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Structure and functioning of the Bay of Biscay ecosystem: A trophic modelling approach

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Abstract :

Characterizing the structure and functioning of marine ecosystems requires a deep understanding of the dynamics of its populations and the biotic interactions among them. To this end, we developed a mass-balanced food-web model of a regional sea in the Northeast Atlantic, the Bay of Biscay (BoB), considering one of the most important anthropogenic disturbance in the area, the fishing pressure.

The food-web model was performed for the whole BoB region for the first time. The model represents the ecosystems in the early 2000s, encompassing 120433 km2 between 0 and 1000 m depth. The model was composed of 52 functional groups, ranging from primary producers to top predators, and considering both Spanish and French fishing fleets. Input data included biomass obtained locally from bottom trawl and acoustic surveys, data from stock assessment, official fishery statistics, published and unpublished data on stomach content analyses and the use of empirical equations to estimate consumption and production rates.

Our results highlight the importance of the pelagic domain, since the main trophic flows are determined by the interaction between phytoplankton, zooplankton and forage fishes. The role of the detritivore pathway was also relevant due to the relatively high abundance of detritivores organisms and the large percentage of primary production flowing to the detritus. Forage fish have resulted to be a key compartment fostering the connectivity between the benthic and pelagic domains. Pelagic sharks, dolphins, anglerfish, large hake and large demersal fishes were identified as potential keystone functional groups in the BoB model. The results also showed an intense exploitation by fisheries in early 2000s.

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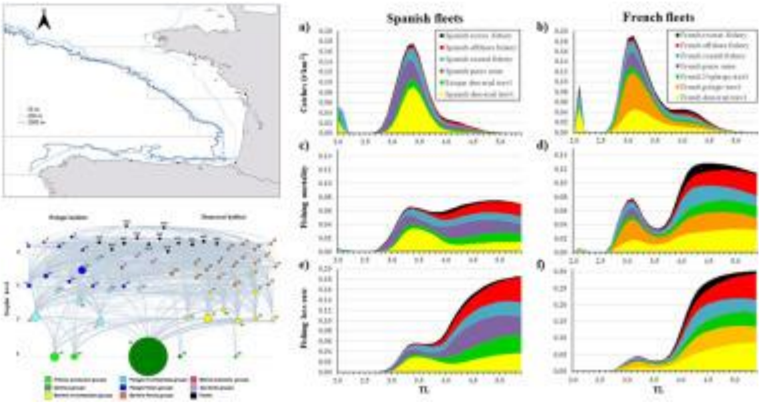
Different strategies between Spanish and French fleets were also found. French fleets were mainly focussed on low trophic level forage fish (e.g., sardine and anchovy) and had larger impacts on higher trophic levels, while Spanish fleets mostly focussed on higher trophic level forage fishes (e.g., mackerel, horse mackerel and blue whiting) but also targeting sardine and anchovy; and displayed lower impacts on higher trophic levels. Overall, our model demonstrates the importance of combining data sources from different countries to regionally address the sought-after implementation of the ecosystem-based management approach.

Graphical abstract



Highlights

► We characterize the structure and functioning of the whole Bay of Biscay with a food web model. ► The model highlights the dominance of the pelagic domain and the importance of the detritivore pathway. ► Forage fish play a key role in fostering the connectivity between the benthic and pelagic domains. ► The results show an intense exploitation by fisheries in early 2000s. ► The model highlight different strategies between Spanish and French fleets.

Keywords : Ecopath model, Food-web model, Ecosystem-Based management, fishing impacts, Bay of Biscay

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1. Introduction

Fishing pressure on marine resources and ecosystems has grown dramatically since the mid XX century (Worm and Branch 2012; Link and Watson 2019). While global marine catches increased from the 1950s to 1990s and then started a steady decline (Pauly and Zeller 2016), fishing effort and efficiency have continued to increase (Bell, Watson et al. 2017; Rousseau, Watson et al. 2019) and fishing activities have expanded their geographic and bathymetric coverage (Swartz, Sala et al. 2010; Watson and Morato 2013). Therefore, the overall limits of sustainable exploitation may have been overpassed (Worm and Branch 2012).

Within the European Union context, although fishing pressure has declined since 2000, overexploitation of marine resources is still widespread (Gascuel, Coll et al. 2016; Fernandes, Ralph et al. 2017; Froese, Winker et al. 2018). In addition, Atlantic European waters are widely impacted by other human activities (Halpern, Frazier et al. 2015) including the increasing effects of climate change (Perry, Low et al. 2005; Baudron, Brunel et al. 2020).

The current EU fisheries framework in Atlantic waters uses single-species stock assessment to inform management decision for several commercially targeted species based on Total Allowable Catches (TACs) and quotas. Single-species management generally attempt to maintain populations of target species ignoring most environmental and trophic interactions as well as other human impacts. However, managing marine resources and ecosystems is becoming increasingly complex as interacting and cumulative anthropogenic impacts are rising up rapidly (Halpern, Frazier et al. 2015). Therefore, there is an urgent need to move towards more comprehensive frameworks such as the ecosystem-based management (EBM) (Rosenberg and McLeod 2005; Long, Charles et al. 2015). The EBM considers the relationship and interdependence of the entire ecosystem, which include marine organisms, environment and multiple human activities. Ecosystem modelling contributes to EBM implementation by providing a framework for integrating available information about trophic interactions, interactions with environmental factors and human pressures such as fishing (Plagányi 2007). They have been proven to be useful to provide understanding of the structure and functioning of marine ecosystems, estimate the impacts of human activities, assess the effects of the environment, evaluate the impact of management measures and give support to the decision-making progress (Collie, Botsford et al. 2014; Acosta, Wintle et al. 2016; EMB 2019). For such purposes, the Ecopath with Ecosim (EwE) approach has been widely applied to model aquatic ecosystems (Colléter, Valls et al. 2015).

The Bay of Biscay (thereafter BoB), a gulf located in the northeastern Atlantic Ocean, is a complex and highly productive area due to upwelling events, especially in the Iberian continental shelf, and river run-offs, mainly from French rivers (e.g., the Loire and Gironde). It corresponds biogeographically to a subtropical/boreal transition zone, so it supports a wide and diverse number

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of marine organisms (OSPAR 2000). In addition, it hosts important habitats and biodiversity spots (i.e., canyons and seamounts) (Sánchez, Serrano et al. 2008; Louzao, Anadón et al. 2010) and species of interest for conservation such as cetaceans and seabirds (García- Barón, Authier et al. 2019). The BoB is subjected to intense anthropogenic activities such as fishing, shellfish farming and aquaculture, and marine transport, and other anthropogenic pressures such as climate change, invasive species, tourism and agriculture-industrial induced pollution (Lorance, Bertrand et al. 2009; Borja, Amouroux et al. 2019). Fishing activities in the Bay of Biscay involve Spanish and French fleets, which are characterized by a wide range of fishing gears and techniques, targeting a large number of species, particularly in the demersal habitat (Daurès, Rochet et al. 2009). As other European ecosystems, the BoB experienced an increasing fishing effort and capacity until the 1990s, when several stocks showed an alarming state of depletion (Garcia and De Leiva Moreno 2005). However, since the Common Fisheries Policy reform in 2002, fishing effort has been reduced (Mesnil 2008; ICES 2018). Nevertheless, the expected positive effects for target species and ecosystems due to these fishing reductions have not been observed (Rochet, Daurès et al. 2012; Gascuel, Coll et al. 2016; Froese, Winker et al. 2018). In fact, several analysis showed intense fishing impact and changes in the trophic structure of the ecosystem during the last decades (López López 2017; Moullec, Gascuel et al. 2017; Preciado, Arroyo et al. 2019).

In this study, we have developed for the first time a food web model of the BoB including simultaneously Spanish and French waters. Previously, smaller areas were modeled in the region corresponding to the International Council for the Exploration of the Sea (ICES) divisions (8ab and 8c) (Sánchez and Olaso 2004; Lassalle, Lobry et al. 2011; López López 2017; Moullec, Gascuel et al. 2017). However, hydrodynamic events, ecological features and management criteria (e.g,, the presence of several shared stock) in the area demand to analyze the BoB as an ecological entity (Valdés and Lavin 2002; Borja, Amouroux et al. 2019), what motivates the development of a larger model in order to move towards an EBM in the area. Therefore, the objectives of the present study were:

a) To characterize the structure and functioning of the whole BoB ecosystem during the early 2000s;

b) To evaluate the ecological role of important species of the ecosystem; and

c) To assess the impact of fishing activity on the structure and functioning of the ecosystem

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2. Materials & Methods

2.1. Study area and time period

This study encompasses the BoB ecosystem, from Brest (Brittany, France) to Cabo de Finisterre (Galicia, Spain) (Fig. 1), including the ICES divisions 8abc (Fig. 1). The model comprises the continental shelf and upper slope, between 0 and 1000 m isobaths, covering an area of 120433 km^2. The BoB model represents the mean ecosystem functioning over the 2000-2003 period, which is the first period for which more reliable and available data exists, especially regarding the catch statistics.

