



Climate-induced changes in ocean productivity and food-web functioning are projected to markedly affect European fisheries catch

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ABSTRACT: In European waters, climate-induced changes in ocean conditions will alter marine ecosystems, leading to potential repercussions for the European fisheries and the status of exploited species. Here, we used a new version of the EcoTroph model, forced by a regional high-resolution coupled hydrodynamic–ecosystem model, to investigate the effects of climate change on biomass and catch in 15 areas (ICES divisions) of the European Atlantic shelf ecosystems. Based on the projected changes in temperature, zooplankton and benthic secondary producers, we modeled the changes in biomass and catch at each trophic level by the end of the 21st century. We projected that total biomass and catch for the whole Atlantic European seas would decrease by 11.5 and 10.0%, respectively, by 2090–2099 relative to 2013–2017 under a ‘no mitigation’ greenhouse gases emissions scenario (RCP8.5). The projected decrease in catch is 310 000 or 240 000 t by 2090–2099 under a high (RCP8.5) or a moderate (RCP4.5) emissions scenario, respectively. Some areas, such as the Celtic Sea, would be more affected than others, while the climate impact on the benthic-demersal biomass and catches would be more pronounced, especially toward the higher trophic levels. Our study suggests that climate change may strongly impact European fisheries, with ecological consequences and potential socio-economic repercussions. Future studies using alternative climate and ecosystem models would allow the exploration of uncertainties in projected biomass and catch. While fisheries management is required to adapt to these changes, the projected impacts on catch cannot be avoided without aggressive mitigation of greenhouse gas emissions.

KEY WORDS: Marine food web · Biomass flow · Climate change · EcoTroph · Fishing · Trophic ecology · Ecosystem modeling

1. INTRODUCTION

Climate change is altering ocean conditions with consequences on the structure and functioning of marine ecosystems (Bindoff et al. 2019, Tittensor et al. 2021). In the Northeast Atlantic Ocean, climate-induced shifts in distributions and the concomitant effects on community structure of fish stocks have

already been shown for benthic and demersal communities (Perry 2005, Poulard & Blanchard 2005, Dulvy et al. 2008, Baudron et al. 2020) as well as for pelagic communities (Hughes et al. 2014, Montero-Serra et al. 2015). These changes are generally associated with an expansion of populations located at the northern boundary of a species’ range, while populations located at the southern boundary tend to

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contract (Poloczanska et al. 2016). Changes in species distribution under ocean warming reshape community structure, with increases in dominance of warm-water species and decreases in cold-water species (ter Hofstede et al. 2010, Simpson et al. 2011, Montero-Serra et al. 2015).

The continued reshaping of the structure of marine ecosystems under climate change in the 21st century may induce profound negative consequences on the future fisheries production of European seas. Previous work integrating ecophysiology and phytoplankton dynamics projected a decrease in maximum fisheries catch potential of exploited fish and invertebrate stocks in the Northeast Atlantic under climate change by 2050 (Cheung et al. 2011). However, such projections do not account for the cascading effects of changes in fish stocks on ecosystem structure and function (Cheung et al. 2016). Moreover, changes in fishing levels will also add to, and potentially interact with (Perry et al. 2010, Planque et al. 2010), climate-related changes in fish stocks and ecosystems (Cheung et al. 2011, 2018, Blanchard et al. 2011). To generate scenarios that are more representative of the reality of European fisheries, it is important to consider the current fishing exploitation patterns and plausible fishing scenarios for the future.

In a recent study, the EcoTroph modeling framework was used to explore the future of marine consumer biomass and trophic structure at the global scale (du Pontavice et al. 2021). In EcoTroph, the trophic functioning of aquatic ecosystems is modeled as a continuous flow of biomass surging up the food web, from lower to upper trophic levels (TLs), through predation and ontogenic processes (Gascuel 2005, Gascuel & Pauly 2009, Gascuel et al. 2011). Du Pontavice et al. (2021) projected that the alterations of the trophic functioning of marine ecosystems would lead to a global decline in consumer biomass as well as in the abundance of predators. These projections, however, did not consider the effects of fishing exploitation. Moreover, the global-scale EcoTroph simulations do not adequately resolve the physical, biogeochemical and ecological dynamics of marine ecosystems at the scale of European waters, such as the dynamics of coastal waters in Earth system models (Asch et al. 2016) and pelagic–benthic linkages (du Pontavice et al. 2021). The pelagic–benthic linkages are particularly important for food webs of continental shelf ecosystems such as European seas (Blanchard et al. 2011, Woodland & Secor 2013, Kopp et al. 2015).

Here, we developed a new version of the EcoTroph approach, coupling both the pelagic and demersal

pathways, to project the climate- and fishing-induced changes in biomass and fisheries catch in European waters in the 21st century under 2 contrasting greenhouse gas emissions scenarios. Our study focused on the European continental shelf that ranges from the Portuguese waters to the North Sea, divided for management purposes into 15 ICES divisions (International Council for the Exploration of the Sea) (Fig. 1). In each of the divisions (called ‘study areas’ in this study), we applied the EcoTroph approach to model the ecosystems and calculate the biomass and production for each TL. We accounted for the pelagic–benthic linkages by subdividing the biomass flows into pelagic and benthic–demersal pathways, accounting for the flows from the pelagic to the latter pathways. Furthermore, the EcoTroph simulations were driven by the projection of ocean conditions from a regional, high-resolution coupled hydrodynamic–ecosystem model under 2 greenhouse gas emissions scenarios. In addition, we explored the effects of the inclusion of fishing scenarios on the projected biomass and catch in European marine ecosystems.

As a first step, the model was applied for the period 2013–2017 to establish a reference state of the 15 study areas. Then, based on 2 Representative Concentration Pathways (RCPs), we explored the potential changes in biomass and fisheries catch in the 15 study areas between 2020 and 2099.

2. MATERIALS AND METHODS

2.1. Regional model for low trophic levels

In order to consider the effects of climate change on both the secondary production entering the ecosystem and the functioning of the food web of higher TLs, EcoTroph incorporated the outputs of POLCOMS-ERSEM a regional, high-resolution coupled hydrodynamic–ecosystem model for low TLs (Kay 2020). We used the zooplankton and benthic secondary producer biomass time series based on the outputs from the ERSEM model v15.06 (Butenschön et al. 2016). ERSEM is an ecosystem model with a focus on marine biogeochemistry, pelagic plankton and benthic secondary producers. It simulates the cycles of carbon and the major nutrient elements (nitrogen, phosphorus and silicon) within the marine environment. ERSEM is coupled to a regional ocean circulation model, POLCOMS (Proudman Oceanographic Laboratory Coastal Ocean Modelling System; Kay 2020), with a grid resolution of

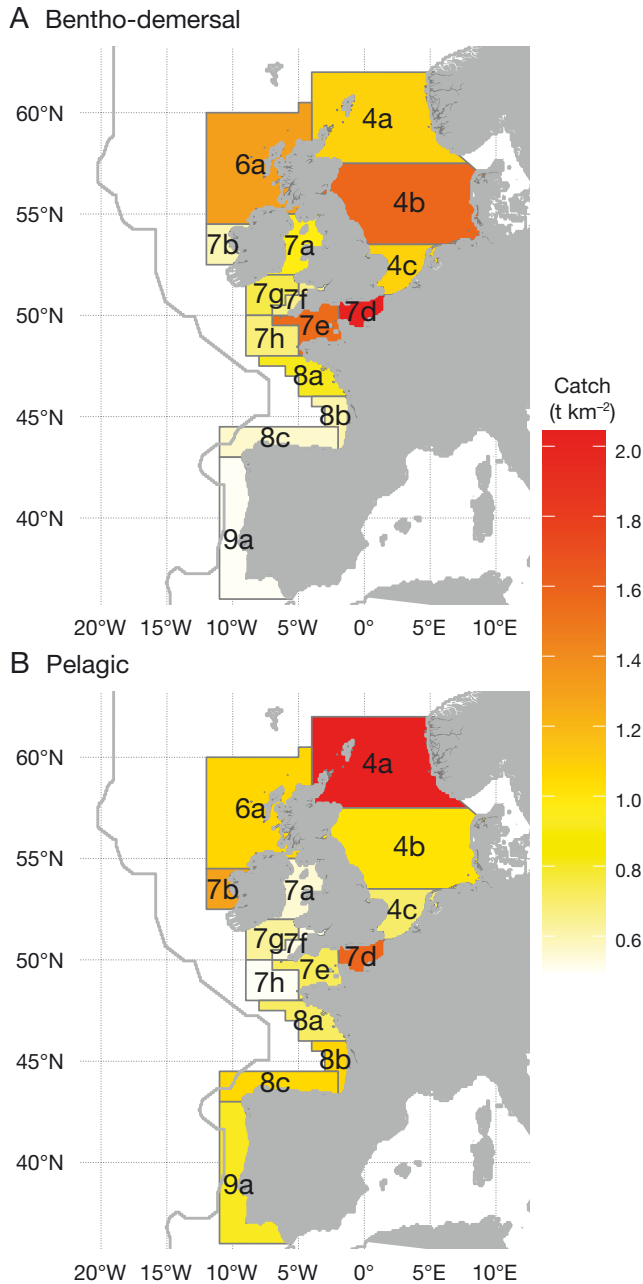


Fig. 1. Study areas and fisheries catch per unit area (t km^{-2}) in 2013–2017. The spatial distribution of the annual average catch per area (km^2) between 2013 and 2017 is represented for (A) pelagic and (B) benthic-demersal species in the 15 study areas (ICES divisions). The gray line is the boundary of the POLCOMS-ERSEM model, while codes of each division refer to the numbering used by the International Council for the Exploration of the Sea

0.1° latitude \times 0.1° longitude. The coupled hydrodynamic biogeochemical model is driven at the open ocean boundaries by an Earth system model developed at the Max Planck Institute (MPI-ESM-LR; Giorgetta et al. 2013) and run as part of the Coupled

Model Intercomparison Project Phase 5 (CMIP5), in combination with downscaled atmospheric forcing data generated by the Swedish Meteorological and Hydrological Institute Rossby Centre Regional Atmospheric Model, also driven by MPI-ESM-LR.

