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FEATURE ARTICLE

Rebuilding Mediterranean marine resources under climate change

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ABSTRACT: The Mediterranean Sea ranks among the most overexploited and fastest-warming ocean regions. This situation calls for urgent development of global change scenarios and models of marine biodiversity to anticipate changes and support ecosystem-based management strategies across the entire Mediterranean Sea. Using a new end-to-end modelling chain for the whole Mediterranean Sea, we explored the potential effects of changes in fishing pressure on marine resources and ecosystem structure and functioning under a worst-case climate change scenario (RCP8.5). We found that a decrease in fishing mortality or an improvement in fishing selectivity could increase the total biomass and total catch of high trophic level species by the middle and end of the 21st century, especially the biomass of demersal, large pelagic and benthic species, thereby reversing the projected climate-induced decrease in their biomass and catch by the end of the century in the western Mediterranean basin. In contrast, climate change could offer opportunities for some eastern Mediterranean fisheries to increase catches of thermophilic and/or exotic species benefiting from new favourable environmental conditions. Based on a suite of ecological indicators, our results indicated clear positive effects of a more sustainable fisheries management on ecosystem structure and functioning. However, a decrease in fishing pressure may not fully compensate for climate-induced changes on marine resources and ecosystems, but rather buffer some projected negative impacts. Our study highlights the need for a more sustainable exploitation of fisheries resources to restore marine ecosystems and increase their resilience in a global change context.

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An artisanal fishing vessel on the shores of Milos, a Greek island in the Aegean Sea.

Photo: Laure Velez

KEY WORDS: Fishing scenarios · Climate change · Biodiversity · End-to-end model · OSMOSE model · Mediterranean Sea

1. INTRODUCTION

Mediterranean marine ecosystems are largely impacted by climate change and overexploitation of marine resources (Micheli et al. 2013, Halpern et al. 2015, Marbà et al. 2015, Colloca et al. 2017). Recent research suggests that fish life history and physiological traits have changed, spatial distributions of fish

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have shifted northward and eastward, and the community structure and composition of Mediterranean Sea flora and fauna is undergoing rapid modification (Damalas et al. 2015, Arndt et al. 2018, Azzurro et al. 2019). The current fisheries management system in the Mediterranean region appears to have failed to protect biodiversity and secure living marine resources for future generations (Tsikliras et al. 2015, Cardinale et al. 2017, Colloca et al. 2017). For example, fisheries selectivity associated with high juvenile mortality is a characteristic feature of Mediterranean fisheries, with the catch composition of most of the commercial stocks dominated by 0-group to 2 yr old specimens and characterized by a low occurrence of large individuals (Colloca et al. 2013). In addition, the current fishing mortality for all species and management units combined has been, on average, 2.5 times higher than that corresponding to the maximum sustainable yield (MSY) (Vasilakopoulos et al. 2014, FAO 2020), the target for European fisheries. Given the poor economic and ecological situation of Mediterranean fisheries, the management strategies in place have largely proved ineffective in achieving the objectives of the European Common Fisheries Policy and Marine Strategy Framework Directive (e.g. MSY and Good Environmental Status of ecosystems), and the Sustainable Development Goals of the United Nations (Colloca et al. 2017, Raicevich et al. 2017, Vielmini et al. 2017). Rebuilding the size and trophic structure of fish communities and preserving species richness are critical for increasing the resilience and maintaining the productivity of marine ecosystems under climate change (e.g. Brander 2010, Grafton 2010, Gaines et al. 2018).

Beyond climate change and fishing, anthropogenic pressures such as pollution, biological invasions and habitat destruction have also contributed to a decline in the biodiversity and overall health status of Mediterranean ecosystems (Coll et al. 2010, 2012, Ramírez et al. 2018). Pressures have the potential to act in synergy to shape and modify biodiversity patterns, ecosystem functioning and the goods and services they provide, especially seafood production (Carozza et al. 2019, Lotze et al. 2019).

In a recent paper, Moullec et al. (2019a) projected that, under the worst-case IPCC scenario for greenhouse gas concentrations (Representative Concentration Pathway, RCP, 8.5), the total biomass and catch of high trophic level species in the Mediterranean Sea would increase by 22 and 7 %, respectively, by the end of the 21st century. However, these global increases masked strong spatial and interspecific contrasts. Projected increases were mainly due to an increase in the biomass of smaller, pelagic, thermophilic and/or exotic species at relatively low trophic levels and located in the southeastern part of the basin. In contrast, fisheries catches were projected to decrease in the whole western basin, particularly for several species of high commercial interest (e.g. European hake *Merluccius merluccius*, red mullet *Mullus barbatus* and Mediterranean horse mackerel *Trachurus mediterraneus*) by the end of the century (Moullec et al. 2019a). All of these findings call for an urgent development of scenarios that can be tested using models of marine biodiversity in order to anticipate changes and support ecosystem-based management strategies at the whole Mediterranean scale.

By examining a range of plausible futures based on potential trajectories of drivers (e.g. fishing management strategies, climate change; Kreiss et al. 2020, Pinnegar et al. 2021), exploratory scenarios can contribute to assessing and anticipating the impacts of drivers on biodiversity and ecosystem services in order to identify potential solutions to mitigate them (IPBES 2016). Most projections of changes in marine populations or biodiversity in the Mediterranean Sea have been restricted to specific regions, levels of biological organization or single drivers and have ignored trophic interactions. Thus, previous studies have not included potential interactions between drivers and between species (e.g. Maravelias et al. 2014, Libralato et al. 2015, Stergiou et al. 2016, Corrales et al. 2018). There is an urgent need to develop new operational tools that explicitly include spatial and multispecies dynamics to make projections of the impacts of various anthropogenic drivers (e.g. fishing activities) on marine biodiversity to support management decisions and effective, ecosystem-based fisheries management (EBFM) in the Mediterranean Sea (Coll et al. 2013, Lehuta et al. 2016, Peck et al. 2018). Ecosystem models represent key quantitative tools that can integrate available knowledge on the ecosystem at different scales to make projections of the consequences (i.e. benefits and trade-offs) of future management decisions (Plagányi 2007, Collie et al. 2016, Lehuta et al. 2016).

Here, we projected and assessed the effects of fishing scenarios at the whole Mediterranean scale by considering the entire life cycle of several interacting species, species distribution shifts, and changes in trophic interactions and in plankton production in a climate change context. We used a recently developed, end-to-end modelling chain at the Mediterranean scale (Moullec et al. 2019b), integrating the dynamics of the physics, of the biogeochemistry and of living organisms, from plankton to fish and macroinvertebrates. We aimed to explore how the Mediterranean marine ecosystem and resources would potentially respond to combined changes in climate and fisheries management strategy by projecting 2 types of plausible fishing scenarios during the 21st century: (1) a general improvement of the fishing size selectivity and (2) changes in fishing pressure in a climate-change context.

2. MATERIALS AND METHODS

2.1. End-to-end modelling chain

We used an integrated modelling chain (hereafter named OSMOSE-MED) including a high-resolution regional climate model (CNRM-RCSM4; Sevault et al. 2014, Darmaraki et al. 2019), a regional biogeochemistry model (Eco3M-S; Auger et al. 2011) and a multispecies and individual-based model (OSMOSE; Moullec et al. 2019b) to project fishing management scenarios in the Mediterranean Sea under the very high greenhouse gas emission scenario RCP8.5 (Moullec et al. 2019a). The CNRM-RCSM4 model is driven by atmosphere and ocean lateral boundary conditions extracted from a general circulation model (CNRM-CM5; Voldoire et al. 2013). Eco3M-S is driven by the atmosphere and ocean outputs of CNRM-RCSM4. At the upper end of the ecosystem, the multispecies dynamic model OSMOSE is forced by the biogeochemistry outputs (i.e. plankton production) of Eco3M-S. The present modelling chain was fully described by Moullec et al. (2019a,b); thus, only a brief description of OSMOSE is given in the present study.

OSMOSE covers the whole Mediterranean basin under a regular grid of 20 × 20 km (6229 cells). It represents the Mediterranean food web from plankton functional groups to the main apex predatory fish and macroinvertebrate species over the period 2006–2013 (Moullec et al. 2019b). OSMOSE-MED is therefore a climatological model which represents an average state over the period 2006–2013. The one-way coupling between Eco3M-S and OSMOSE was realized through the predation process, with planktonic organisms (phyto- and zooplankton) serving as potential prey fields for the high trophic level species (Travers-Trolet et al. 2014a). High trophic level species (n = 97, comprising 82 fish species, 5 cephalopod species and 10 crustacean species, mainly shrimps), accounting for around 95% of total declared catches (83 exploited species) in the region in 2006–2013, were explicitly modelled, i.e. from eggs to the adult life stage. We acknowledge that the number of species considered in this study is low in view of the high species richness in the basin (ca. 714 Mediterranean marine species for fishes alone) and that some species not modelled here could play key trophic roles in the ecosystem. Nevertheless, the ecological processes and the species considered here represent the best biological knowledge currently available in the Mediterranean region (Dimarchopoulou et al. 2017). Major processes of the life cycle, i.e. growth, predation, reproduction, natural and starvation mortalities, as well as fishing mortality were modelled step by step (a 2 wk period in this study) (see Moullec et al. 2019b for more details on the structure and parameterization of OSMOSE, and https://documentation.osmose-model.org for a general description of the model). In OSMOSE, species interact through predation in a spatial and dynamic way (Shin & Cury 2001, 2004). The predation process occurs when there are both spatio-temporal co-occurrence and size compatibility between a predator and its prey. Maximum and minimum predator/prey size ratios govern predator–prey interactions. The food web structure thus emerges from these local individual interactions (Travers et al. 2009, Travers-Trolet et al. 2014b).

