ELEMENTA
Science of the Anthropocene

Ouled-Cheikh, J, et al. 2022. Fisheries-enhanced pressure on Mediterranean regions and pelagic species already impacted by climate change. *Elem Sci Anth*, 10: 1. DOI: https://doi.org/10.1525/elementa.2022.00028

RESEARCH ARTICLE

Fisheries-enhanced pressure on Mediterranean regions and pelagic species already impacted by climate change

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Marine species are widely threatened by anthropogenic activities, including fishing and human-induced climate change. However, geographically broad and spatially explicit assessments of the simultaneous impacts of these major threats at regional scales are mostly lacking due to the practical challenges of surveying vast geographical areas and obtaining adequately resolved data. Yet, these assessments are key for identifying highly and cumulatively impacted areas and species that should be prioritized for conservation through knowledge-based management strategies. Here, we analysed a 26-year (1993–2018) time series of highly resolved remotely sensed environmental data to evaluate changes in optimal habitat availability (i.e., extent of marine areas encompassing optimal environmental conditions) for 15 species representative of small, medium and large pelagic fish inhabiting the Mediterranean Sea Large Marine Ecosystem. We then combined spatial and temporal data on fishing pressure and changes in optimal habitats to identify areas of high risk of cumulative impacts. Overall, results show how most of the studied Mediterranean pelagic species experienced a reduction in optimal habitat availability over the past decades. The few species that showed positive trends in optimal habitat availability expanded only to a small degree and hence were unlikely to compensate for the loss of key functional roles at the group level. Habitat loss concentrated in the western and central regions. Similarly, fishing pressure was found to be higher in these regions, thus overlapping with the areas experiencing a higher reduction of optimal habitat. Small and large pelagic fish were the most impacted groups, having a larger proportion of their distributions in highly, cumulative impacted areas. Redistributing fishing pressure and reducing it in highly impacted areas may alleviate the overall cumulative pressure on pelagic stocks, contributing to the necessary shift to sustainable and resilient fisheries that would ensure food security and a healthy ecosystem in this highly impacted basin.

Keywords: Safe operating space, Mediterranean, Pelagic fish, Cumulative impact analysis, Climate change, Fisheries

Introduction

Human activities threaten the health of ecosystems worldwide across a range of ecological scales, from the effects on organism physiology to changes in the function and structure of entire ecosystems (Steffen et al., 2011; Birnie-Gauvin et al., 2017; Nolan et al., 2018). Marine ecosystems have been largely impacted by the synergistic interactions between anthropogenic activities across vast distances (Halpern et al., 2008) and through human-driven climate change (Halpern et al., 2019). Combined, these main threats can produce changes in physical and oceanographic properties of the oceans and marine productivity patterns, with far-reaching consequences for marine species and food webs (Steinacher et al., 2010; Lenoir et al., 2020; Pontavice et al., 2020; Voosen, 2020; Boers, 2021). These threats may jeopardize important marine ecosystem services such as seafood provision (McClanahan et al., 2015), which currently poses a first-order global challenge, particularly in a world with an ever-growing human population (1.05% yr^{-1}; United Nations, 2019), an increasing fish demand (doubled by 2050; Naylor et al., 2021), and the reach of maximum catches, which is currently covered by the production of fish in aquaculture systems according to the Food and Agriculture Organization (FAO, 2020).

Spatially explicit assessments of fishing and climate impacts at regional scales are still limited, given the

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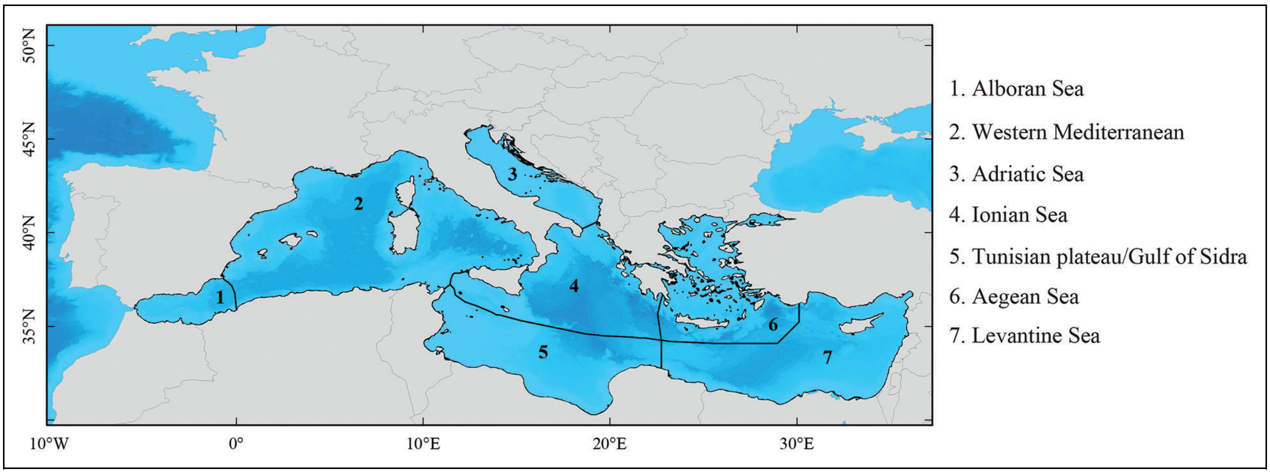

Figure 1. Mediterranean Sea basin, our study zone, divided into marine ecoregions. In addition to these ecoregions (from Spalding et al., 2007), we refer to wider geographic sections of the Mediterranean using the following terminology: western Mediterranean (Alboran Sea and Western Mediterranean Sea marine ecoregions), central Mediterranean (Adriatic Sea, Ionian Sea and Tunisian plateau/Gulf of Sidra marine ecoregions) and eastern Mediterranean (Aegean Sea and Levantine Sea marine ecoregions).

scarcity of data with the required spatiotemporal resolution and the need to integrate information from multiple jurisdictions. There is an urgent need for regional impact assessments that consider both fishing and climate change effects to establish an integrated vision of the impacts to which marine ecosystems are exposed. In addition, these impacts are unevenly distributed in time and space (Halpern et al., 2008), which makes the implementation of spatially explicit approximations of impact distribution a priority to identify those areas where combined impact of fisheries and climate change can bring ecosystems to states beneath their functional thresholds (Houk et al., 2018; Ramírez et al., 2022). Within this context arises the concept of Safe Operating Space (SOS, sensu Rockström et al., 2009), which can be defined as a multidimensional space with climate and human impacts as axes or dimensions that set the bounds for ecosystems to maintain a desirable state of conservation. The SOS framework applied to the management of highly impacted marine systems argues that reducing fishing pressure in those highly impacted areas could be an efficient management strategy to alleviate the pressure upon these systems in front of the effects of climate change (Ramírez et al., 2018; Ramírez et al., 2021; Ramírez et al., 2022).

The Mediterranean Sea (30°N–46°N, 6°W–36°E; **Figure 1**) is considered a biodiversity hotspot because it comprises less than 1% of the global ocean yet contains up to 18% of the world's macroscopic marine species, of which around 30% are endemic (Bianchi and Morri, 2000; Coll et al., 2010; Coll et al., 2012). Due to its semi-enclosed nature (i.e., water renovation occurs mainly in the Strait of Gibraltar; Coll et al., 2010), the Mediterranean Sea shows a northwest–southeast gradient in temperature, salinity and primary productivity and is heavily impacted by global warming, showing a steeper warming rate than the global average (Lionello and Scarascia, 2018; Salat et al., 2019). Furthermore, the Eurasian landmass prevents species from escaping the warming basin (Ben Rais Lasram et al., 2010; Poloczanska et al., 2013). Most fish stocks in the Mediterranean Sea are exploited at unsustainable rates (FAO, 2020), which, in combination with climate change, have turned the Mediterranean into one of the most impacted seas in the world (Giorgi, 2006; Kim et al., 2019). The Mediterranean Sea is usually regarded as a "giant mesocosm," as it holds processes, features and gradients that occur at a global scale, too, such as species redistributions, biomass fluctuations or the heterogeneous distribution of fishing pressure (García Molinos et al., 2016; Free et al., 2020; Ojea et al., 2020; Pinsky et al., 2020). Therefore, the development of an SOS framework in the Mediterranean Sea considering both fishing pressure and climate change is very valuable, as it can provide high quality information for the search of solutions to global issues such as food security (Pinsky et al., 2018).