We used 2 sets of POLCOMS-ERSEM outputs: the mean annual carbon biomass of zooplankton and benthic secondary producers from 2006 to 2099. In ERSEM, zooplankton was subdivided into 3 size classes of zooplankton categorized as heterotrophic flagellates, microzooplankton and mesozooplankton, while benthic secondary producers included 3 types of benthic fauna: suspension feeders, deposit feeders and meiobenthos (Butenschön et al. 2016). Furthermore, we used the sea surface temperature (SST) as a climate forcing of biomass transfer processes accounted by EcoTroph (transfer efficiency, TE, and flow kinetics). The trends in secondary producers and SST are presented in Section S1 in the Supplement (www.int-res.com/articles/suppl/m713_p021_supp.pdf).

The variables were available in a 2-dimensional horizontal grid of $0.1^\circ \times 0.1^\circ$ covering the Northwest European shelf (see the spatial extent of the model in Fig. 1). The outputs of POLCOMS-ERSEM were available for the period from 2006 to 2099 for 2 RCPs (van Vuuren et al. 2011): RCP4.5, representing a scenario under which global radiative forcing level would rise in the first half of the 21st century then stabilize, reaching 4.5 W m^{-2} in the year 2100 (‘moderate mitigation’ scenario); and RCP8.5, representing continuously rising radiative forcing leading to 8.5 W m^{-2} in 2100 (‘no mitigation policy’ scenario).

2.2. Study area and fisheries

Our study focused on the European continental shelf from the North Sea to the Strait of Gibraltar, divided into 15 ICES divisions (Fig. 1), including the North Sea (4a–c), Western Scotland (6a), Irish Sea (7a), Western Ireland (7b), Celtic Sea (7f–h), English Channel (7e,d), Bay of Biscay (8a,b) and Iberian Coast (8c and 9a). We focused on these 15 areas since they are the most productive and exploited areas of the European continental shelf managed or co-managed by the European Union (before Brexit). Moreover, these areas offer the best spatial resolution at which catches are reported by governmental statistical offices, and were spatially covered by the coupled hydrodynamic–ecosystem model POLCOMS-ERSEM.

Catch data from 2013 to 2017 were obtained from the ICES data collection (ICES 2020). The fisheries catch statistics were reported annually by the national offices, and then prepared and published by ICES in the official catch statistics dataset for the Northeast Atlantic. The catch statistics included catch of fish, crustaceans, molluscs and other aquatic organisms, at the spatial resolution of ICES divisions. A low proportion of catch was reported for a pool of 2 or 3 ICES divisions. These catches were distributed among divisions proportionally to the mean allocated catch of the period. For each species, we assigned a trophic pathway (pelagic or benthodemersal) based on their feeding affinity reported in FishBase (www.fishbase.org; Froese & Pauly 2000) and SeaLifeBase (www.sealifebase.org; Palomares & Pauly 2020). If information on feeding affinity was not available, we used information on their associated habitat to categorize their trophic pathway. Furthermore, the TL of each species was also obtained based on estimates from FishBase and SeaLifeBase.

2.3. The EcoTroph model

2.3.1. General EcoTroph modeling framework

In EcoTroph, the ecosystem trophic functioning is modeled as a continuous flow of biomass surging up the food web, from lower to higher TLs, through predation and ontogenic processes (Gascuel 2005, Gascuel & Pauly 2009). The ecosystem is represented by a continuous distribution of the biomass along TLs, i.e. a biomass trophic spectrum (Gascuel et al. 2005). Biomass enters the food web at TL = 1, as generated by the primary producers and recycling by the microbial loop. Then, at TLs higher than 2, the biomass is composed of heterotrophic organisms with mixed diet and fractional TLs resulting in a continuous distribution of biomass along TLs. This distribution is represented using small trophic classes, aggregating all organisms of the related TL. Hence, EcoTroph represents the entire marine community as a TL distribution. In this approach, species identity is not resolved and marine organisms are instead combined into classes based only on their TLs. As a convention (and based on previous studies; Gasche et al. 2012, du Pontavice et al. 2021), we considered trophic classes of width $\Delta\tau = 0.1$ TL to be an appropriate resolution, and a range starting at TL = 2 (corresponding to the first-order consumers) up to TL = 5.5, sufficient to cover all top predators in marine systems (Pauly 1998, Cortes 1999). The detail of the EcoTroph

equations and the mathematical development are fully detailed in Gascuel et al. (2011) and du Pontavice et al. (2021).

First, the core equation of EcoTroph is the continuous biomass flow (i.e. the quantity of biomass moving up through TL τ at every moment t) such that:

$$\Phi(t, \tau) = B(t, \tau) K(t, \tau) \quad (1)$$

where $\Phi(t, \tau)$ is expressed in $t \text{ yr}^{-1}$, $B(t, \tau)$ is the density of biomass at TL = τ expressed in $t \text{ TL}^{-1}$, and $K(t, \tau)$ is the flow kinetics expressed in TL yr^{-1} . $K(t, \tau)$ measures the speed of the biomass flow in the food web, from low to high TLs.

Under steady-state conditions, Eq. (1) becomes:

$$B(\tau) = \frac{\Phi(\tau)}{K(\tau)} \quad (2)$$

A discrete approximation of the continuous distribution $B(\tau)$ is used for mathematical simplification (see du Pontavice et al. 2021). The model state variable becomes B_τ , the biomass (in t) under steady-state conditions within the trophic class $[\tau, \tau + \Delta\tau]$, and Eq. (2) becomes:

$$B_\tau = \frac{1}{K_\tau} \Phi_\tau \Delta\tau \quad (3)$$

where Φ_τ and K_τ are the mean biomass flow (in $t \text{ yr}^{-1}$) and the mean flow kinetics (in TL yr^{-1}) within the trophic class $[\tau, \tau + \Delta\tau]$, respectively. K_τ varies per trophic class and is directly defined using mean values per trophic class based on an empirical model (Gascuel et al. 2008; see Section 2.3.2).

The biomass flow $\Phi(\tau)$ is not conservative and is expressed as a decreasing function of TL:

$$\Phi(\tau + \Delta\tau) = \Phi(\tau) \exp(-\mu_\tau \Delta\tau) \quad (4)$$

where μ_τ (expressed in TL⁻¹) represents the mean natural losses within the trophic class $[\tau, \tau + \Delta\tau]$ through non-predation mortality, excretion and respiration. It defines TE within the trophic class $[\tau, \tau + \Delta\tau]$, such that TE = $\exp(-\mu_\tau)$.

Finally, EcoTroph defines the biomass flow $\Phi(\tau)$ as a density of production at TL = τ . Therefore, the production P_τ of the trophic class $[\tau, \tau + \Delta\tau]$ is:

$$P_\tau = \int_\tau^{\tau+\Delta\tau} \Phi(\tau) d\tau = \Phi_\tau \Delta\tau \quad (5)$$

Production is commonly expressed in $t \text{ yr}^{-1}$, which implicitly refers to the conversion of biomass eaten at TL $\tau-1$, into predator tissues whose mean TL is τ . Therefore, in a TL-based approach such as EcoTroph (wherein the width of trophic classes may be different from 1 TL), production has to be expressed in $t \text{ TL yr}^{-1}$, i.e. tonnes moving up the food web by 1 TL on average during 1 yr.