A niche modelling approach based on environmental data (i.e. temperature and salinity) has been used to generate high trophic level species presence/absence maps (i.e. climate suitability habitats) in the Mediterranean Sea (Moullec et al. 2019b). Species distribution models developed and calibrated under present conditions were then used to project the environmental niche of species in 2 time slices, 2021–2050 and 2071–2100 (Moullec et al. 2019a, 2022) using future temperature and salinity projections from CNRM-RCSM4 under the very high emission RCP8.5 scenario (Sevault et al. 2014). Temperature and salinity variables (from CNRM-RCSM4) thus indirectly forced OSMOSE-MED both through species distributions and plankton production. To take into account plankton production changes, biogeochemical projections (i.e. plankton production) from Eco3M-S under the RCP8.5 emission scenario were used (see Moullec et al. 2019a for further details).

A classic likelihood-based objective function was used to fit the OSMOSE-MED to biomass and catch data, and to estimate only a few species parameters (e.g. larval mortality and fishing mortality) using an optimization algorithm. OSMOSE-MED was then validated against independent data sets at different hierarchical levels: from individual (e.g. species composition of the diets while only size-based predation rules were modelled) to community levels (e.g. mean trophic level) following an approach similar to pattern-oriented modelling (Grimm et al. 2005). All of these aspects were detailed by Moullec et al. (2019a,b).

2.2. Fishing scenarios and simulation design

Two different plausible fisheries management strategies were simulated and assessed separately.

2.2.1. Change in fishing selectivity

The first set of fishing scenarios involved the size-selectivity of fisheries, one of the main problems encountered with Mediterranean fisheries, especially trawlers which are characterized by a critical combination of high fishing effort and low size at first capture for most commercial species (Colloca et al. 2013, 2017, Vitale et al. 2018). Changes in selectivity could theoretically correspond to changes in mesh size of fishing gears or alternative selection tools and technical solutions (e.g. sorting grids) as requested by international programs (FAO 2020). To reflect a change in the overall fishing selectivity, various multipliers (λ) varying between 1.1 and 1.75 were applied to the length at first catch (*Lc*) of each exploited species (i.e. length at recruitment) that is an input parameter of the OSMOSE model (Shin & Cury 2001, 2004) and defined as spatially uniform at the basin scale. Present day lengths at first catch were extracted from the fisheries data collection of the Joint Research Centre (https://datacollection.jrc.ec.europa.eu). New lengths at catch were computed as follows:

$$Lc_{exploited\ species} = \lambda \times Lc_{current} \quad (1)$$

where $\lambda \in \{1.1, 1.2, 1.3, 1.4, 1.75\}$, and $Lc_{current}$ corresponds to the current length at first catch of the targeted species.

In line with previous studies assessing changes in the exploitation schemes of Mediterranean species (Colloca et al. 2013, Maravelias et al. 2014, Vasilakopoulos et al. 2014, Tserpes et al. 2016), 2 supplementary scenarios of size selectivity were tested with the length at first catch corresponding to either the size at maturity (*Lmat*) of exploited species or to the optimal length at first catch (*Lopt*) defined for each exploited species. *Lopt* is considered a target reference point to avoid growth and recruitment overfishing. Following Froese et al. (2016), *Lopt* was calculated as follows:

$$Lopt = \frac{L_{\infty}(2 + 3\,F/M)}{(1 + F/M)\,(3 + M/K)} \quad (2)$$

where L_{∞} and K are parameters of the von Bertalanffy growth model, M is the natural mortality rate, and F is the present-day fishing mortality rate of the exploited species. Natural mortality rates of each species were computed from the outputs of the OSMOSE model. For all species considered in this study, *Lc* was, on average, 25 and 40% lower than *Lopt* and *Lmat*, respectively. Scenarios of size selectivity corresponding to a 50 and 75% increase in *Lc* were in general closest to length at first catch corresponding to *Lopt* and *Lmat*, respectively.

2.2.2. Change in fishing mortality

A second set of fishing scenarios involved changes in fishing mortality rates. For each fishing scenario, the multiplier α, varying from 0.25 to 1.4, was applied to the current fishing mortality rates, here considered as spatially uniform at the basin scale:

$$F_{exploited\ species} = \alpha \times F_{current} \quad (3)$$

where $\lambda \in \{0.25, 0.5, 0.6, 0.7, 0.8, 0.9, 1, 1, 1.2, 1.3, 1.4\}$, and $F_{current}$ corresponds to the current fishing mortality vector of exploited species, that was estimated during the calibration of OSMOSE to observed biomass and catch data in the Mediterranean Sea in 2006–2013 (see Moullec et al. 2019b for more details on the estimation of fishing mortality rates).

At the Mediterranean scale, during the period 2006–2013, the F/F_{MSY} ratios were, for example, on average 6, 2, 1.9 and 4.1 for European hake, European anchovy *Engraulis encrasicolus*, European pilchard *Sardina pilchardus* and red mullet, respectively. A reduction in fishing mortality could correspond to new fishing regulations proposed by the European Commission consisting of a reduction in fishing effort, spatio-temporal closures and/or a reduction in the fishing fleet capacity over the whole Mediterranean basin (European Commission 2003, 2018, STECF 2016). Alternatively, because Moullec et al. (2019a) projected an increase in total biomass and catch by the middle and end of the 21st century under the RCP8.5 climate change scenario, and because a growing demand for seafood is anticipated globally (FAO 2020), fishing scenarios simulating an increase of up to 40% were also considered.

2.2.3. Simulation design

Given the inherent stochasticity of OSMOSE, 10 replicated simulations in each time period and scenario were run and averaged. For each of the 3 time slices (2006–2013, referred to hereafter as the baseline; 2021–2050; and 2071–2100), simulations were run for 110 yr to ensure sufficient spin-up time (i.e. OSMOSE-MED reached a steady state) and only the last 10 yr were averaged to analyse the outputs. Note that the time of a simulation with OSMOSE (110 yr) is completely independent of the time dynamic in OSMOSE and that 110 yr of simulations simply allow reaching an equilibrium in the outputs. The 2 time slices, 2021–2050 and 2071–2100, were chosen to represent potential mid-term and long-term environmental conditions and to allow comparisons with previous studies in the Mediterranean Sea.

2.3. Indicators of ecosystem structure and functioning

A selection of ecological indicators reflecting different levels of biological organization was used to detect a wide range of fishing-induced impacts in a climate change context (Table 1) (Moullec et al. 2019a). Most of the retained ecological indicators were selected by the IndiSeas programme to track fishing impacts in a context of a changing environment. They were tested against several performance criteria, namely sensitivity, specificity and responsiveness (Rice & Rochet 2005, Shin et al. 2012, 2018, Briton et al. 2019, Halouani et al. 2019).

For each fishing scenario (*sc*) and each period (*period*), the relative change in indicators (*Ind*) is calculated as:

$$\Delta Ind_{sc}^{period} = \left(\frac{Ind_{period,sc} - Ind_{Baseline}}{Ind_{Baseline}}\right) \times 100 \qquad (4)$$

where baseline (*Baseline*) represents the period 2006–2013, in terms of fisheries pressure and climate conditions.

To assess changes in the spatial distribution of total catches, impacts of fishing scenarios were assessed by mapping relative changes in catches by Geographical Sub-Area (GSA) (i.e. operative areas for which boundaries were established by the General Fisheries Commission for the Mediterranean Sea; https://www.fao.org/gfcm/en/), and using only 2 contrasted scenarios simulating a decrease or an increase of 40% in the fishing mortality under the climate change scenario RCP8.5, by the end of the century (2071–2100).

A multivariate analysis (principal components analysis, PCA) based on ecological indicator values projected for the different fishing scenarios and time periods was used to explore potential ecosystem changes in an integrated way. Only the first 2 PCA dimensions were conserved for the analysis. All analyses were performed using R version 3.5.1 (R Core Team 2018).