Pelagic fish species are under high fishing pressure in the Mediterranean Sea due to their high commercial values, and the fact that their catches account for >50% of the total fish catches in the basin (FAO, 2020). Although most pelagic species share life-history traits such as rapid life cycles, high adult motility, planktonic larval stages, and low levels of dependence on benthic habitat (Alheit and Peck, 2019), biomass and distribution responses to climate and fishing pressure vary between species. For example, the distribution range of Round sardinella *Sardinella aurita* has expanded in response to warming conditions (Sabatés et al., 2006), while stocks of some commercial species, such as European anchovy *Engraulis encrasicolus*, Atlantic bonito *Sarda sarda* and European sardine *Sardina pilchardus* are showing signs of depletion (Coll and Bellido, 2020; FAO, 2020; General Fisheries Commission for the Mediterranean, 2021). Due to their roles in providing food security and the structuring and functioning of marine food webs (Cury et al., 2000; Pikitch et al., 2013; Piroddi et al., 2015), holistic and integrative assessments of these species that combine climate and

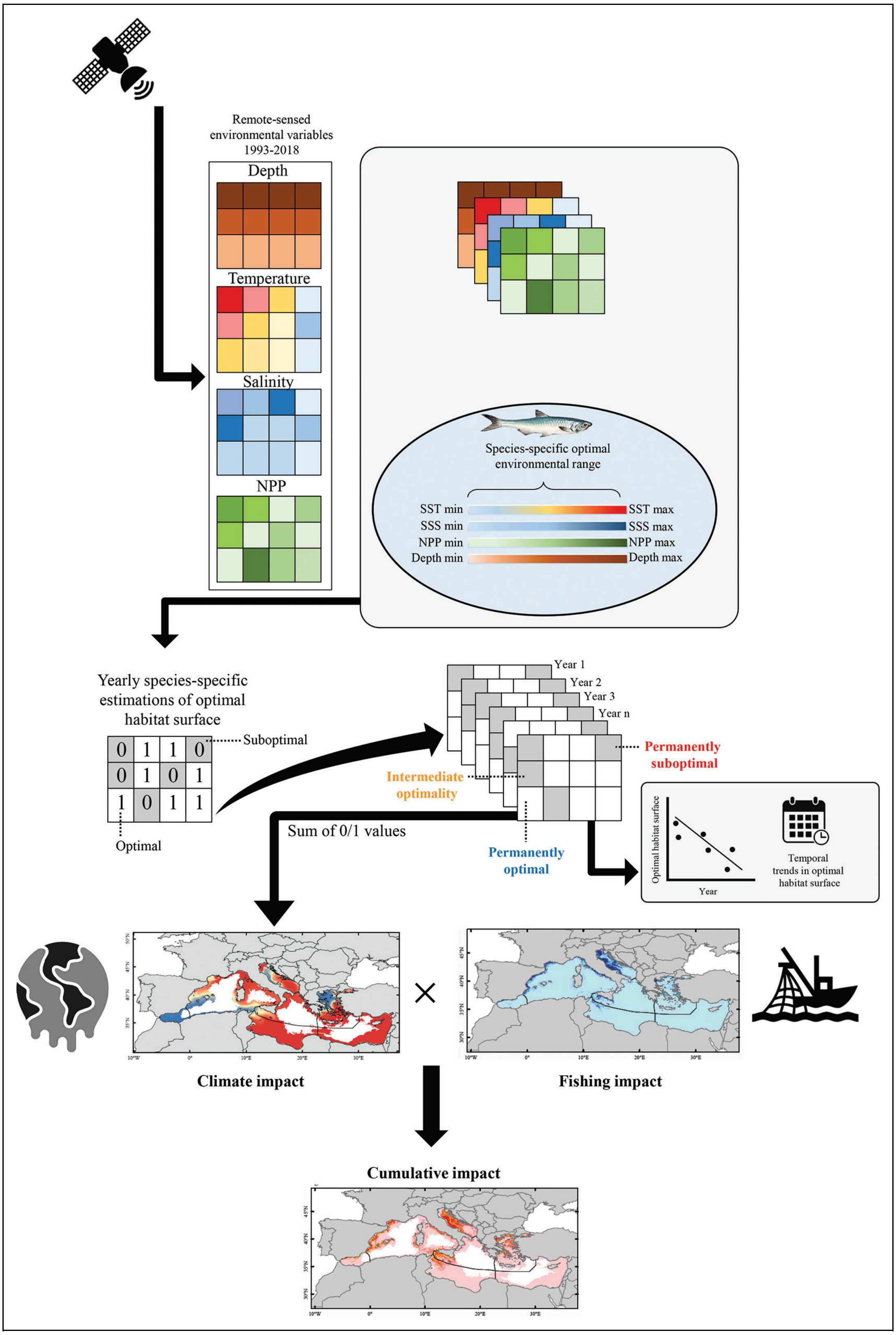

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Figure 2. Visualization of the methodology used.

fishing impacts can help to develop comprehensive management plans of impacted marine ecosystems.

Previous research has shown how the simultaneous impact of climate forcing and fishing pressure may affect the dynamics of small pelagic fish species in the northwestern Mediterranean and Adriatic Sea (e.g., Ramírez et al., 2018; Ramírez et al., 2021). However, integrative assessments of fishing and climate change impact on multiple pelagic fish species across the entire Mediterranean basin are lacking. This study aims to fill this gap by

Table 1. Pelagic fish study species, split by size category, with habitat information extracted from Froese and Pauly (2000)

Size Category	Latin Name	Common Name	Habitat
Small	*Engraulis encrasicolus*	European anchovy	Pelagic-neritic
	Sardina pilchardus	European sardine	Pelagic-neritic
	Sardinella aurita	Round sardinella	Pelagic-neritic
Medium	*Lepidopus caudatus*	Common scabbardfish	Benthopelagic
	Scomber colias	Atlantic chub mackerel	Pelagic-neritic
	Sphyraena sphyraena	European barracuda	Pelagic-neritic
	Trachurus mediterraneus	Mediterranean horse mackerel	Pelagic-oceanic
	Trachurus trachurus	Atlantic horse mackerel	Pelagic-neritic
Large	*Euthynnus alletteratus*	Little tunny	Pelagic-oceanic
	Katsuwonus pelamis	Skipjack tuna	Pelagic-oceanic
	Mobula mobular	Giant devil ray	Pelagic-neritic
	Prionace glauca	Blue shark	Pelagic-oceanic
	Sarda sarda	Atlantic bonito	Pelagic-neritic
	Thunnus thynnus	Atlantic bluefin tuna	Pelagic-oceanic
	Xiphias gladius	Swordfish	Pelagic-oceanic

analysing 15 commercial and non-commercial representative of small, medium and large pelagic fish species inhabiting the whole Mediterranean Sea and their requirements for depth, sea surface temperature (SST), sea surface salinity (SSS), and net primary productivity (NPP) (**Figure 2**). By combining long-term (1993–2018) spatially explicit trends, we first performed a climate-risk assessment by evaluating changes in their optimal habitat availability; i.e., the extent of marine areas encompassing optimal environmental conditions. We then overlaid these areas with available, high-resolution fisheries data (Global Fishing Watch, http://globalfishingwatch.org/; Kroodsma et al., 2018) to identify areas at high risk of cumulative impacts. We hypothesized that highly and "doubly" impacted areas would have patchy distributions across the Mediterranean Sea, as climate and fishing impacts are not evenly distributed throughout the basin, and their overall cumulative footprint may have different effects on pelagic species and functional groups. Management and conservation actions within the SOS framework in these "doubly" and highly impacted areas could potentially contribute to the conservation of marine ecosystems and the sustainable exploitation of the pelagic fish community in this "sea under siege" (Coll et al., 2012; Micheli et al., 2013).