2.3.2. Flow kinetics and trophic transfer efficiency

The flow kinetics measures the velocity of biomass transfers through all groups from primary producers to top predators in an unexploited ecosystem (Gascuel et al. 2008). To estimate the flow kinetics at TL = τ and as in du Pontavice et al. (2021), we used an empirical equation (Gascuel et al. 2008) as a function of SST and TL (τ):

$$K_{\tau} = 20.19 \times \tau^{-3.26} \times \exp(0.041 \times SST) \quad (6)$$

In EcoTroph, trophic transfer takes into account the losses at each trophic class, and is defined such that $\mu_{\tau} = -\ln(\text{TE})$ (Eq. 4). In this study, we used the temperature-dependent TE estimates for temperate ecosystems derived from the empirical equation of du Pontavice et al. (2019):

$$\text{TE} = e^{(-2.119 - 0.034SST)} \times 1.079 \quad (7)$$

The relationship between TE and SST was obtained from combined global fisheries catch data and information on fish life-history traits (du Pontavice et al. 2019). These estimates of TE were calculated between TL = 2.5 and TL = 4 in all the temperate coastal ecosystems (see supplementary information of du Pontavice et al. 2019).

The flow kinetics (K) and TE are directly linked to SST, and their variations reflect the changes in species assemblages induced by ocean warming (Gascuel et al. 2008, du Pontavice et al. 2019, 2021). These 2 parameters indicate that biomass flows tend to be slow and efficient in cold waters and faster and less efficient in warmer waters.

Finally, we used SST projections from POLCOMS-ERSEM to estimate K_{τ} (Eq. 6) and TE (Eq. 7) per TL.

2.3.3. Integration of fishing effects in EcoTroph

Firstly, biomass flow is affected by fishing through the fishing loss rate (φ), which is defined by the ratio of catch and production within the trophic class [τ , $\tau + \Delta\tau$] as: $\varphi_{\tau} = \frac{Y_{\tau}}{P_{\tau}}$, where Y_{τ} represents the annual catch at TL = τ . Hence, in an exploited ecosystem, the biomass flow is defined as:

$$\Phi(\tau + \Delta\tau) = \Phi(\tau) \exp(-\mu_{\tau} \Delta\tau) (1 - \varphi_{\tau})^{\Delta\tau} \quad (8)$$

Secondly, the model takes into account the effect of fishing mortality on the life expectancy of organisms and on their K_{τ} . It is calculated for the exploited state following the methodology developed by Gascuel et al. (2008, 2011) and is defined as:

$$K_{\text{exploited}, y, \tau} = K_{y, \tau} \left[1 + \alpha \frac{B_{\text{exploited}, \text{pred}, y}^{\gamma} - B_{\text{unexploited}, \text{pred}, 2013-2017}^{\gamma}}{B_{\text{unexploited}, \text{pred}, 2013-2017}^{\gamma}} \right] + F_{\tau} \quad (9)$$

Fishing reduces the life expectancy of individuals and thus reduces the time they spend in a trophic class; therefore, K is faster with a higher fishing mortality rate, $F_{\tau} = \frac{Y_{\tau}}{B_{\tau}}$. Additionally, the kinetics can be altered by climate change and fishing. A reduction in predators decreases the predation mortality rate of their prey, and such top-down control is introduced into the model by Eq. (9). Hence, the kinetics depends partly on the changes in exploited biomass of predators in year y ($B_{\text{exploited}, \text{pred}, y}$) compared to the biomass of the unexploited ecosystem during the reference period ($B_{\text{unexploited}, \text{pred}, 2013-2017}$). The coefficient α defines the intensity of top-down control, and may vary between 0 (no top-down control) and 1 (all natural mortality depends on predator abundance). The coefficient γ varies between 0 and 1 and defines the functional relationship between prey and predators. In this study, we used the conventional value of $\alpha = 0.5$, which is assumed to be an intermediate top-down intensity (Gascuel et al. 2011), and $\gamma = 0.8$, which is a non-linear functional relationship between prey and predator. A sensitivity analysis (Section S2 in the Supplement) explored different top-down control intensity with $\alpha = 0$ (no top-down control), $\alpha = 1$ (top-down driven ecosystem), $\gamma = 0.5$ (non-linear functional relationship between prey and predator) and $\gamma = 1$ (linear functional relationship between prey and predator).

2.3.4. Ecosystem model structure with two trophic pathways

To represent the trophic structure of marine food webs on the continental shelf more accurately, the biomass flow in EcoTroph was divided into 2 trophic pathways: a pelagic pathway that is fueled by zooplankton biomass, and a benthic-demersal pathway fueled at its base by benthic fauna (Fig. 2). In the pelagic pathway, species were assumed to feed exclusively on pelagic prey. In contrast, species belonging to the benthic-demersal pathway feed on benthic and pelagic prey (Woodland & Secor 2013, Kopp et al. 2015, Giraldo et al. 2017, Day et al. 2019). In this study, we included the energy flow from the pelagic to the benthic-demersal pathway in EcoTroph, assuming that, in each EcoTroph trophic class, a fraction of the biomass flow in the pelagic pathway is transferred to

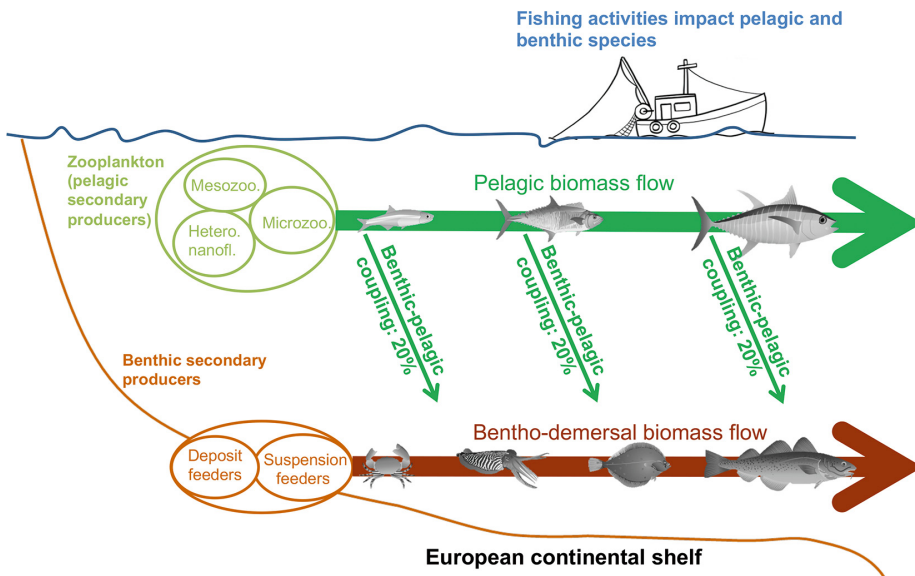


Fig. 2. Schematic representation of the EcoTroph model in the European continental shelf sea. The downward green arrows represent the biomass flow from pelagic to benthic-demersal pathways, assumed to be 20% of the flow at each trophic level

the flow in the benthic-demersal pathway. The intensity of the benthic–pelagic coupling was set to 20% for all TLs, and intensities of 5% and 40% were tested to evaluate the sensitivity of the model outputs to the intensity of the coupling (Section S3 in the Supplement).

2.3.5. Forcing the base of the food web with POLCOMS-ERSEM

Previous studies incorporated projected changes in net primary production as a driver for simulating ecosystem dynamics using the EcoTroph model (Tremblay-Boyer et al. 2011, du Pontavice et al. 2021). Instead, we used the biomass of secondary producers (zooplankton and benthos) projected by the POLCOMS-ERSEM model as a lower TL forcing. This reduces the uncertainties associated with making assumptions on biomass flow between the primary and secondary producers (Eddy et al. 2021).

The biomass of the 3 groups of zooplankton were aggregated and summed to constitute the biomass entering the pelagic food web, while 2 groups of benthos (suspension feeders and deposit feeders) were aggregated and summed to constitute the biomass entering the benthic-demersal food web. Deposit feeders are organisms living within the sediment that eat detritus and smaller organisms of the meiobenthic group. So, only a fraction of their biomass (which depends on the biological and behavioral features) is accessible for the higher TLs (Tableau et al. 2015). We set this accessible fraction to 20%, which means that we used 20% of the deposit feeder biomass.

The biomass of zooplankton and secondary producers (benthos) are incorporated in EcoTroph by assuming they constitute the bulk of the biomass between TL = 2 and TL = 2.5. Hence, the EcoTroph models were initialized by estimating the pelagic and benthic-demersal mean biomass flow between TL = 2 and TL = 2.5 ($\Phi_{2-2.5}^{\text{pelagic}}$ and $\Phi_{2-2.5}^{\text{benthic-demersal}}$, respectively) based on the flow equation under steady-state conditions (Eq. 3) within the trophic class [2, 2.5] using zooplankton biomass for the pelagic pathway (Eq. 10) and secondary producer biomass for the benthic-demersal pathway (Eq. 11):

$$\Phi_{2-2.5}^{\text{pelagic}} = \frac{B_{\text{zooplankton}} \bar{K}_{2-2.5}}{0.5} \quad (10)$$

$$\Phi_{2-2.5}^{\text{benthic-demersal}} = \frac{B_{\text{benthos}} \bar{K}_{2-2.5}}{0.5} \quad (11)$$

where $\bar{K}_{2-2.5}$ is the mean flow kinetics between TL = 2 and TL = 2.5.

