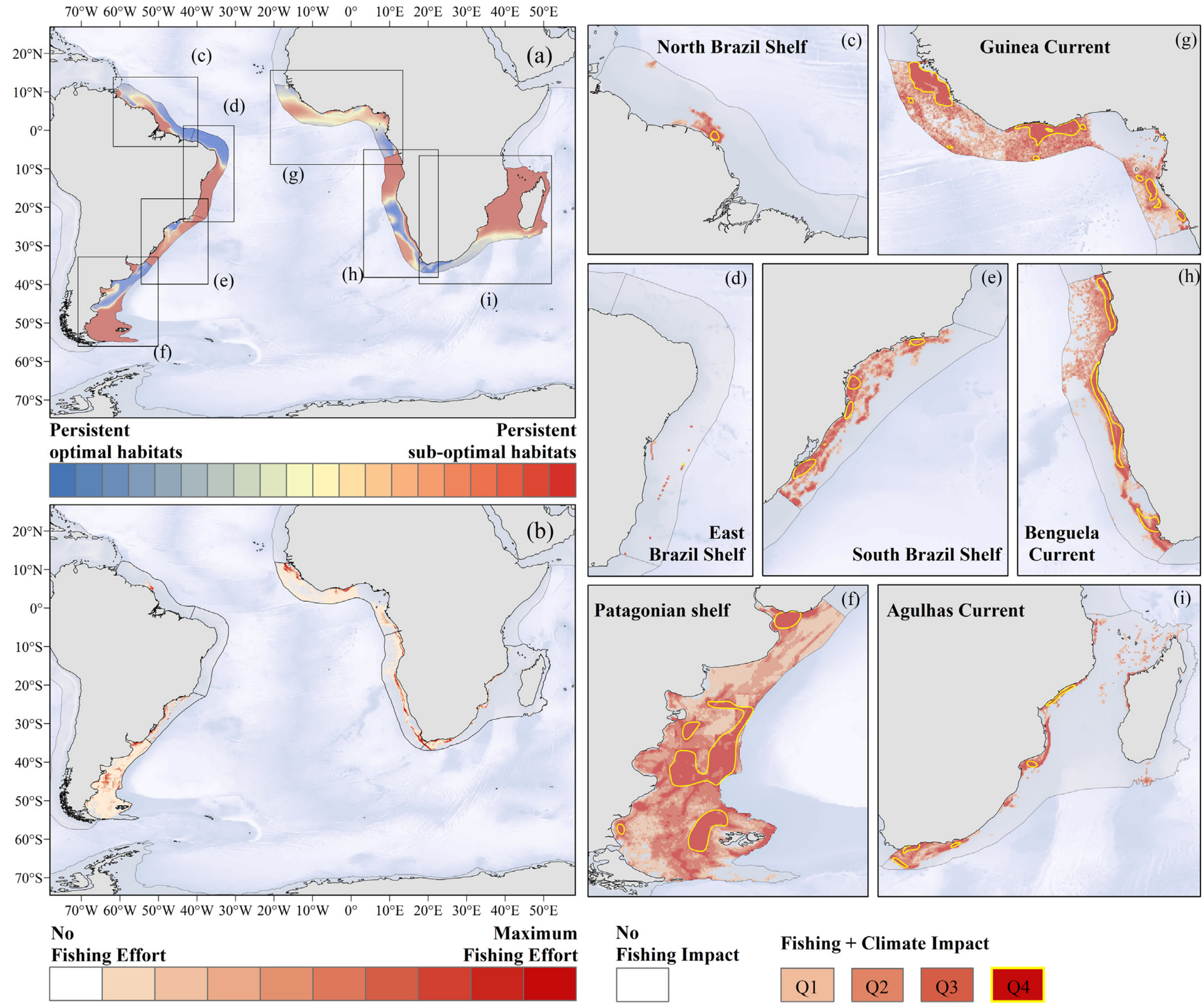

Fig. 5. Our proxy to (a) climate impacts on species' optimal habitat distributions (i.e., the persistency of optimal habitats, see Methods and Figs. S2 to S5) is combined with the (b) spatial distribution of fishing pressure (combining trawlers and purse seiners, data from GFW) to provide a spatial-explicit proxy to the cumulative impact of climate effects and fishing pressure (c to i). Colours for the cumulative impact represents marine areas categorized in quartiles (Q1 to Q4) according to the magnitude of the cumulative effect.