Ecological and fishery characteristics were used to establish the bathymetric limits of the model. As such, coastal waters were included as they represent important feeding and nursery areas for many species, and since they constitute the main fishing grounds of the coastal artisanal fishery and recreational fishers; while the limit of 1000 m is assumed to cover almost all fishing activities and it corresponds to the bathymetric limit of some important stocks such as anglerfish (*Lophius* spp.) and hake (*Merluccius merluccius*) (Persohn, Lorance et al. 2009).

Regarding the latitudinal limits, the BoB is a well-differentiated unit due to geomorphological, oceanographic and biological features and management criteria (Valdés and Lavin 2002; Borja, Amouroux et al. 2019), although the BoB is included within the Lusitanian and South European Atlantic Shelf ecoregion (Spalding, Fox et al. 2007), which also included the Iberian coast.

2.2. The Ecopath modelling approach

The Ecopath with Ecosim (EwE) version 6.6.3 (Christensen and Walters 2004; Christensen, Walters et al. 2008) was used to construct the food web model of the BoB. The static Ecopath model was used to provide a quantitative representation of the food web in terms of biomass and flows for the early 2000s. The food web is modelled using functional groups, which consist of the major biological components of the ecosystem. Functional groups can be ontogenic fractions of a species, single species or groups of species that share common ecological traits such as feeding habits, predators and habitats (Christensen, Walters et al. 2008; Heymans, Coll et al. 2016).

Ecopath is based on the assumption of mass-balance over a time period and it is parameterized by two master equations, one describing the production (Eq. 1) and the second describing the energy balance (Eq. 2) of each functional group (Christensen and Walters 2004; Christensen, Walters et al. 2008).

Production = predation mortality + fishing mortality + other mortality + biomass accumulation + net migration (Eq. 1)

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Consumption = production + respiration + unassimilated food (Eq. 2)

For each functional group, three of the four basic parameters (biomass (*B*), production (*P/B*) and consumption (*Q/B*) rates, and ecotrophic efficiency (*EE*)) are required and the fourth is estimated through the mass balance routine. In addition, the diet composition for each functional group and the catch by fleet and functional group is required to define prey-predator relationships and represent the impact of fishing, respectively. A detailed explanation of the algorithms and equations of the approach and its main advantages and limitations are described in Christensen and Walters (2004) and Heymans, Coll et al. (2016).

2.3. Functional groups and input data

For the definition of the functional groups, previously developed models in the area (Sánchez and Olaso 2004; López López 2017; Moullec, Gascuel et al. 2017) were considered. Functional groups were defined based on the commercial importance of the species, data availability and ecological features of the species such as diet composition and bathymetric distribution (Table 1). Specifically, main target species were modeled separately such as bluefin tuna (*Thunnus thynnus*), albacore (*T. alalunga*), mackerel (*Scomber* spp.), horse mackerel (*Trachurus* spp.), sardine (*Sardina pilchardus*), anchovy (*Engraulis encrasicolus*), anglerfish, sea bass (*Dicentrarchus labrax*), megrim (*Lepidorhombus* spp.), common sole (*Solea solea*), mullets (*Mullus* spp.) and Norway lobster (*Nephrops norvegicus*). Hake was split into two age groups (i.e. multi-stanza groups) (large hake, i.e. ≥ 27 cm of total length and small hake < 27 cm) attending fisheries and ecological reasons. For example, the minimum conservation reference size in Atlantic waters for hake is of 27 cm and, therefore, landings can be attributed to large hake while discards can be associated to small hake. In addition, 27 cm is near the size where hake change its diet and thus the ecological role, becoming one of the top predators of the system (Velasco and Olaso 1998; Mahe, Amara et al. 2007). In total, the BoB model encompasses 52 functional groups, including 3 primary producers, 16 groups of invertebrates, 23 groups of fish, 4 groups of elasmobranchs, 2 groups of cetaceans, 2 groups of seabirds and 2 groups of detritus (natural detritus or “marine snow” and discards) (see Supplementary Online Material (SOM hereafter) 1 for details on species composition). In addition, the fishery was divided into 13 fishing fleets covering both coastal and offshore metiers, considering pelagic and demersal components: i.e., fleets were defined based on the area they operate (France and Spain, and coastal and offshore) and the characteristics of fishing gears (pelagic and demersal trawl, purse seine, artisanal and recreational). Specifically, Basque and Spanish demersal trawls were considered as separated fleets because they mainly operate in ICES 8ab and 8c respectively, while a specific French demersal trawl targeting Norway lobster was defined. In addition, the “artisanal” fleet, which includes a large amount of passive fishing gears and metiers (e.g., longlines, pots, traps and gillnets) were split into coastal and

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offshore fishing fleets to take into account the spatial distribution, fishing capacity and target species.

Input parameters for the species and functional groups were mainly obtained from published literature and unpublished information in the study area from the Spanish Institute of Oceanography (IEO), the French Research Institute for Exploration of the Sea (IFREMER) and AZTI (see SOM 1 for further details and references). Biomass were obtained using data from (1) the bottom trawl surveys (swept-area method) DEMERSALES and EVHOE (ICES 2017) for demersal species; (2) the acoustic surveys PELACUS and PELGAS for pelagic species (Masse, Uriarte et al. 2018), (3) stock assessment (ICES 2019), (4) visual surveys for mammals and seabirds (Laran, Authier et al. 2017; Pettex, Laran et al. 2017), (5) complementary information found in the literature and (6) estimated by mass balancing using realistic EE values (Heymans, Coll et al. 2016). Most of the data (demersal and acoustic surveys and stock assessment) corresponds to the study period (2000-2003) and an average value was estimated. Visual surveys include seasonal information, which were averaged, and correspond to different periods and, therefore, we reconstructed the biomass using the trends observed by Authier, Dorémus et al. (2018). Production (P/B) and consumption (Q/B) rates were estimated from empirical equations (Heymans, Coll et al. 2016), acquired from the literature or derived from other models developed in the area. The trophic information to populate the diet matrix was compiled using published and unpublished results on stomach content analyses, giving preference to local or surrounding areas. Remarkably, we used the dietary preferences of 35 fish species based on specimens collected during the DEMERSALES trawl surveys for the 2000-2003 period. For migratory species (large pelagic fishes, marine mammals and seabirds), a fraction of the diet was set as import based on the time that they spent feeding outside the system (Christensen, Walters et al. 2008; Heymans, Coll et al. 2016). Official landings were obtained from IEO and AZTI databases, Ministry of Agriculture, Fisheries and Food of the Spanish Government, and the Ministry of Agriculture and Food of the French Government. Landings for tuna species (bluefin tuna and albacore) came from ICCAT databases. Percentages of discards were obtained from local studies such as Rochet, Arregi et al. (2014), AZTI database, Ruiz, Louzao et al. (2021) and Melnychuk, Morissette et al. (2001). Finally, recreational fisheries catch were obtained from Gordoa, Dedeu et al. (2019), Dedeu, Boada et al. (2019) and Herfaut, Levrel et al. (2013). As the estimated catches of these studies did not match to our study period, we reconstructed the catches to the 2000-2003 period using the evolution of the catches estimated by the Sea Around Us project (http://www.seaaroundus.org/).

2.4. Pre-balancing and balancing analyses

Ecologically and thermodynamically balanced Ecopath model should comply the following requirements: (1) estimated EE < 1 for all functional groups, (2) values of P/Q (production/consumption rate) fall between 0.1 and 0.35 with the possible exception of fast growing groups, (3) R/A (respiration/food assimilation) < 1, (4) R/B (respiration/biomass) values fall between 1 and 10 for fishes and higher values for small organisms, (5) NE (net efficiency of food conversion) > PQ and (6) P/R (production/respiration) < 1 (Christensen, Walters et al. 2008; Heymans, Coll et al. 2016) (SOM 2).

Initial results of the BoB model showed that the EE > 1 for 15 functional groups. To achieve the mass-balance conditions, we applied a manual procedure following the best practice guidelines of the approach (Heymans, Coll et al. 2016) and a top-down strategy (starting from the groups with higher trophic levels). Within this context, the PREBAL analysis (Link 2010) was used to ensure that the input data falls within general ecological principles and, together with the pedigree index (see section 2.5), to prioritize and justify which input values should be modified during the balancing procedure. For additional information on the application of the PREBAL procedure see SOM 3. After that, diet matrix was slightly modified (see SOM 4 for the final diet matrix). The input parameters of the balanced model can be found in Table 1.

2.5. Pedigree index and quality of the model

The pedigree routine (Christensen and Walters 2004) was used to describe data origin and quality, quantify the uncertainty associated with the input parameters and to guide modifications made in balancing the model. Pedigree values were assigned for each input data, which then were used to estimate the pedigree index for the overall model. The pedigree index ranges between 0 (low quality) and 1 (high quality), allowing a description of the quality of the model. The index values and confidence intervals for the pedigree analysis are described in SOM 5.

2.6. Model analyses and ecological indicators

2.6.1. Ecosystem structure and functioning traits

To analyse the food-web structure of the BoB model, biomass, trophic flows and trophic levels (TL) were visualized using the flow diagram and the Lindeman spine (Lindeman 1942). The Lindeman spine aggregates flows and biomasses into discrete TLs while the detritus box was separated from the primary producers to display the amount of energy moving through it.

