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How will the cumulative effects of fishing and climate change affect the health and resilience of the Celtic Sea ecosystem?

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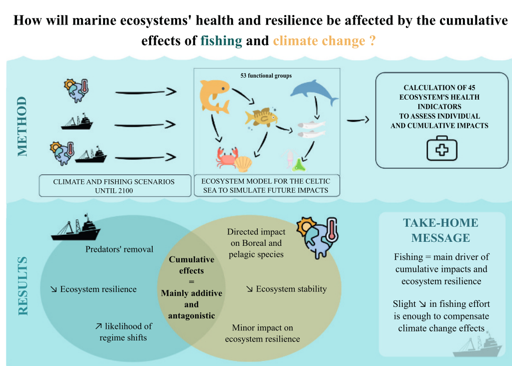
HIGHLIGHTS

- Climate change impacts Boreal, pelagic species and ecosystem stability.
- Fishing is predicted to increase the likelihood of a regime shift.
- Predicted cumulative effects are mainly additive and antagonistic.
- Climate change had minor impacts on ecosystem recovery to fishing.
- Fishing is the main driver of cumulative impacts and of ecosystem resilience.

GRAPHICAL ABSTRACT



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ABSTRACT

Ecosystems are subject to increasing anthropogenic pressures worldwide. Assessing cumulative effects of multiple pressures and their impacts on recovery processes is a daunting scientific and technical challenge due to systems' complexity. However, this is of paramount importance in the context of ecosystem-based management of natural systems.

Our study provides major insights into the assessment of cumulative effects on Northeast Atlantic ecosystems. Using an Ecopath with Ecosim (EwE) tropho-dynamic model for the Celtic Sea ecosystem including 53 functional groups, we (1) assess individual and cumulative effects of fishing and climate change and (2) explore the impact of fishing intensity and climate change on ecosystem resilience. Various levels of increasing fishing intensities are simulated over the whole 21st century, by forcing the EwE model with time series of sea temperature, primary production and secondary producer's biomass from the regional POLCOMS-ERSEM climate model, under both RCP4.5 and RCP8.5 scenarios. Cumulative impacts on the ecosystem's health and its capacity to recover after the cessation of fishing activities were assessed through a set of 45 indicators (biomass-based, diversity, trait-based and habitat-based indicators), using a theoretical non-fishing and climate-constant scenario as a reference.

Our results reveal climate change impacts on Boreal, pelagic species and on ecosystem stability. Fishing preferentially removes apex predators and is predicted to increase the likelihood of a regime shift by decreasing ecosystems' capacity to recover. Predicted cumulative effects are mainly additive and antagonistic but synergies

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are observed for high fishing effort levels, and finally climate change had minor impacts on ecosystem recovery to fishing. Fishing is shown to be the main driver of cumulative impacts and of ecosystem resilience over the next decades. Our results suggest that slight reduction in fishing effort is enough to compensate the impact of climate change. Future research should then be directed towards exploring and evaluating ecosystem-based climate-adaptive fisheries management strategies.

1. Introduction

Humans affect natural systems in many ways including climate change, direct exploitation of living resources, propagation of invasive alien species, land or sea use change and pollution (Brondízio et al., 2019). Large amounts of literature addressed the effects of single pressures on specific species or ecosystem components. However, current challenges lie in understanding the cumulative impacts of multiple anthropogenic stressors on the different facets of biodiversity and the ecosystem services they provide. Depending on the local context some studies have documented that multiple stressors applying in concert can exacerbate negative impacts on ecosystems while others have predicted dampened effects (Crain et al., 2008).

Gradual and accumulated changes in abiotic and biotic conditions brought about by multiple stressors can trigger losses in resilience (Möllmann and Diekmann, 2012). Resilience is defined as the ability to absorb disturbance and bounce back to an equilibrium state where relationships between populations and variables are maintained (Holling, 1973; DeAngelis, 1980). The loss of resilience makes ecosystems more vulnerable to changes that they were previously able to absorb, decreases the distance between two stable states, increasing the probability of the ecosystems shifting from a stable state to another. Such a process might lead to a less desirable state and to a loss of ecosystem functions and services (Folke et al., 2004; Bernhardt and Leslie, 2013).

Marine ecosystems are subject to two major stressors: fishing and climate change (e.g. Chapman, 2017). Fishing has a long-lasting and strong direct impact on communities by decreasing the exploited species' biomass. The selective removal of targeted species and large individuals have indirect effects through trophic interactions (Estes and Palmisano, 1974; Mumby et al., 2006) changing species assemblages and reducing mean trophic levels at the ecosystem scale (Pauly et al., 1998; Myers et al., 2007; Anderson et al., 2008; Nye et al., 2013). Fishing techniques such as bottom trawling can cause high mortality or displacement of benthic epifauna by physical disturbance in the wake of towed bottom gears, thus removing potential prey available to predatory fish (Collie et al., 2017). Overall, overfishing of piscivores and apex predators has been well documented as a cause of reduced resilience in ecosystems, altering their ability to recover and increasing the likelihood of regime shifts to alternative states (Scheffer et al., 2005; Daskalov et al., 2007; Pelletier et al., 2020).

Climate change modifies abiotic components of marine systems including increases in water temperature, acidification or decreases in the level of dissolved O_2 (Williamson and Guinder, 2021; IPCC, 2023). Changes in abiotic components have direct effects on ecosystem biotic compartments. These effects extend from phytoplankton to higher trophic levels, including a decline in net primary production (Bindoff et al., 2019; IPCC, 2023), physiological, biological and ecological species responses (Koenigstein et al., 2016) and changes in distribution patterns of species (Dulvy et al., 2008). For example, temperature evolution will lead to changes in energy metabolism. Coping with stress consumes energy which might reduce energy allocated to growth and reproduction (Chapman, 2017). Changes in the biomass and productivity of different ecosystem compartments are in turn reverberated throughout the ecosystem also altering trophic structure and functioning (Dulvy et al., 2008; Guibourd de Luzinais et al., 2023). According to Guibourd de Luzinais et al. (2023), total consumers biomass is projected to decrease by 2100 more than net primary production will decrease. Such direct and indirect modifications also increase the probability of reduced ecosystem resilience to anthropogenic perturbations (Bernhardt and Leslie, 2013) like fishing.

Scientific literature has documented that fishing and climate change acting in concert can have enhanced (Gissi et al., 2021; Hidalgo et al., 2011) or mitigated (Darling et al., 2010) negative impacts on some marine species and communities than either pressure alone, depending on local context. The literature review of Gissi et al. (2021) showed that climate change has generally intensified the effects of local pressures at species level, but that the direction and intensity of interactions between pressures depend on the context and vary between and within ecosystems. Additionally, resource exploitation has been shown to weaken the resistance and resilience of ecosystems to environmental changes due to climate change (Planque et al., 2010; Gissi et al., 2021).

The management of marine systems has been increasingly oriented towards ecosystem-based approaches i.e. Ecosystem-Based Management (EBM), with the objective of maintaining ecosystem in healthy, productive, and resilient conditions (Borja, 2014; Delacámara et al., 2020). Managing for resilience involves maintaining ecosystem health, but also rebuilding ecosystem functions and structure through restoration. Levin et al. (2009) provided a framework for organizing science to inform decisions in marine EBM, i.e., Integrated Ecosystem Assessments (IEAs), as there is little practical advice on how to do this. This framework includes the identification of critical drivers for ecosystem management and specific pressures on ecosystems. In this context, assessing cumulative impacts of multiple pressures on marine ecosystems, being able to disentangle them and exploring the capacity of ecosystems to recover in the face of multiple pressures is paramount (Borja, 2014; Pope et al., 2014; Allen et al., 2011). Additionally, regime shifts have important management implications, as restoring regimes that are considered favorable may require drastic and costly management actions (if ever possible). Understanding the dynamics of recovery is thus crucial (Möllmann and Diekmann, 2012).