Material and methods

Optimal habitat availability

In order to define optimal habitat areas for our study species, we obtained the species environmental preferences and occurrences from AquaMaps (https://www.aquamaps.org; Kaschner et al., 2019). For thousands of marine species, AquaMaps provides environmental preferences for depth, SST, SSS and NPP, and the probability of occurrence at particular locations (latitudes and longitudes) throughout species distribution ranges. Here, we first subset AquaMaps occurrences within the Mediterranean Sea with probabilities higher than 90%, and with a number of observations larger than 5. We then defined the species-specific optimal environmental thresholds for the Mediterranean region as the minimum and maximum values of the environmental variables (i.e., depth, SST, SSS and NPP) for selected occurrences (Figures S1–S15).

To produce spatially explicit assessments of the distribution of optimal habitat for our study species, we downloaded depth information from the ETOPO1 Global Relief Model (NOAA, https://www.ngdc.noaa.gov/mgg/global/). Spatiotemporal trends in SST (°C), SSS (practical salinity) and NPP (mol m^{-3}) were sourced from the Global Ocean Physics and Biogeochemistry Reanalyses (GLOBAL_REANALYSIS_PHY_001_030 for SST and SSS, and GLOBAL_REANALYSIS_BIO_001_029 for NPP) of the EU Copernicus Marine Environment Monitoring Service (https://marine.copernicus.eu/). Environmental time series were restricted to the 1993–2018 period, the time period for which SST, SSS and NPP data are available.

Because of the high environmental heterogeneity of the Mediterranean Sea, many divisions have been suggested to split the basin into ecological sub-regions (FAO, 1990–2021; Spalding et al., 2007; Notarbartolo di Sciara and Agardy, 2010). Here we used the Mediterranean marine ecoregions (Spalding et al., 2007), as they are considered to capture much of the oceanographic variability in the Mediterranean Sea (**Figure 1**). All of the species considered in the study are part of the pelagic fish community of the Mediterranean Sea, including small,

Table 2. Results of Pearson correlation tests between estimates of yearly optimal habitat surface and biomass data extracted from the Sea Around Us Project (Palomares et al., 2020; Pauly et al., 2020)[a]

Species[b]	Marine Ecoregion[b]	Correlation Coefficient	*P*-value
Engraulis encrasicolus	Alboran Sea	**−0.699**	**<0.01**
Sardina pilchardus	Alboran Sea	0.137	0.54
Engraulis encrasicolus	Western Mediterranean	0.278	0.21
Sardina pilchardus	Western Mediterranean	**0.549**	**<0.01**
Lepidopus caudatus	Western Mediterranean	**0.502**	**<0.05**
Sarda sarda	Western Mediterranean	0.312	0.16
Engraulis encrasicolus	Adriatic Sea	–0.086	0.70
Sardina pilchardus	Adriatic Sea	**−0.490**	**<0.05**
Lepidopus caudatus	Adriatic Sea	–0.273	0.22
Sarda sarda	Adriatic Sea	–0.292	0.19
Engraulis encrasicolus	Ionian Sea	0.336	0.13
Sardina pilchardus	Ionian Sea	**0.485**	**<0.05**
Engraulis encrasicolus	Aegean Sea	–0.023	0.92
Sardina pilchardus	Aegean Sea	0.046	0.84
Sarda sarda	Aegean Sea	**0.440**	**<0.05**

[a] Boldface values indicate significant correlations.

[b] Biomass data were not available for all of our study species and marine ecoregions.

medium and large-sized species with commercial and non-commercial interest. Distributions range from neritic to oceanic habitats (**Table 1**).

Based on species-specific optimal environmental thresholds, as calculated from the AquaMaps occurrence data from the Mediterranean Sea in combination with depth profiles and time series of SST, SSS and NPP, we evaluated how the surface of optimal environmental habitat (i.e., the spatial intersect of areas encompassing optimal environmental conditions) varied both temporally (yearly; 1993–2018) and spatially within the Mediterranean Sea. First, we estimated the surface area (in km^2 and % relative to the maximum surface area recorded in the 1993–2018 period) of species-specific optimal habitats on a yearly basis, for the whole study period, in each marine ecoregion. The relativization to the maximum surface area was done in order to have comparable outputs among species. These estimates were used as a surrogate for optimal habitat availability and to evaluate the temporal trends (1993–2018) in optimal habitat availability through linear regressions with a Gaussian distribution following previous analyses (Ramírez et al., 2021; Ramírez et al., 2022). We used the slopes (and significances; *P*-value) of these linear regressions as estimates for the magnitudes of observed changes.

To evaluate the climate-driven environmental effects on the availability and distribution of optimal habitats, we quantified habitat persistency on a per-pixel basis by counting how many years (for the 1993–2018 period) each pixel was identified as optimal in terms of SST, SSS and NPP, individually. Spatial outputs for each feature ranged from 0 (all years categorized as suboptimal; i.e., permanently suboptimal conditions) to 26 (all years categorized as optimal; permanently optimal conditions across all climate drivers). As a proxy for the overall persistency of optimal environmental conditions, we used multiplicative equally weighted combination of feature-specific outputs (i.e., SST, SSS and NPP outputs). Although we assumed here that optimal ranges of SST, SSS and NPP equally contribute to the distribution of species, our approach can be revisited and refined by incorporating the relative weights that these multiple drivers may have in shaping species-specific distributions. Depth was considered *a posteriori* to define the plausible areas where species live, which were calculated by cropping the optimal habitat persistency areas to preferred depth range of each species. This procedure was applied at the species level and by species size groups (i.e., small, medium and large pelagic species or "pelagics"; **Table 1**) to provide a more general and interpretable output.

In order to validate our approach with an independent dataset, we evaluated if our estimates of species-specific trends in optimal habitat availability corresponded to trends in fish biomass of the Sea Around Us project (SAUP; Palomares et al., 2020; Pauly et al., 2020). The Pearson's correlation test was used to obtain the relationships between the yearly surface of optimal habitat and the yearly biomass estimates per marine ecoregion to correlate our estimates with the changes in fish abundance. This analysis was limited to those species and marine ecoregions for which estimates were available in SAUP (**Table 2**).

The overlapping impact of fishing

Spatially explicit estimates of fishing effort were obtained from Global Fishing Watch (GFW; Kroodsma et al., 2018; accessed on July 2021 from the Google Earth Engine: https://developers.google.com/earth-engine/datasets). We summed daily fishing records to obtain spatially explicit totals for the 2012–2016 period. Our analyses focused on main fishing gears targeting small, medium and large pelagic fish species: we considered purse seiners and trawlers for small pelagics, purse seiners for medium pelagics, and drifting long liners, purse seiners, fixed gear and jiggers for large pelagics.

Before overlapping fishing pressure information with our proxy for climate impacts on species optimal habitat distributions, we normalized both information layers from 0 to 1. We then estimated the cumulative impact of our proxies for climate effects and fishing pressure by multiplying the two layers. 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/or climate impacts) to 1 (i.e., maximum fishing/climate impacts) for areas that were most impacted by both stressors. Non-zero values were subsequently categorized into quartiles that express the magnitude of the cumulative impacts (Q1 to Q4). Areas within the Q4 quartile can be interpreted as most impacted by climate change and fishing pressure simultaneously.

Datasets used, temporal and spatial cover and methodological comment

Some inherent limitations in our work arise from the used datasets. First of all, temporal correspondence is lacking between spatially explicit estimates of fishing effort from Global Fishing Watch, which covers the period between 2012 and 2016, and the environmental data from EU Copernicus Marine Environment Monitoring Service, which extend from 1993 to 2018. This lack of correspondence leads to the assumption that spatial patterns of fishing activity did not vary extensively during our study period, which has already been indicated by Kroodsma et al. (2018), who showed that fisheries have low sensitivity to environmental and economic variation. However, this mismatch could be masking some spatiotemporal variability that we could not capture in our approach, which means that our results on doubly impacted areas should be understood as conservative. Also, at local scales (and particularly in the southern part of the basin) we are lacking most of the fishing effort data due to low usage of automatic identification system (AIS) transmitters (Kroodsma et al., 2018; Merino et al., 2019; see https://globalfishingwatch.org/data/radar-illuminated-ocean/). As our approach can be revisited and applied at many different locations, future assessments at sub-regional scales, including information on artisanal or small-scale fisheries, would be important to complete the current lack of information in some parts of the Mediterranean. This lack could be overcome by using recent advances in vessel-detection technology such as the usage of synthetic aperture radar, although current data availability is restricted to 2021, which would reduce the temporal window covered by fishing effort information.