2.4. Simulation experiments

2.4.1. EcoTroph model for the reference period 2013–2017

We defined the reference state of the ecosystems in the 15 study areas by modeling the biomass trophic structure in 2013–2017 using EcoTroph based on TE and K driven by SST and secondary production (see biomass spectrum in each study area in Section S4 in the Supplement). The estimated annual average SST and biomass of secondary producers (zooplankton and benthic secondary producers) entering the

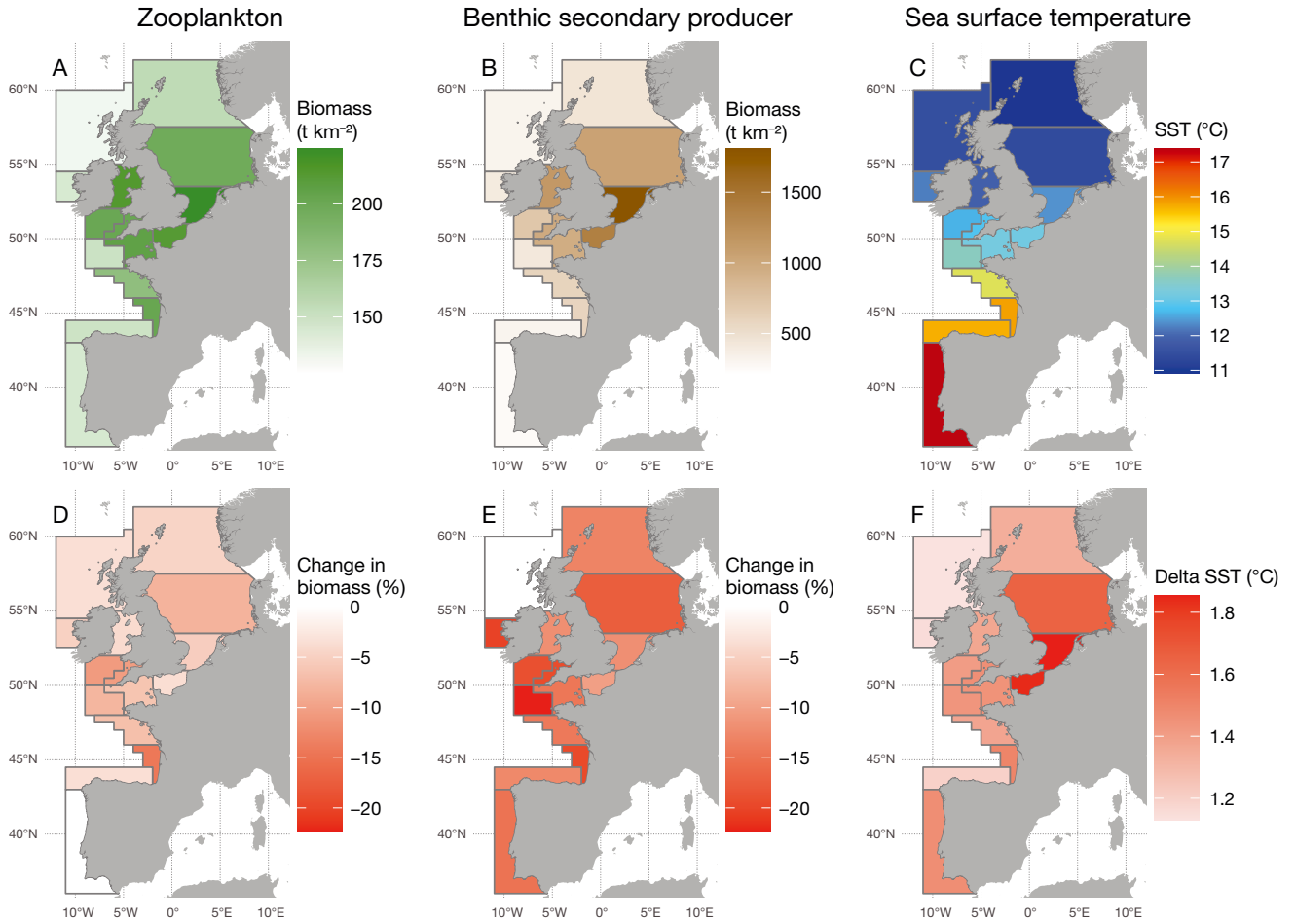


Fig. 3. (A–C) Biomass of secondary producers per unit area (t km^{-2}) and sea surface temperature (SST) in 2013–2017 and (D–F) their changes in 2090–2099 under RCP8.5. Left: zooplankton biomass, center: benthic secondary producer biomass, right: SST. While the changes in zooplankton and secondary producer biomass are calculated as the percentage of change in 2090–2099 compared to 2013–2017, the change in SST is the difference between the mean SST in 2090–2099 and 2013–2017 (Delta SST)

food web from each study area was obtained from the ERSEM outputs (Fig. 3A,B). In each study area, fishing activities were represented by the annual average total catch per TL over the reference period. Biomass was simulated for the period 2013–2017 and used as the reference state to calculate changes by the end of the century (Section S5 in the Supplement).

2.4.2. Projecting future biomass and catches

We projected changes in biomass and catch in the 15 study areas between 2020 and 2099, under the RCP4.5 and RCP8.5 scenarios, and a constant fishing mortality scenario in which future fisheries catch the same proportion of the biomass at each TL as 2013–2017. In this scenario, the mean projected catch at

year y (between 2020 and 2099; $Y_{y,\tau}$) at TL τ was estimated as:

$$Y_{2099,\tau} = F_{\tau} \times B_{2099,\tau} \quad \text{where} \quad F_{\tau} = \frac{Y_{\text{ref},\tau}}{B_{\text{ref},\tau}} \quad (12)$$

F_{τ} , $Y_{\text{ref},\tau}$ and $B_{\text{ref},\tau}$ are the fishing mortality, catch and biomass, respectively, at TL τ for the reference period (2013–2017). $B_{2099,\tau}$ is the biomass at TL τ in 2090–2099.

Changes in SST and the biomass of secondary producers were projected by ERSEM between 2020 and 2099 under RCP4.5 and RCP8.5 (Section S1 in the Supplement; Fig. 3D–F). We present the majority of the results in changes in biomass and catch by 2090–2099 relative to the reference period (2013–2017) and for 3 aggregates: pelagic consumers (TL ≥ 2.5 , excluding the secondary producers as they are inputs), benthic-demersal consumers (TL ≥ 2.5) and total consumers (TL ≥ 2.5).

2.4.3. Simulations to identify the drivers of the biomass and catch changes

A last set of simulations was designed to identify the drivers of the changes in total consumer biomass and trophic structure. Hence, 4 biomass flow parameters were investigated: (1) the production entering the pelagic food web (zooplankton), (2) the production entering the benthic food web (benthic secondary producers), (3) the trophic TE and (4) the flow kinetics.

In order to understand how biomass and catch responded to climate-induced changes in the 4 parameters, we ran 4 sets of simulations. In each simulation, we isolated one biomass flow parameter, which varies over the projection period, while the others remained constant and equal to their mean values during the reference period 2013–2017. The

sensitivity to biomass flow parameters was studied using the RCP8.5 scenario.

All analyses and simulations were performed in the R environment (R Core Team 2021).

3. RESULTS

3.1. Climate-change effects on total biomass and catch

Aggregating across the 15 study areas on the European continental shelf, total biomass in the 21st century was projected to decrease by 11.5% under RCP8.5 and 7.6% under RCP4.5 by 2090–2099 relative to the period 2013–2017 (Fig. 4A). Notably, under RCP8.5, biomass was projected to decrease abruptly between 2040 and 2060, increase briefly in