However, understanding cumulative impacts remains a daunting scientific and technical challenge due to the complexity of the systems and the trophic interactions (Billick and Case, 1994; Crain et al., 2008; Foley et al., 2017; Hodgson and Halpern, 2019; Hodgson et al., 2019; Stock et al., 2023). Specific vocabulary and theoretical concepts have been developed to assess, quantify and interpret "cumulative effects" (Crain et al., 2008), which can either be the exact sum of individual pressure's effects i.e. "additive", higher, i.e. "synergistic", or lower, i.e. "antagonistic" (Folt et al., 1999; Crain et al., 2008; Hodgson and Halpern, 2019). In practice, disentangling the effects of distinct environmental drivers and human stressors by historical data analysis is difficult because the effect of one driver on the response variable may depend on other drivers (Cao and Wang, 2023). Modelling tools make it possible to free oneself from this constraint comparing scenarios with individual and cumulative effects. Among available modelling tools, ecosystem models allow to better understand cumulative pressures through their direct and indirect effects (Ainsworth et al., 2011; Stock et al., 2023) because of their holistic representation of ecosystems extending from primary producers to large predators and including the impact of fisheries, of the abiotic environment and trophic interactions (Coll et al., 2015; De Mutsert et al., 2021).

The aim of this paper is to show how a tropho-dynamic model such as Ecopath with Ecosim ecosystem model (henceforth EwE; Polovina, 1984, Christensen and Walters, 2004), can be used to assess the cumulative impact of multiple stressors and to explore the capacity of an ecosystem to recover from a degraded state. We applied this approach to the continental shelf of the Celtic Sea, one of the most heavily exploited seas of the northeast Atlantic for more than a century (Guénette and Gascuel, 2012). Between the 1950s and 1990s, the area experienced an increase in fishing pressure leading to sharp declines of commercial species biomass and substantial reduction in some large demersal fish. After a period of stabilization, fishing effort was reduced in the mid-2000s due to the implementation of constraining management measures, allowing only a partial recovery of the ecosystem to a level similar to that of the 1980s (Hernvann and Gascuel, 2020). Due to particular hydrodynamic conditions the Celtic Sea has been less impacted by climate change warming effect than neighbouring areas (Simpson et al., 2011; Hernvann and Gascuel, 2020). However, historical data analysis and modelling works are already revealing the emerging effect of climate change through the looming threat of a decline in cold-water-affiliated Boreal species (Lynam et al., 2010; Hernvann et al., 2020).

Using an EwE ecosystem model for the Celtic Sea, we address several questions (1) What will be the individual and cumulative effects of fishing and climate change on the ecosystem in the future? (2) How does the fishing intensity impact the capacity of ecosystem to recover from fishing impacts? (3) Is climate change preventing the ecosystem post-fishing recovery? To this aim, various levels of increasing fishing intensities are simulated over the whole 21st century, by forcing the EwE model with parameters of sea temperature, primary production and secondary producer's biomass from the regional POLCOMS-ERSEM climate model, under both RCP4.5 and RCP8.5 scenarios. The ecosystem state under individual and cumulated pressures and its capacity to recover to fishing are assessed through a set of indicators (biomass-based, community composition, trait-based and habitat-based indicators), using a theoretical non-fishing and climate-constant scenario as a reference. Climate change is expected to have a major impact on Boreal biomasses and ecosystem stability through a more variable environment. Reductions in primary production due to climate change are expected to have a greater impact on the biomass of planktivorous species than on piscivores. Conversely, fishing is expected to have greater effects on piscivore biomasses, mean lengths and mean trophic levels. We hypothesize that cumulative climate change and fishing will have synergistic effects on biomasses and diversity within the ecosystem, and that these synergisms will prevent ecosystem recovery after fishing.

2. Material and methods

2.1. Ecosystem model

An EwE (Polovina, 1984; Christensen and Pauly, 1992; Christensen and Walters, 2004) ecosystem model was built for the Celtic Sea continental shelf area (Hernvann et al., 2020). It was upgraded to assess the effects of climate and fishing on the ecosystem. It now covers the 2003–2020 historical period (for which fishing effort data are available) and is developed at an annual time step (technical annex from Appendix 1 to 19). It represents the ecosystem thanks to 53 functional groups among which 2 seabirds' groups, 2 cetaceans and seals' groups, 31 fish groups (22 demersal and 9 pelagic; either multispecies or monospecific), 2 cephalopods' groups, 9 benthos groups, 4 zooplankton groups and 2 phytoplankton groups. A detritus and a bacteria group are also included. Among the fish groups, 9 demersal commercial single species groups (referred as "multi-stanza" groups) are separated in several life stages to consider ontogenetic changes (e.g., productivity changes, diet shift ...). 3 functional groups are divided into Boreal and Lusitanian subgroups to better represent the effect of temperature changes on species due to climate change (other groups already having a majority of either Boreal or Lusitanian species included). According to the EwE modelling principles, functional groups exchange matter and energy through trophic interactions set by an initial prey-predator diet matrix defined at the starting year of the model, i.e., 2003. The Ecosim model was fitted over the 2003–2020 period, using 121 observation time series (biomass, biomass indices and catches; see Appendix 12).

Over 53 functional groups, 40 are targeted by fisheries which consist in 44 fishing fleets: 16 United Kingdom fleets, 15 French fleets, 8 Irish fleets, 3 Spanish fleets and 2 fleets belonging to other countries fishing to a lower extent in the area. Fleets are defined as a combination of four variables: country, gear type, vessel length and species targeted. Fishing pressure is represented using forcing fishing effort time series, built from fisheries dependent databases (Appendix 12; Zanzi and Holmes, 2017, Gibin et al., 2021). The environment is represented through biotic and abiotic drivers: temperature, primary production, plankton and benthos biomass time series. Sea Surface and Sea Bottom annual Temperature's series (resp. SST and SBT) are coupled with 36 species functional responses to temperature (niche models; Appendix 14). The 36 responses correspond to functional groups for which enough data of sufficient quality are available to model and predict the species' response to water temperature (i.e., mainly fish groups). Thus, any variation in temperature directly affects species consumption to represent the effect of temperature on species. Primary production time series drive the phytoplankton groups production rate. Zooplankton and benthos biomass time series (i.e., for mesozooplankton, microzooplankton, suspension and deposit feeders, and meiobenthos) drive the interaction between these groups and their preys or predators. Plankton and benthic biomass are not used as absolute biomass drivers in the model because data on those groups are highly uncertain. All environmental drivers are issued from the regional biogeochemical POLCOMS-ERSEM model (Butenschön et al., 2016; Kay et al., 2018) and yearly averaged on the 2003–2020 period.

Long-term simulations are carried out from 2021 to 2099, integrating both climate and fishing scenarios. Simulations are analyzed to identify i) individual effects of climate change and fishing ii) cumulative effects of climate change and fishing and iii) the recovery capacity of ecosystem when fishing stops.

2.2. Climate scenarios

To assess the effects of climate change on the ecosystem and its resilience, climate projection time series are used for each of the biotic and abiotic variables likely to be impacted by climate change (and considered in the model: phytoplankton, zooplankton, benthos and temperatures variables). Climate projection data are extracted from the POLCOMS-ERSEM model outputs (Kay et al., 2018) and yearly averaged for the whole Celtic Sea area over the 2021–2099 forecast period. Two CO_2 emissions mitigation scenarios are considered (Appendix 13): The Representative Concentration Pathways (RCP) 4.5 corresponding to an intermediate scenario of Greenhouse Gas (GHG) emissions and the RCP8.5 representing a scenario of high GHG emissions. In order to have a climate reference simulation integrating natural environmental variations, a no climate change scenario (noCC; Appendix 13) is built by detrending biotic and abiotic projection time series of the RCP4.5 (the closest to the current situation). The trend is detected by an Ensemble Empirical Mode Decomposition method (Wu et al., 2007, 2011).

2.3. Fishing scenarios

The impacts of fishing on the ecosystem and its resilience, are investigated through various fishing effort scenarios. In each scenario, a given fishing pressure is applied on the ecosystem from 2021 onwards until being suddenly interrupted in 2070. The simulation then ends in 2099. The 50-years fishing period allows the model to react to fishing while giving enough time for climate change to occur so as to study the cumulative effects of both pressures. The 30-year unfished period is considered long enough for the ecosystem to potentially recover based on the mean generation time of commercial fish stocks (Lynam et al., 2023). The various intensities simulated correspond to multipliers applied to the effort averaged over the last three years of the hindcast period (hereafter referred as "mE") ranging from 0 to 2 with 0.2

increments.

2.4. Ecosystem state's indicators

A set of biomass-based, diversity-based, trait-based and habitat-based indicators are used in order to assess the climate and fishing effects on the ecosystem state and its resilience (Table 1; technical details in Appendix 20). They were chosen on the basis of previous studies, mainly the Seawise European project (Lynam et al., 2023), and IndiSeas European project (Shin et al., 2010b) and additional literature on indicators (Bourdaud et al., 2016; Beukhof et al., 2019). They are all considered to address the criteria of a good indicators defined by Rice and Rochet (2005).