3. RESULTS

3.1. Projected changes in biomass and catch

In the baseline period (current environmental conditions), considering a decrease by 40% of the fishing mortality, the total biomass and total catch were predicted to increase by 3 and 6%, respectively (Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m708p001_supp.pdf). At the end of the century (2071–2100), under the same fishing scenario but considering climate-induced changes (RCP8.5), total biomass and total catch were projected to increase by 27 and 7%, respectively (Tables S1 & S2). More surprisingly, under RCP8.5, a 40% increase in the fishing mortality would make total biomass and total catch increase by 20 and 19%, respectively, by the end of the century (no change in biomass and an increase in total catch of only 8% under the same fishing scenario in the baseline period, Tables S1 & S2). However, the projected changes in total biomass and total catch masked strong spatial and inter-species changes. By the end of the century, the bulk of the increase in total biomass and catch is located in the eastern part of the basin, while the overall western part could experience a decrease in catch by up to 23% under fishing status quo scenarios (i.e. current fishing mortality and selectivity) (Fig. 1). However, a 40% decrease in fishing mortality showed clear benefits for the total catch in the western basin, with most GSAs experiencing a trend reversal, with an increase in catch up to 20% by the end of the century (Fig. 1). For instance, total catch in the Gulf of Lions (GSA7), projected to decrease by 17% by the end of the century under RCP8.5 and fishing status quo scenario, could increase by 10%, with a 40% decrease in fishing mortality. In the eastern part of the basin, a decrease in fishing mortality would lead to an additional increase in catch by 14% compared to the fishing status quo scenario projected by the end of the century under climate change. In the western basin, under the same decrease in fishing mortality, the increase

Table 1. Ecological indicators used to assess the impacts of fishing scenarios on Mediterranean marine resources and ecosystem structure and functioning. *TL*: trophic level

Indicator	Description
Biomass and catch-based	
Total biomass	Total biomass of all fish and macroinvertebrate species ($TL > 2$) (Hilborn & Walters 1992)
Total catch	Total catch of exploited species (Zeller & Pauly 2007)
Demersal biomass	Total biomass of demersal species
Small pelagic biomass	Total biomass of small pelagic species
Other pelagic biomass	Total biomass of all pelagic species other than small pelagics
Benthic species	Total biomass of benthic species
Size-based	
Large fish indicator (LFI_{40})	Proportion of the biomass of large fish and macroinvertebrates in the community $LFI_{40} = {}^{B_{40}}\!/_{B}$ where B_{40} is the biomass of organisms larger than 40 cm, and B is the total biomass of all species (Greenstreet et al. 2011, Modica et al. 2014)
Mean maximum length in community ($MMLc$)	Reflects the relative abundances of large and small species $MMLc = \sum_i N_i \overline{L_{\max,t}} / N$ where N_i is the abundance of species i, N is the total abundance, and $\overline{L_{\max,t}}$ is the maximum average size of species i (Jennings et al. 1999, Nicholson & Jennings 2004, Shin et al. 2005)
Slope of size spectrum	The size spectrum is the distribution of fish by size class. Here, we used fish numbers by size class of 5 cm over a range of 20 to 200 cm. In $\log_{10}$ scales, the size spectrum was approximated by a decreasing linear function (Rice & Gislason 1996, Shin & Cury 2004, Shin et al. 2005)
Trophic-level based	
Mean trophic level of community ($MTLc$)	Average species trophic levels weighted by species biomass $MTLc = \sum_i TL_i \, {}^{B_i}\!/_{B}$ where TL_i is the trophic level of species i, B_i is the biomass of species i, and B is the total biomass (Pauly et al. 1998, Shannon et al. 2014, Reed et al. 2017)
Marine trophic index (MTI)	Mean trophic level of catch excluding all low trophic level species with $TL < 3.25$ $MTI = \sum_{i\,(TL>3.25)} (TL_i)(Y_i) / \sum_{i\,(TL>3.25)} Y_i$ where Y_i is the catch of species i (Pauly & Watson 2005)

in catch was mainly due to the increase in biomass of demersal (e.g. *Merluccius merluccius*), pelagic species other than small pelagics (e.g. *Xiphias gladius*) and benthic species (e.g. *Mullus barbatus barbatus*), while the increase in the eastern part was linked to the boom of thermophilic and/or non-native small pelagic species (e.g. *Etrumeus teres*). By the end of the century, under a scenario combining the climate change RCP8.5 and a 40% decrease in fishing mortality, the decline in the total catch in the Adriatic Sea is projected to be more pronounced due to the decrease in small pelagic species (e.g. *Sardina pilchardus*) induced by the increased predator biomass (i.e. demersal biomass). Under the opposite fishing scenario, simulating an increase in fishing mortality by 40%, the decrease in catch in the western basin is projected to be less important than under fishing status quo scenario. This change is due to the increase in biomass of small pelagic species (e.g. *Engraulis encrasicolus*), whereas demersal (e.g. *Merluccius merluccius*) and large pelagic species (e.g. *Coryphaena hippurus*) sharply decrease. In the eastern part of the basin, total catch is projected to increase with a 40% increase in fishing mortality combined with RCP8.5, compared to the fishing status quo scenario by the end of the century. This global increase is due to the boom of the biomass of small pelagic species, thermophilic and/or non-native species, while the biomass of demersal or other pelagic species (mainly large pelagics) is projected to decline.

Regardless of the considered period, an increase in fishing mortality in the 21st century, even by only 10%, could lead to a decrease in demersal and other pelagic (mainly large pelagic fish species) biomass

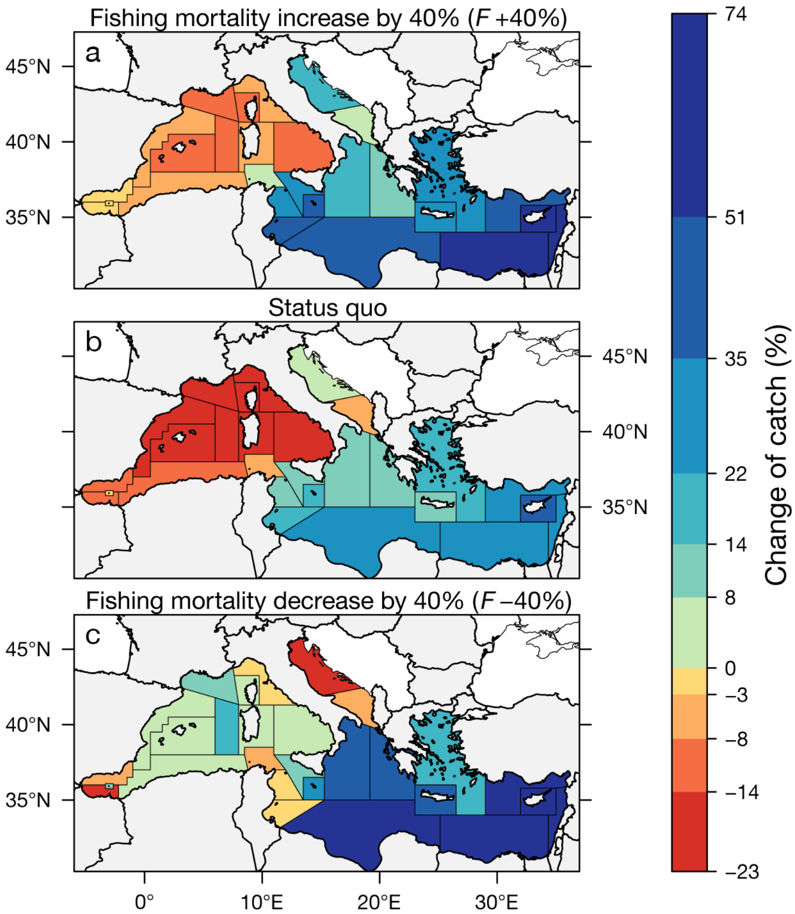

Fig. 1. Projected relative changes in catch by the end of the century (2071–2100), by geographical sub-area, resulting from the RCP8.5 climate change scenario combined with 3 different fishing scenarios: (a) increase by 40% of the fishing mortality; (b) status quo, i.e. current fishing mortality and selectivity; (c) decrease by 40% of the fishing mortality). Changes were compared to the baseline period (2006–2013). Under the fishing scenario simulating a 40% increase in fishing mortality, the slight increase in catches in the western Mediterranean Sea is due to the increase in biomass of small pelagic species, whereas demersal and large pelagic species, the main predators of small pelagic species, are projected to decrease. In contrast, a decrease in fishing mortality by 40% could lead to higher catches in the western part due to the increase in biomass of demersal, pelagic species other than small pelagics and benthic species

(Fig. 2). For example, in the baseline period, an increase in fishing mortality of 40% could lead to a decrease in demersal and other pelagic biomass by up to 14 and 4%, respectively, and the yields could decrease by ca. 26 and 4%, respectively. Under the climate change RCP8.5 scenario, the same negative trends were projected but with a higher magnitude. For the 2 future periods (2021–2050 and 2071–2100), small pelagic species (forage species) and benthic species are expected to benefit from the removal of demersal and large pelagic species (Fig. 2). Considering a 40% increase in fishing mortality, their biomass was projected to increase by ca. 33 and ca. 50%, respectively, by the end of the century. In contrast, a global decrease in fishing mortality by 75% would lead to an increase in biomass for demersal, other pelagic and benthic species up to 48, 104 and 74%, respectively, in the baseline period (i.e. without climate change) and up to 58, 102 and 122%, respectively, under RCP8.5 by the end of the century. As a comparison, under the status quo fishing scenario combined with RCP8.5, the biomass of demersal and benthic species was projected to increase by ca. 3 and 32%, respectively, by the end of the century. Small pelagic species may not benefit from the global decrease in fishing mortality as a result of increased predation pressure from demersal and large pelagic species. However, the climate change induced increase in plankton production counterbalanced the increase in predation pressure. As a result, the biomass of small pelagic species was projected to increase by 5% at the end of century, under a 75% reduction in fishing mortality combined with RCP8.5.