Results

We found contrasting trends in the availability of optimal habitat across species and ecoregions. Generally, our results highlighted a reduction in optimal habitat availability for most of the studied species (**Figure 3**). We identified a few exceptions, which are mainly found in the Western Mediterranean and Alboran Sea marine ecoregions (i.e., for round sardinella *Sardinella aurita*, Mediterranean horse mackerel *Trachurus mediterraneus*, European barracuda *Sphyraena sphyraena* and Giant devil ray *Mobula mobular*), and a significantly increasing trend for Mediterranean horse mackerel.

Despite the general trend of reductions, magnitudes were unequal among regions (**Figure 3**). In the Western Mediterranean marine ecoregion species lost the largest amount of optimal habitat surface, mainly affecting two small pelagic fish species (i.e., European sardine and European anchovy), with European sardine experiencing the largest loss in optimal habitat surface within this region and in the whole Mediterranean Sea. In contrast, in the adjacent marine ecoregion of the Alboran Sea small pelagics were not impacted, but large species such as swordfish and Atlantic Bluefin tuna lost the most optimal habitat surface. Medium pelagics (Mediterranean horse mackerel and European barracuda in particular) were most impacted in the central Mediterranean Sea (including Adriatic, Ionian and Tunisian Plateau/Gulf of Sidra), followed mainly by the three species of small pelagic fish. Regarding large pelagics, giant devil ray lost most optimal habitat surface across the central Mediterranean (**Figure 3**). The eastern Mediterranean Sea (including Aegean and Levantine Sea regions) was found to be permanently suboptimal for most of the species (**Figures 4A**, **5A**, **6A**), thus leaving little room for decreases in optimal habitat availability. The Aegean Sea did not show particularly large decreases in optimal habitat surface for the study species (**Figure 3**). The Giant devil ray was the only species with a significant loss of optimal habitat surface in the Levantine Sea.

Regarding spatial persistency of optimal habitat availability, we found that most of the Mediterranean Sea basin had a large area of persistent suboptimal conditions for small, medium and large pelagic species (**Figures 4A**, **5A**, **6A**). Small pelagics had the largest proportion of persistently suboptimal habitat surface, followed by large and medium pelagics (**Figures 4A**, **5A**, **6A**). The latter two groups had a larger proportion of intermediate levels of optimal habitat persistency, meaning that the optimality of those areas varied over time. Conditions were generally better at the beginning of our study period than at the end. We also identified some exceptions of persistent optimal habitat conditions in the Alboran Sea, parts of the northernmost section of the Adriatic Sea, and the innermost part of the Aegean Sea (**Figures 4A**, **5A**, **6A**).

As in the case of optimal habitat reductions, fishing pressure was not evenly distributed spatially, with highest

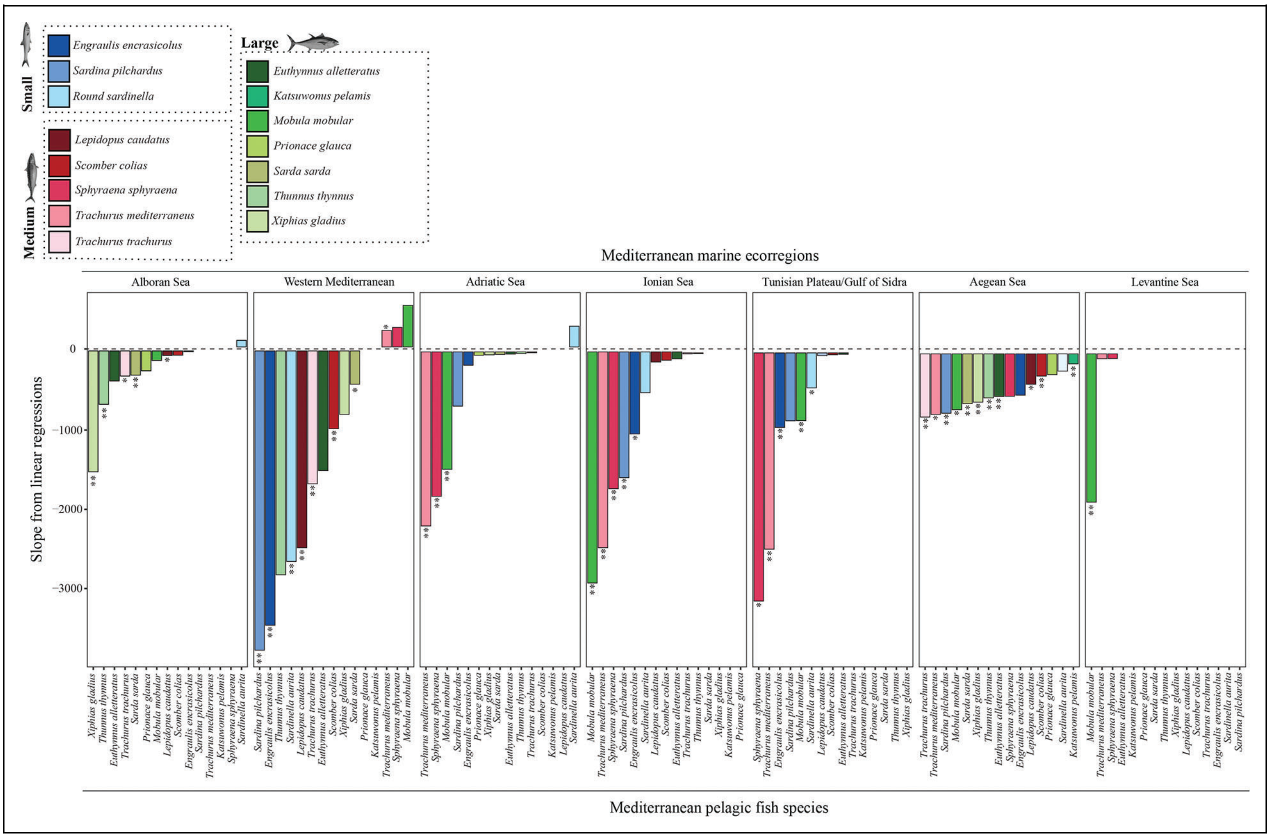

Figure 3. Linear regression slopes (yearly optimal habitat availability) by marine ecoregion and pelagic fish size category. Barplots colour-coded for pelagic fish size category and ordered from large to small slopes. Asterisks denote statistically significant linear regressions (*, P-value < 0.05; **, P < 0.01).

pressures in the western and central Mediterranean (mostly Spain, southern Sicily, eastern and western Italy and Croatia) by predominantly trawl, purse seine and long-line vessels (**Figures 4B**, **5B**, **6B**). The easternmost marine ecoregions of the Mediterranean Sea did not show particularly large fishing pressures compared to the western ecoregions, with limited fishing pressure along the coasts of the Aegean Sea, southern Turkey and Cyprus.

Overlap of climate and fishing impacts highlighted areas where the largest fishing pressure and large persistency of suboptimal conditions overlapped extensively (**Figures 4C**, **5C**, **6C**). Overall, highly cumulatively impacted areas (Q4 zones) were quite similar spatially for small, medium and large pelagics, although with lesser impacts for the latter two groups. The Alboran Sea marine ecoregion had the lowest proportion of high-impact areas except for large pelagics. In contrast, the Adriatic Sea marine ecoregion consistently had the largest proportion of its area (30–45%) within high impact zones, followed by the Western Mediterranean marine ecoregion (particularly Eastern Spain and Western Italy; approximately 25%). The remaining marine ecoregions also showed large proportions of high-impact zones (around 15–25% of their total surface), with particularly intense spots such as the Strait of Sicily in the Ionian Sea or Southern Turkey in the Levantine Sea (**Figure 7**).

The validation of our results through biomass data from SAUP showed that, in some cases, the correlations were as expected (i.e., being positive; $r > 0$, P-value < 0.05), meaning that larger optimal habitat surface estimates coincided with larger biomasses (**Table 2**). This relationship was particularly the case for European sardine and silver scabbardfish in the Western Mediterranean marine ecoregion, European sardine in the Ionian Sea, and Atlantic bonito in the Aegean Sea. However, we encountered a few cases with negative correlations, such as European anchovy in the Alboran Sea and European sardine in the Adriatic Sea.