the oceans, highlighting tropical and sub-tropical areas as those of special concern because of the impact of shifting environmental conditions (Burrows et al., 2011; Ramírez et al., 2017). Shifts towards higher latitudes in ocean water isotherms (the so-called velocity of climate change) have also been reported to be more intense in low-latitude regions of the South Atlantic Ocean (Burrows et al., 2011). Finally, projected impacts of climate change on marine communities based on Marine Ecosystem Models (MEMs, some of which account for food-web dynamics) have also revealed that the areas around the tropics are likely among the most impacted of marine regions, and less suitable for a range of species (Coll et al., 2020; Lotze et al., 2019; Tittensor et al., 2021). This is partly because no communities of organisms from warmer regions exist to replace those moving out of the tropical and sub-tropical regions (Burrows et al., 2011). Additionally, marine species in the tropics are believed to have smaller thermal safety margins as they live closer to their upper thermal limits (Pinsky et al., 2019). As the ocean warms, tropical species will likely fall out of their optimal thermal ranges and be forced to shift their distributions towards higher latitudes (Burrows et al., 2011; Lenoir et al., 2020; Pinsky et al., 2019).

Scarce information is available on the shifting distributions of small and medium size pelagic fish from our study area to evaluate their analogous responses to observed environmental shifts (based on the BioShifts geodatabase, Comte et al., 2020; Lenoir et al., 2020). However, pole-wards shifts in the distribution of pelagic and demersal fish species have been reported in the northern areas of the Benguela Current (i.e. Angola). While, latitudinal shifts of species in central (Namibia) and southern (South Africa) areas have occurred in both directions (van der Lingen et al., 2006; Yemane et al., 2014). Similarly, we observe no clear reductions in optimal habitat availability for pelagic species associated with latitudinal shifts off Namibia and South Africa. Instead, our results point to an eastward shift in optimal habitat availability for the commercially and ecologically important Southern African anchovy (*Engraulis encrasicolus*) and pilchard (*Sardinops sagax*). This result corresponds with the widely reported eastward shifts in the distribution of these pelagic species (Coetzee et al., 2008; Roy et al., 2007; van der Lingen et al., 2006), as well as with the negative impacts on the important seabird community of the Southern Benguela that largely rely on these species for prey (Crawford et al., 2019, 2007).

According to our results, the most vulnerable and socioeconomically constrained developing nations in the Atlantic Ocean, particularly those near the equator, have already experienced the most striking deteriorating trends in optimal environmental conditions for pelagic fish species. These trends will likely exacerbate in the future (Boyce et al., 2020), potentially leading to reductions in species abundance and changes in community compositions, and reshaping patterns of provisioning services (Burrows et al., 2011; García-Molinos et al., 2016). Therefore, these nations are likely to experience greater local changes due to poleward range shifts (Wiens, 2016) and will likely face greater economic constraints. This may widen the existing equity gaps among sovereign states, potentially leading to substantial conflict (Boyce et al., 2020; Mendenhall, 2020; Ojea et al., 2020; Spijkers et al., 2019).

While environmental shifts, particularly in isotherms, explain a substantial variation in rates of marine species (Sunday et al., 2015), some species have shifted their ranges faster than environmentally expected (Pinsky et al., 2013; Poloczanska et al., 2013; Sunday et al., 2015), or even in the “wrong” direction (Fuchs et al., 2020; Rivadeneira and Fernández, 2005). This could be partly explained by particular intrinsic traits that may enhance or buffer species vulnerability to climate impacts. For instance, adult and larval mobility has been revealed as an essential trait shaping species' responses to environmental shifts (Raventos et al., 2021; Sunday et al., 2015). Our study targets pelagic fish species, which have a notable capacity to swim and thus to actively shift their distributions towards more suitable habitats (Sunday et al., 2015). However, recent studies have shown contrasting results when looking at different organisms such as benthic invertebrates (Fuchs et al., 2020; Sunday et al., 2015). Therefore, our approach can be extended to other organisms to explore whether our results are observed in different species groupings.