Improving size-selectivity is expected to benefit demersal, other pelagic and benthic species which showed an increase in biomass in response to increased length at first catch, whereas an opposite trend was found for small pelagic species. Marked positive changes in biomass appeared only from an increase of at least 30% of the length at first catch (Fig. 2).

Our projections suggested that acting on both fishing mortality and fishing selectivity would be beneficial to some species of high commercial interest which were projected to decrease in biomass due to climate change if no change in management was undertaken. For instance, the biomass of European hake was projected to decrease by 26% by the end of the century as a result of climate change (RCP8.5) and business as usual fisheries management. By contrast, it was projected to increase by 30% if fishing mortality was reduced by 40%, thereby offsetting negative effects of climate change. On the other

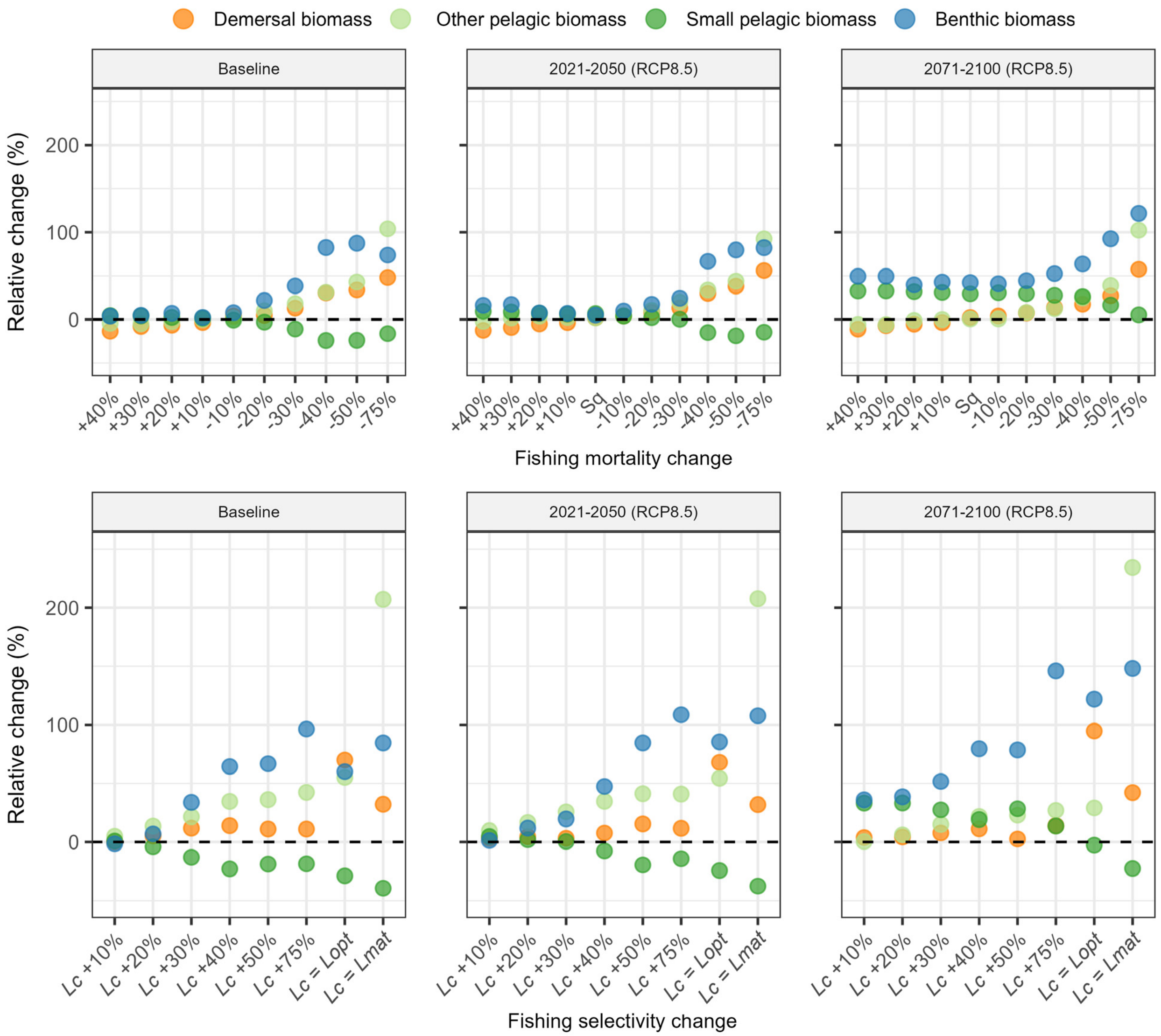

Fig. 2. Projected relative change in biomass under climate change (RCP8.5) and various fishing scenarios. Changes were compared to current status quo scenario (dashed line) with climate and fishing conditions in 2006–2013. *Lc*: length at first catch; *Lmat*: length at maturity; *Lopt*: optimal length; Sq: status quo. Biomasses were aggregated according to habitat

hand, due to trophic interactions, the biomass of European anchovy, projected to increase by 35% by the end of the century under climate change (RCP8.5) and status quo fishing scenarios, would only increase by 4% if a decrease of 40% in fishing mortality was applied.

3.2. Projected changes in trophic indicators

The mean trophic level of the community (*MTLc*; based on species composition in the ocean) showed an overall positive trend, with lower fishing mortalities and larger size at first catch for all considered periods with or without climate change (Fig. 3). However, due to climate change, regardless of the type of fishing scenarios, the *MTLc* is globally projected to decrease by the end of the century compared to the baseline period. Only a reduction of at least 50% in fishing mortality or an increase of at least 75% in length at first catch would be likely to maintain or slightly increase the *MTLc* compared to the baseline period (Fig. 3). Due to changes in the biomass of demersal and benthic species, which are affected by an increasing predation pressure induced by the large increase in large pelagic species, the marine trophic index (*MTI*; reflecting species composition of the catch) could decrease under the most 'impacting' fishing