Discussion

By combining long-term, spatially explicit trends in environmental conditions with available distributions of fishing pressure, we identified marine areas and pelagic species within the Mediterranean Sea that are most impacted by both climate change and fishing pressure. Our results highlight optimal habitat loss for the vast majority of the species studied over the 1993–2018 time period. This finding is in agreement with previous studies in the area, and underscores that the Mediterranean Sea is highly impacted by climate change (Claudet and Fraschetti, 2010; Coll et al., 2012; Ramírez et al., 2018). Marine species distributions have been shown to closely track shifting environmental conditions (Pinsky et al., 2013; Pinsky et al., 2019; Lenoir et al., 2020). Accordingly, we argue that the environmental changes that we detected can affect species biomass and spatial

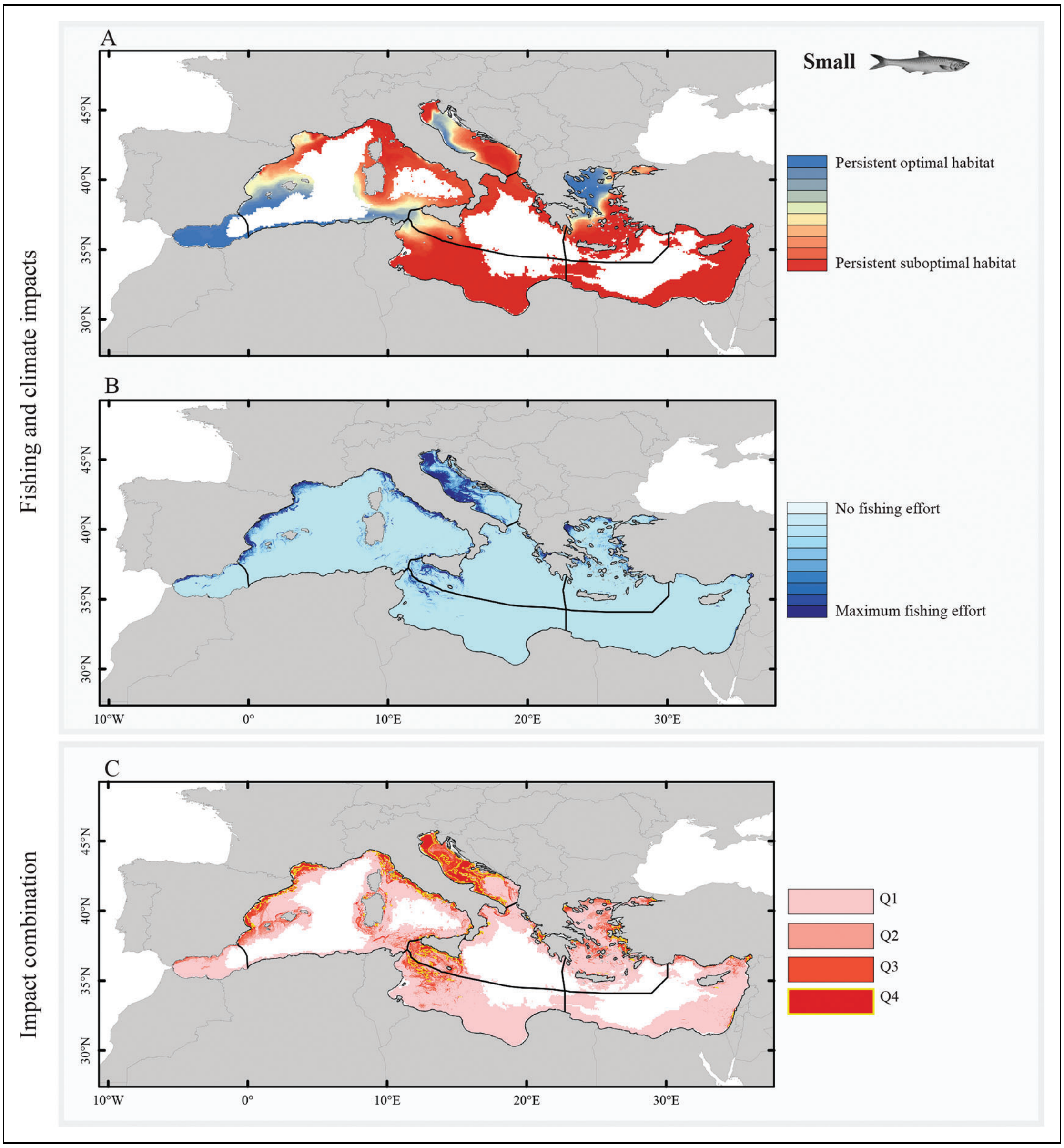

Figure 4. Risk assessment components for small pelagic fish in the Mediterranean Sea split by marine ecoregions. Combined assessments for European anchovy, European sardine and round sardinella: (A) optimal habitat persistency along the 1993–2018 period; (B) fishing effort based on Global Fishing Watch data (2012–2016); and (C) combined impact of (A) and (B) with categorization by quartiles (Q1–Q4).

distribution, which can ultimately have ecosystem-level consequences and impacts on fishing catches and seafood provision (Ramírez et al., 2022).

Complementing previous studies, our work identifies key areas and pelagic species that are likely the most affected by the simultaneous impacts of shifting environmental conditions and fishing pressure over time. The magnitudes and directions of these trends contrast among species and marine ecoregions, with the steepest decreases occurring in the western and central regions. We detected very few cases with an increase of optimal habitat availability. Moreover, the magnitude of increase in those cases was small (e.g., for round sardinella in the Western Mediterranean marine ecoregion), which indicates that losses of functional roles from some species (e.g., European sardine) may not be compensated by a biomass increase of other similar species that could be favoured by shifting environmental conditions such as round sardinella (Sabatés et al., 2006). This likely lack of compensation could imply changes in the overall functioning of the Mediterranean food web, as small pelagic fish species play important functional roles such as the transfer of energy from lower to higher trophic level organisms (Palomera et al., 2007; Coll et al., 2008; Albo-Puigserver et al., 2016). Worryingly, we also found a high spatial congruence between fishing pressure and suboptimal environmental conditions for pelagic species, thus suggesting that fisheries and climate-driven environmental impacts could push the pelagic fish communities beyond safe limits (i.e., outside of their SOS).

At the basin scale, small pelagic fish suffered the largest loss of optimal habitat and showed the largest highly