Table 1
: Set of ecosystem state's indicators. *Indicators indicated by "*" are the one calculated only to study the climate change effects on the ecosystem.*

Indicator abbreviation and name	Calculation's scale(s)	Description and interest of the indicator
Biomass-based indicators		
Biomass	All species, all fish, class, guild and province*	Aggregation of species biomass at a certain scale. Used to monitor changes in composition within the ecosystem.
1/CV Inverse coefficient of variation	Total biomass*	Determining ecosystem stability by quantifying biomass variations. The greater the metric, the less variations occur, the more stable the ecosystem.
Diversity indicators		
Shannon Shannon diversity index	All species, all fish, class, guild	Usually quantify species diversity including species richness and evenness in the community. Here, quantifies species evenness as the number of EwE functional groups is stable in time.
Trait-based indicators		
API Apex Predator Index	All fish	Proportion of higher TL predators among predators. Indicates the ecosystem trophic health as having top predators bring stability within the ecosystem (Allesina and Tang, 2012). The higher, the better health.
MTL Mean Trophic Level	All species, all fish, class, guild	Mean TL of the community. Indicator which measure the impact of fishing by the removal of higher trophic level targeted species.
Prop_pred Predators' proportion	All fish	Proportion of predators within the community. Indicator of the ecosystem trophic health as having predators bring stability within the ecosystem (Allesina and Tang, 2012). The higher, the better health.
MML Mean Maximum Length	All species, all fish, class, guild	Mean maximum length within the community. Used to track length composition changes within the community.
LSI Large Species Index	All fish, class	Large species proportion within the community. Used to track length composition changes within the community.
CWV_Linf Community Weighted Variance of the L_{inf} trait	All fish, class	Variance of the L_{inf} trait. High values indicate a trait divergence (better resilience of the community) while low values indicate convergence.
Habitat-based indicators		
CTI Community Temperature Index	All species*, all fish*, class*, guild*	Mean "preferred temperature" of the community. Used to track changes in temperature community niche due to water temperature increases.

Indicators are calculated from simulations outputs on specific periods (depending on the question, see the 2.5- Result analysis section) using the R software (R Core Team, 2024). To assess the pressures' impact at several ecological scales, several scales of calculation are considered: all species (including TL higher than the one of zooplankton groups), all fish, position in the water column (either demersal or pelagic, hereafter "class"), trophic guild (planktivore/benthivore/piscivore) or the biogeographical province (either Boreal or Lusitanian). The functional group attributions to the different ecological scales (Appendix 1) was made using FishBase (http://www.fishbase.org, accessed 02/2024) for the position in the water, Thompson et al. (2020) for the trophic guild and two different literature sources (Jiming, 1982; Hernvann, 2020) for biogeographical provinces.

2.5. Result analysis

Results are analyzed with regard to several scientific questions, which determine the studied period, the reference scenario, the compared simulations and the comparison metrics (Table 2). In order to study individual and cumulative effects of climate and fishing, the ecosystem state (assessed through ecosystem indicators) is analyzed in the 2060s at the end of the perturbation period once a 50-years perturbation has been applied. The ecosystem's capacity to recover is studied in the 2090s at the end of the recovery period after 30 years without fishing.

For questions 1 and 2, the individual effects of climate change and fishing are studied through the whole set of ecosystem indicators. For question 3, the direction of cumulative effects compared to the direction

Table 2
: Analysis carried out for each question.

Questions	Period	Reference simulation	Scenarios	Comparison metric
1- What is the individual effect of climate change?	2060s	NoCC mE = 1	3 climatic scenarios in a fishing status quo	% change of indicators compared to the reference
2- What is the individual effect of fishing?	2060s	NoCC mE = 1	11 fishing scenarios in a no climate change context	% change of indicators compared to the reference
3- What is the direction of cumulative effects?	2060s	NoCC mE = 0	33 climate and fishing scenario combination	Effects direction of sensitive indicators
4- Are cumulative effects additive?	2060s	Three climate scenarios mE = 0	33 climate and fishing scenario combination	Delta for sensitive indicators
5- What is the impact of a fishing perturbation on recovery processes?	2090s	NoCC mE = 0 (no fishing since 2020)	11 fishing scenarios in a no climate change context	% change of each indicator value between the investigated mE and the reference
6- Does climate change affect recovery processes after a fishing perturbation?	2090s	mE = 0 (no fishing since 2020) for the three climate scenarios	33 climate and fishing scenario combination	Delta' for sensitive indicators

of individual effects is studied through indicators termed "sensitive indicators", selected in each indicators' category to represent 95 % of the variance of the total set of indicators in this category. Thus, selected indicators are the ones sensitive to cumulated pressures. Direction is studied to assess which pressure drives cumulative effects. In question 4, the antagonistic/additive/synergistic nature of effects is also studied on sensitive indicators. For question 5, the influence of the fishing pressure intensity on ecosystem recovery is studied through the whole set of indicators, recovery being the process by which the ecosystem returns to a situation similar to the one predicted with no fishing over the whole century. Finally, question 6 raises the ability of climate change to impact ecosystem's recovery through sensitive indicators. Sensitive indicators are here selected in the same way as before but calculated over a different period.

For question 4, a metric termed Delta is calculated as the difference between the absolute predicted cumulative effects and the theoretical sum of individual effects, those effects being quantified as a percentage of change relative to the reference value for each indicator (the reference run is listed in Table 2). Thus, Delta $>$ 0 means absolute cumulative effects are higher than additive ones suggesting effects' synergism. Conversely, Delta $<$ 0 would reflect an antagonism. We considered effects to be additive if $|\text{Delta}|$ was $<$5 %.

For question 6, predicted effects of fishing on the recovery are compared between climate scenario, relative to a reference scenario with no fishing between 2020 and 2099, for which we assume the ecosystem to be totally recovered by the end of the run. Thus, for a given effort multiplier, results obtained with RCP 4.5 and RCP8.5 are respectively compared to a noCC scenario via a Delta' metric which is a difference in absolute values of change (see metric in Table 2, question 4) reported between RCPs and the noCC situation. Delta' $>$ 0 means that for a given mE, the indicator does not recover as much as in the considered RCP scenario than it does for the noCC scenario. Conversely, Delta' $<$ 0 indicates an increased recovery in the climate change scenario compared to the noCC one.

3. Results

3.1. Climate change effect on the ecosystem: A pelagic and boreal-directed effect, also affecting ecosystem stability

The effects of climate change in the Celtic Sea (RCP scenarios) are assessed on each category of ecosystem indicators relative to a reference scenario, i.e., a scenario with no climate change.

Climate change lead to variations in biomass. In fact, it leads to opposite trends in the biomass of all species (−3.2 % and 3.2 % for RCP4.5 and RCP8.5 respectively) mainly driven by variations in benthic biomass. Declines in fish biomass are predicted for the 2060s (by 6.8 % and 6.5 % for RCP4.5 and RCP8.5 respectively, Fig. 1) mainly driven by pelagic groups declining (until −12.3 % for the worst climatic scenario) but also demersal ones (between −3 and − 5 % according to the climatic scenario). Among trophic guilds, planktivores and piscivores biomasses are the most affected (respectively −8.1 % and − 10.1 % for the worst climatic scenario). The worst biomass-based changes are the Boreal biomass decline (until −18.0 % for the worst scenario) and the reduced ecosystem stability (1/CV also drops sharply by −27.5 % and − 44.9 % for RCP4.5 and RCP8.5 respectively).

Overall, climate change reduces the diversity of several ecosystem compartments (Appendix 21). In fact, climate change slightly reduces the global evenness (Shannon index all species; −1.0 % for the intermediate scenario and − 3.4 % for the worst scenario) whereas fish evenness remains unchanged due to conflicting signals in the diversity index of the different compartments. In fact, pelagic and piscivores gain in evenness while demersal, planktivores and benthivores lose.