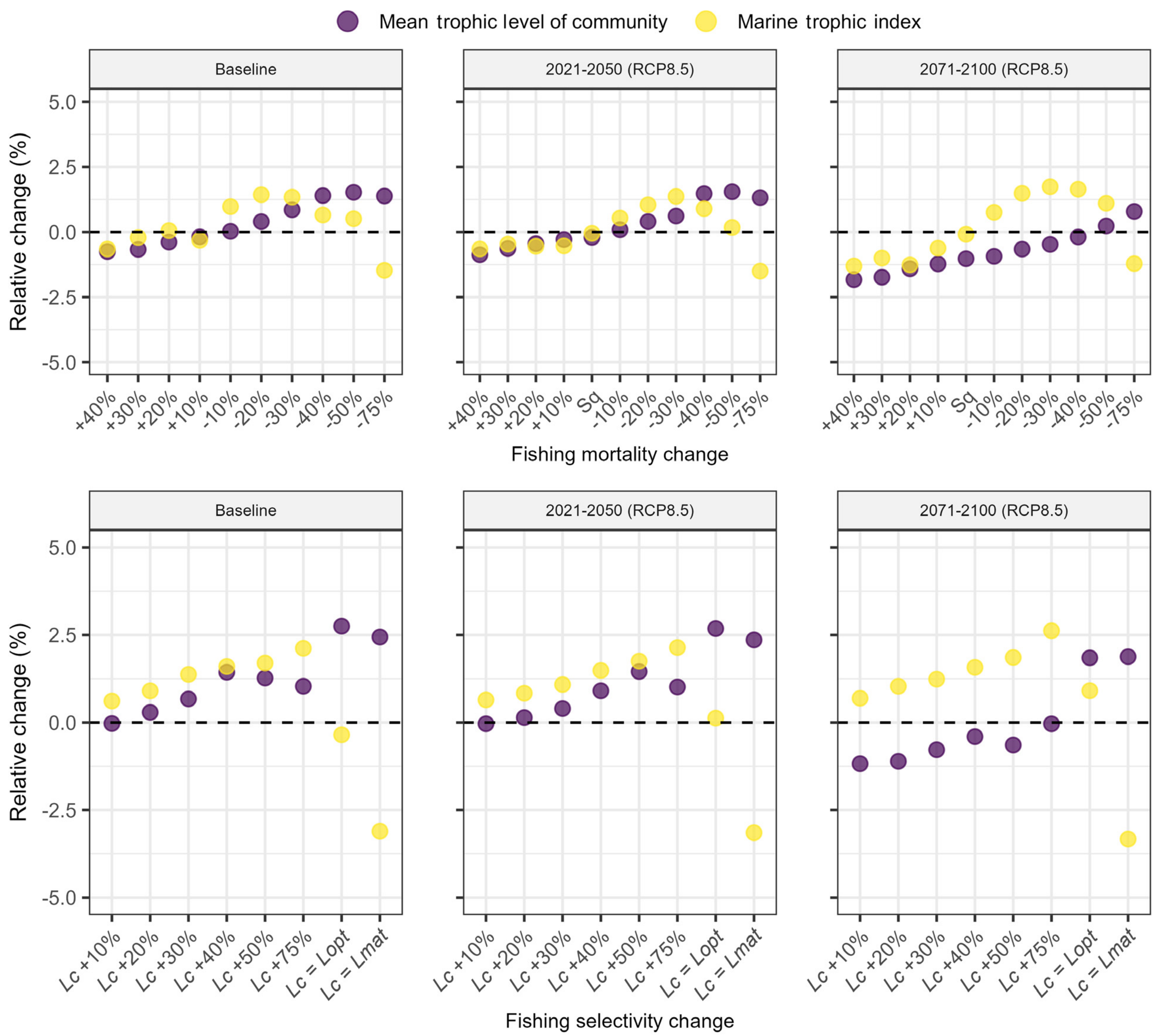

Fig. 3. Projected relative change in the mean trophic level of the community and the marine trophic index under climate change (RCP8.5) and various fishing scenarios. Changes were compared to current status quo scenario (dashed line) with climate and fishing conditions in 2006–2013. Abbreviations as in Fig. 2

scenarios (i.e. *F* of –50%, *F* of –75%, *Lopt*, *Lmat*). In all considered periods, fishing scenarios involving moderate changes in size-selectivity (i.e. an increase in length at first catch from 20 to 75%) appeared to be the most effective to maintain or increase *MTLc* and *MTI* simultaneously.

3.3. Projected changes in size-based indicators

Among the size-based indicators, the large fish indicator (*LFI*) was clearly the most responsive indicator to changes in fishing pressure (Fig. 4). In the baseline period (with current climatic conditions), the *LFI* was predicted to increase by up to 106% with a 75% decrease in fishing mortality and to decrease by up to 18% with a 40% increase in fishing mortality. By the end of the century, under RCP8.5 and considering a decrease by 75% or an increase by 40% in fishing mortality, the *LFI* was projected to increase by 91% and to decrease by 32%, respectively. As a comparison, the *LFI* was projected to decrease by ca. 16% under fishing status quo and the RCP8.5 climate change scenario by the end of the century. A decrease in fishing mortality could thus lead to a greater proportion of large individuals in the system, even in a climate-change context. With change in size-selectivity, the *LFI* remained almost stable or

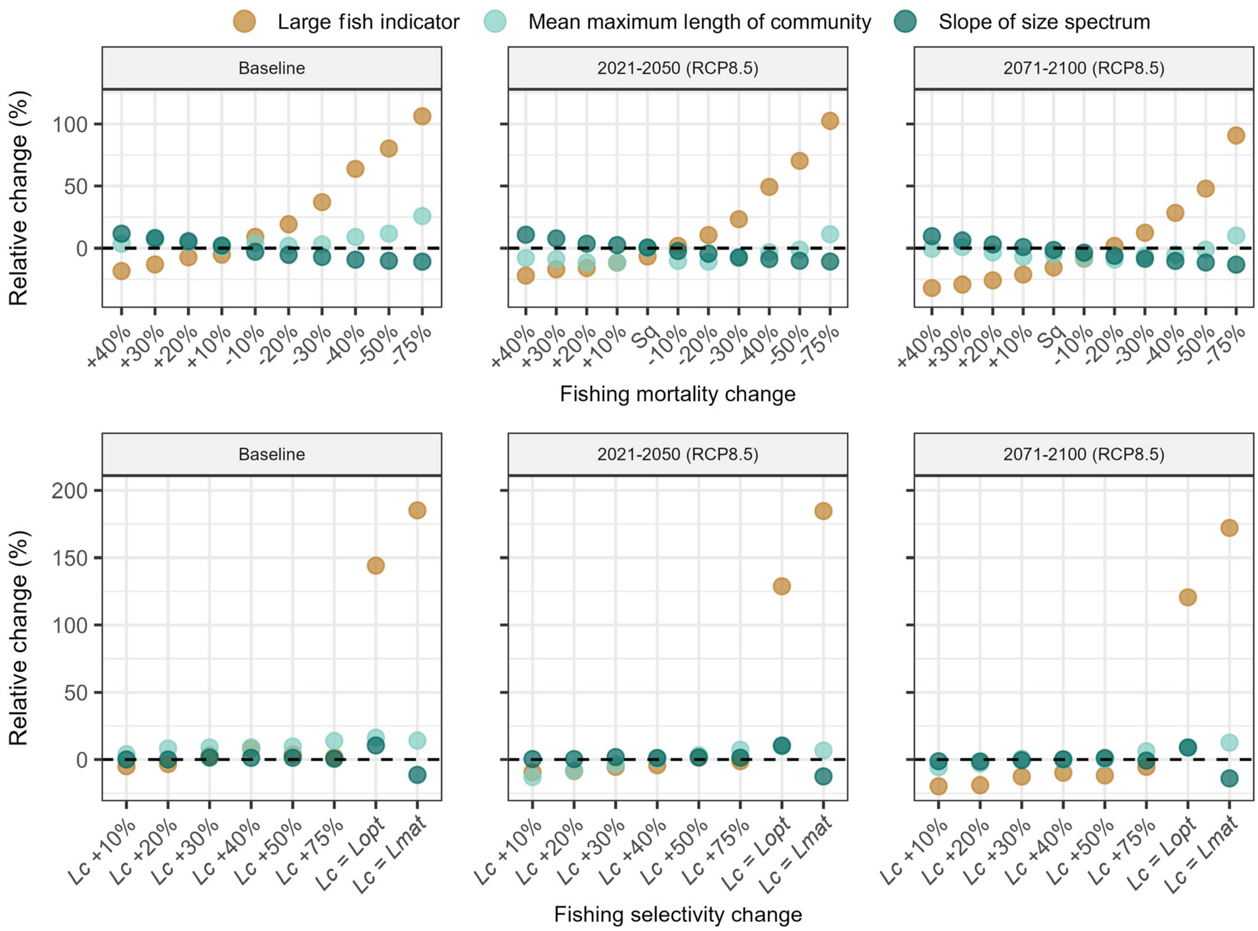

Fig. 4. Projected relative changes in the large fish indicator, the mean maximum length of the community and the slope of size spectra under climate change (RCP8.5) and various fishing scenarios. Changes were compared to current status quo scenario (dashed line) with climate and fishing conditions in 2006–2013. Abbreviations as in Fig. 2

slightly decreasing in all fishing scenarios, except in the 2 size-selectivity scenarios Lopt and Lmat: in all considered periods (with climate change or under current climatic conditions), only the *Lopt* and *Lmat* scenarios were projected to induce a large increase in the *LFI*, from 121 to 185%.

The mean maximum length of the community (*MMLc*) showed non-trivial trends (Fig. 4). In the baseline period, an increase in the fishing mortality of 30% could lead to an increase by 7% in the *MMLc*, resulting from a decrease in the largest individuals, followed by an increase in the medium-sized fish, and in turn a decrease in small individuals. By the middle and end of the century, under RCP8.5 and fishing status quo scenario, the *MMLc* was projected to decrease by ca. 10 and 5%, respectively. However, by decreasing the fishing mortality by 75% or by increasing the length at first catch in the same proportion, the *MMLc* was projected to increase by 10 and 6%, respectively, by the end of the century under RCP8.5.

The slope of the community size spectrum (from 20 to 200 cm) steepened with increasing fishing mortality (the absolute value increased) with or without climate change (Figs. 4 & 5). It remained stable for most fishing scenarios involving a change in size-selectivity, except for Lopt and Lmat scenarios (Figs. 4 & 5). There was no clear change of slope between periods. However, increasing the length at first catch up to the length at maturity or to the optimal length reference point was projected to increase oscillations of the community size spectra (Fig. 5; Fig. S1).