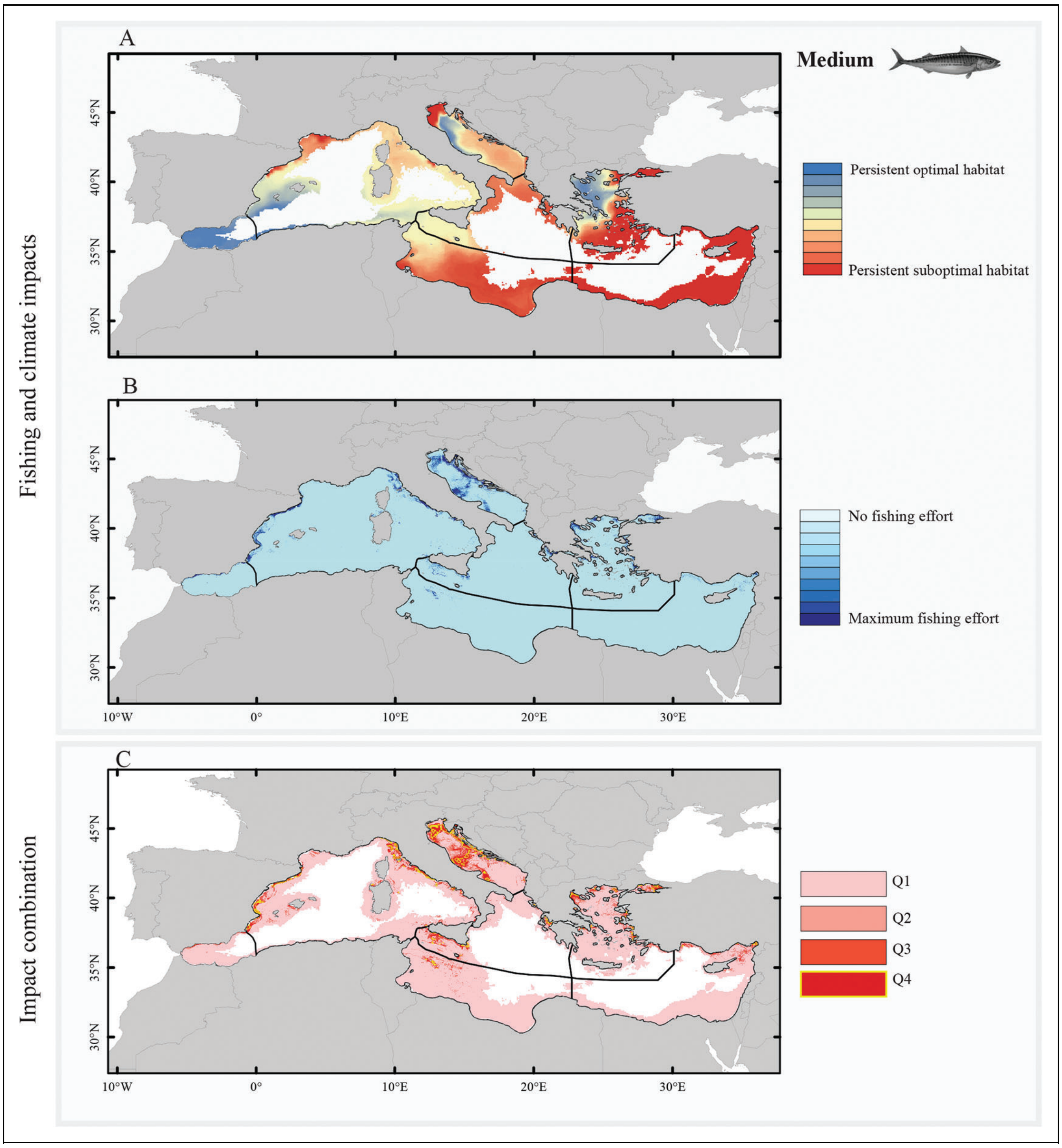

Figure 5. Risk assessment components for medium pelagic fish in the Mediterranean Sea split by marine ecoregions. Combined assessments for common scabbardfish, Atlantic chub mackerel, European barracuda, Mediterranean horse mackerel and Atlantic horse mackerel: (A) optimal habitat persistency along the 1993–2018 period; (B) fishing effort based on Global Fishing Watch data (2012–2016); and (C) combined impact of (A) and (B) with categorization by quartiles (Q1–Q4).

impacted areas. Small pelagic fish are known to suffer rapidly from both environmental changes and overfishing, which may result into stock depletions or collapses with broader ecological impacts (Palomera et al., 2007; Roux et al., 2013; Essington et al., 2015; Fernandes et al., 2017). In particular, European sardine from the Western Mediterranean marine ecoregion was the most impacted species (followed by European anchovy) in the Mediterranean basin in terms of optimal habitat surface loss for the study period. This result is in line with the sensitivity of the species towards warming conditions of the basin (Palomera et al., 2007; Pennino et al., 2020; Albo-Puigserver et al., 2021), and it coincides with a worrying situation for the sustainable exploitation of the fish stocks targeted by Spanish and French Mediterranean fisheries (General Fisheries Commission for the Mediterranean, 2021). Interestingly, habitat suitability has also decreased for round sardinella, a thermophilic species whose distribution range in the western Mediterranean expanded northward in the past decades due to warmer conditions (Sabatés et al., 2006). However, successful reproduction of the round sardinella also requires high chlorophyll levels in summer (Ben-Tuvia, 1973; Schismenou et al., 2008; Sabatés et al., 2009), which are currently low in most of the Mediterranean Sea and have been predicted to decrease even more in a warmer world (Macias et al., 2015). Hence, according to our results, round sardinella is unlikely to expand further and may not be an ecological substitute for European sardine in the future, which may be substituted by other, currently less abundant

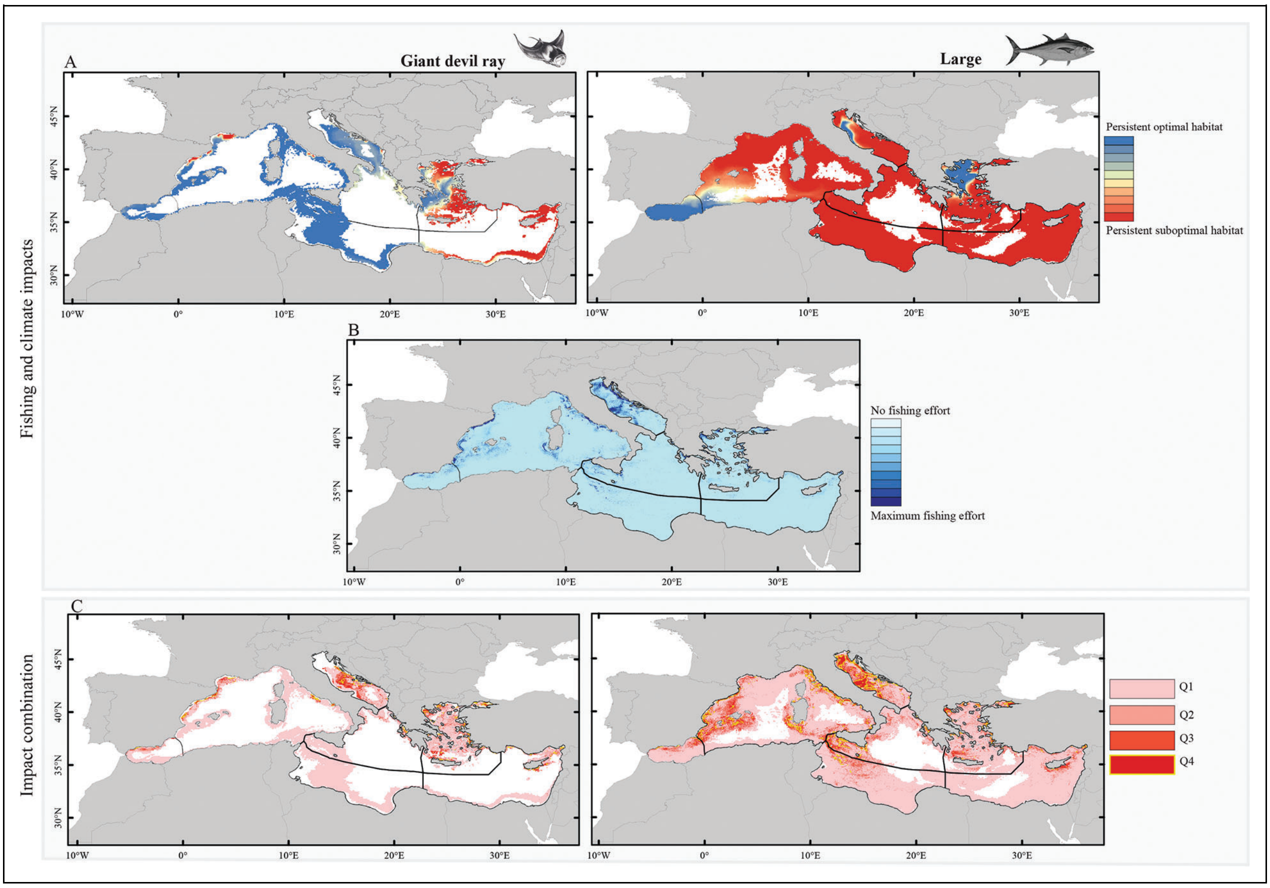

Figure 6. Risk assessment components for large pelagic fish in the Mediterranean Sea split by marine ecoregions. Left: Giant devil ray. Right: Combined assessments for little tunny, skipjack tuna, blue shark, Atlantic bonito, Atlantic bluefin tuna, and swordfish. (A) Optimal habitat persistency along the 1993–2018 period; (B) fishing effort based on Global Fishing Watch data (2012–2016); and (C) combined impact of (A) and (B) with categorization by quartiles (Q1–Q4).

species such as the picarel *Spicara smaris*, which is the dominant zooplanktivore over the continental shelf of the Balearic Islands, Crete and Cyprus (i.e., warm, oligotrophic areas), but which is not important in terms of fishing catches (SAUP; Palomares et al., 2020; Pauly et al., 2020). Other species that may be shifting their distributions into the Mediterranean through the Suez Canal are Lessepsian migrants from the Red Sea (Ben Rais Lasram et al., 2008). Although our approach would allow the consideration of these and other invasive species, only two of them (rainbow sardine *Dussumieria acuta* and yellowstripe barracuda *Sphyraena chrysotaenia*) support local fisheries and have not been included due to the scarcity of data.