Trait-based indicators' (Appendix 21) reveal the climate change impact on predators. The predators proportion drops due to environmental changes (−8.8 % and − 13.8 % for RCP4.5 and RCP8.5 respectively), with a stronger impact on intermediate trophic level predators (API rises by 6.2 % and 7.0 % for RCP4.5 and RCP8.5 respectively). These trophic consequences on predators, coupled with the decline in pelagic biomasses, influence the pelagic length traits. In fact, climate change reduces the intermediate trophic level predators (i.e., horse

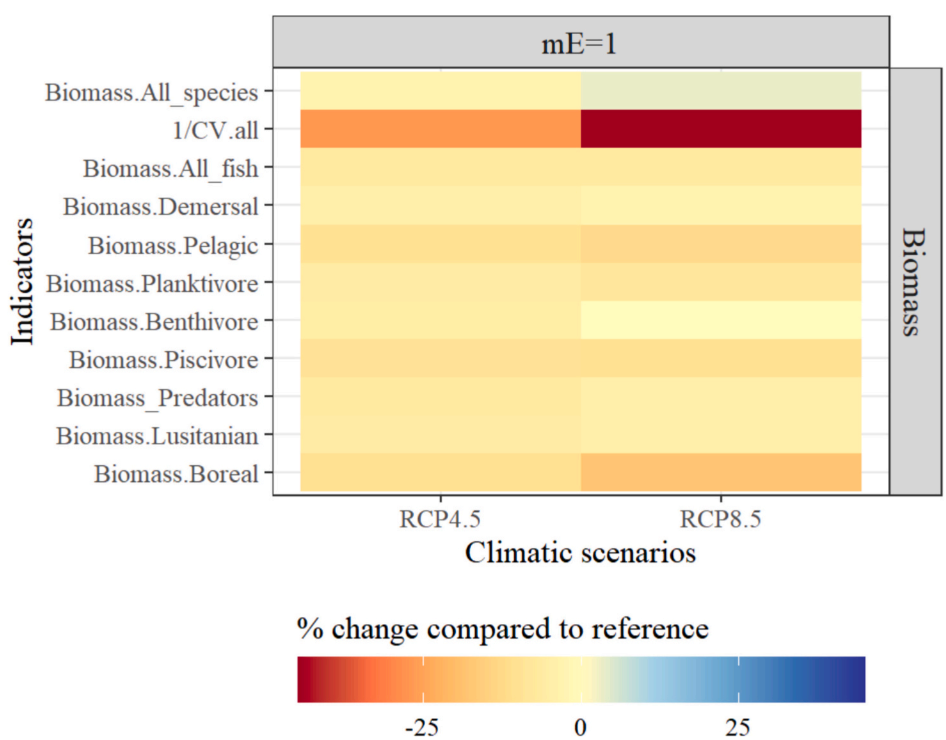

Fig. 1. : percentage of change in the biomass indicators compared to the reference (no climate change) in the 2060s decade. *In these 3 runs, fishing effort remains at status quo level, mE = 1.*

mackerel), which are larger than the average pelagic fish, thus slightly reducing the maximum length of pelagic fish (i.e. MML). Those changes in size composition however increase the resilience of pelagic communities (i.e., divergence of the L_{inf} trait within the pelagic community by the removal of intermediate size pelagic individuals). Other trait-based indicators (e.g., the Mean trophic level MTL) are insensitive to climate change (maximum variation of 1.7 % in absolute value compared to the reference).

Finally, habitat-based indicators exhibit low sensitivity to climate change (Appendix 21; maximum variation of 2.5 % in absolute value compared to the reference).

3.2. Fishing effect on the ecosystem: The removal of piscivores

The effect of fishing in the Celtic Sea is investigated by analyzing the response of biomass indicators to various fishing effort multipliers, compared to a reference scenario with fishing status quo (mE = 1) (Fig. 2, all runs with no climate change). The fishing effect on biomasses is analyzed when increasing or decreasing effort compared to reference.

Piscivores and predators are identified as highly impacted by fishing. Increasing fishing effort little influences the biomass of all species but decreases the fish biomass (−5.8 % for the worst fishing scenario). Most fish compartments lose biomass when fishing effort rises (i.e., pelagic, demersal, benthivores, piscivores and predators until mE = 1.6), with the loss being focused on pelagic fish and piscivores across all effort multipliers (resp. -10.0 % and − 14.2 % compared to the status quo for mE = 2) and predators for mE<1.6 (−15.9 % compared to status quo when mE = 1.4). Surprisingly, beyond the 1.6 effort threshold, those groups appear to benefit from fishing (+14.8 % compared to status quo when mE = 2). Reducing fishing effort has greater impacts, leading to biomass gains across all fish groups (e.g., +110.3 % for predators if mE = 0) except for planktivores whose biomass remains stable across the effort range. Reducing the effort increases some planktivores biomass due to fishing cessation but also decreases the biomass of non-exploited planktivory species because of their predators' re-increasing.

Fishing does not strongly influence overall species diversity due to opposite signals within the community (Appendix 22). Fishing decreases benthivores diversity (−23.6 % compared to the status quo for mE = 2) while increasing the diversity of pelagic, planktivores and especially piscivores (non-monotonic small increase for pelagic and planktivory fish, +27.7 % for piscivores compared to the status quo at mE = 2).

Trait-based metrics reveal the impact of fishing on piscivores (Appendix 22): increasing effort drops the predator proportion (−8.0 % compared to the reference for the worst scenario), with the drop being directed on higher trophic level predators up to mE = 1.6 (i.e., API declines; −11.9 % compared to the reference for mE = 1.4). As higher predators decrease for a fishing effort between 1.2 and 1.6, larger individuals are removed (i.e., fish and piscivore MML drop by −4.9 % compared to the status quo for mE = 1.4). The removal of larger individuals decreases the resilience of pelagic communities and increases the one of demersal communities (convergence of CWV_Linf for pelagic fish and divergence for demersal ones). When the effort multiplier exceeds 1.6, some of the observed trends change: fishing still removes higher predators and larger individuals, however the release in predation causes the biomass of some predators to re-increase (e.g., cod), resulting in a positive impact on several length-based indicators compared to mE = 1.4 (i.e., MML fish, MML piscivores, all LSI metrics and variance of L_{inf} trait for pelagic fish).

In contrast, trophic-level based indicators such as MTL are not sensitive to fishing (maximum variation of 2.7 % in absolute value compared to the reference).

3.3. Cumulative effects mainly driven by fishing

Cumulative effects induced by the interaction between both pressures are analyzed with regard to their direction compared to individual effects (climate change on one side, fishing on the other) for a selection of sensitive indicators (Fig. 3). For the analysis, effects on indicators where both pressures act in the same direction are referred to as 'analogue effects,' whereas effects where pressures act in opposite directions are described as "opposed effects".

When the individual effects of fishing and climate change are

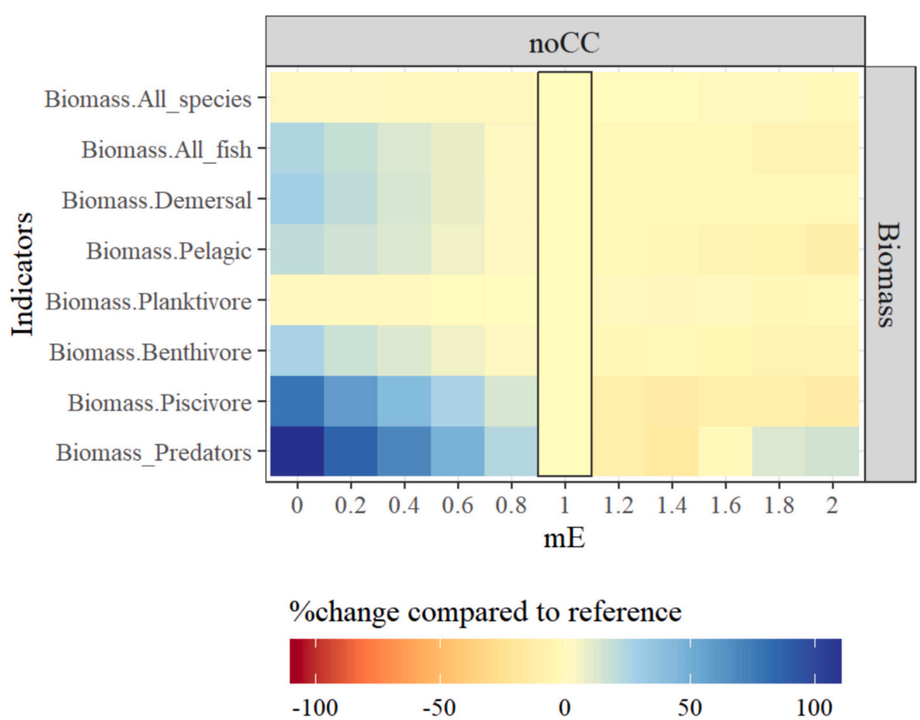

Fig. 2. : Percentage of change in the biomass indicators compared to the reference (i.e. fishing status quo with no climate change) in the 2060s decade. *The reference is indicated by a black rectangle.*