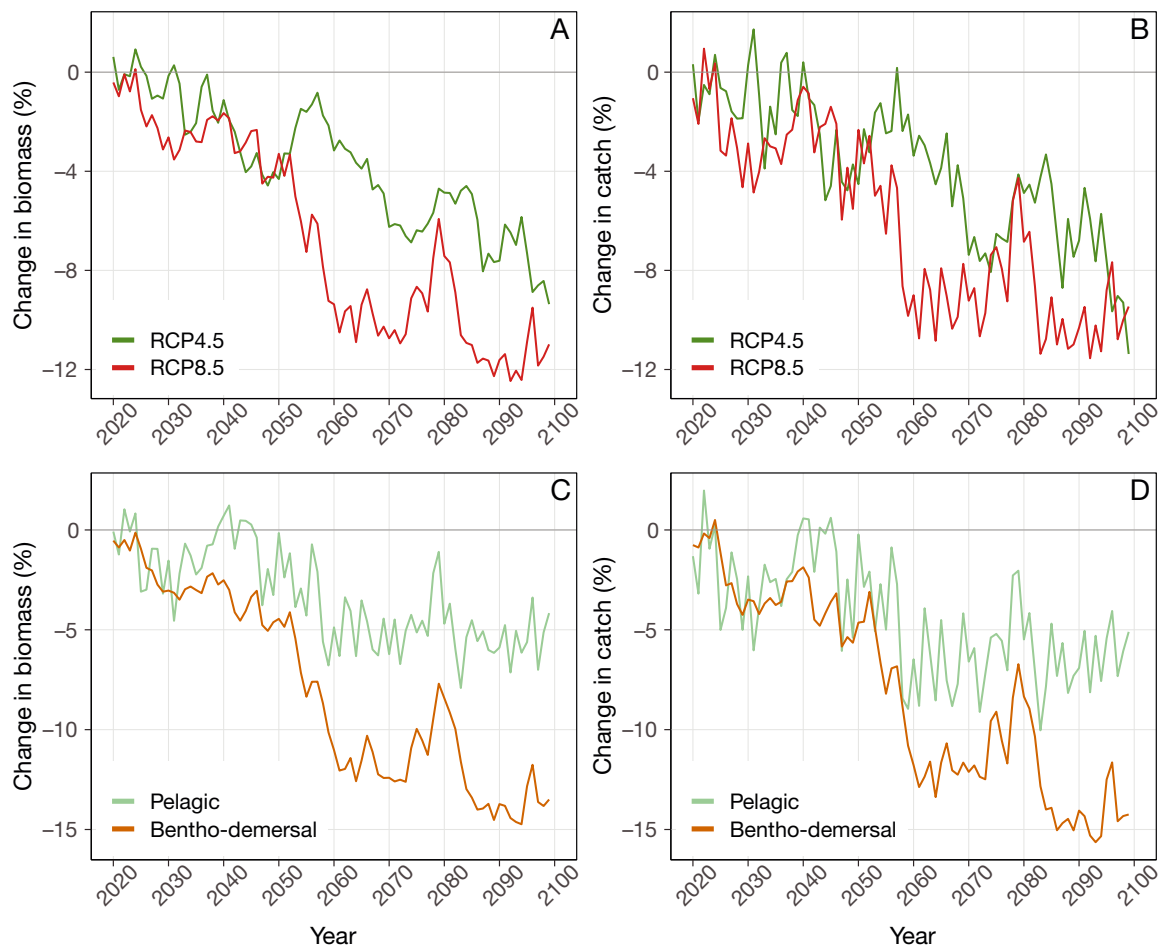


Fig. 4. Projected changes in biomass and catch from the European continental shelf trophic systems. The projected change in (A) total ($TL \geq 2.5$) biomass and (B) catch between 2020 and 2100 relative to the reference period (2013–2017) is presented under RCP4.5 (green) and RCP8.5 (red). (C,D) Projected changes in biomass and catch for pelagic and benthic-demersal ecosystem components under RCP8.5. The changes in biomass and catch presented in the figure are calculated by summing the biomass and catches of the 15 areas we considered in this study

2070–2080 but then continue to decrease afterward. The projected total catch followed a similar trend and exhibited a decrease of 10.0% under RCP8.5 and 7.8% under RCP4.5 by 2090–2099 (Fig. 4B). This represents a large catch reduction of 310 000 t under RCP8.5 and 240 000 t under RCP4.5. By 2040–2049, EcoTroph projected a loss of catch of 87 000 and 92 000 t under RCP8.5 and RCP4.5, respectively. The decrease in total biomass and catch was projected to be 8.1% and 8.3%, respectively, larger for the benthodemersal ecosystem component than for the pelagic one by 2090–2099 under RCP8.5 (Fig. 4C,D). Hence, the benthodemersal catch was projected to decrease by 13.7%, being 210 000 t by 2090–2099,

while the pelagic catches were projected to decrease by 5.4%, being 100 000 t under RCP8.5 (Fig. 4C,D).

The projected changes in total biomass and catches varied between the study areas in the European continental shelf sea, with the Celtic Sea (7h, g, f), west Ireland (7b), the middle of the North Sea (4b) and the Southern Bay of Biscay (8b) having the largest projected decreases (Fig. 5A,D). In these 6 study areas, the total decrease in biomass was, on average, 14.8% (14.0–16.0%) by 2090–2099 relative to 2013–2017 under RCP8.5, and total catches were projected to decrease, on average, by 15.4% (10.3–19.8%). These stronger projected decreases in the 6 aforementioned study areas are induced by a decrease in ben-

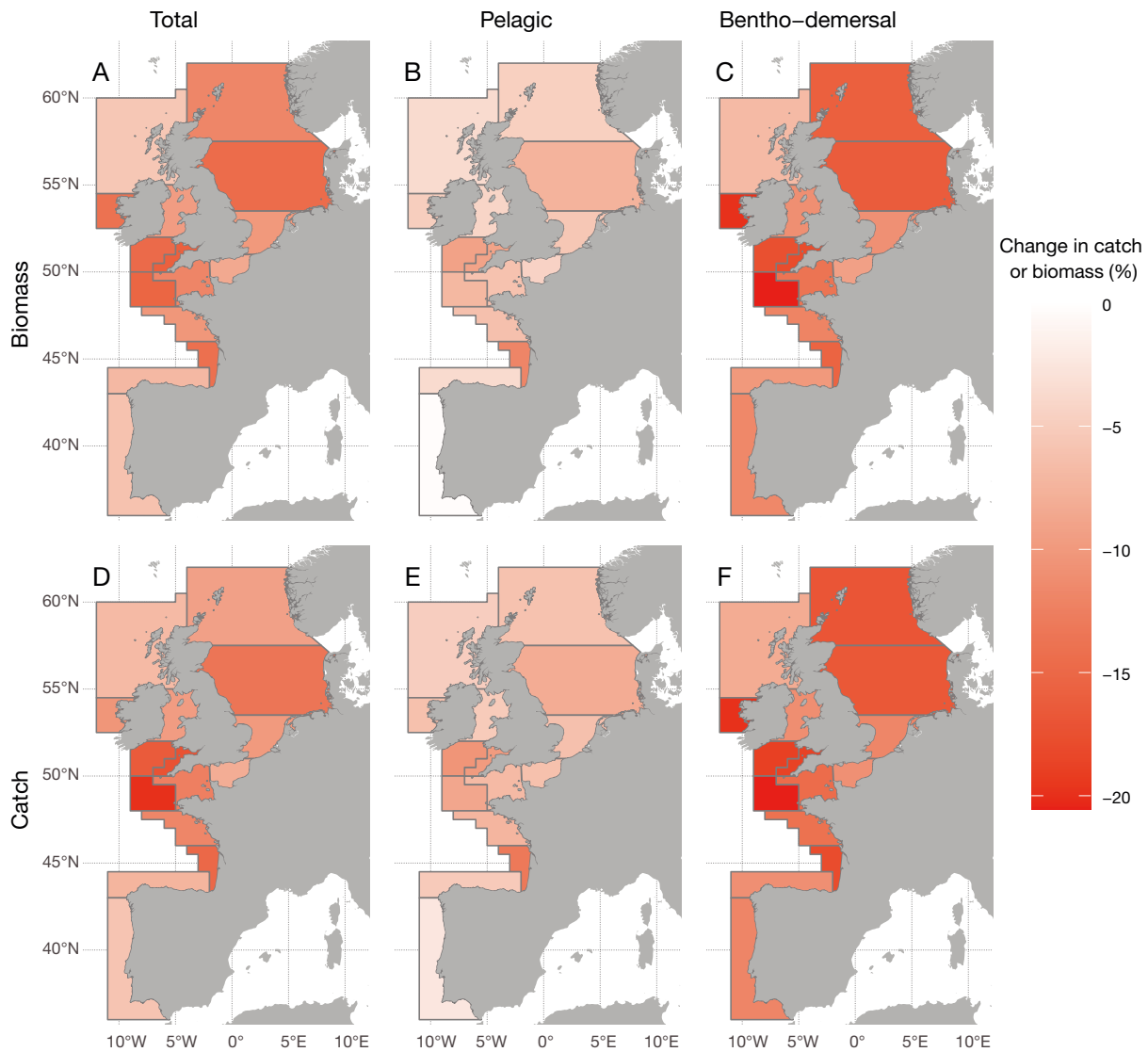


Fig. 5. Changes in biomass and catch in 2090–2099 relative to 2013–2017 under RCP8.5. The changes in total biomass (top panels) and catch (bottom panels) were aggregated for (A,D) the entire ecosystem, (B,E) the pelagic ecosystem component and (C,F) the benthodemersal ecosystem component

tho-demersal biomass and catch (Fig. 5C,F) as well as a larger decrease in pelagic biomass and catch in the southern Bay of Biscay (Fig. 5B,E). Overall, our simulations showed larger projected decreases in biomass and catch for the benthic-demersal ecosystem component in the study areas compared to the pelagic one.

3.2. Climate-change effects on the food web

The biomass projected by EcoTroph over the European continental shelf was dominated by the benthic-demersal ecosystem components at all TLs (Fig. 6A). On average, the benthic-demersal components represented 73.1 and 71.2% of the total biomass of the trophic system in 2013–2017 and 2090–2099, respectively (Fig. 6A). Conversely, lower TL catches were made up of pelagic and benthic-demersal species, while mid-TLs were dominated by pelagic catches (around 75% between TL = 3.3 and TL = 3.7) and higher TL catches were dominated by benthic-demersal catches (more than 83% for TL \geq 4) (Fig. 6B). The pelagic and benthic-demersal biomass and catch were projected to decrease at every TL (Fig. 6).