Contrasting shifts in optimal environmental conditions and species distributions might be explained by decoupling between the metrics used to define environmental shifts and the fine-scale temporal and spatial aspects of the environment likely driving species distribution (e.g., duration of the summer season, local minimum temperature in winters; Poloczanska et al., 2013; Sunday et al., 2015). Accordingly, our spatially explicit assessments of optimal habitats should be considered with caution and used only as a proxy to climate-driven environmental impacts likely affecting species distribution. Also, our assessments do not consider evolutionary processes, acclimation, or potential changes in species interactions that may lead species to persist in sub-optimal environmental conditions, occupy new niches or even disappear from previously preferred environmental ranges (Pinsky et al., 2020; Rilov et al., 2019; Woodin et al., 2013). Despite these considerations, our results evaluate the uneven distribution of environmental shifts and identify potentially highly impacted marine areas that are more prone to fall out their SOS and thus deserve conservation priority to prevent collapses, even in the face of large uncertainty (Rilov et al., 2019; Willcock et al., 2016).

4.2. The overlapping impact of fisheries

A high fishing pressure may increase the vulnerability of marine systems to climate-driven shifts in environmental conditions (Coll et al., 2019; Planque et al., 2010). Overall, historical trends reveal that fish catches have decreased through the study period for most Central and Southern Atlantic Ocean regions (decreasing trends in fish catches are reported for 22 out of 27 EEZs, Fig. 4). This coincides with global declining trends in fishing catches (Pauly and Zeller, 2016) and is particularly true for those EEZs impacted the most by declining trends in optimal environmental conditions for those pelagic species included in our assessments (but see Brazil and Guyana, Fig. 5). However, catch data provided by SAU reflect changing fish biomasses, and varying fishing efforts and efficiencies (Pauly et al., 2013). The impossibility of teasing apart these underlying processes prevents drawing firm conclusions on the long-term trends and the underlying processes driving these trends, particularly when SAU data is used alone (Pauly et al., 2013).

Rather than showing an “optimistic” scenario, where declining trends in fishing catches are due to management actions (i.e., decreasing fishing pressure) that may buffer environmental impacts, our results likely show a historic overfishing trend that may aggravate synergistically climate-driven environmental impacts on fish populations (Coll et al., 2008; FAO, 2020; Kleisner et al., 2013; Roux et al., 2013). In fact, finer-scale analyses on the distribution of fishing pressure revealed that fishing activities are primarily concentrated in areas where fish catches have declined (e.g., the Patagonian Shelf or the Guinea and Benguela Currents). In these regions, the overlapping impact of climate change and fishing pressure has likely synergistically impacted small and medium size pelagic species, causing declining trends in population / stock biomasses and, hence, their catches (Coll et al., 2019; Ramírez et al., 2021; Saraux et al., 2019). Furthermore, recent spatially-explicit stock assessments indicate that fishery biomasses (populations / stocks that are vulnerable to fishing gears) in these areas have declined over the last decades, often reaching biomass levels below the optimal deemed for achieving Maximum Sustainability Yield (B_{MSY} Palomares et al., 2020; see also Table S4 and SAU).

The uneven distribution of environmental shifts and fishing pressure reported in this study might be not informative of future trends and patterns (Rilov et al., 2019). For contributing to an adaptive and effective management of fisheries, our SOS framework must be periodically revisited to provided updated spatial assessments on the overlapping distribution of climate-driven environmental changes and fishing pressure. It is also worth noting that our spatial assessments are rather conservative and may only represent a relatively small fraction of the highly impacted marine areas that deserve conservation priority. This is so because fishing gears target additional species besides the ones our study focuses on. Also, the spatial distribution of fishing pressure from GFW largely relies on the automatic identification system (AIS) for fishing vessel monitoring, which might be lacking in developing nations, and does not account for artisanal fisheries or illegal, unreported, and unregulated (IUU) fishing. Recent technological advances in remote sensing tools and modelling techniques (e.g., those based on satellite radar and night-light imagery, Oozeki et al., 2018; Santamaria et al., 2015) have the potential to revolutionize the way we remotely observe the oceans and monitor fishing activities (including IUU, Oozeki et al., 2018). These new observations can be integrated in spatially detailed analysis like ours when available.