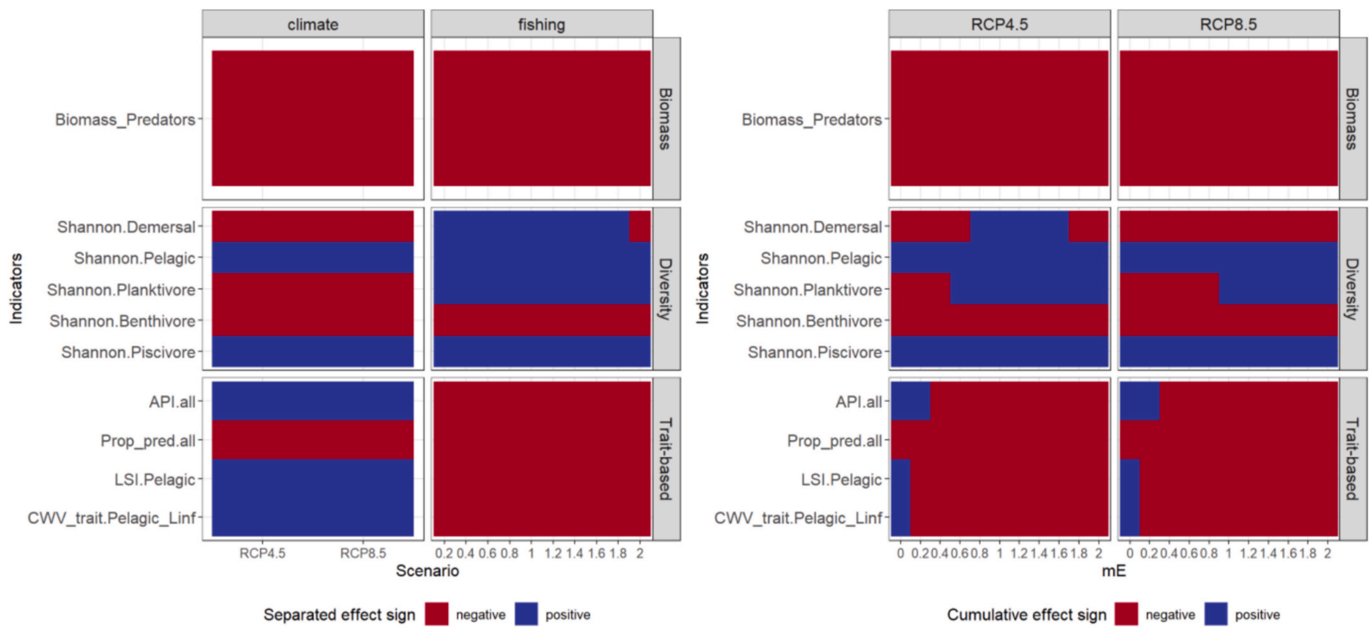

Fig. 3. : Comparison of individual and cumulative effects of fishing and climate change for sensitive indicators.

analogue, either positive or negative, cumulative effects logically have the same direction (e.g., Biomass of predators, biodiversity Shannon indicators for pelagic, benthivore and piscivore grouping). When individual effects are opposed, fishing effects appear predominant and determine the direction of the cumulative effects (e.g., pelagic LSI). Thus, change in fishing has greater impact on the general characteristics of the Celtic Sea ecosystem than climate change, even under the worst climate scenario. However, logically, under low fishing effort, climate effects tend to drive cumulative effects (e.g., API for mE = 0.2). In fact, the lowest effort multipliers represent exceptions where climate impacts determine the cumulative effects (e.g., API for mE = 0.2). Under stronger climate change (RCP8.5) such exceptions extend to higher fishing effort multipliers, particularly for community biodiversity (e.g., demersal and planktivores' Shannon index), suggesting that climate change has a stronger impact on biodiversity than fishing.

3.4. Are cumulative effects additive, synergistic or antagonistic?

Cumulative effects are mainly additive, but the nature of cumulative effects depend on the considered indicator (Appendix 23–24).

In detail, a sharp synergism is predicted in piscivore diversity with increased fishing (i.e., Shannon index; Delta of +38,2 % for mE = 2 in the RCP8.5) meaning that the diversity is higher than expected. Cumulative effects are non-proportional to the RCP scenario intensity as predicted changes between RCPs are relatively similar. Conversely, an antagonism is predicted for some other indicators, meaning that the cumulative effects are lower than expected (additive): predators' biomass, the API, the pelagic LSI and the pelagic variance of L_{inf} until

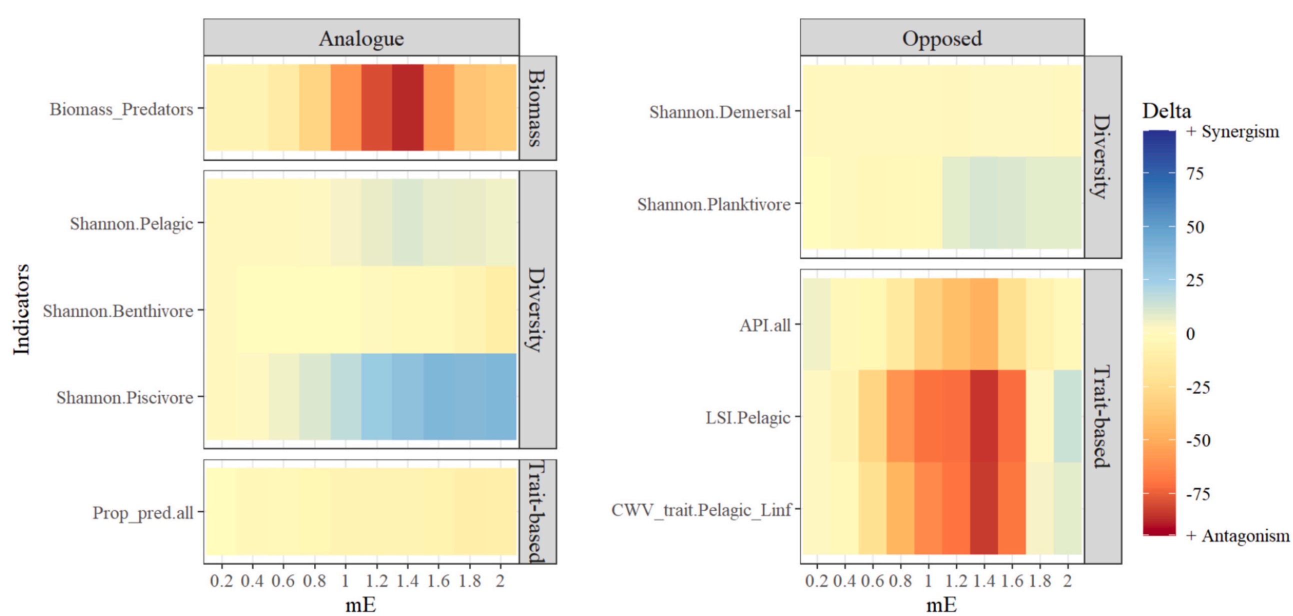

Fig. 4. : Absolute difference between cumulative (observed) and additive (theoretical sum) effects of fishing and climate change for a given mE in the 2060s for RCP8.5. The left panel presents the indicators for which fishing and climate have analogue effects. The right one presents the indicators for which fishing and climate have opposed effects.

mE = 1 (Fig. 4; resp. Delta of −87.6 %, −32.5 %, −57.9 %, −57.3 % for mE = 1.4 in the RCP8.5). Up to mE = 1.6, the higher the fishing pressure, the stronger the antagonism. The interaction between climate change and fishing induces a smaller negative effect than expected on large species and higher trophic levels predators (e.g., Delta <0 for predators' biomass and for the pelagic large species index). The fishing-climate interaction has a greater impact than expected for higher fishing efforts. In fact, the antagonism decreases and a slight synergism begins for the pelagic LSI and the pelagic L_{inf} variance especially for the RCP8.5 (resp. delta of +9.7 % and + 6.2 % for mE = 2 in the RCP8.5). In other words, up to a specific effort level, the fishing-climate interaction leads to lower effects than expected. Beyond this effort level, the interaction changes the nature of cumulative effects.