We also used several ecological indicators that describe the structure and functioning of the ecosystem and the general state of the ecosystem according to Odum (1969) and Odum (1971): (1) Total system throughput (TST, $t \cdot km^{-2} \cdot year^{-1}$), estimated as the total flows in the ecosystem (sum of all consumption, exports, respiration and flow to detritus); (2) total biomass (TB, $t \cdot km^{-}$

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^{2}); (3) Total Production (TP, t·km^{-2}·year^{-1}); (4) Net Production (NP, t·km^{-2}·year^{-1}), (5) total primary production/total respiration (Pp/R); (6) total primary production/ total biomass (Pp/B, t·km^{-2}·year^{-1}); (7) system omnivory index (SOI), (8) Finn's cycling index (FCI, %) and (9) Finn's mean path length (PL) (Odum 1969; Finn 1976; Christensen 1995; Christensen, Walters et al. 2008; Heymans, Coll et al. 2014). We estimated the transfer efficiency (TE), which represents the average energy transferred to higher trophic levels through consumption or exported out of the ecosystem (e.g., by the fishery). We also calculated the mean trophic level of the community (mTLco) by weighting the TL of each functional group by its relative contribution to the total consumer biomass in the system and excluding the TL = I (primary producers and detritus).

2.6.2. Ecological roles of functional groups

We used the Trophic Level (TL) (Lindeman 1942) defined by the model to assess the ecological position of the functional groups of the BoB model. We also employed the Omnivory Index (OI), calculated as the variance of the TL of their prey, to analyse the trophic specialization. The Mixed Trophic Impact (MTI) analysis was performed to assess the direct and indirect impacts in the food web of changes in the biomass of a group (Ulanowicz and Puccia 1990; Christensen, Walters et al. 2008). From the MTI, we estimated the relative total impact (RTI), that assesses the overall effect of each functional group through the sum of all the MTI (excluding the effect on the group itself). Finally, the keystoneness index developed by Valls, Coll et al. (2015) was estimated to identify potential keystone species within the ecosystem. A keystone group is considered a species with a large and broad impact on the food web despite its low biomass (Paine 1966; Paine 1969; Valls, Coll et al. 2015).

2.6.3. Impacts of fishing on the food web

The MTI was also used to quantify the direct and indirect impacts of each fishing fleet on the functional groups and the potential competition between fleets. We also analysed fishing mortalities (F) and exploitation rates (fishing mortality/total mortality, F/Z). While the former quantifies the fishing pressure relative to the biomass present in the ecosystem, the latter make it relative its overall production capacity. At the ecosystem level, we estimated the total catches, including landing and discards, the Primary Production required to sustain the fisheries (%PPR), the Gross Efficiency (GE) of the fishery (ratio of total catches to net primary production) and the mean trophic level of the catch (mTLc), which was calculated for each fishing fleet and for the whole fishery within the ecosystem.

In addition, we have used the trophic spectrum analysis (Gascuel, Bozec et al. 2005), which is a very synthetic graphical representation of a given ecosystem parameter (in our case catches, fishing mortalities and fishing loss rates (catches/production)) along the TL. Fishing loss rate

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reflects the level of the production extracted each year for each TL and provides an idea of the fishing impacts at the ecosystem level. We performed this analysis splitting the fleets of France and Spain to evaluate differences on the exploitation regimes between both countries.

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3. Results

3.1. Ecosystem structure and functioning traits

Total biomass of the ecosystem (excluding detritus groups) was 75 t·km^{-2} (Table 2), represented mainly by zooplanktonic groups (26.0%), pelagic fishes (22.5%), benthic invertebrate groups (21%), phytoplankton groups (17.5%), large crustacean groups (FG 34-38) (7.3%), demersal fish groups (4.9%) and cephalopods (1%) (Table 1). The overall trophic flows among functional groups (FG hereafter) showed that in early 2000 most of the flows to detritus (90%), production (96%) and consumption (74.5%) were related to the pelagic compartment mainly due to the contribution of planktonic groups, which are highly productive, fuel the food web but for which a substantial part of the production is not consumed (EE of 0.55 and 0.75 for small and large phytoplankton) (Table 1 and 3). If only higher trophic levels (>3) are considered, the pelagic compartment represented 78.2%, 75.4% and 73.8% of the flows to detritus, production and consumption respectively (Table 1 and 3). The 39.1% of the flows in the BoB ecosystem model in the early 2000s were consumed, 29.6% were flowing to detritus, 17.9% were exported and 13.5% were respired (Table 2).

The visualization and quantification of the biomasses and trophic flows among the functional groups highlighted the complexity of the ecosystem due to a large number of connections between them (Fig. 2). In addition, important fluxes from phytoplankton (FG 49-50) and detritus (FG 52) were found (Fig. 2). In fact, consumption on detritus box accounted for 30.3% of the total consumption within the system (results not shown). The flow diagram also pointed out an important benthic-pelagic coupling (Fig. 2). Indeed, benthic and pelagic pathways are well differentiated (Fig. 3). Below TL 4, around 60% of the production is allowed by the energy issued from phytoplankton, except in TL 2.3. Benthic-pelagic coupling mostly operates from TL 3 in two ways, from the detritus to the pelagic and from the pelagic (phytoplankton) to the benthos. The contribution of detritus to pelagic production between TL3 and TL4 is around 25% while the contribution of phytoplankton to benthic production remains marginal. Near TL4, an upward shift (7 folder) is observed in the production of demersal groups, which is fuelled at 50% by energy from pelagic origin. Within this context, forage fish played an important role transferring energy from the pelagic compartment (planktonic groups) to higher trophic levels (both demersal and pelagic predators). For all these groups, 36.5% of the energy transferred to higher trophic levels was consumed by demersal predators while 63.5% was predated by pelagic groups (results not shown). Similarly, an upward shift in the contribution of benthic-originating energy in the benthic domain is observed (Fig. 3).

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Concerning the Lindeman spine, our results showed that most of flows and biomasses were concentrated in TL I, II and III (Fig. 4). TL I generated 60.71% of the TST, followed by TL II (30.7%). Alive biomass was concentrated in TL II (40.6%), followed by TL III (26.9%) and TL I (18.3%) (Fig. 4). An important relationship between TL II and detritus was observed, as TL II represents the main consumer and generator of detritus (Fig. 4). Exports (i.e., catches) were primary located on TL III (50.4%), followed by TL IV (31%), TL II (10.9%) and TL V (7.7%) (Fig. 3). The transfer efficiency (TE) decreased with TL (Fig. 4) and the mean TE for the entire ecosystem was 17.5 (Table 2).

When taking into account all the groups included in the model, the mTLco for the BoB model was 1.42. If groups with TL = 1 (i.e., phytoplankton and detritus groups) were excluded, the mTLco was 2.7 (Table 2), highlighting the important biomass of low pelagic and benthic trophic levels.

3.2. Ecological roles of functional groups

Functional groups ranged from TL = 1 for primary producers (FG 48-50) to TL = 4.55 for pelagic sharks (FG 6) (Fig. 2 and Table 3). The top predators (TL >4) of the ecosystem were dolphins (FG 4), demersal sharks (FG 5), pelagic sharks (FG 6), bluefin tuna (FG 9), albacore (FG 10), other large pelagic fishes (FG 11), anglerfish (FG 198), sea bass (FG 19), large hake (FG 21) and large demersal fishes (FG 28) (Table 3). Invertebrate groups displayed TLs between 2.02 and 3, except cephalopods, which presented higher TLs (Table 3). TL of fishes ranged between 3.09 and 4.35 while sharks presented high TLs values (>3.9) (Table 3). Seabirds groups presented lower TLs (Table 3). Most of the groups presented high Omnivory Index (OI) (Table 3). However, several functional groups such as other planktivorous fishes, anglerfish, common sole, polychaetes, echinoderms and microzooplankton presented low values (Table 3), indicating a high trophic specialization (i.e., feeding almost exclusively on organism within the same TL).

The Ecotrophic Efficiency (EE) was high for most of the groups (Table 1), indicating that most of the total production of these groups was consumed (through predation) or taken by the fishery. Lower EE were obtained for top predators that are scarcely consumed and/or moderately fished (e.g., albacore), groups that spend part of their time outside of the ecosystem (e.g., marine mammals, seabirds, mackerel, bluefin tuna and albacore) or highly abundant groups (e.g., phytoplankton and zooplankton) (Table 1).

In general, most functional groups had a negative impact on themselves through competition for resources, as well as a strong negative impact on their main prey because of predation (Fig. 5). For example, large hake had a particularly negative impact on itself and on small hake, in line with cannibalism, and sardine. The MTI analysis also highlighted a remarkable positive impact of basal groups (e.g., detritus and phytoplankton and zooplankton groups) through the food web, up to top predators (Fig. 5). The RTI values suggested that these functional groups are the most impacting groups of the ecosystem (Fig. 6). This analysis also highlighted remarkable impacts of forage fish groups mostly negative on their lower TL prey (e.g., macrozooplankton for mackerel, horse mackerel, blue whiting, and sardine; and positive on higher TL predators (e.g., sardine for pelagic sharks, other large pelagic fishes, anglerfish and large hake) (Fig. 5). Forage fish also appeared to have a negative impact on their competitors (e.g., sardine vs anchovy, mackerel vs horse mackerel) as suggested by the trophic niche overlap indices that can be derived from the diet matrix. This analysis also showed a low impact through the food web of several functional groups such as benthic primary producers, Norway lobster, deep sea fishes and mullets (Fig. 5). This is notably in line with specific behaviour limiting predation risk (burying Norway lobster), or particular species distribution (very deep areas for deep sea fish, and very coastal and shallow waters for mullets).