3.4. Multivariate analysis of fishing and climate change scenarios

The first 2 dimensions of the PCA explained 68.7% of the variance (Fig. 6; Figs. S2–S5). *MTLc, MMLc, LFI,* demersal biomass, other pelagic biomass and benthic biomass variables were positively correlated

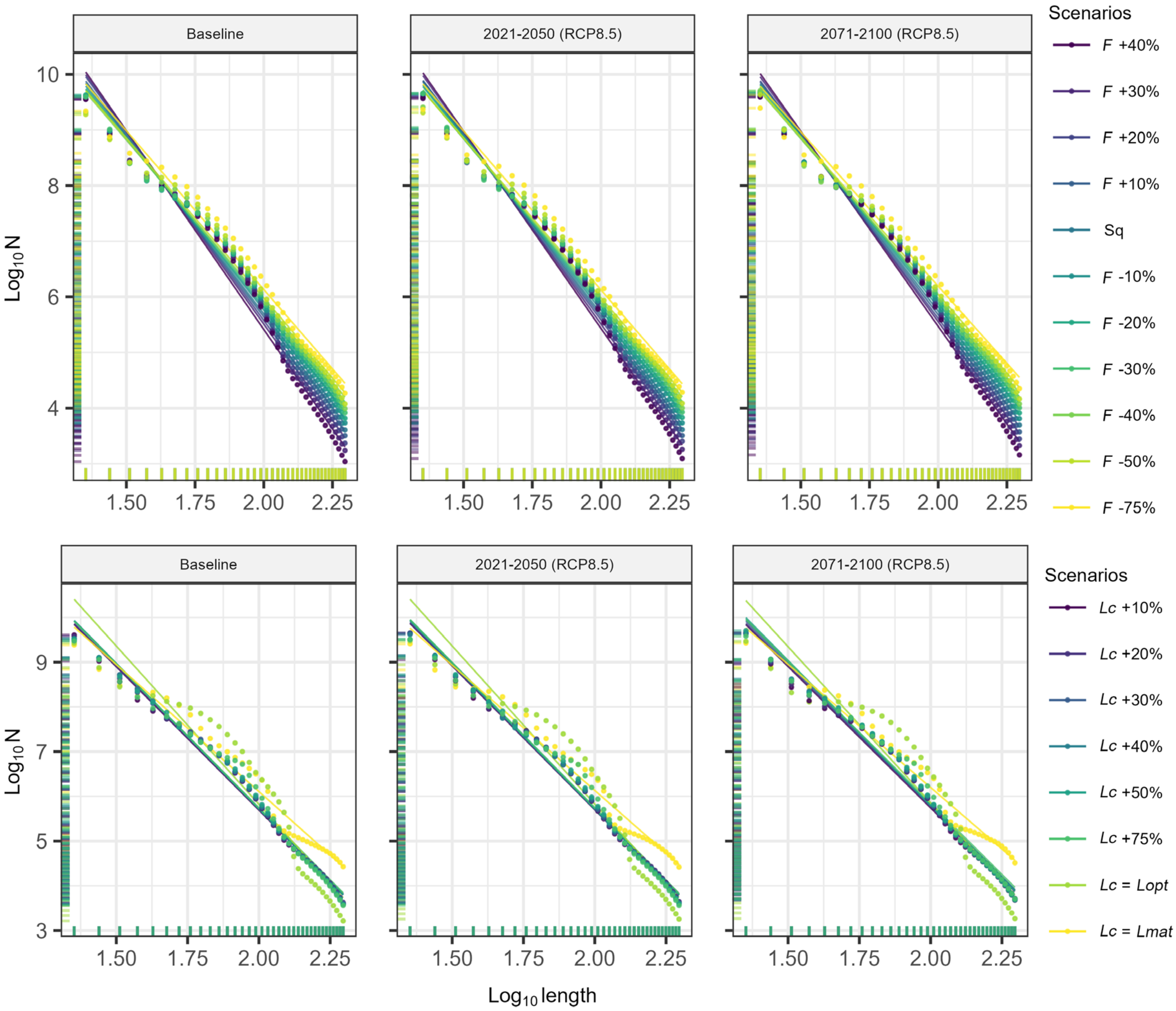

Fig. 5. Projected community size spectra (log-log scale; abundance N per 5 cm size-class between 20 and 200 cm) under climate change (RCP8.5) and various fishing scenarios. Linear regressions were applied. *F*: fishing mortality rate; other abbreviations as in Fig. 2. Marks on the axes represent the coordinates of each point

with each other and negatively correlated with total catch, small pelagic biomass and *MTI*. The first axis opposed fishing scenarios, leading to an increase in biomass of demersals and pelagic species other than small pelagics (i.e. mainly large pelagic species) and associated with higher values of *LFI* and *MTLc* to fishing scenarios, inducing an increase in small pelagic biomass and a decrease in the latter indicators. The second axis opposed fishing scenarios, leading to a higher total biomass, a higher biomass of small pelagic species, a higher absolute value of the slope of the size spectrum to fishing scenarios leading to higher *MTI* and *MTLc* values (Fig. 6). The PCA showed that, by the end of the century, under the RCP8.5 climate change scenario combined with any of the fishing scenarios, the structure and functioning of the Mediterranean Sea would progressively evolve towards higher total biomass, with an increasing proportion of small pelagic species in the community and a decrease in large individuals (*LFI, MMLc*) and higher trophic level species (*MTLc*). Fishing scenarios that could slightly buffer such climate-induced changes in species composition were all oriented toward a decrease in the fishing mortality and an increase in the length at first catch (e.g. *F*−50%, *F*−75%, *Lc*+40%, *Lc*+75%, *Lopt* or *Lmat*) (Fig. 6; Fig. S5). In contrast, an increase in fishing mortality (e.g. *F*+30% or *F*+40%) could accentuate the impacts on the structure and functioning of the Mediterranean Sea as shown by the slight shift towards lower values of *MTLc, MMLc, LFI* or demersal and large pelagic biomass along dimension 1 of the PCA.

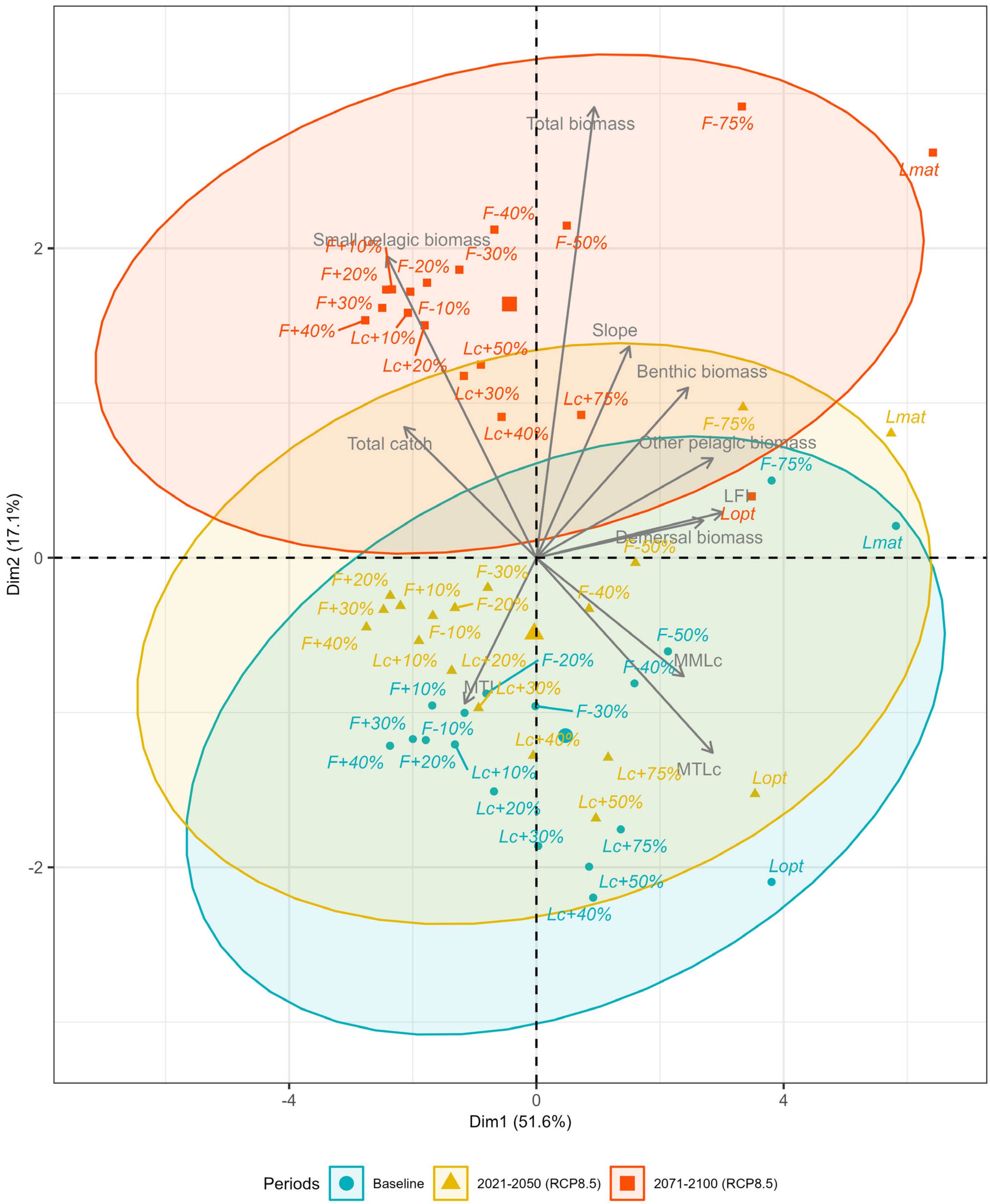

Fig. 6. Principal components analysis (PCA) of the 54 simulated fishing scenarios (18 fishing scenarios per period) under the baseline (2006–2013, blue) and future periods under RCP8.5 scenario (2021–2050, yellow; 2071–2100, red). Ellipses represent concentration ellipses at normal probability. Abbreviations as in Figs. 2 & 5, and Table 1

4. DISCUSSION

While previous modelling approaches in the Mediterranean Sea have focused on climate change impacts on specific biological compartments (e.g. Albouy et al. 2012, Chefaoui et al. 2018, Benedetti et al. 2019) or local ecosystems (Libralato et al. 2015, Hattab et al. 2016, Corrales et al. 2018), here we project the effects of climate change and fisheries management strategies at the whole Mediterranean scale and in an integrated way, i.e. considering explicit and consistent changes in regional climate, ocean dynamics, nutrient cycles, plankton production, shifts in species distributions, their life cycles and their trophodynamic interactions (Moullec et al. 2019a).