In a business-as-usual scenario (i.e., mE = 1), the fishing-climate interaction shows some strong antagonistic and synergistic effects (i.e., predators' biomass, API, pelagic LSI and pelagic L_{inf} variance).

3.5. Beyond a threshold, increasing fishing pressure would impair the ability of ecosystems to recover

To disentangle the effects of fishing and climate change on ecosystem recovery capacity, we first investigated the impact of various fishing efforts applied over 40 years (2020 to 2060) on recovery processes in a no climate change scenario. Simulations are compared to a reference state, here defined as a system unfished since 2020. Overall, the Celtic Sea ecosystem recovers from the fishing perturbation except for piscivores and pelagic fish, and climate change has no impact on the ecosystem capacity to recover.

In detail, for fishing pressures lower than status quo (mE = 1), all biomass indicators recover in the 2090s from the fishing perturbation, with indicators' values approaching the reference values (see Fig. 5). Conversely, increasing fishing pressure above status quo levels prevents recovery for piscivores, predators and pelagic fish. In fact, pelagic fish recovery is particularly negatively impacted for an effort multiplier between 1.2 and 1.6 (approximately −5 % compared to the reference for mEs in [1.2;1.6]). Piscivores' and predators' recovery processes are increasingly affected with the effort intensification (resp. -6.9 % and + 8.4 % compared to the reference for mE = 2).

Diversity and trait-based indicators confirm that intense fishing pressures impair the ecosystem capacity to recover, even in a no climate-change context (Appendix 25). For low fishing intensities, the diversity recovers (changes <2.0 % compared to the reference); but for higher fishing intensities (i.e., mE exceeding 1.8) the diversity of benthivores' and piscivores' does not (−6.0 % and + 6.3 % respectively, compared to the reference for mE = 2). For a high fishing intensity, another three trait-based indicators do not recover (API, the pelagic LSI and the pelagic L_{inf} variance; Appendix 25; difference of 10–15 % for some scenarios compared to the reference). Then, the impact of climate change on the ecosystem ability to recover from fishing is investigated using the same set of fishing scenarios (Fig. 6). Overall, climate change does not sharply impair indicators' recovery. In fact, little differences occur between climate scenarios for biomass and diversity indicators (maximum Delta' around 2 % in absolute value). However, climate change impacts the recovery of two trait-based indicators: the pelagic LSI and the pelagic L_{inf} variance. For lower effort multipliers, climate change slightly increases both indicators' recoveries (Delta' between 0 and − 3 %), while a decreased recovery is expected for multipliers between 1 and 1.6 (Delta' between 3 and 7 %). Climate change amplification (i.e., RCP8.5) decreases indicators' recovery compared to RCP4.5 (i.e., Delta' values <0 less negative and Delta' values >0 more positive).

4. Discussion

4.1. SST rising and zooplankton losses drive climate directed impacts on boreal and pelagic compartments

Environmental projections into the 2060s strengthen the current evidence of deborealization of the northeast Atlantic ecosystems due to climate change impacts, even if warm-affiliated Lusitanian species are

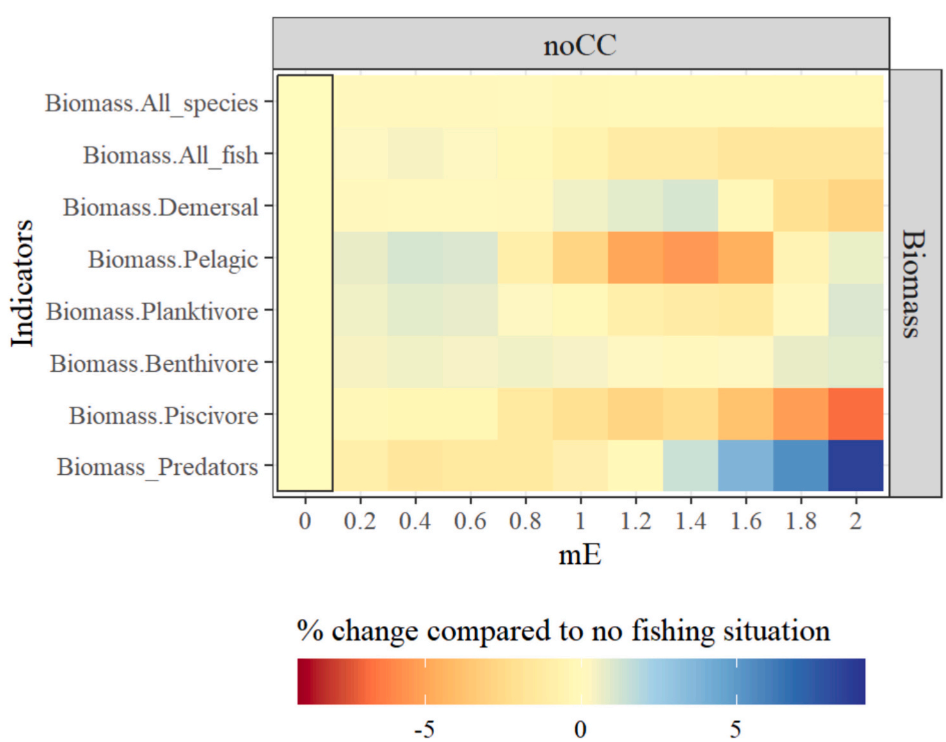

Fig. 5. : Percentage of change at the end of the recovery period (2090s) in the biomass indicators, compared to the reference (i.e. no fishing since 2020 in a no climate change context) according to fishing scenarios. *The reference is indicated by a black rectangle; each fishing scenario refers to a given fishing effort multiplier applied all along the 2020–2060 simulation period.*

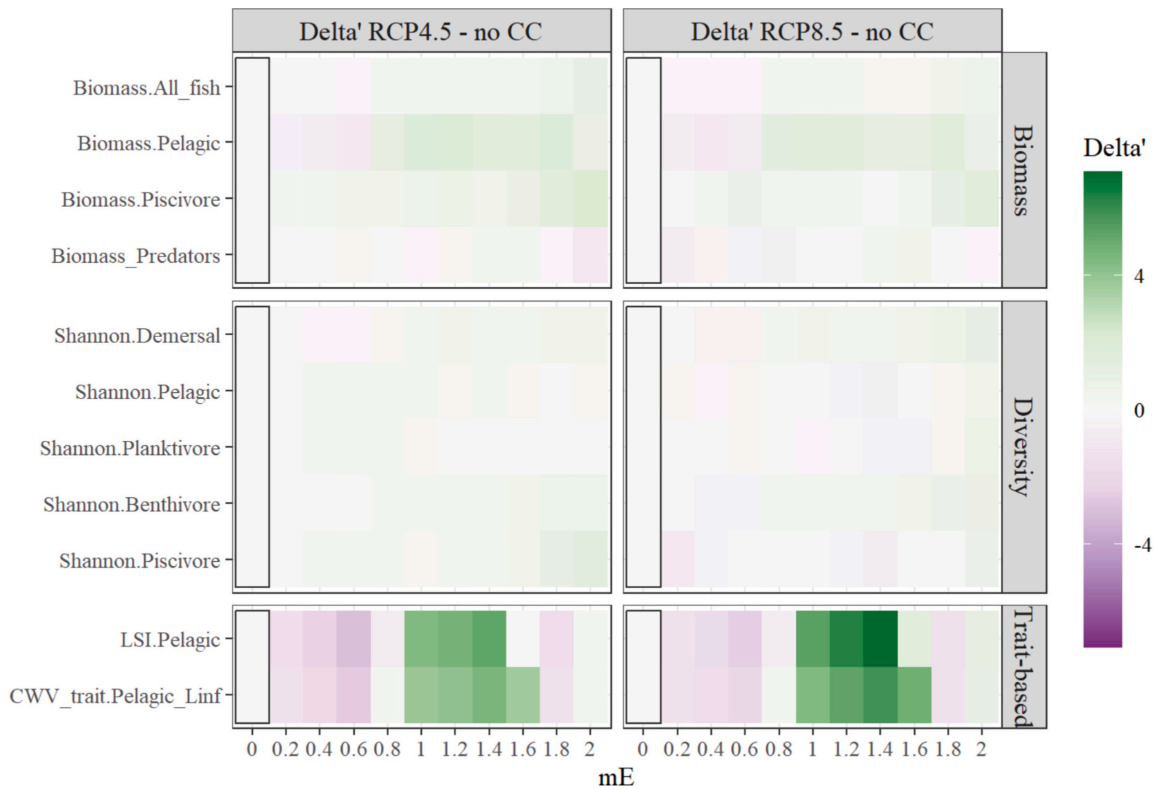

Fig. 6. : For a given effort multiplier, difference in the % of change in the considered metric relative to the reference (no fishing since 2020) between the RCPs and the noCC scenarios. *The reference is indicated by a black rectangle; each fishing scenario refers to a given fishing effort multiplier applied all along the 2020–2060 simulation period.*

also affected. The Boreal species decline (i.e. by 17 % for RCP8.5) at the southern limit of their boundary due to climate change has already been demonstrated in other data analysis works (Rijnsdorp et al., 2009; Lynam et al., 2010; Ter Hofstede et al., 2010; Heath et al., 2012) or modelling research works in the area (Rijnsdorp et al., 2009; Heath et al., 2012; Hernvann, 2020; Maltby et al., 2020). This decline is usually associated to a northward shift of species distribution towards colder waters or in a deepening phenomenon in which species shift to deeper isobaths to fulfill their thermal niche (Heath et al., 2012; Maltby et al., 2020).