Pelagic sharks (FG 6), dolphins (FG 4), anglerfish (FG 18), large hake (FG 21) and large demersal fishes (FG 28) were identified as potential keystone functional groups in the BoB model (Fig. 6a,b). In addition, demersal sharks (FG 5), other large pelagic fishes (FG 11), sea bass (FG 19), small demersal fishes (FG 30), benthic cephalopods (FG 32) and albacore (FG 10) could be also suggested to play a keystone role within the ecosystem (Fig. 6). Polychaetes (FG 40), macrozooplankton (FG 45), mesozooplankton (FG 46), microzooplankton (FG 47) and small and large phytoplankton (FG 49-50) also played an important role within the BoB ecosystem (Fig. 6b).

3.3. Impacts of fishing on the food web

Total catches were 3.06 $t \cdot km^{-2} \cdot year^{-1}$, landings and discards representing 70% and 30% respectively (Table 2). Exploitation rates (F/Z) were high (>0.5, indicating that more than 50% of the total mortality was due to fishing activities) for bluefin tuna, anglerfish and large hake (Table 3). In addition, demersal and pelagic sharks, albacore, sea bass and large demersal fishes presented large exploitation rates (Table 3). The GE of the fishery was 0.002 while the percentage of primary production required to sustain the fisheries (%PPR) was 9.2% (Table 2). The analysis of the total catch by fleet indicated that the Spanish demersal trawl, Spanish purse seine, French demersal trawl and French pelagic trawl had the highest catches in the area (Table 4 and Fig. 7a,b). The mTLc by fleet indicated that the French purse seine and the French coastal fishery presented the lowest values, while the French and Spanish offshore fleets had the highest mTLc (Table 4).

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The MTI analysis highlighted the main interactions between fishing fleets and functional groups (Fig. 5). This analysis showed that the 13 fleets had negative impacts on themselves and, in general, to a lesser extent on other fleets. However, remarkable impacts between different fleets were found, indicating direct and indirect competition between fleets for marine resources. For example, the Spanish demersal trawl impacted negatively on the Spanish coastal fishery, while the French demersal trawl impacted negatively on the Basque demersal trawl and French offshore fishery. Also, the French coastal fishery impacted negatively on the French recreational fishery respectively. In addition, the French pelagic trawl and the Spanish purse seine had impacts between them (Fig. 5).

The trawling fleets of Spain (Spanish and Basque) and France (demersal and pelagic) had the most widespread impacts on the ecosystem (Fig. 5). The analysis indicated strong negative impacts of fleets on several target species. For example, Spanish purse seine and French pelagic trawl had strong impacts on bluefin tuna and albacore, while trawling fleets of Spain (Spanish and Basque) and France (demersal and Nephrops) had large impacts on anglerfish. Both recreational fleets (Spanish and French) caused high impacts on sea bass. Vulnerable species such as seabirds and dolphins were negatively impacted by Spanish and French purse seine and coastal fishery, and dolphins were largely negatively impacted also by Spanish offshore fishery and French pelagic trawl. Pelagic sharks were highly impacted by Spanish and French offshore fishery. In addition, the MTI analysis suggested a low impact of discards at the ecosystem scale. However, seabirds, Norway lobster and pelagic crab were highly positively impacted by discards.

Trophic spectrum comparisons between French and Spanish fleets suggested that they exploit differently the BoB food web. The trophic spectrum of the catch indicated that most of the catch is concentrated in a narrow TL (TL between 3 and 3.5) in both fishing fleets, indicating the predominance of forage fish, and with a smaller peak at TL around 2, corresponding to suspensivores and detritivores (Fig. 7a and b). Forage fish (TL between 3 and 3.5) represented the greatest part of the catch while high TL (TL>4) cannot be neglected, especially for the French fleet (Fig. 7a and b). Spanish fleets concentrated most of their catches on TL around 3.2-3.5, while French fleets catches focus on TL around 3 (Fig. 7a and b). In fact, while French fleets caught 61.7% and 88.4% of total sardine and anchovy catches respectively, Spanish fleets caught 77.9, 68.1 and 95% of total mackerel, horse mackerel and blue whiting catches (species with higher TL (Table 3)) (results not shown). Fishing mortality reached a maximum of 0.07 in the Spanish fleet while it reached a maximum of 0.12 in the French fleet, both at higher TL (Fig. 7c and d). The fishing mortality spectrum showed an increase of F for the Spanish fleets between TL 2.6-3.3 and a nearly constant F on higher TL, while F for the French fishing fleets showed two peaks in TL 3 and TL 4 (Fig. 7c and d). The fishing loss rate analysis reached a maximum of 0.18 and 0.3 at the

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highest TL for the Spanish and French fishing fleets respectively (Fig. 7e and f). Offshore and recreational fleets (both Spanish and French) presented larger fishing loss rates in higher TL (TL > 4). As in the fishing mortality spectrum, the fishing loss rate decreased between TL 3.1 and 3.6 for the French fleet (Fig. 7f).

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4. Discussion

Contrary to the models previously developed in the area (Sánchez and Olaso 2004; Lassalle, Gascuel et al. 2012; López López 2017; Moullec, Gascuel et al. 2017), the present study characterized the structure and functioning of the whole ecosystem in the Bay of Biscay. By representing the food web of a more coherent entity in terms of geomorphological, oceanographic and biological features, this model may substantially improve our understanding of the Bay of Biscay dynamics over the recent decades. Since the spatial extent of the model also matches the spatial distribution of several fish stocks and represents both Spanish and French fleets that closely interact, the present model may efficiently assess the impacts of fishing at the ecosystem scale during the early 2000s both on the continental shelf and on the upper continental slope. Thus, the BoB model represents an important step towards the implementation of an ecosystem-based management in this area.

The pedigree index obtained for the BoB model (0.69) pointed out the good quality of the model (Morissette 2007; Lassalle, Bourdaud et al. 2014) due to the specific efforts made to include as much as local and contemporary data as possible when setting up the model, especially regarding biomass estimates and diet information. In addition, some of the fishing mortalities estimated by the model are in line with the results of stock assessment (ICES 2019; ICES 2019; ICES 2019; ICES 2019; ICES 2019) as well as other analysis (Raveau, Macher et al. 2012) and further ecosystem models (Sánchez and Olaso 2004; Moullec, Gascuel et al. 2017) in the study area. Finally, the consistency of the model was reinforced by the application of the PREBAL analysis. All the modelling efforts carried out here are crucial to ensure the reliability of diagnoses and simulations that will be made in the future work.

Although the most updated and accurate available data was used, substantial uncertainty exists. As in all ecosystem modelling approach, part of this uncertainty is related to the model structure, i.e. the way that groups were built with regard to specific purposes of the study. Within this context, the model was developed focussing mainly on fish groups to account for the effect of fishing, and, therefore, some interesting interactions between other species or groups may be hidden and/or some analyses may be biased (e.g., keystoneness). Additionally, some information gaps remain, notably regarding biomass estimates for benthic primary producers, gelatinous plankton, bivalves, crustacean groups, mesopelagic fishes and pelagic sharks, which were not available and represents a major limitation of the present study. This is particularly important for species that are thought to play an important role in marine ecosystems such as gelatinous plankton (Lamb, Hunter et al. 2019), mesopelagic fishes (Irigoien, Klevjer et al. 2014; Martin, Boyd et al. 2020) and pelagic sharks (Dulvy, Baum et al. 2008). In addition, pelagic and demersal scientific surveys are carried out in different seasons (spring and autumn, respectively), which

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could have important implications in our modelling exercise as distribution and abundance of species could vary seasonally (Lam, Cheung et al. 2008; Vilas, Pennino et al. 2019). Also, although quantitative information of stomach content analysis for fish species were accurate and abundant, diet information of other groups was scarce (e.g., many benthic invertebrates organisms). Finally, although official landings and discards were included by using the best available information, the reconstruction of catches of recreational fishers represent a major limitation, despite doing the best assumption, due to their uncertainty and their large impacts on coastal species and ecosystems (Hyder, Weltersbach et al. 2018; Hyder, Maravelias et al. 2020). Continued data collection is important to improve data availability and its quality and, thus, improving the model.

4.1. Ecosystem structural and functioning traits

Total trophic flows and biomass in the BoB model presented lower values than other ecosystem models developed in the area (Sánchez and Olaso 2004; López López 2017; Moullec, Gascuel et al. 2017; Veiga-Malta, Szalaj et al. 2019). However, these differences could be attributed to the spatial extent of the models. In particular, the BoB model included the continental shelf and upper slope (up to 1000 m), while the other models developed in the area included only the continental shelf. In addition, these coastal ecosystem models are more productive due to the influence of the Galician upwelling system in the Cantabrian Sea model and large river discharges and the Landes coastal upwelling system in the French Bay of Biscay (Borja, Amouroux et al. 2019).