Although we focus here on LMEs (and associated EEZs), where most nations fish predominantly, an area of intense fishing pressure also occurs in the South Atlantic high seas, driven mainly by the fishing activity of few countries such as Spain and Japan (Kroodsma et al., 2018). Satellite remote sensing records for key environmental features that are presumed to drive fish abundances and distributions, along with spatially-explicit quantifications of fishing effort, are now provided at the global scale and for relatively long periods (Kroodsma et al., 2018; Ramírez et al., 2017). Accordingly, our SOS approach has the potential to be extended to the high seas (and other geographical areas or climatic zones) to identify those areas deserving conservation priority in the face of climate change.

4.3. SOS for fisheries in a shifting environment

The pervasive consequences of climate-driven marine species redistribution can be aggravated by fisheries, with far-reaching social-ecological implications for ecosystem functioning and human well-being (Chen et al., 2011; Lenoir et al., 2020; Mendenhall, 2020; Ojea et al., 2020; Pecl et al., 2017; Poloczanska et al., 2013). Therefore, managing and anticipating the consequences of climate-driven species redistribution requires a better understanding of these environmental shifts, particularly when they may affect shared resources such as transboundary fish stocks that are also subjected to intense harvesting pressure (Ojea et al., 2020; Pinsky et al., 2020).

Local to transnational joint efforts to reduce fishing pressure in marine areas where the availability of optimal habitats is decreasing may support long-term sustainable fisheries by enhancing fish stocks' resilience in the face of climate change (Ramírez et al., 2021, 2018, 2017). To date, shifting species distributions have been largely neglected in international agreements regarding climate impacts on natural systems and human societies

(Free et al., 2020; Ojea et al., 2020; Pecl et al., 2017; Pinsky et al., 2018). Local to international fisheries are clearly underprepared for geographic shifts in commercial species (Pinsky et al., 2018; Ramos Martins et al., 2021), despite the fact that planning for species redistributions could substantially reduce the impacts that a changing climate may pose with few trade-offs against current policies (Free et al., 2020; Pinsky et al., 2020).

Sustainable governance of shared stocks will require proactive cooperative approaches to identify and manage highly impacted areas and fish stocks on the move that can provide useful insights to guide future multi-scale and cross-border initiatives. Pioneer initiatives already exist, such as the "The Accra Declaration on environmentally sustainable development of the LME of the Gulf of Guinea", which aims at institutionalizing a new ecosystem-wide paradigm for joint and collaborative actions by the 16 countries in the Guinea Current to preserve the living marine resources (Ibe and Sherman, 2002; Ukwe et al., 2006). In the Benguela Current LME, Angola, Namibia and South Africa ratified the Benguela Current Convention in 2014, supporting a five-year strategic action programme based on Transboundary Diagnostic Analysis (TDA) whereby transboundary challenges are identified and prioritized (Neto and Jardim, 2016). Based on TDA, policy actions were identified in an attempt to optimize social and economic benefits while mitigating environmental and ecological issues, notably included to "improve the understanding and predictability of climate change impacts and climate variability" and to "reduce threats to species and habitats" (Neto and Jardim, 2016). These and similar initiatives can benefit from our assessment of the spatial congruence between climate and fishing impacts, along with their inclusion within a SOS framework. International initiatives hold large potential, such as the Southern African Development Community (SADC) Programme for Transfrontier Conservation Areas (TFCAs), which recognizes that management of shared natural resources has the potential to meaningfully contribute to both the conservation of biodiversity and the socio-economic development of local communities. Spatially-explicit assessments of the distribution of climate and fishing impacts can be relevant for defining and implementing relevant TFCAs, especially in the tropical and subtropical regions where projected changes in community compositions and contemporary cumulative human impacts largely overlap (Boyce et al., 2020; García-Molinos et al., 2016). Next steps for the SOS framework should incorporate future projections under different scenarios of fishing and climate change to anticipate future management options and best alternatives.

Additional information

Correspondence and requests for materials should be addressed to FR (ramirez@icm.csic.es). Spatially explicit outputs produced in this work will be provided in geotiff for easy visualization using GIS (geographic information system) software. This information will be hosted on the Spanish National Research Council [Consejo Superior de Investigaciones Científicas (CSIC)] digital repository (https://digital.csic.es/). The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

FR, JS and MC conceived the work; MC provided the funding; FR extracted and analysed the data and drafted the paper. All authors contributed substantially to the interpretation of results, and the writing, reviewing and editing of the work.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.155480.

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