Our simulations also reveal the pelagic-directed effect of climate change (i.e., impact focused on pelagic compartments). Biomass and mean maximum length of pelagic compartments decrease as a potential result of increasing SST and decreasing food availability for pelagic fish which feed on mesozooplankton. The higher sensitivity to climate change of the pelagic compartment compared to the bentho-demersal ones are in line with SST being more rapidly impacted by global change than SBT (RCP scenarios more distinct for SST than for SBT, and distinct earlier in time, see Appendix 13). The integration of zooplankton biomass projections from POLCOMS-ERSEM into our model represents a significant improvement over previous versions (Hernvann, 2020; Hernvann et al., 2020), and allows to integrate the indirect impact of climate change on small pelagic fish through trophic interactions via bottom-up processes (Rijnsdorp et al., 2009; Muhling et al., 2017). Although the POLCOMS-ERSEM phytoplankton and temperature hindcasts have been compared to historical observations, the zooplankton hindcast has not (Vega and Marsh, 2020). However, we advocate that POLCOMS-ERSEM projections are the best sources available for zooplankton and benthic groups at the regional level (i.e., large temporal coverage, several climatic scenarios available, fine spatial scale) and represent forcings rarely included in ecosystem modelling approaches.

The interactions between zooplankton and pelagic fish are complex and some determinant aspects are not included in our model such as: zooplankton nutritional quality (bioenergetic mismatch; Dam and Baumann, 2017, Menu et al., 2023), spatio-temporal match-mismatch between zooplankton and pelagic fish (Durant et al., 2007; Rijnsdorp et al., 2009; Dam and Baumann, 2017; Muhling et al., 2017) and the match-mismatch between specific zooplankton species and specific fish species stage (e.g. importance of the *Calanus finmarchicus* zooplankton species for some fish larval stages in the North Atlantic (Beaugrand et al., 2003, Lynch et al., 2011). Therefore, it can be assumed that the climate change impact on pelagic fish is under-estimated in this work, as climate change is expected to reduce zooplankton quality and such prey/predator match-mismatches.

Our simulations also suggest decreasing trends in piscivore biomass as a response to climate change, thus highlighting the impacts through bottom-up propagation. This result is driven by the decline in the horse mackerel biomass. The trophic guilds used to compute trophic indicators rely on seminal work for the North Sea by Thompson et al. (2020) whereas the diet matrix of our trophic model is based on Celtic Sea datasets. The interpretation of trophic indicators is thus limited by the potentially large temporal and spatial variability in diet composition that may occur (Amelot et al., 2023b). However, assessing climate change effects at the trophic guilds level requires working with this type of metrics.

In this work, only the long-term effects of climate change were considered, as a finer time scale is needed to study short-term effects. However, short-term effects are also likely to occur in the Celtic Sea through extreme events. Among such events, marine heatwaves are prolonged periods of anomalously high SST (i.e. temperature extreme events), and may induce migrations, adaptations or mortality depending on organisms (Guibourd de Luzinais et al., 2024; Castrillo-Acuña et al., 2024). The frequency and the duration of heatwaves are expected to increase in the northwest European shelf despite weak water stratification (Chen and Staneva, 2024). In temperate biomes, marine heatwaves are expected to decrease fish biomass, particularly predators biomass, leading to changes in ecosystem structure associated with a reduced capacity to recover (Guibourd de Luzinais et al., 2024). Such events may exacerbate the effects of climate change on pelagic and predators reported in this study.

4.2. Climate change increases ecosystem instability

RCP scenarios simulations lead to a more variable total biomass (i.e., 1/CV indicator) as well as a reduction in piscivores' biomasses. More precisely, climate change reduces the proportion of predators, apex predators (i.e., API) and piscivores biomass. Such features are known to affect ecosystem stability (Shin et al., 2010a; Allesina and Tang, 2012) and thus ecosystem resistance and resilience. Climate change reduces most fish evenness (i.e. Shannon indices), which might affect ecosystem stability as well, even if the diversity-stability relationship remains unclear in the literature depending on the scales and habitats on which diversity is measured (Cusson et al., 2015). The pelagic evenness is yet predicted to rise with climate change, but this evolution is due to the small number of groups in the compartment. This raises questions about the relevance of using the Shannon diversity index when diversity is described with a small number of species/groups.

4.3. Fishing preferentially removes piscivore fish

Biomasses, trophic and length indicators reveal multi-level impacts of fishing on the ecosystem. Fishing has logically a strong impact on high trophic levels (i.e., TL > 3.5), as they are the most targeted by fisheries. Through top-down processes (predation release), the increased fishing pressure benefits to lower trophic levels, less targeted by fisheries, resulting notably in more planktivorous fish. Conversely, a slight effort reduction is enough to increase the predator biomass compared to the status quo, and thus to compensate the impact of climate change. In fact, an effort reduction of 20 % (mE $= 0.8$) would already largely mitigate climate change effects on piscivores and predators.

For multiple indicators, the ecosystem smoothly and monotonically reacts to fishing (e.g., predator proportion, pelagic LSI…). Beyond mE $=$ 1.6, an abrupt change of trend is however observed, suggesting that a "regime shift" phenomenon may occur where the ecosystem is evolving from a stable state to another with different characteristics (Möllmann and Diekmann, 2012). Very high fishing efforts have a counterintuitive positive effect on predators. The shift corresponds to the transition from a state where anglerfish and hake are abundant top predators to another where fishing drastically reduces their biomass. In this second state, the predation release on forage fish and other preys (i.e., pouts, blue whiting and cod) increases food availability for other top-predators (i.e., pelagic sharks). This predicted community shift may be associated with an overestimation of anglerfish predation on adult cod in our model. However, such regime shifts have already been observed in several marine and estuarine ecosystems (Möllmann and Diekmann, 2012; Chevillot et al., 2016) and overfishing is known to cause shifts due to top-predation releases (Scheffer et al., 2005; Daskalov et al., 2007; Österblom et al., 2007). Yet, regime shifts are difficult to anticipate and predict accurately, mainly because of ecosystem plasticity. Indeed, the biological responses of species and the underlying biological processes are susceptible to change (to shift) under conditions very distinct from those used to calibrate and validate the model parameters.

Finally, we recognize that scenarios of constant, uniform effort across fleets are theoretical. Nonetheless, the model integrates fine-resolution fleets and is driven by fleet effort time series. This will allow further work on exploring more realistic fisheries management scenarios by fleet to mitigate the effect of climate change on ecosystem functioning while maintaining the provision of ecosystem services.

4.4. Cumulative effects of fishing and climate change will not be simply additive

Simulations carried out to study the cumulative effects of climate change and fishing on future ecosystem trajectories reveal that climate change has a subtler effect (smaller magnitude of changes in indicators) than fishing. When fishing decreases, climate change displays more visible impacts on indicators. The level of fishing pressure in the Northeast Atlantic is therefore likely to determine the observed cumulative effects in future decades, implying climate change effects on marine ecosystems structure and functioning could be, at least partially, compensated by a reduction in fishing pressure.

The largest differences between cumulative and additive effects of fishing and climate change are mostly due to antagonisms. In particular, at near status quo fishing pressure and even in a strong climate change context, the simulated cumulative effects of fishing and climate change on predator biomass are smaller than expected. This result suggests that the interaction between climate change and fishing mitigates the individual effects of pressures on predator biomass, revealing some community changes among predator species.