Most of the biomass and production are located within the pelagic domain as highlighted in previous studies (Sánchez and Olaso 2004). In fact, the main trophic flows in the BoB are defined by the trophic interaction between phytoplankton, zooplankton and forage fishes, making the BoB a pelagic dominated ecosystem especially in low trophic levels (Lavin, Valdes et al. 2006; Cresson, Chouvelon et al. 2020). While at low TL, the phytoplankton to pelagic pathway dominated the trophic flows, at higher TL, there is no dominance of the energy pathways. Our results also pointed out the importance of the benthic-pelagic coupling. However, this benthic-pelagic coupling in the BoB changes in both intensity and way along TLs. For low TL it is relatively low and dominated by pelagic to benthos pathway except in TL 2.3, due to the high biomass of detritus feeder decapods in this specific TL. Benthic-pelagic coupling mostly operates from TL 3 in two ways, from the detritus to the pelagic and from the pelagic to the benthos. The former is mainly enabled by detritus consumed by zooplankton, pelagic crab and zooplankton feeding shrimps, in turns propagating through the trophic networks up to forage fish. The second is mainly due to the consumption of forage fishes including mackerel, horse mackerel, blue whiting, sardine and anchovy, by mesopredator fish like hake or anglerfish. In addition, the importance of the ecosystem production to phytoplankton pathway would be underestimated

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since our analysis did not disentangle the detritus pathway fueled by the primary production that is not consumed. The high productivity and more limited energy transferred to benthos makes possible the coexistence of both demersal and pelagic high trophic level species (van Denderen, Lindegren et al. 2018). However, a large part of the primary production flows to the detritus as a particulate organic matter, corroborating previous studies in the area (OSPAR 2000; Sánchez and Olaso 2004). As a consequence, a large amount of energy is available for suspension feeders (e.g., zooplanktonic shrimps, bivalves, polychaetes, echinoderms, other invertebrates) and deposit feeders (e.g., polychaetes, benthos and detritus feeders decapods, suprabenthos, other invertebrates), which in the study area represented a large part of the biomass of the ecosystem, and highlight the detritivore energy pathway for benthic communities and organisms, in line with other studies (Sánchez and Olaso 2004; Le Loc'h, Hily et al. 2008; Lassalle, Lobry et al. 2011). The clear identification of relatively independent benthic and pelagic pathways from low to medium trophic levels in our study is consistent with the patterns observed in extensive analysis of fish isotopic signatures (Chouvelon, Spitz et al. 2012; Chouvelon, Spitz et al. 2012). Transfer efficiency within the ecosystem was high, which is in line with the results of other models carried out in the area (Sánchez and Olaso 2004; Moullec, Gascuel et al. 2017) as well as other models developed in the Iberian peninsula (Torres, Coll et al. 2013; Corrales, Coll et al. 2015; Veiga-Malta, Szalaj et al. 2019).

According to Odum proposals (Odum 1969), several ecological indicators suggested that the Bay of Biscay ecosystem was stressed and at developing stage in early 2000s (Table 2). This is consistent with other ecosystem models in the study area (Sánchez and Olaso 2004; Moullec, Gascuel et al. 2017). For example, while total primary production/total respiration (Pp/R) is expected to approach one as an ecosystem matures (Christensen 1995), Pp/R was higher than 1 in the BoB, suggesting that more energy is produced than respired within the ecosystem. While total primary production/total biomass (Pp/B) is expected to decrease in mature ecosystems, it is fairly high in the BoB ecosystem, indicating low levels of biomass accumulation within the system. Net system production, which decreases in mature ecosystems, presented a high value. The Finn's Cycling Index (FCI), which represent the proportion of the total flows that is recycled and tends to increase as the system matures (Finn 1976), had a moderate value. In addition, food web complexity indices such as the System Omnivory index (SOI) and Finn's mean path length (PL) were low, suggesting that the BoB network is more chain-like than web-like.

4.2. Ecological role and trophic interactions

Similar TLs were found in other ecological models in the study area (López López 2017; Moullec, Gascuel et al. 2017). For example, anglerfish, large hake, dolphins and large pelagic fishes were also found as a top predators in the Cantabrian continental shelf (Sánchez and Olaso 2004; López

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López 2017) as well as the French Bay of Biscay (Moullec, Gascuel et al. 2017). Seabirds had low TL values due to the high contribution of discards in their diet, which in EwE is considered as a detritus group (TL = 1).

The MTI highlighted that groups at the base of the food web (e.g. detritus and phytoplankton and zooplankton groups) may have large impact through the food web, indicating their importance within the system and suggesting possible bottom-up effects (Cury, Shannon et al. 2003; Ware and Thomson 2005). In that sense, several studies have shown the potential role of bottom-up processes in population dynamics and ecosystem structure in the BoB (Stenseth, Llope et al. 2006; Borja, Fontán et al. 2008; Lassalle, Lobry et al. 2011). The MTI, as well as the flow diagram, also pointed out that forage fish play an important role within the BoB ecosystem, as reported by other studies in the area (Preciado, Velasco et al. 2008), accounting for an important part of the total flows of the ecosystem, having wide impacts through the food web and playing a noticeable role in the benthic-pelagic coupling. To a lower extent than bottom-up control of low TL, the MTI showed important impacts of forage fishes on lower and higher trophic levels, which could indicate a possible top-down control on plankton and bottom-up control on predators (Cury, Bakun et al. 2000; Cury, Shannon et al. 2003). The bottom-up impact of forage fish may be considered with regard to their high biomass levels in the Bay of Biscay. Moreover, the substantial overlap in the diets of forage fish may induce competition between species and might dampening top-down effect on zooplankton (Bachiller and Irigoien 2015). Such species transfer energy from phytoplankton and zooplankton to higher trophic levels (Cury, Bakun et al. 2000; Pikitch, Rountos et al. 2014), being some predators very dependent on forage fishes (large proportion of forage fishes in their diets) such as seabirds, pelagic sharks and several demersal predators (e.g., hake and anglerfish). Nonetheless, precisely assessing the impact of pelagic species on the dynamic of their predators remains challenging as trophic interactions at its level are particularly complex (Astarloa, Louzao et al. 2019). In addition, forage species are of great importance of the fishery in the BoB, as well as worldwide (Pikitch, Rountos et al. 2014), as they represented 57.5% of the total catch (Table 3). Within this context, our study also shows a remarkable role of blue whiting, as highlighted in previous analysis (Silva, Azevedo et al. 1997; Preciado, Velasco et al. 2008). This occurs due to its high abundance (Sánchez, Blanco et al. 2002), its wide bathymetric distribution (from mid-shelf to the slope) (Carrera, Meixide et al. 2001) and its vertical migrations (Bailey 1982), making it possibly the only forage species available in the deep demersal community. In fact, blue whiting constitutes an important food resource for demersal species such as hake, anglerfish and other piscivorous fishes (Velasco and Olaso 1998; Preciado, Velasco et al. 2006; Mahe, Amara et al. 2007; Preciado, Velasco et al. 2008).

Sharks, dolphins, anglerfish, large pelagic fishes, hake and demersal piscivorous were also found as potential keystone in other ecosystem models in the area (López López 2017; Moullec, Gascuel

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et al. 2017) as well as other models developed in the Iberian peninsula (Torres, Coll et al. 2013; Corrales, Coll et al. 2015; Veiga-Malta, Szalaj et al. 2019) and North-East Atlantic waters (Morato, Lemey et al. 2016). In fact, piscivorous fishes, dolphins and sharks have been suggested to play important roles in the structure and functioning of marine ecosystems (Baum and Worm 2009). Regarding hake, it has been suggested to play a prominent role within the ecosystem as a top predator that competes for food resources with other demersal and pelagic predators and, at the same time, an important prey of other keystone species such as dolphins (Santos, German et al. 2013; Korta, García et al. 2015). The keystoneness of the foresaid species, which are top predators in the ecosystem, may suggest that they drive ecosystem dynamics through top-down control. Other species were found to play an important role within the system (polychaetes, zooplanktonic groups and phytoplankton), as highlighted by Lassalle, Lobry et al. (2011), but it is due to their high abundance, and therefore they could be identified as dominants/structuring groups within the ecosystem (Power, Tilman et al. 1996; Heymans, Coll et al. 2012).

4.3. Impacts of fishing

The results of this study confirmed that commercial and non-commercial fishing played an important role on the BoB ecosystem dynamics. Total catches were high, suggesting an intensive rate of exploitation by fishing fleets. This result was higher than in previous models from the French Bay of Biscay (Moullec, Gascuel et al. 2017), but much lower than the results obtained in the Cantabrian continental shelf (Sánchez and Olaso 2004). These differences could be related to different bathymetric extension of the model, different time periods and different origin of the data. The percentage of primary production required to sustain the fisheries was lower than other models developed in the area (Sánchez and Olaso 2004; Lassalle, Lobry et al. 2011; Veiga-Malta, Szalaj et al. 2019), as well as other temperate ecosystems (Pauly and Christensen 1995). However, the gross efficiency of the fishery was higher than the mean global value (0.0002) (Christensen, Walters et al. 2008), suggesting a high impact of fisheries. In addition, several groups presented higher exploitation rates than a suggested general reference point for exploited marine resources (F/Z=0.5) (Rochet and Trenkel 2003) or large exploitation rates (close to 0.5), indicating the overexploitation of several species or functional groups in the Bay of Biscay.