Those areas showing permanent suboptimal conditions for small pelagic fish, as the Ligurian Sea (northern Western Mediterranean marine ecoregion), Ionian Sea, Tunisian Plateau/Gulf of Sidra and Levantine Sea, were generally not identified as doubly impacted areas because of the low fishing pressure, which may reflect that these areas were not ever suitable as fishing grounds during our study period. These areas contrast with those that have intermediate values of optimal habitat persistency, such as the northeastern coast of Spain and western coast of Italy, where most of the Western Mediterranean marine ecoregion zones of cumulative climate and fisheries impacts occur. Environmental conditions were likely good enough to support a strong fishing pressure at the beginning of the study period (1993), but deterioration of environmental conditions may not have been accompanied by the necessary reduction of fishing pressure, resulting in a high cumulative impact. Indeed, fishing effort in these areas is strong compared to other Mediterranean areas (e.g., the Levantine Sea marine ecoregion), as they host the largest trawling and purse-seining fleet of the Mediterranean Sea (Sbrana et al., 2010; Ramírez et al., 2018).

In contrast, the adjacent Alboran Sea marine ecoregion had a mild fishing pressure and was consistently identified as a spot with persistent optimal conditions for all of the examined small pelagic fish. This assessment may be a consequence of the lower temperatures of surface waters flowing in from the Atlantic Ocean, which makes this ecoregion more resilient to warming. Other regions that were generally identified as persistently optimal for small pelagic fish were the northernmost part of the Aegean Sea and a small section of the Northern Adriatic Sea. Nevertheless, the Adriatic Sea is one of the most heavily human-impacted zones of the Mediterranean (Lotze et al., 2011), where intense fishing pressure coincides with already "poor" environmental conditions for small pelagics due

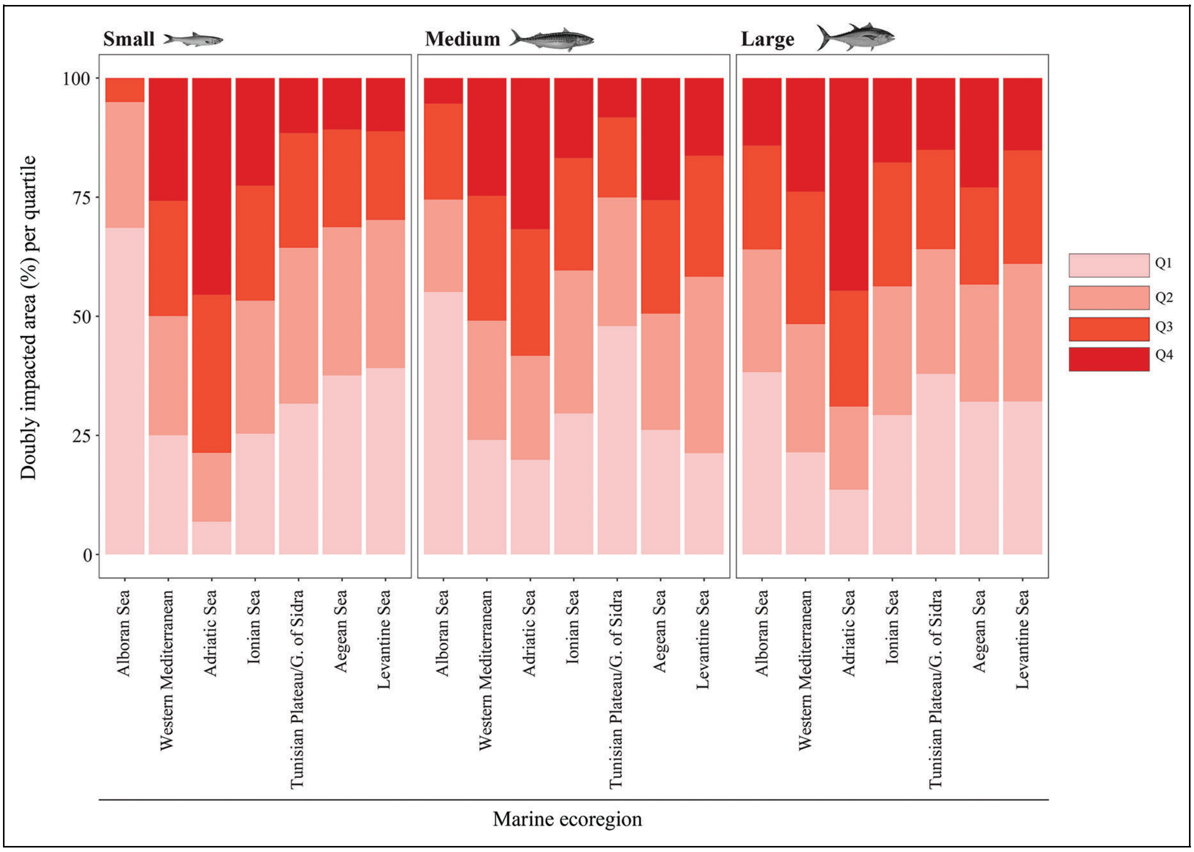

Figure 7. Percentage (%) of surface for each marine ecoregion in the Mediterranean Sea. Percentages split by fish size category (small, medium, and large) and colour-coded by impact magnitude (quartiles Q1–Q4).

to riverine runoff induced eutrophication (Vighi et al., 1991; Sfriso, 2021). We thus identified most of the Adriatic Sea as a permanently suboptimal area for small pelagics (with little room for further decreases) and, hence, a highly and cumulatively impacted zone. Even if environmental conditions have been permanently suboptimal in most of the Adriatic Sea, fishing pressure remains very high. This situation constitutes another example of how fishing pressure has not been reduced to adapt to environmental conditions, in line with the current overfished state of several fish stocks within this marine ecoregion (UNEP-MAP-RAC/SPA et al., 2015). Small pelagic fish also showed a strong reduction of their optimal habitat surface in the Ionian Sea marine ecoregion, with a high-impact zone centered in the Strait of Sicily, mainly due to local trawling fisheries supported by an upwelling system (Russo et al., 2014; Di Lorenzo et al., 2018).

In contrast to small pelagic fish, medium pelagic species showed intermediate optimal habitat persistency in the Western Mediterranean and Adriatic Sea marine ecoregions, including the Strait of Sicily. This pattern, however, results from the contrasting responses of two groups of species, because optimal habitat availability declines for common scabbardfish, Atlantic horse mackerel and Atlantic chub mackerel but remains largely unchanged for Mediterranean horse mackerel and European barracuda (see species-specific results in Supplementary Material). The contrast between Atlantic and Mediterranean horse mackerels is particularly illustrative, as the former is a cold-water species whose abundance is highly dependent on bottom temperature, whereas the Mediterranean horse mackerel is more thermophilic (Milisenda et al., 2018). Hence, species replacement is expected in the foreseeable future within the group of medium pelagics, which is also probably the case for the European barracuda and the yellowmouth barracuda (*Sphyraena viridensis*). Both species occur in the Mediterranean and have been misidentified for a long time (Relini and Orsi-Relini, 1997), which leads us to question the accuracy of the information extracted from AquaMaps. If the yellowmouth barracuda is actually more thermophilic than European barracuda, the results reported here may be indicative of species replacement, as for horse mackerels.

Regarding large pelagic fish species, we observed massive losses of optimal habitat surface for most of the investigated species, except for the giant devil ray. Swordfish and the four species of tuna considered are targeted by specific fisheries (Coulter et al., 2020), while blue sharks are frequently bycaught by bottom trawlers and purse seiners in the western Mediterranean (Nuez et al., 2021). Conversely, aerial surveys have revealed a previously unexpected abundance of giant devil ray in the Adriatic Sea (Fortuna et al., 2014) and the western Mediterranean (Nortarbartolo di Sciara et al., 2015), but rays are not a widespread bycaught species. Furthermore, swordfish, the four tuna species and blue sharks occupy high trophic levels in the Mediterranean (i.e., they are top predators; Cardona et al., 2015), whereas mobulid rays rely primarily on pelagic crustaceans (Couturier et al., 2012; but see Barría et al., 2015). The overall evidence supports that fishing and loss of optimal habitat may combine to reduce the populations of large pelagic fishes with a high trophic position in the Mediterranean, whereas giant devil ray may thrive in most of the central and western Mediterranean unless their fishing pressure increases. This shift may result in major changes in the structure of marine pelagic food webs, considering the major ecological differences between giant devil rays and the other species of large pelagics.