Effects tend to be synergistic when fishing pressure is very high, suggesting that increasing fishing pressure to extreme levels would increase the probability to observe synergisms and regime shifts. Crain et al. (2008) analyzed 171 scientific articles to synthetize the cumulative effects' nature of 78 stressors' pairs, and noticed that the interactions between stressors were equally likely to be antagonistic (38 % of studies) as they were to be synergistic (36 %). The nature of the interaction strongly relies on the level of response to the effects and the scale at which these effects are measured. As a result, the response can be antagonistic at the indicator level (here guild or community) but synergistic at the population or species level. More interestingly, Crain et al. study (2008) highlights the lack of Cumulative Effects Assessment (CEA) at the ecosystem scale and a lack of fishing-directed studies. Our study contributes to fill this gap. Nevertheless, future work on cumulative effects would benefit from the integration of other important stressors known to impact population dynamics such as habitat loss.

4.5. Recovery capacity is determined by the intensity of historical harvesting

Simulations suggest that the recovery capacity of the ecosystem is driven by the historical level of fishing pressure. Ecosystem recovery occurs within 20 years of no fishing when the previously applied fishing pressure was at or below status quo, while intensive fishing pressure prevents the rebuilding of indicators and is likely to induce a regime shift in the ecosystem. The non-recovery of some indicators post high fishing levels is rather logical knowing that regime shifts are likely to impact the resilience of ecosystems (De Young et al., 2008; Möllmann and Diekmann, 2012) and thus their capacity to recover. However, the predicted changes compared to the reference (i.e., no fishing situation) are relatively small, even for high multipliers, except for predators and piscivores, suggesting overall pretty good recovery capacity of the Celtic Sea ecosystem and a strong resilience to high fishing intensity. This last result should be taken with care, knowing the fast reactivity of EwE models in general (ICES, 2019) and for the Celtic Sea one particularly (Appendix 18).

At the historical level of fishing, little differences are observed between climate change scenarios, which suggests that climate change does not seem to deeply alter the resilience of the Celtic Sea ecosystem. However, the lack of sensitivity of the post-fishing recovery to climate change could be attributed to the potential underestimation of climate change in long-term climate projections (2090s).

4.6. Model-based CEAs: Capabilities and weaknesses of EwE?

This study is a first model-based assessment of the individual and cumulative effects of fishing and climate change in a northeast Atlantic ecosystem by 2060. By disentangling the importance of the two major current and/or future stressors on the ecosystem, this study provides relevant insights for ecosystem-based fisheries management. While the consequences of climate and fishing scenarios are explored through a wide diversity of methods (e.g. in the area; Amelot et al., 2023a, Kempf et al., 2022, Lynam et al., 2010), cumulative effects and their antagonistic or synergistic nature are rarely assessed (Crain et al., 2008). CEAs are of paramount importance to scientists and stakeholders in order to design the more appropriate mitigation measures (De Young et al., 2008; Foley et al., 2017; Hodgson et al., 2019), highlighting the interest of this study.

However, predicting cumulative effects remains challenging given the variety of response types and scales, and the complex interactions occurring within biological systems (Crain et al., 2008; De Young et al., 2008; Hodgson and Halpern, 2019; Hodgson et al., 2019; Stock et al., 2023). Among existing modelling frameworks, EwE offers the ability to model responses to stressors across different ecological levels (from species to ecosystem) and to address different ecological complexities such as indirect effects of stressors through trophic interactions (Hodgson and Halpern, 2019; Stock et al., 2023). In the end, due to the heavy data requirement and the strong model assumptions, many sources of uncertainty remain. Uncertainty being difficult to quantify and propagate within mechanistic ecosystem models (Hill et al., 2007; Gilbert et al., 2024), it remains rather difficult to explore the full potential range in cumulative effects. Moreover, the lack of process-informed foundation in EwE is also a limitation as the impacts of pressures on processes cannot be fully addressed and understood. For instance, temperature increases due to climate change have an effect on the growth process at the physiological level of organisms, which is not explicitly modelled in EwE, but only implicitly modelled through the consumption rate modulation by the functional responses of species to temperature. Synthetic tools such as EwE are therefore to be used in association with process-informed models to better understand and forecast the effects of climate change (Koenigstein et al., 2016).

4.7. Sensitivity of indicators in relation to model structure and assumptions

All ecosystem state metrics were chosen to address the criteria of a good indicator as defined by Rice and Rochet (2005), which includes the responsiveness of the indicator to pressure. However, some of the selected indicators were not highly reactive to fishing and/or climate change in our simulations, such as: Mean Trophic Levels (MTL) and Community Temperature Index (CTI). The lack of reactivity to climate change of MTL could be due to the model structure, and more specifically to: 1) the fact that the model does not allow the inclusion of new species in the diet of predators while climate change could induce such diet changes with the decrease in prey availability (Amelot et al., 2023b), 2) the structure of functional groups, which hides biomass variations across species within each group. CTI indicators were also chosen to be responsive to climate change as they define the mean "preferred temperature" of the community (Devictor et al., 2008; Cheung et al., 2013). Thus, their value is expected to increase with climate change by removing cold-water-affiliated species. The lack of responsiveness here is probably due to the fact that changes in zooplankton have greater impacts on the ecosystem than changes in temperature. This study underlines the challenge to study cumulative effects and the ecosystem recovery using a specific set of indicators. In fact, indicators are analyzed in relation to a reference, and it is sometimes difficult to know whether a change in the indicators value is a 'positive' or 'negative' change for the ecosystem. This difficulty is extensively discussed in the literature dedicated to assess a 'good ecological status' for ecosystems (Borja et al., 2013).

Finally, an ecosystem like the Celtic Sea is characterized by a high spatial variability in abiotic components (e.g. Seabed substrates; https://emodnet.ec.europa.eu/en) and by a series of complex gradients in these components (Hernvann et al., 2020). Habitat diversity induces a diversity of species assemblages (Trenkel et al., 2005), which strongly structures the spatial distribution of fishing effort (Mateo et al., 2017; Moore et al., 2019), resulting in multiple ecotones with different functions (Hernvann et al., 2020). Spatializing the EwE model could help to further explore the spatial impacts of climate change, such as deepening effects (Dulvy et al., 2008) or northward redistribution of species (Maltby et al., 2020). Spatialization of indicators, made possible by the EwE spatialization into an Ecospace model, would help to understand how this overall picture of impacts is modulated by the strong spatial heterogeneity.

5. Concluding remarks

Using an ecosystem model, this study provides a first assessment of the individual and cumulative effects of climate change and fishing on a Northeast Atlantic ecosystem (i.e., the Celtic Sea) and its resilience over the next century. There has been no previous predictive research in this area and rare studies in adjacent seas (Coll et al., 2016; Serpetti et al., 2017). Studies about combined pressures exist, pressures are not necessarily modelled/specified in the same way (e.g. constant model drivers for some climate scenarios; Coll et al., 2016, Serpetti et al., 2017), and impacts are mainly analyzed in terms of changes in the biomass of commercial species (Travers-Trolet et al., 2014; Coll et al., 2016; Serpetti et al., 2017) rather than with a set of global indicators of ecosystem condition (Ainsworth et al., 2011; Olsen et al., 2018). More specifically in the south Catalan sea, the EwE-based study of Coll et al. (2016) reported synergistic but also antagonistic effects of fishing and climate change on the biomass of commercial species. This study has integrated surface and bottom salinity drivers in addition to SST, SBT and primary production and has focused the study on biomasses of commercial species.

In the context of EBM, this study allows for a better understanding of the cumulative effects of climate change and fishing, which is a first step for the Integrated Ecosystem Assessments to operationalize EBM. This study highlights the need for fisheries management to mitigate the effects of climate change, particularly at the level of Boreal, pelagic and intermediate trophic level predators. Reducing fishing pressure would automatically benefit top predators and globally allow the ecosystem to recover. Future research should now be directed towards exploring climate-adaptive fisheries management scenarios that could potentially have less impact on ecosystem health while maintaining a sustainable activity for fishermen and food supply for the world's population.

CRediT authorship contribution statement

M. Potier: Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **M. Savina-Rolland:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **P. Belloeil:** Software, Resources, Methodology, Investigation, Formal analysis. **D. Gascuel:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **M. Robert:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.178942.

Data availability

Data will be made available on request.

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