The mTLc indicated high exploitation on medium trophic level organisms, due to the dominance of forage fishes (e.g., sardine, anchovy, mackerel, horse mackerel and blue whiting). This indicator could be associated with the “fishing down marine food webs” concept, when catches of large, long-lived and predatory species tend to decline faster than smaller, short-lived and low trophic levels species (Pauly, Christensen et al. 1998; Pauly and Watson 2005). In fact, Guénette and Gascuel (2012) showed a decline of the mTLc in the French Bay of Biscay between 1950 and 2008, while Sánchez and Olaso (2004) evidenced a large decline of the mTLc of demersal

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fisheries between 1983 and 1999. Using a non-model approach, Arroyo, Safi et al. (2019) showed different trends of this ecological indicator in both shelves, with a slight increase in the Cantabrian Sea for TL>4 and a significant decline in French waters for TL>3.25. These contrasting results showed the relevance of combining different approaches to identify ecological trends in such key indicators.

By fleets, Spanish purse seine has a higher mTLc than the French purse seine due to its landings of bluefin tuna and albacore, target species in France of the pelagic trawl. Overall, French fleets presented low mTLc. This is due to the low catches of mackerel, horse mackerel and blue whiting of French fleets, species that have TLs around 3.5 (higher than sardine and anchovy). The French coastal fishery had lower mTLc than the Spanish coastal fishery due to its landings of benthic primary producers and because mackerel is a target species of Spanish coastal fishery. Both offshore fleets (Spanish and French) presented the lowest catches. However, they presented the highest mTLc because they target on top predators such as anglerfish, hake and large demersal fishes.

The MTI analysis highlighted a wide and large impact of trawls through the food web, as indicated by Preciado, Arroyo et al. (2019). However, larger impacts of Spanish purse seine, Spanish coastal fishery and French offshore fishery on bluefin tuna, albacore, pelagic sharks and vulnerable species such as marine mammals and seabirds were observed. In fact, bycatch has been identified as one of the main threats in the Bay of Biscay for marine mammals and seabirds (García-Barón, Santos et al. 2019). In addition, some species were highly impacted by discards such as Norway lobster, seabirds and pelagic crab as discards constitutes an important food resource for these species. Our results also pointed out several strong impacts of recreational fisheries. Indeed, this fleet is gaining importance (Hyder, Weltersbach et al. 2018; Hyder, Maravelias et al. 2020) and in some cases it is considered in the management of marine resources (e.g., sea bass) (ICES 2019).

The trophic spectrum of the catch highlights different strategies of the fleets. The French fleets were more diverse, as they exploited more intensively low (TL = 2) and high (TL > 4) trophic levels than Spanish fleets. In addition, French catches were mainly focussed on sardine and anchovy (TL ≈ 3), while Spanish catches targeted at a wider variety of forage fishes, including sardine and anchovy, but also mackerel, horse mackerel and blue whiting. In addition, the fishing mortality and fishing loss rate spectrums have evidenced these strategies. Fishing mortality (F) and fishing loss rate between TL 2 and 3.2 presented similar profiles in both fleets, while from TL = 3.2 and forward the fleets of both countries presented different strategies, especially due to the low catches of mackerel, horse mackerel and blue whiting, and higher catches on higher TL (TL > 4) of French fleets. The fishing loss rate in all fleets revealed that fishing had larger impacts at higher TL, especially for offshore and recreational fleets (both Spanish and French). In fact,

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impacts on low and medium TL (TL between 2 and 3.5) appear to be low due to the large biomass and production of these organisms. In contrast, impacts on higher TL species is larger due to their low biomass and production rates.

4.4. Concluding remarks

The strong interactions between compartments (benthic-pelagic coupling) and species/functional groups, the presence of several multispecific fisheries targeting numerous species and the noticeable impacts of fishing at species and ecosystem level, suggest that the current management scheme in the BoB, based on single species stock assessment, should be improved to incorporate ecosystem attributes. Future work should include the calibration and fitting of the static model to available time series of historical data through the temporal dynamic module Ecosim (Walters, Christensen et al. 1997), including other impacts such as climate change in order to assess historical and future cumulative impacts on the ecosystem dynamics of the BoB. This is especially urgent within the context of the global change (e.g., ocean warming and changes in primary production) (Hoegh-Guldberg and Bruno 2010; Doney, Ruckelshaus et al. 2012) and the safe operational space (Rockström, Steffen et al. 2009; Steffen, Richardson et al. 2015), which make the consideration and assessment of cumulative impacts one of the grand challenges in marine ecosystem management. Therefore, this model represents an important step towards the implementation of the EBM in the BoB, which is also a requirement under the Marine Strategy Framework Directive (MSFD) and Common Fishery Policy. Indeed, the EwE approach has already been proved to derive useful indicators described under the attributes of the MSFD (Rombouts, Beaugrand et al. 2013; Piroddi, Teixeira et al. 2015; Safi, Giebels et al. 2019) as well as to be a key tool for strategic and tactical management and provide support to the decision-making progress.

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Table 1. Initial (in bold) and estimated input data of the Bay of Biscay model. B = final biomass (t·km^{-2}); P/B = production/biomass (year^{-1}); Q/B = consumption/biomass (year^{-1}); EE = ecotrophic efficiency; P/Q = production/consumption ratio. (*) indicates groups that were considered within the pelagic domain.

	Functional group	**B**	**P/B**	**Q/B**	**EE**	**P/Q**
1	Diving and pursuit divers’ seabirds*	**0.001**	**0.09**	**66.69**	0.19	0.001
2	Surface feeders seabirds*	**0.003**	**0.09**	**61.77**	0.19	0.001
3	Baleen whales*	**0.04**	**0.04**	**4.12**	0.00	0.01
4	Dolphins*	**0.07**	**0.13**	**12.33**	0.18	0.01
5	Demersal sharks	**0.13**	**0.58**	**4.93**	0.79	0.12
6	Pelagic sharks*	0.07	0.24	**2.36**	**0.50**	**0.10**
7	Deep sea sharks	**0.05**	**0.49**	**4.45**	0.44	0.11
8	Rays and skates	**0.17**	**0.63**	**5.29**	0.53	0.12
9	Bluefin tuna*	**0.06**	**0.43**	**3.10**	0.66	0.14
10	Albacore*	**0.50**	**0.41**	**3.30**	0.38	0.12
11	Other large pelagic fishes*	0.27	**0.52**	**3.96**	0.70	0.13
12	Mackerel*	**6.95**	**1.09**	**6.63**	0.24	0.16
13	Horse mackerel*	**2.39**	**1.11**	**6.51**	0.91	0.17
14	Sardine*	**1.79**	**1.64**	**8.66**	0.91	0.19
15	Anchovy*	**0.51**	**1.75**	**9.22**	0.97	0.19
16	Other planktivorous fishes*	**1.15**	**1.61**	**8.71**	0.92	0.19
17	Mesopelagic fishes*	1.05	1.87	**10.37**	0.80	**0.18**
18	Anglerfish	**0.18**	**0.42**	**3.44**	0.70	0.12
19	Sea bass	**0.17**	**0.64**	**5.23**	0.80	0.12
20	Blue whiting*	**1.97**	**1.16**	**7.02**	0.94	0.17
21	Large hake	**0.34**	**0.50**	**3.20**	0.74	0.16
22	Small hake	**0.05**	**1.25**	**8.90**	0.94	0.14
23	Poor cod	**0.45**	**0.97**	**6.71**	0.91	0.14
24	Megrim	**0.04**	**0.98**	**6.52**	0.93	0.15
25	Common sole	**0.20**	**0.89**	**5.90**	0.90	0.15
26	Flatfishes	**0.12**	**1.10**	**6.86**	0.91	0.16
27	Mullets	**0.07**	**1.06**	**6.63**	0.94	0.16
28	Large demersal fishes	**0.46**	**0.57**	**4.71**	0.73	0.12
29	Medium demersal fishes	**0.22**	**0.89**	**6.14**	0.98	0.15
30	Small demersal fishes	**0.93**	**1.20**	**7.07**	0.94	0.17
31	Deep sea fishes	**0.07**	**0.77**	**5.74**	0.88	0.14
32	Benthic cephalopods	**0.44**	**1.70**	**9.82**	0.91	0.17
33	Squids*	**0.28**	**1.80**	**11.70**	0.98	0.15
34	Norway lobster	**0.11**	1.83	**7.34**	0.91	**0.25**
35	Pelagic crab*	0.55	2.64	**10.56**	**0.95**	**0.25**
36	Zooplankton feeding shrimps	1.33	**3.20**	**12.48**	**0.90**	0.26
37	Benthos feeders decapods	1.82	**2.10**	**8.28**	**0.80**	0.25
38	Detritus feeders decapods	1.59	2.38	**9.14**	**0.80**	**0.26**
39	Bivalves	0.82	**3.24**	12.96	**0.80**	**0.25**
40	Polychaetes	**3.91**	**5.68**	**24.25**	0.72	0.23
41	Suprabenthos	**2.51**	**9.41**	37.64	0.69	**0.25**
42	Echinoderms	**1.12**	**1.72**	**7.13**	0.72	0.24

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43	Other invertebrates	**7.23**	**3.50**	14.00	0.66	**0.25**
44	Gelatinous plankton	1.01	**8.00**	**40.00**	**0.80**	0.20
45	Macrozooplankton	**5.10**	**13.00**	**46.50**	0.58	0.28
46	Mesozooplankton	**7.70**	**25.00**	**90.00**	0.83	0.28
47	Microzooplankton	**5.50**	**45.28**	150.93	0.79	**0.30**
48	Benthic primary producers	0.49	**2.70**	-	**0.20**	-
49	Small phyoplankton	**8.28**	**153.00**	-	0.55	-
50	Large phytoplankton	**4.72**	**118.00**	-	0.75	-
51	Detritus	**173.61**	-	-	0.40	-
52	Discards	**0.91**	-	-	0.91	-

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Table 2. Summary statistics and ecological indicators for the Bay of Biscay ecosystem model.