The marine ecoregion where the optimal environmental conditions for large pelagic fishes appeared to be the most degraded was the Alboran Sea, where, contrastingly, we did not find optimal habitat surface loss for small or medium pelagic species. The highly migratory nature of some of the large pelagic species, such as Atlantic bluefin tuna, may reduce the impact of decreases in optimal habitat, as these species only traverse the Alboran Sea from the Atlantic Ocean to the spawning zones in predominantly the Western Mediterranean marine ecoregion (i.e., Balearic Islands, Northern Sicily, Malta; Medina et al., 2002; Corriero et al., 2005) and other zones further East (Karakulak et al., 2004).

We may expect that those species that increased their overall optimal habitat surface could have larger biomasses and thus be more available for fisheries, increasing catches and *vice versa*. However, the correlation between our annual optimal habitat surface estimates and biomasses extracted from SAUP was only positive and significant for three species (European sardine, silver scabbardfish and Atlantic bonito) in three marine ecoregions (Western Mediterranean, Ionian Sea and Aegean Sea). In the case of European sardine, this result supports the existence of an actual biomass decline linked to the deterioration of environmental conditions (Coll and Bellido, 2020; Pennino et al., 2020). Inconsistencies between our results (i.e., trends in optimal habitat availability) and biomass estimates for other species could be due to a range of factors, including the effect of fisheries harvesting or inaccuracy in biomass estimates. They could also be a consequence of inherent limitations of our methodological approach. For instance, we considered that SST, SSS and NPP contributed equally to species distributions, which may actually vary among species and geographic areas. Also, a decoupling may exist between the metrics used here to define environmental shifts and the fine-scale temporal and spatial aspects of the environment driving species biomass and distribution (e.g., duration of the summer season, local minimum temperature in winters; Poloczanska et al., 2013; Sunday et al., 2015). Moreover, our analyses may be sensitive to potential auto-correlation among environmental divers. Also, our assessments do not consider evolutionary processes, acclimation, and potential changes in species interactions that may lead species to persist in suboptimal environmental conditions, occupy new niches, or even leave previously preferred environmental ranges (Pinsky et al., 2020). Also, our approach may fail at local scales, as we do not have species-specific fine scale movement data (e.g., tracking data), and we rely on their static environmental envelopes, without considering their much more complicated life cycles, which include in some cases migrations (e.g., bluefin tuna), local scale movements in search of prey, or different life-history stages (e.g., larvae may have different environmental requirements than adults). To overcome these methodological constraints, our approach could be revisited in search of local, fine-scale patterns, using much more detailed data on local fisheries and species.

Accordingly, our spatially explicit assessments of optimal habitats should be interpreted with caution and used only as a proxy for the climate-driven environmental impacts that are likely to affect species distributions and biomass. Despite these limitations, our results provide a first comprehensive evaluation of the uneven distribution of environmental shifts likely affecting a good representation of species from the pelagic community of the Mediterranean Sea. Moreover, we identified potentially highly impacted species and marine areas that are more prone to fall outside of their SOS and thus deserve conservation priority in order to prevent collapses and foster potential catch reductions. However, our basin-scale assessment is limited by the availability of AIS data for North African countries, related to the minimal use of on-board transmitters and lack of terrestrial receptors (Kroodsma et al., 2018; Merino et al., 2019). For this reason, our results on doubly impacted areas should be understood as conservative. The lack of AIS data ultimately imposes severe limitations on performing SOS analysis in the southern Mediterranean Sea, which may mask highly and simultaneously impacted areas that need urgent consideration (Coll et al., 2010). This problem is particularly important with the ever-advancing climate crisis, in which local administrations cannot make immediate, tangible policy changes to counter climate impacts. A recent suggestion is that fisheries could be reallocated to low-impacted, “resilient” areas where “oceanographic processes drive range expansion opportunities that may support sustainable growth in the medium term” (i.e., climate change “bright spots”; Queirós et al., 2021). This reallocation could only be implemented through sustainably managed fisheries supported by rigorous spatial-temporal analysis, as climate change bright spots may act as climate refuges for many species (e.g., Pennino et al., 2020). We acknowledge that the SOS framework offers a medium-term solution; in the long term, sustainable ecosystems can only be ensured through a global reduction in greenhouse gas emissions in combination with an ecosystem-based approach to manage exploitation. This view is in line with the fact that a significant number of stocks are projected to either shift their distributions or collapse under future climate change (Le Bris et al., 2018; Oremus et al., 2020). As the global human population is still growing (United Nations, 2019), satisfying seafood demand may be harder, in particular in countries where terrestrial food production is scarce (Naylor et al., 2021). Therefore, the results shown here reinforce the urgent need to address the multi-faceted crisis of biodiversity loss and climate change impacts that we are currently facing. Species redistribution will likely reshape the spatial patterns of catches across regions and fishing sectors (Cheung et al., 2010; Ramirez et al., 2022), which may lead to further increasing impacts on marine resources with increased risk for substantial geopolitical conflict at the global scale (Pecl et al., 2017; Pinsky et al., 2018; Boyce et al., 2020; Mendenhall et al., 2020). Our approach, based on risk assessment methods within a SOS framework, can be applied globally to contribute to the assessment on how to reach a balance between the conservation and sustainable exploitation of marine ecosystems. It could provide key insights to adapt current and future fisheries to climate change, in a way that keeps socio-ecological impacts at a minimum.

Data accessibility statement

The source data on which we base our findings are all open access and can be found at https://www.aquamaps.org/ and https://marine.copernicus.eu/. All of the generated TIF files will be available at the public repository https://digital.csic.es/ upon publication. All the code used in our analyses is stored in a dedicated GitHub repository and will be available upon request via the authors.

Supplemental files

The supplemental files for this article can be found as follows:

Figures S1–S15. PDF

Funding

JO was supported by Universitat de Barcelona through the PREDOCS-UB grant (2021). MC received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 869300 (FutureMARES project) and the Spanish project ProOceans (Ministerio de Ciencia e Innovación, Proyectos de I + D + I (RETOSPID2020-118097RB-I00). FR was supported by the Spanish government through the "Severo Ochoa Centre of Excellence" accreditation (CEX2019-000928-S) and the Ramón y Cajal programme (Spanish Ministerio de Ciencia e Innovación, RYC2020-030078-I). JO, FR and MC acknowledge the institutional support of the "Severo Ochoa Centre of Excellence" accreditation (CEX2019-000928-S). FR also acknowledges support by the Spanish government through the project SOSPEN (grant agreements N° PID2021-124831OA-I00, Spanish Ministerio de Ciencia e Innovación).

Competing interests

All authors declare that they have no conflicts of interest.

Author contributions

Contributed to conception and design: MC, FR.

Contributed to acquisition of data: JO, MC, FR.

Analysis and interpretation of data: JO, MC, LC, JS, FR.

Drafted and/or revised the article: JO, MC, LC, JS, FR.

Approved the submitted version for publication: JO, MC, LC, JS, FR.

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How to cite this article: Ouled-Cheikh, J, Coll, M, Cardona, L, Steenbeek, J, Ramírez, F. 2022. Fisheries-enhanced pressure on Mediterranean regions and pelagic species already impacted by climate change. *Elementa: Science of the Anthropocene* 10(1). DOI: https://doi.org/10.1525/elementa.2022.00028

Domain Editor-in-Chief: Jody W. Deming, University of Washington, Seattle, WA, USA

Associate Editor: Laurenz Thomsen, Department of Marine Sciences, University of Gothenburg, Gothenburg, Sweden

Knowledge Domain: Ocean Science

Published: October 26, 2022 **Accepted:** August 23, 2022 **Submitted:** February 11, 2022

Elem Sci Anth is a peer-reviewed open access journal published by University of California Press.