4.1. Potential trade-offs between conservation and exploitation

Our results highlight that under current environmental conditions (i.e. baseline), a reduction in fishing mortality or an increase in fishing selectivity could result in an increase in the biomass and catch of demersal, large pelagic species and benthic biomass. The resulting increased predation mortality exerted on small pelagics would reduce their biomass. Such a trophic cascade has already occurred in the Mediterranean Sea (Lotze et al. 2011, Coll & Libralato 2012), projected for the Israeli continental shelf under climate change (Corrales et al. 2018), simulated in a marine protected area under various fishing management scenarios (Albouy et al. 2010) and observed in other ecosystems in the world (Daskalov et al. 2007, Andersen & Pedersen 2010, Szuwalski et al. 2017). From an ecosystem perspective, small pelagics may not benefit as much from a global decrease in fishing pressure. Using a monospecific approach, Colloca et al. (2013) showed the positive effect of an exploitation at optimal length (*Lopt*) on the biomass of demersal and large pelagic fish stocks and the negative impact on the biomass of European anchovy stocks. The authors explained their results by the fact that *Lopt* was estimated lower than the current length at catch of European anchovy (Colloca et al. 2013). In our study, *Lopt* was estimated higher than the current length at catch, hence suggesting a major role of trophic interactions in population and community dynamics.

In contrast, for all considered periods, with or without climate change, we found that a global increase in fishing mortality would be beneficial to small pelagic species, and thus to total catches, due to the release of predation by species at the top of the food chain (Baum & Worm 2009, Steneck 2012). Such a trophic cascade has been demonstrated to be responsible for the high reported wild catches in areas of the world with minimal management measures in place and intense fishing, which is the case for the Mediterranean Sea (Szuwalski et al. 2017). Our simulations thus emphasized the emergence of winner and loser species from different management strategies. This point questions the relevance of several target reference points (e.g. MSY) established by single-species assessments to reach EBFM goals (Walters et al. 2005, Karp et al. 2019) and highlights the need to consider trade-offs between ecosystem management objectives and commercial interests (Engelhard et al. 2014, Andersen et al. 2015, Essington et al. 2015). As mentioned by Koehn et al. (2017), trade-offs exist between the revenue generated by harvesting forage fish species directly versus leaving them in the ocean and harvesting their predators, which generally have a higher economic value per catch unit (FAO 2020). In addition, increasing fishing pressure could certainly increase total fishery productivity by removing predatory fish but with detrimental effects on biodiversity and ecosystem functioning (Andersen et al. 2015, Szuwalski et al. 2017). Future studies assessing fishing scenarios under climate change should consider different trade-offs between objectives (for example, between minimizing ecosystem impacts and maximizing catches and profits) and across interacting species (Jacobsen et al. 2017). Under current climate conditions and fishing scenarios aiming at reducing fishing impacts, all ecological indicators obtained in our study (excepted the *MTI*) underlined a potential restoration of the structure and functioning of the Mediterranean ecosystem as well as of marine resources, some of which are of high commercial interest in the region (e.g. European hake, red mullet or deep-water rose shrimp). These results are in line with past studies showing the benefits of reducing fishing activities in the Mediterranean Sea (e.g. Vasilakopoulos et al. 2014, Tserpes et al. 2016, Corrales et al. 2018). On the contrary, our projections showed that an increase in fishing mortality, even moderate, could lead to a decrease in the biomass of demersal or large pelagic species (here included in other pelagic species), estimated to be highly overexploited by our OSMOSE model and by current stock assessments (FAO 2020). An increase in fishing pressure could therefore lead to changes in trophic functioning and increases in abundance of species with higher turnover rates, of smaller size and at low trophic levels, as suggested by our ecological indicators and as observed by hindcast studies in the Adriatic Sea, the Catalan Sea, the Aegean Sea or at the Mediterranean scale (Coll et al. 2009, Lotze et al. 2011, Piroddi et al. 2017). An increase in fishing mortality would then make the Mediterranean ecosystem and marine resources more sensitive to climate forcing, with implications for fisheries sustainability and biodiversity conservation (Perry et al. 2010, Hidalgo et al. 2011).

Our projections under a worst-case climate change scenario (RCP8.5, 2021–2050 and 2071–2100 periods) showed that a reduction in fishing mortality or a larger length at first catch could dampen some climate-induced changes on ecosystem structure and functioning and likely rebuild overexploited marine resources by the middle and end of the century. In addition, by the end of the century, climate change and the projected increase in plankton production, which would be beneficial to planktivorous fish (Moullec et al. 2019a), could mitigate the negative impact induced by the increase in predation by large demersal and pelagic species on small pelagic biomass under fishing reduction and size-selectivity scenarios. However, we showed that the increase in small pelagic fish is mainly driven by thermophilic and/or non-native fish species such as *Etrumeus teres* in the southeastern part of the basin (Moullec et al. 2019a), raising new questions on the potential of fishers, markets and seafood consumers to adapt to this projected change (Galil 2008, Lam et al. 2016, Weatherdon et al. 2016). For certain fisheries in the eastern Mediterranean Sea (e.g. in Turkish or Egyptian waters), these increases in the biomass of non-native species, such as *E. teres*, may offer new opportunities to increase catches and therefore income for fishermen (Farrag 2010).

Recent studies conducted in the Mediterranean Sea at local (Corrales et al. 2018) and global scales (e.g. Carozza et al. 2019, Lotze et al. 2019, Sumaila et al. 2019) also demonstrated the numerous benefits of a higher regulation of fishing activities on marine ecosystems and resources even, and especially, in a climate change context. Our results were partially in line with these studies. Most of them projected a significant decrease in global biomass and/or catch under climate-induced changes and suggested that improvements in fishery management could offset the negative consequences of climate change and lead to ecosystems with higher total biomass and catch. In our case, trade-offs exist because fishing regulation could be beneficial for the global ecosystem structure and functioning but not as much for the total biomass and catch (as increasing large-fish biomass could decrease the small-fish biomass), for which increases, mainly in the eastern Mediterranean part, are projected under climate change. From an Ecopath with Ecosim model, Corrales et al. (2018) also shown that climate change could increase the total biomass in the Israeli continental shelf due to the increase in primary producers and alien fish by the middle of the century. In the Gulf of Gabès, Hattab et al. (2016) projected changes in the ecosystem functioning, with more smaller-sized species composing the food web structure under a high-emissions scenario.

In the RCP8.5 climate change scenario, we projected a decrease in the total catch across all western Mediterranean Sea waters (up to 23%) by the end of the century under status quo fishing. An increase in fishing mortality could exacerbate the projected trend of climate change effects on the ecosystem structure and functioning, with an increase in smaller size and lower trophic level species (forage fishes) and a decrease in demersal and large pelagic species in the community, weakening the fishing activity in this part of the basin. In contrast, a reduction in fishing mortality would result in a greater catch by the end of the century than during the baseline period (2006–2013), composed of individuals and species of larger size and higher trophic levels, generally associated with higher prices in the Mediterranean Sea (FAO 2020). Reflecting the proportion of large predatory fish in the catch, the *MTI* was projected to respond in a non-monotonous way to reduced fishing mortality or increased size at first catch, first increasing but then decreasing if fishing mortality was reduced by more than 30% or if the size at first catch was at Lopt or Lmat. Species at medium trophic levels, between 3.25 and 4.0, which composed the bulk of the total biomass, were indeed affected by an increasing predation pressure induced by the large increase in large pelagic species, thus driving the decrease in *MTI*. The projected change will likely be associated with a tropicalization of the catch, a phenomenon already taking place in the Mediterranean Sea (Tsikliras & Stergiou 2014).