The EcoTroph projections under RCP8.5 showed that the declines in biomass at higher TLs are more pronounced with an increasing difference of impacts between the low and high TLs throughout the 21st

century (Fig. 7A,C). Focusing on the period 2090–2099, we showed that the magnitude of the projected decreases in biomass was lower for the lower and mid-TLs until TL = 4.3. Then, the decrease of the top-down intensity led an enhancement of the projected decrease in biomass along the TLs. Specifically, biomass is projected to decrease by 11.1% at lower TLs (between TL = 2.5 and TL = 4) and 19.3% at higher TLs (between TL = 4.5 and TL = 5.5) under RCP8.5 (Fig. 7C). A similar trend was observed for the higher TL catches (TL \geq 3.8), while the effects appeared to be weaker for the mid-TLs (Fig. 7B,D). This can be explained by the combination of 2 factors: (1) the mid-TL catches were dominated by pelagic species (Fig. 6B) and (2) zooplankton biomass, which fuels the pelagic ecosystem component, was projected to be less impacted by climate change in the POLCOMS-ERSEM model (Fig. 3D). The projected changes in biomass and catch by 2090–2099 highlighted that the benthic-demersal ecosystem component was more affected than the pelagic one at all TLs, with a marked top-down effect (Fig. 7E,F).

3.3. Climatic drivers of the changes in biomass and catch

Different climate-related drivers (changes in temperature and secondary production), as well as TE

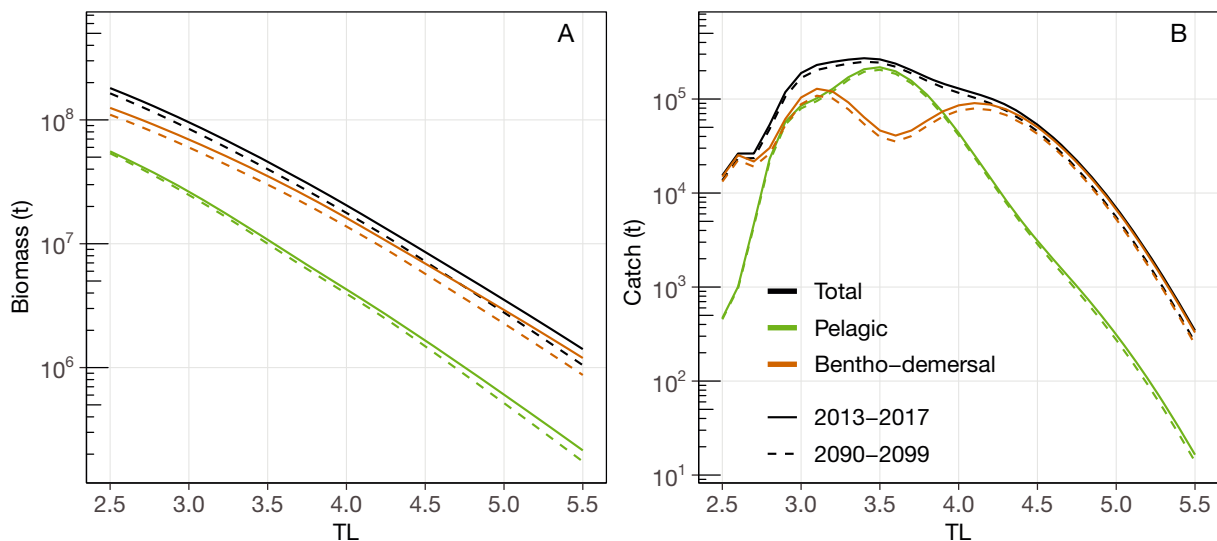


Fig. 6. Projected changes in biomass and catch from the European continental shelf at each trophic level. EcoTroph projections of (A) biomass and (B) catch trophic spectra (i.e. biomass and catch distribution across trophic levels) for the pelagic and benthic-demersal ecosystem components for the period 2013–2017 (solid lines) and for the period 2090–2099 (dashed lines) under RCP8.5. The changes in biomass and catch presented in the figure are calculated by summing the biomass and catches of the 15 areas we considered in this study

and flow kinetics, affected the projected changes in biomass and catch differently. The temperature-induced decrease in TE caused a projected decline in total biomass and catch that was limited at low TLs but amplified along the food web (blue lines, Fig. 8).

Further, the temperature-induced increase in K was negatively related to the total biomass and catch (red lines, Fig. 8). This negative effect of change in K was homogeneous across all TLs for biomass and catch (see Eq. 7).

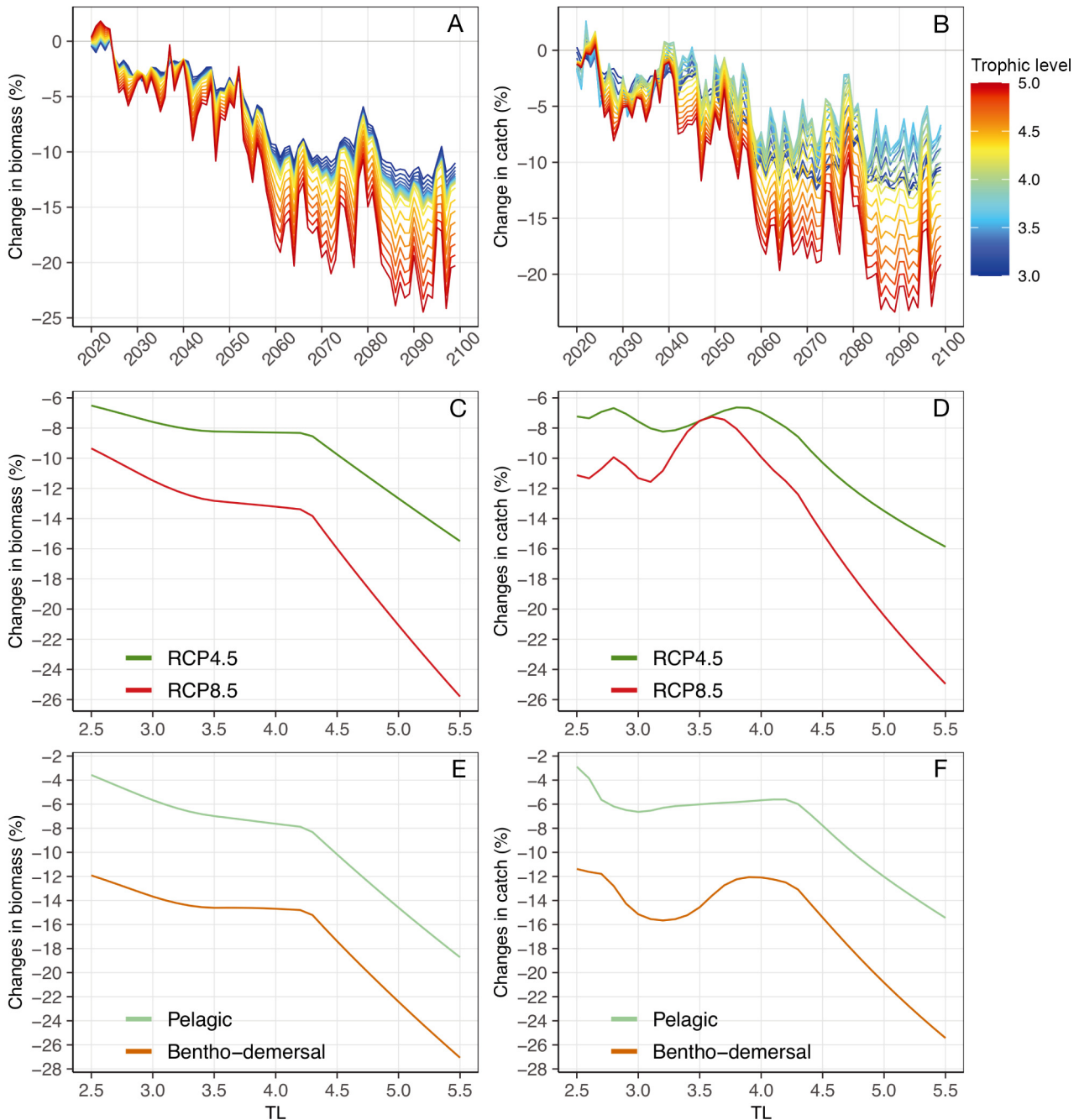


Fig. 7. Projected changes in (left) biomass and (right) catch from the European continental shelf at each trophic level. (A,B) Changes in biomass and catch for each trophic class of width 0.1 trophic level (TL) between TL = 3 and TL = 5 in 2090–2099 relative to 2013–2017 under RCP8.5. (C,D) Projected changes in biomass and catch at each trophic class in 2090–2099 relative to 2013–2017 for RCP4.5 and RCP8.5. (E,F) Projected changes in biomass and catch at each trophic class separately for the pelagic and benthic-demersal components in 2090–2099 relative to 2013–2017 for RCP8.5. The changes in biomass and catch presented in the figure are calculated by summing the biomass and catches of the 15 areas we considered in this study