Indicators	**Value**	**Units**
Sum of all consumption	2312.30	$t\cdot km^{-2}\cdot year^{-1}$
Sum of all exports	1058.11	$t\cdot km^{-2}\cdot year^{-1}$
Sum of all respiratory flows	796.62	$t\cdot km^{-2}\cdot year^{-1}$
Sum of all flows into detritus	1747.85	$t\cdot km^{-2}\cdot year^{-1}$
Total system throughput	5914.87	$t\cdot km^{-2}\cdot year^{-1}$
Sum of all production	2455.23	$t\cdot km^{-2}\cdot year^{-1}$
Calculated total net primary production	1825.12	$t\cdot km^{-2}\cdot year^{-1}$
Total primary production/total respiration	2.29	
Total primary production/total biomass	24.34	
Net system production	1028.50	$t\cdot km^{-2}\cdot year^{-1}$
System omnivory index (SOI)	0.27	
Finn's cycling index (of total throughput) (FCI)	9.73	% of TST
Finn's mean path length (PL)	3.19	
Total biomass (excluding detritus)	75.00	$t\cdot km^{-2}$
Mean trophic level of the community (mTLco)	1.42	
mTLco (excluding TL = 1)	2.70	
Total catches	3.06	$t\cdot km^{-2}\cdot year^{-1}$
Total landings	2.15	$t\cdot km^{-2}\cdot year^{-1}$
Total discards	0.91	$t\cdot km^{-2}\cdot year^{-1}$
Mean trophic level of the catch (mTLc)	3.37	
Primary production required to sustain the fisheries (PPR, considering PP + detritus)	9.24	%
Gross efficiency (catch/net p.p.)	0.002	
mean Transfer efficiency	17.46	%
Ecopath pedigree	0.69	

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Table 3. Output estimates the Bay of Biscay model. TL = Trophic Level; F = fishing mortality (year^{-1}); M2= predation mortality (year^{-1}); M0 = other natural mortality (year^{-1}); F/Z = exploitation rate (fishing mortality (F) / total mortality (Z)); OI= Omnivory index; FD = flow to detritus (t·km^{-2}·year^{-1}).

Functional group	TL	F	M2	M0	F/Z	OI	FD
Diving and pursuit divers' seabirds	3.98	0.02	0.00	0.07	0.19	0.73	0.01
Surface feeders seabirds	3.81	0.02	0.00	0.07	0.19	0.89	0.04
Baleen whales	3.64	0.00	0.00	0.04	0.00	0.92	0.03
Dolphins	4.40	0.02	0.00	0.11	0.18	0.20	0.18
Demersal sharks	4.01	0.25	0.21	0.12	0.44	0.32	0.14
Pelagic sharks	4.55	0.09	0.03	0.12	0.37	0.20	0.04
Deep sea sharks	3.94	0.11	0.11	0.28	0.22	0.42	0.06
Rays and skates	3.83	0.17	0.17	0.30	0.26	0.28	0.24
Bluefin tuna	4.29	0.27	0.01	0.15	0.63	1.39	0.05
Albacore	4.27	0.15	0.00	0.25	0.37	1.36	0.46
Other large pelagic fishes	4.17	0.06	0.30	0.16	0.12	0.11	0.26
Mackerel	3.56	0.07	0.19	0.84	0.06	1.02	15.03
Horse mackerel	3.39	0.17	0.84	0.10	0.15	0.11	3.35
Sardine	3.11	0.16	1.34	0.15	0.10	0.27	3.35
Anchovy	3.09	0.55	1.15	0.06	0.31	0.26	0.98
Other planktivorous fishes	3.22	0.09	1.39	0.13	0.06	0.08	2.16
Mesopelagic fishes	3.08	0.00	1.49	0.37	0.00	0.27	2.56
Anglerfish	4.35	0.29	0.00	0.13	0.69	0.09	0.15
Sea bass	4.19	0.26	0.26	0.13	0.40	0.20	0.20
Blue whiting	3.46	0.10	0.99	0.07	0.08	0.12	2.91
Large hake	4.33	0.28	0.09	0.13	0.56	0.11	0.26
Small hake	3.77	0.30	0.88	0.07	0.24	0.27	0.09
Poor cod	3.57	0.09	0.79	0.08	0.10	0.18	0.64
Megrim	3.67	0.29	0.63	0.07	0.29	0.39	0.06
Common sole	3.14	0.29	0.51	0.09	0.33	0.05	0.25
Flatfishes	3.34	0.27	0.73	0.10	0.24	0.25	0.17
Mullets	3.35	0.21	0.79	0.06	0.20	0.16	0.10
Large demersal fishes	4.18	0.23	0.18	0.15	0.41	0.21	0.51
Medium demersal fishes	3.69	0.20	0.67	0.02	0.22	0.28	0.27
Small demersal fishes	3.13	0.14	0.98	0.08	0.12	0.43	1.38
Deep sea fishes	3.77	0.06	0.62	0.09	0.07	0.17	0.08
Benthic cephalopods	3.42	0.19	1.37	0.15	0.11	0.20	0.62
Squids	3.89	0.12	1.64	0.04	0.07	0.27	0.67
Norway lobster	2.91	0.40	1.27	0.16	0.22	0.39	0.18
Pelagic crab	3.00	0.01	2.50	0.13	0.00	0.52	1.24
Zooplankton feeding shrimps	2.94	0.00	2.88	0.32	0.00	0.32	3.75
Benthos feeders decapods	2.92	0.05	1.63	0.42	0.02	0.29	3.79
Detritus feeders decapods	2.39	0.00	1.90	0.48	0.00	0.34	3.66
Bivalves	2.14	0.14	2.45	0.65	0.04	0.18	4.81
Polychaetes	2.06	0.00	4.06	1.62	0.00	0.06	63.24
Suprabenthos	2.14	0.00	6.53	2.88	0.00	0.14	35.56
Echinoderms	2.07	0.05	1.18	0.49	0.03	0.07	3.73

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Other invertebrates	2.13	0.00	2.29	1.21	0.00	0.13	49.19
Gelatinous plankton	2.95	0.00	6.40	1.60	0.00	0.25	9.70
Macrozooplankton	2.64	0.00	7.55	5.45	0.00	0.33	122.66
Mesozooplankton	2.18	0.00	20.70	4.30	0.00	0.15	310.29
Microzooplankton	2.02	0.00	35.73	9.55	0.00	0.02	384.58
Benthic primary producers	1.00	0.05	0.49	2.16	0.02	0.00	1.06
Small phyoplankton	1.00	-	83.79	69.21	0.00	0.00	573.03
Large phytoplankton	1.00	-	88.53	29.47	0.00	0.00	139.08
Detritus	1.00	-	-	-	-	0.42	0.00
Discards	1.00	-	-	-	-	0	0.09

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Table 4. Catch ($t \cdot km^{-2} \cdot year^{-1}$) and mean trophic level of the catch (mTLc) for the different fleets in the Bay of Biscay model.

Fleet	**Catch**	**mTLc**
Spanish demersal trawl	0.55	3.42
Basque demersal trawl	0.15	3.35
Spanish purse seine	0.36	3.39
Spanish coastal fishery	0.21	3.34
Spanish offshore fishery	0.06	3.88
French demersal trawl	0.44	3.32
French pelagic trawl	0.50	3.36
French Nephrops trawl	0.15	3.37
French purse seine	0.15	3.18
French coastal fishery	0.26	3.13
French offshore fishery	0.08	3.83
Spanish recreational fishery	0.05	3.52
French recreational fishery	0.09	3.50

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Fig. 1. The Bay of Biscay (ICES VIIIa,b,c,d), showing the modelled area and depth contours.