As shown by previous studies involving single-species approaches but disregarding climate change impacts, Mediterranean Sea fisheries, particularly in the western basin, will need to adapt by reducing their effort and improving selectivity of their gear to be sustainable (Tsikliras et al. 2015, Cardinale et al. 2017, Vitale et al. 2018). Many studies reported positive effects of increased size selectivity on the population dynamics of the main targeted species in the Mediterranean Sea; however, management targets could only be achieved through a radical change in fisheries selectivity (Maravelias et al. 2014, Tserpes et al. 2016). With decreased fishing mortality and increased gear selectivity, Mediterranean stocks, especially demersal stocks for which the current selectivity is poor, could be more resistant to fishing pressure and could produce higher, long-term yields (Vasilakopoulos et al. 2014). Nonetheless, the beneficial effects of increasing the size at first catch on ecosystem structure and functioning are debated (e.g. Rochet et al. 2011, Breen et al. 2016, Law et al. 2016). Some studies indicated that the combination of heavy fishing with minimum-size regulations was a major disruption to the structure and function of aquatic ecosystems (Law et al. 2015). Here, using different ecological indicators, our results suggest that exploiting species at their size at maturity (*Lmat* in this study) or at an optimal length (*Lopt*; Froese et al. 2016) could minimize fishing impacts on ecosystem structure but could also destabilize (i.e. amplify oscillations) of the biomass flow in the community size spectra. Moreover, at current fishing mortality levels, oscillations have wider amplitude with the increase in size-selectivity. Rochet & Benoît (2012) observed the same pattern with a more simplistic size-spectrum model and highlighted a possible risk for population and community dynamics.

4.2. Using multiple ecological indicators to track climate and fishing impacts

Ecosystem-level indicators, such as those used in this study, offer the possibility to track the status of ecosystems and marine resources under climate change and fishing impacts and to support decision-making for an ecosystem approach to fisheries (Fulton et al. 2005, Coll et al. 2016). The non-linear or low responses of some indicators, such as the *MMLc* or the *MTLc*, highlight the need to consider a suite of complementary indicators. All indicators calculated in this study were complementary to provide an overview of ecosystem changes and to detect a large range of impacts from fishing. The use of total biomass or total catch (across all groups) may have masked changes in the species composition of the community or the strong spatial heterogeneity of the impacts. The oscillations along the size spectrum induced by an increase in large individuals and a decrease in smaller organisms were not captured by changes in *MMLc* in fishing scenarios. Our results also indicated that the capacity of an indicator to track fishing effects depended on the fishing management strategy. For example, the slope of the size spectrum remained almost stable for most of the scenarios involving size selectivity changes but showed clear changes with fishing mortality scenarios. For all scenarios, the *LFI*, identified as an indicator for food webs and for monitoring biodiversity in European seas (Shephard et al. 2011, Marshall et al. 2016, Stamoulis & Torreele 2016), appeared as the most suitable to detect a change in ecosystem structure under climate and fishing forcing. This finding is in line with Halouani et al. (2019), who identified the *LFI* as a key size-based indicator to reflect a change in the status of the Gulf of Gabès ecosystem associated with changes in fishing pressure. In our study, changes in *LFI* values were associated with 2 different, co-occurring processes. First, the increase in fishing mortality on already heavily overfished large organisms could lead to the decrease in biomass of organisms >40 cm and the increase in biomass of organisms of lower size and trophic level (due to decreased mortality by predation). In parallel, climate-induced changes could favour the increase in organisms <40 cm, which could amplify the decrease in *LFI* in future periods. The fact that the *LFI* decreases under current fishing mortality (status quo, 'Sq') and climate change scenario suggests that it is robust enough to track climate-induced changes on the size composition of the fish community.

4.3. Limitations and perspectives

While this study represents significant progress in assessing the potential ecosystem effects of different fisheries management strategies under climate change, there are various sources of uncertainty. First, we used a single greenhouse gas emissions scenario, RCP8.5, while there is a strong scientific debate around the plausibility and accuracy of this scenario (e.g. Hausfather & Peters 2020, Schwalm et al. 2020, Arias et al. 2021, Burgess et al. 2022). RCP8.5 is one of the most commonly used scenarios in the climate impact literature, but it is increasingly considered as unrealistic in its assumptions (Kemp et al. 2022, Burgess et al. 2023). Future works using OSMOSE-MED to explore consequences of future management decisions under climate change should therefore consider more plausible median scenarios such as SSP2-3.4 and SSP2-4.5 (Pielke et al. 2022, Burgess et al. 2023). Second, we employed a range of fairly simplistic fishing scenarios that do not incorporate spatial, seasonal or ontogenic variations in the fishing mortality applied to each species. For example, we did not consider adaptive responses of fisheries to potential changes in species abundance and distribution. Third, similar to the study by Cheung et al. (2010), we assumed that the fisheries exploitation tracked the distribution of the target species. Fourth, we simulated global and simultaneous changes in fishing mortality or selectivity for all exploited species, which is unlikely, even if most Mediterranean fisheries are landing multiple species (Stergiou et al. 2003, FAO 2020). Moreover, we used a theoretical fishing fleet targeting all exploited species and did not resolve the different artisanal and industrial fishing fleets operating in the Mediterranean basin. Finally, we used a simple, knife-edge size selectivity, but as the type of fishing selectivity could influence the outcomes of the simulations, future works with OSMOSE should consider different selectivity curves, i.e. either sigmoid functions or Gaussian selectivity curves, that are more realistic (Rochet & Benoît 2012).

There are also uncertainties regarding the whole modelling chain developed in this study, from the regional climate model CNRM-RCSM4 to the higher trophic level model OSMOSE. For example, our results were highly sensitive to forcing by outputs from the lower trophic model (biomass of phyto- and zooplankton groups) estimated by the joint RCSM4/Eco3M-S model. The Eco3M-S biogeochemical model projected an increase in plankton biomass, mainly in the eastern basin (Moullec et al. 2019a), which influenced the overall trends of our fishing scenario outputs. However, there is currently no scientific consensus on the future plankton productivity under climate change in the Mediterranean Sea (Adloff et al. 2015). Some authors argued that primary and secondary production, due to increases in water temperature and stratification (Herrmann et al. 2014), could increase by the end of the century, notably in the eastern basin (Macias et al. 2015), while others projected a global decline in primary production linked to reduced vertical nutrient supply into the photic layer (Steinacher et al. 2010, Richon et al. 2019). The different sources of uncertainty (e.g. structural, linked to model parameterization or to scenarios) need to be addressed in future work to increase the credibility and relevance of ecosystem model projections, but the methods and studies dealing with such challenges are still lacking for complex ecosystem models (IPBES 2016, Payne et al. 2016).

As we only modelled a small range of drivers and impacts in our study, our results are most likely conservative. We did not consider, for instance, other potential effects of climate change and greenhouse gas emissions on marine ecosystems and resources such as the bio-energetic temperature, oxygen and/or pH effects on the eco-physiology of marine organisms, nor the impacts of pollution, habitat destruction or the arrival of new invasive species (Pereira et al. 2010, Micheli et al. 2013, Peck et al. 2018). Such emergent impacts could exacerbate or inverse our projected trends. We also did not consider the bathymetric displacement of species in response to climate warming. Such a vertical displacement, towards cooler and deeper waters, has been reported in the Mediterranean Sea for species such as red mullet or European hake (Galil & Zenetos 2002). The shift in vertical distribution is expected to affect species availability to fisheries and could thus exacerbate the projected decline in commercial catches.

Although the modelling chain used in this study is based on the best ecological knowledge available for the Mediterranean, certain gaps relative to the lack of biological and ecological data on macroinvertebrate species (Dimarchopoulou et al. 2017) as well as the variable quality of commercial fisheries data in the south-eastern Mediterranean Sea, could influence our results in this area (Moullec et al. 2019b).

5. CONCLUSIONS

This study highlights the necessity for western Mediterranean fisheries to move toward a global decrease in fishing mortality, meaning the implementation of non-mutually exclusive management measures such as a decrease in the capacity of the most impacting fishing fleets, i.e. bottom and pelagic trawlers (e.g. Maynou 2014, Corrales et al. 2015, Piroddi et al. 2015); the application of total allowable catches and quota regulation for several species; and/or spatio/temporal closures of fishing activity (STECF 2016, European Commission 2018) to restore ecosystem structure and depleted biomass. Our results also emphasize the need to improve the size selectivity of fishing gear by fixing and strengthening the control on minimum reference sizes and by establishing more restrictive rules on fishing gear (e.g. mesh size). Fisheries management in the Mediterranean basin needs to adapt to climate change (FAO 2020), as we have shown that it impacts marine resources in different ways depending on their location in the basin and in the trophic web, with large demersal and pelagic species in the western Mediterranean Sea likely to be more vulnerable to climate-induced changes. Failure to recognize the impact of warming on climate-sensitive fish stocks and ecosystems could indeed contribute to overfishing (Pershing et al. 2015). In the eastern part, newly arriving species and species benefiting from climate change could offer new opportunities of exploitation if fisheries succeed in targeting only these species. An unselective increase in fishing pressure (i.e. without preferentially targeting species that benefit from climate change) could contribute to the opening of an invasion window (Caplat et al. 2010, Libralato et al. 2015) and exacerbate the destabilization of community structure and the loss of ecosystem resilience to climate-related changes (Libralato et al. 2015, Corrales et al. 2018).

Data availability. The raw data supporting the conclusions of this manuscript will be made available by the authors, without undue reservation, to any qualified researcher.

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