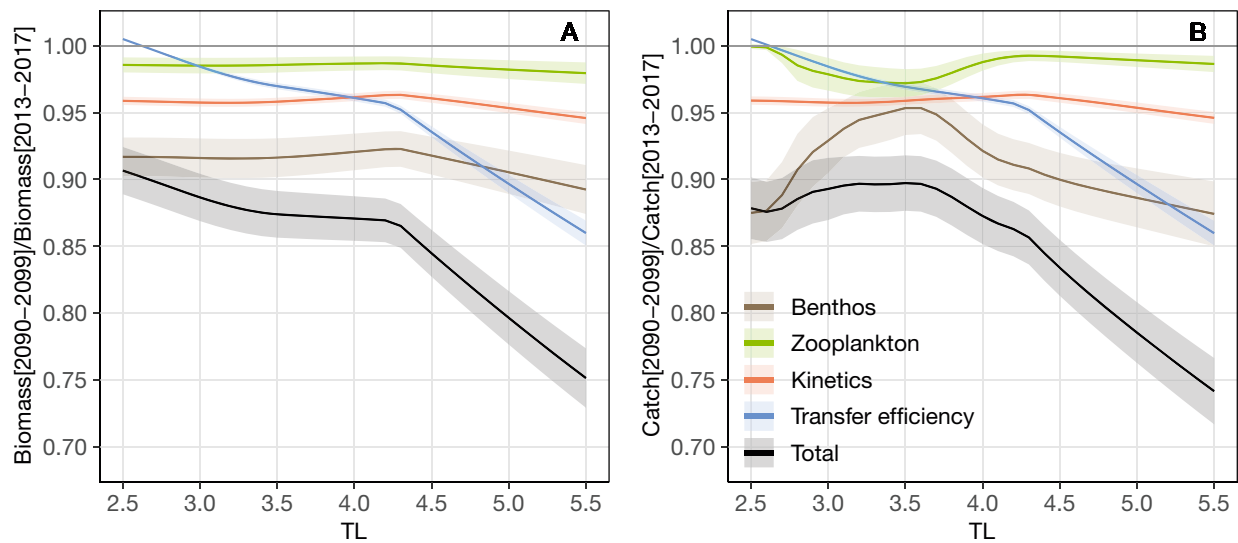


Fig. 8. Drivers of the changes in (A) biomass and (B) catch for the ecosystem. The ratio of catch trophic spectra in 2090–2099 relative to the reference period 2013–2017 derived from the simulations in which each biomass flow parameter is successively isolated (zooplankton, benthic secondary production [benthos], transfer efficiency and flow kinetics). The results are presented for RCP8.5. The shaded areas represent the 95% CI across the 15 study areas

In addition, total biomass was projected to decrease as a result of the decreases in zooplankton and benthic secondary production, with the same effects on all TLs (green and brown lines, Fig. 8A). However, the impact of the decrease in benthic secondary producers was much stronger due to its large climate-induced decrease (brown line, Fig. 8A).

Finally, the projected changes in catch induced by benthic secondary producers were strong at low TLs, and the changes were attenuated until $TL = 3.6$ (brown line, Fig. 8B). Towards the higher TL catches, our projections showed a stronger impact of changes in benthic secondary producers. The reduced impact of secondary production at mid-TLs was directly related to the lower proportion of benthic catches at mid-TLs. Similarly, the impact of the climate-induced changes in zooplankton on the catches was maximal at $TL = 3.6$, where the proportion of pelagic catches is the highest.

This analysis of climate-related drivers also showed that the effects of K , TE and zooplankton were similar across the 15 study areas, while the effects of the climate-induced changes in benthos varied more among the study areas (see low confidence intervals in Fig. 8). This is due to the large spatial variations in the changes in benthic secondary production in the study areas, which are dominated by their benthic-demersal components (see Section 3.2).

4. DISCUSSION

Our results show that biomass and catch in European continental shelf ecosystems are projected to be affected by climate change through alteration of biomass flow. More aggressive mitigation of greenhouse gas emissions can reduce such impacts, while fisheries management is key for adaptation.

4.1. Heterogeneous responses of European continental shelf ecosystems to climate change

The interacting effects of the projected changes in secondary production and ocean temperature under climate change are likely to significantly alter the functioning of marine ecosystems in the Northeast Atlantic. Across all the studied ICES areas, the projected decrease in zooplankton and secondary producer biomass in the 21st century led to changes in biomass flows for both the pelagic and benthic-demersal ecosystem components. Simultaneously, projected ocean warming is expected to affect the flow kinetics and trophic transfer efficiency (Gascuel et al. 2008, du Pontavice et al. 2019). The underlying process is that warmer water temperatures are expected to favor short-lived species with faster metabolic rates across the food webs (Beukhof et al. 2019, du Pontavice et al. 2019, 2021). The increase in dominance of short-lived species is already evidenced in the observed

shifts in species distribution in Northeast Atlantic ecosystems, with increasing dominance of warm-water (shorter-lived) species and decreases in cold-water (longer-lived) species (ter Hofstede et al. 2010, Simpson et al. 2011, Montero-Serra et al. 2015). Hence, on the one hand, warmer temperature accelerates and reduces the efficiency of biomass transfers. On the other hand, the overall climate-induced decrease in secondary production induces an overall decrease of the biomass fueling the food web, which is mainly driven by the decrease in benthic secondary producers. Zooplankton is projected to be less affected by climate change (Section S1 in the Supplement).

The variability of the changes in SST and secondary producers may explain the spatial variations in the response of projected changes in biomass and catch in the European waters. In some study areas, such as in the Atlantic Iberian waters (ICES division 9a) the projected increase in zooplankton was partly compensated by the warming-induced impacts of trophic transfer toward the higher TLs (Fig. S1.10 in the Supplement). In contrast, in other regions such as in the Celtic Sea (7f–h; Fig. S1.9) and the southern Bay of Biscay (8b; Fig. S1.9), the effects of warming and declining secondary production projected by POLCOMS-ERSEM were cumulative and led to large decreases in biomass and catches. Our results also showed that the projections were highly sensitive to climate-induced changes in benthic secondary production, which represented more biomass entering the food web than zooplankton. The EcoTroph projections based on the forecasting simulations from POLCOMS-ERSEM showed that the fishing captures in 3 regions may be more affected by climate change: the Celtic Sea, the middle of the North Sea and southern Bay of Biscay. In parallel, the lower projected climate-induced changes may induce moderate changes in biomass and catches in the Atlantic Iberian waters and Western Scotland (Fig. 5).

Our findings also suggest an amplification of the changes in biomass and catch from low to high TL ecosystem components. This process describes the propagation of the climate signal up from low TLs to upper TLs through the decline (or increase) of biomass along the food web. The stronger decline in biomass and catch of higher TLs arises from reduced TEs associated with increasing temperature. This is consistent with the trophic amplification induced by warming for the higher TLs highlighted at global scale (Lotze et al. 2019, du Pontavice et al. 2021) and locally in the North Sea (Kirby & Beaugrand 2009, Lindley et al. 2010).

4.2. Sensitivity analyses, structural uncertainties and limitations

In this study, we improved the representation of the trophodynamic pathways in EcoTroph by subdividing the ecosystem into pelagic and benthodemersal components. However, our study may have underestimated the degree of coupling in the shallowest study areas (e.g. the Eastern English Channel) by assuming that the production transferred from the pelagic to the benthic pathway is constant over TLs and areas. In contrast, several recent studies showed that the degree of benthic–pelagic coupling varies widely over depth, with stronger coupling in shallow coastal areas in the European continental shelf (Kopp et al. 2015, Giraldo et al. 2017, Cresson et al. 2020). Cresson et al. (2020) highlighted major differences in benthic–pelagic coupling between the Bay of Biscay (8b) and the Eastern English Channel (7d). The consequences of changes in benthic–pelagic coupling on our projections were tested by doubling (40%) and reducing (5%) the production transferred from pelagic to benthic pathways in every study area (Section S3 in the Supplement). The sensitivity analysis showed no effect of the increase in benthic–pelagic coupling on the projected decrease in total biomass, while a higher coupling would lead to a slightly lower decrease in total catch (from 10.0% to 9.7% under RCP8.5) and a lower coupling would lead to a slightly larger decrease in total catch (from 10.0% to 10.2% under RCP8.5) (Section S3 in the Supplement). Increasing benthic–pelagic coupling would reduce the projected climate impacts mainly on the high TL benthodemersal catches by progressively increasing the fraction of pelagic production (which is less affected by climate change) flowing to the benthodemersal compartment (Section S3 in the Supplement). Although the projections were not highly sensitive to benthic–pelagic coupling intensity, quantitative estimates of the spatial and seasonal variability of the coupling may improve the spatial patterns of our projections.

In this study, we considered that each study area is an independent ecosystem without exchange between adjacent ecosystems. In each study area, we assumed that secondary production (zooplankton and benthic secondary producers) fuels the entire ecosystem without seasonal migration (e.g. a species that feeds in one area and is caught in another). This is a reasonable assumption for benthic and demersal species, which are highly dependent on their habitats. However, this assumption is more questionable for pelagic species, since several pelagic fish stocks

in the Northeast Atlantic undertake extensive seasonal migrations (Macer 1977, Uriarte et al. 2001, Hátún et al. 2009, Trenkel et al. 2014). In the future, the model could be further developed by incorporating quantitative knowledge regarding the seasonal migrations within the European continental shelf.

Moreover, the intensity and predator–prey functional relationship of top-down controls were integrated in EcoTroph to account for the effects of the climate-change- and fishing-induced release of predation when climate change and fishing pressure on predators increases. A sensitivity analysis showed that the projected changes in biomass and catch are sensitive to the top-down control intensity (Section S2 in the Supplement). If top-down control is not incorporated into the model, the climate-change- and fishing-induced decrease in high TL biomass does not affect the lower TLs and led to higher climate impacts on total catch (from 10.0 to 14.3% under RCP8.5). In contrast, if a strong top-down control is included in the model, the decrease in high TL biomass led to a release of predation and a lower impact on total catch (from 10.0 to 8.1% under RCP8.5). However, while a strong top-down effect leads to smaller quantitative changes in total biomass and catch, larger qualitative changes are projected in the trophic structure of the food web via chain effects from high to low TLs (Fig. S2.1C in the Supplement). The type of functional relationship (linear or non-linear) of the top-down control has a moderate effect on the changes in total biomass and catch, but does not lead to changes in the trophic structure of the food web. While the projected changes in transfer efficiency and flow kinetics can be a result of changes in species assemblages under ocean warming (Gascuel et al. 2008, du Pontavice et al. 2019), other climate-induced biological responses at individual and population levels that may amplify or temper the climate change impacts on the flow kinetics and trophic transfer efficiency were not represented. We also did not consider the effects of extreme events such as marine heat waves, or the impact of the projected increase in the acidification and reduction in dissolved oxygen in the European seas (Peck et al. 2020). These combined effects may exacerbate the effect of climate change on marine organisms, with great variability in species' responses (Kroeker et al. 2013, Pörtner et al. 2017, Bindoff et al. 2019). Warming and decrease in oxygen content were, notably, projected to impact growth of fish, leading to reductions in individual- and assemblage-level body size (Cheung et al. 2013), which may, in turn, affect trophic interactions and biomass transfers.

Fishing mortality was simulated in each study area based on biomass and catch during the reference period 2013–2017 and then used to estimate the projected catches over the projection period. In order to evaluate the reliability of fishing impacts in 2013–2017, we calculated the ratios between exploited biomass and unexploited biomass (Section S5 in the Supplement). They appeared to be very low compared to the levels of impact found in the literature (Gascuel et al. 2016, Moullec et al. 2017, Abella et al. 2019), especially for the higher TLs. This caused us to underestimate the fishing impacts effect in the European marine ecosystems we considered. One of the reasons could be the potential differences in biomass flow associated with accessible and inaccessible fractions of biomass. In EcoTroph, these differences can be taken into account through different flow kinetics parameters for accessible and inaccessible biomass, respectively (Gascuel et al. 2008, 2011). Further versions of the 2-pathway EcoTroph model should account for such a parametrization. However, this will require the gathering of preliminary information on selectivity in order to represent a realistic pattern of biomass accessibility to fishing in both benthic-demersal and pelagic compartments. The underestimation of fishing impacts could also be induced by potential underestimation or variation of losses at each TL represented by the TE in EcoTroph. Besides these potential uncertainties in biomass flow, the biomass of secondary producers (zooplankton and benthos) projected by POLCOMS-ERSEM could contribute to the underestimation of fishing impacts (e.g. overestimation of zooplankton or benthos biomass). Given the low modeled fishing mortalities we used to estimate the future biomass and catch, our projections are conservative, and the future impact of fishing in a changing climate could not be directly investigated. However, here, we aimed, for the first time at the scale of the whole European continental shelf, to explore the effects of climate-induced changes in ocean productivity and food web function on biomass and catch. To improve the parameterization of the EcoTroph model in Europe, we would need fishing effort estimates spatialized in each study area and assigned to food web components (e.g. benthic-demersal versus pelagic and/or low versus high TLs). Such fine-scale fishing efforts will allow for model calibration using them as an input to the model and not as an output, as we did in this study.

Finally, our findings fully rely on the predictive skills of POLCOMS-ERSEM, which is driven at the open ocean boundaries by one ESM (MPI-ESM-LR).

The latter was developed in the framework of the Coupled Model Intercomparison Project 5 (CMIP5). The high uncertainties in model projections of CMIP5 ESMs (Bopp et al. 2013) must call for caution regarding the ocean condition projections we used in this study. Therefore, other projections from CMIP5 ESMs or from the next-generation CMIP6 ESMs (Kwiatkowski et al. 2020) to drive POLCOMS-ERSEM may be valuable to explore the uncertainties associated with the large-scale change in ocean conditions. The ecosystem component of global ESMs is unlikely to provide good enough representation of benthic–pelagic coupling and secondary production (Drenkard et al. 2021), so regional downscaling with an appropriate ecosystem model is needed. An alternative regional physical–biogeochemical model may provide insights regarding the uncertainties associated with the POLCOMS-ERSEM projections. Finally, simulations from other ecosystem models with different fundamental structures and underlying ecological processes should be produced for the European continental shelf to explore the inter-model spread and put into perspective our projections.

4.3. Contribution of EcoTroph modeling to explore the future of European fisheries

European seas were intensively exploited by fisheries throughout the second half of the 20th century, with a peak at 7.2 million t of catch in the 1970s; these catches were halved by the early 21st century due to overfishing and fishing regulation (Gascuel et al. 2016, Pauly & Zeller 2016). A decrease in fishing pressure was observed over the last 15 yr and the mean fishing mortality rate of assessed stocks was reduced in all the ecosystems in European seas in the Northeast Atlantic (Hernvann & Gascuel 2020, STECF 2022). Over-exploited fish stocks have started to recover slowly, and abundance of fish stocks has increased significantly in recent years (Hernvann & Gascuel 2020, STECF 2022).

The EcoTroph simulations coupled with POLCOMS-ERSEM projected a climate-induced decrease in biomass, which in turn may dramatically impact fishing catches. By 2040–2049, our projections showed a reduction of catches of around 4% and 90 000 t regardless of the emissions scenarios under a constant fishing mortality scenario. In the longer term, by 2090–2099, the loss of catch may reach 310 000 t per year under RCP8.5, which represents nearly the average annual catch of The Netherlands in the Northeast Atlantic between 2013 and 2017 (321 000 t;

https://ec.europa.eu/eurostat/databrowser/view/FISH_CA_ATL27/). Under the medium-low emissions scenario, loss of catch is projected to be smaller, although the magnitude of the loss is still substantial (POLCOMS-ERSEM, RCP4.5). Thus, while the climate-induced reduction of fisheries catches may be inevitable by 2040–2049, induced by biomass decreases, a strong mitigation of greenhouse gas emissions is essential to mitigate the losses by the end of the century. Furthermore, we showed that climate change may lead to spatially heterogeneous modifications in ocean conditions, leading to different levels of impact on the continental shelf, with some areas being potentially more impacted, such as the Celtic Sea, the middle of the North Sea and the southern Bay of Biscay. In parallel, at the species level, the observed shifts in species distribution in European waters (ter Hofstede et al. 2010, Simpson et al. 2011, Montero-Serra et al. 2015, Baudron et al. 2020) are expected to accelerate with the future changes in ocean conditions. Hence, European fisheries may face to 2 major issues: declines of total catch and changes in species composition of the catch, which would result in socio-economic and potential political repercussions (especially in the context of Brexit). As suggested by Baudron et al. (2020), a revision of the principle of ‘relative stability’ in catch quota allocation (fixed allocation key based on historical catch for each country) would be necessary to address some economic and political issues related to the changes in species assemblages. Although we did not analyze explicitly the role of fishing to mitigate the impacts of climate change in biomass and catch, European fisheries should also anticipate the expected losses in catch, which may counterbalance the slow recovery in stock abundance observed over the last decade. More precautionary management, for example targeting the maximum economic yield and therefore a lower fishing mortality, could at least partially balance the reduction in biomass and avoid or mitigate any reduction in profitability (Cheung et al. 2022). Careful management has demonstrated its capacity for rebuilding exploited stocks in Europe (e.g. in the Northeast Atlantic, biomass of assessed stocks in 2020 was 35 % higher than in 2003; STECF 2022) and it can be a powerful means to mitigate and adapt to climate change impacts.

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