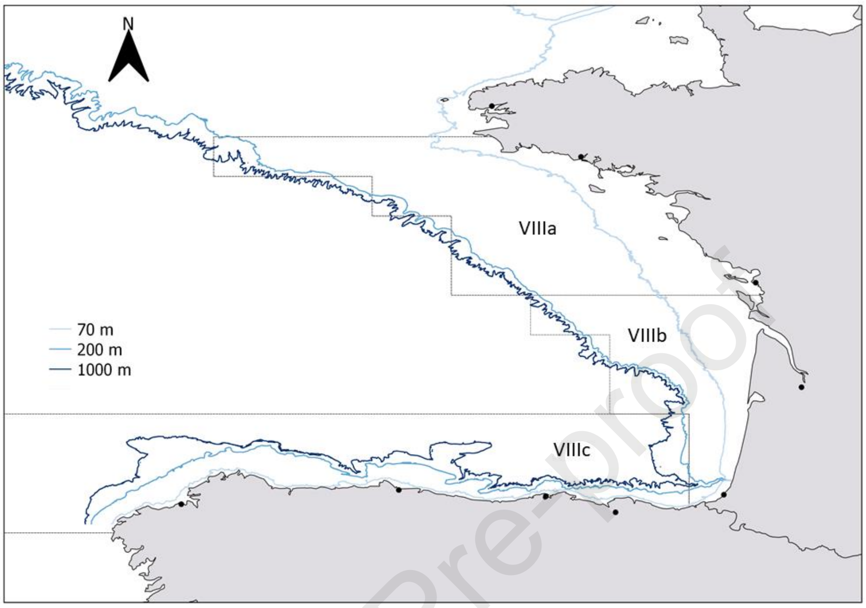

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Fig. 2. Flow diagram of the Bay of Biscay model representing the early 2000s. The numbers identify the functional groups of the model (listed in Table 1). Fleets: SDT = Spanish demersal trawl; BDT = Basque demersal trawl; SPS = Spanish purse seine; SCF = Spanish coastal fishery; SOF = Spanish offshore fishery; FDT = French demersal trawl; FNT = French Nephrops trawl; FPS = French purse seine; FCF = French coastal fishery; FOF = French offshore fishery; SRF = Spanish recreational fishery; FRF = French recreational fishery. The size of each circle is proportional to the biomass of the functional group. The thickness of the connecting lines is proportional to the magnitude of the flows.

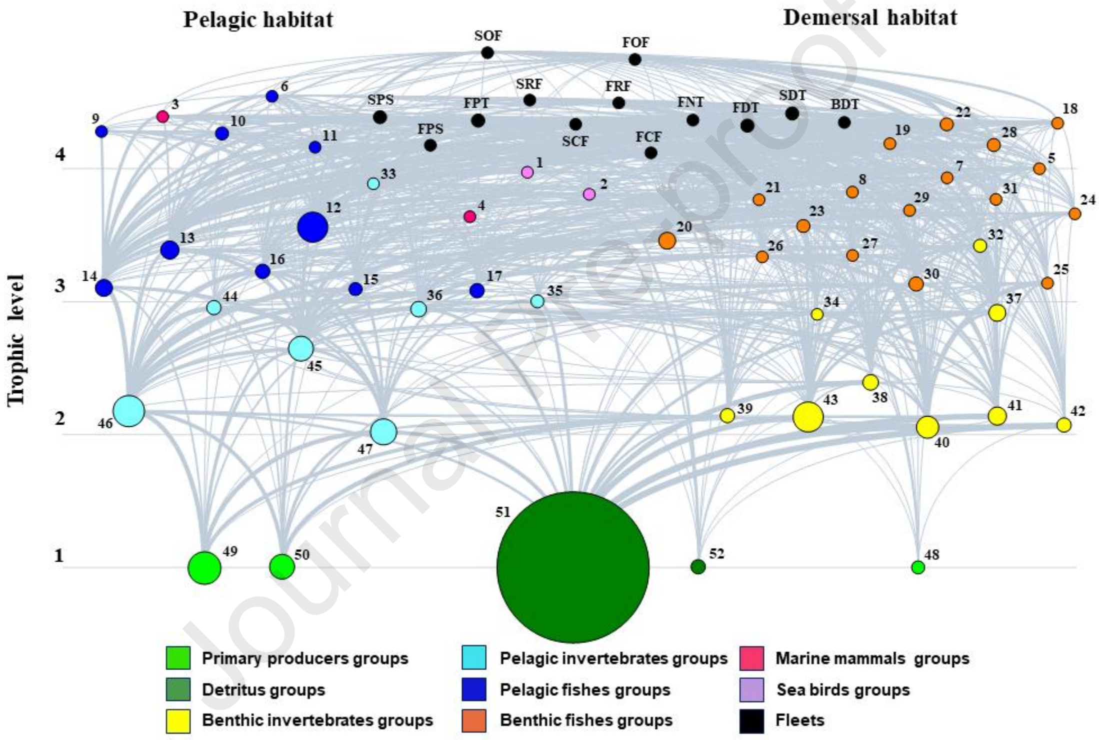

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Fig. 3. Proportion of the benthic and pelagic production (P) that is fueled by phytoplankton primary production and detritus (detritus and discards) in the Bay of Biscay.

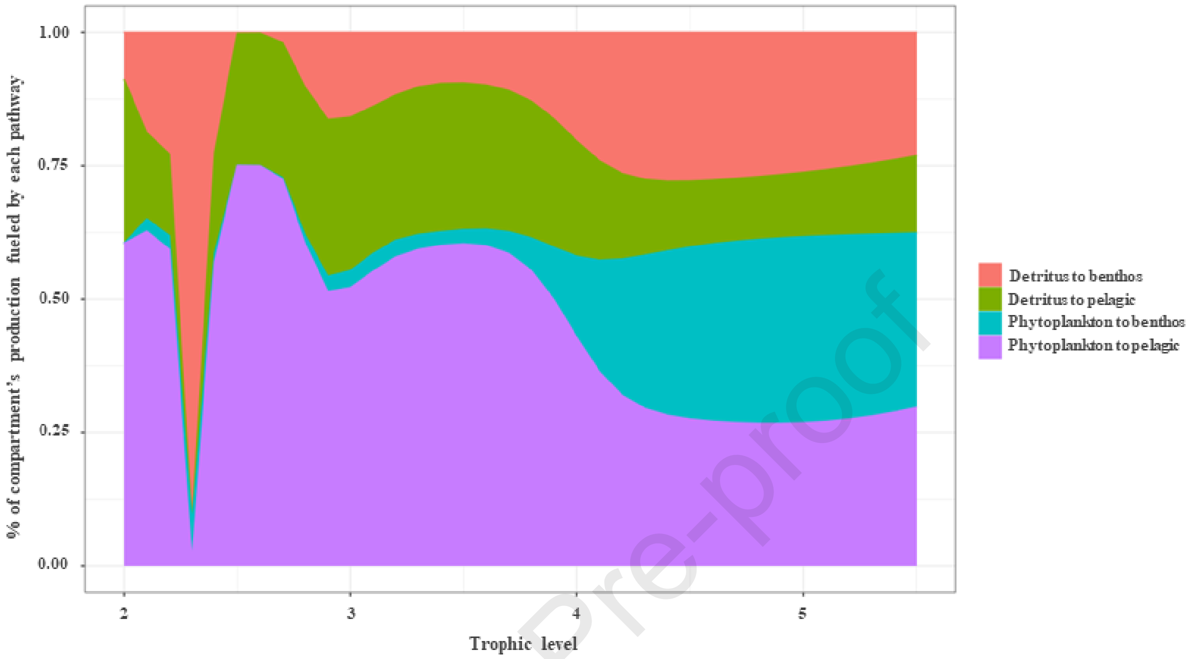

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Fig. 4. Lindeman representation of the Bay of Biscay ecosystem model, organized by integer trophic levels (TL). TL I is separated in primary producers (P) and detritus (D). Flows are represented in t·km^{-2}·year^{-1} and biomass in t·km^{-2}.

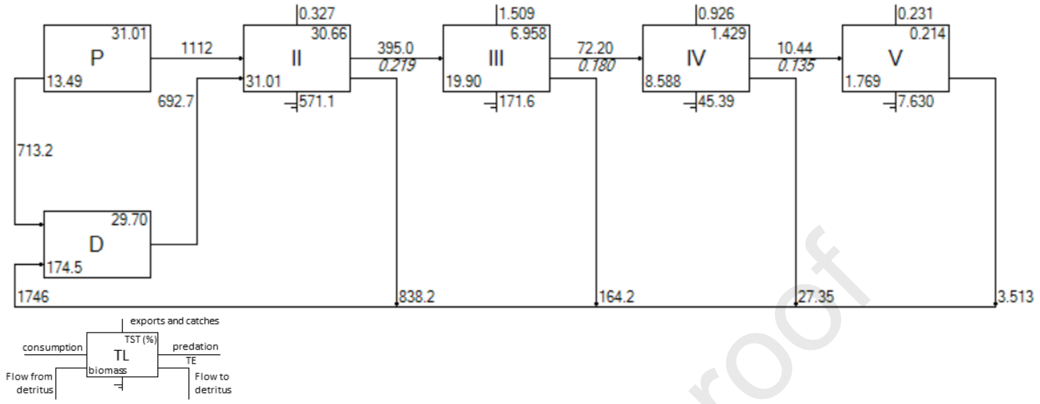

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Fig. 5. Mixed Trophic Impact (MTI) analysis of the Bay of Biscay ecosystem for early 2000s. Negative (red) and positive (blue) impacts are represented.

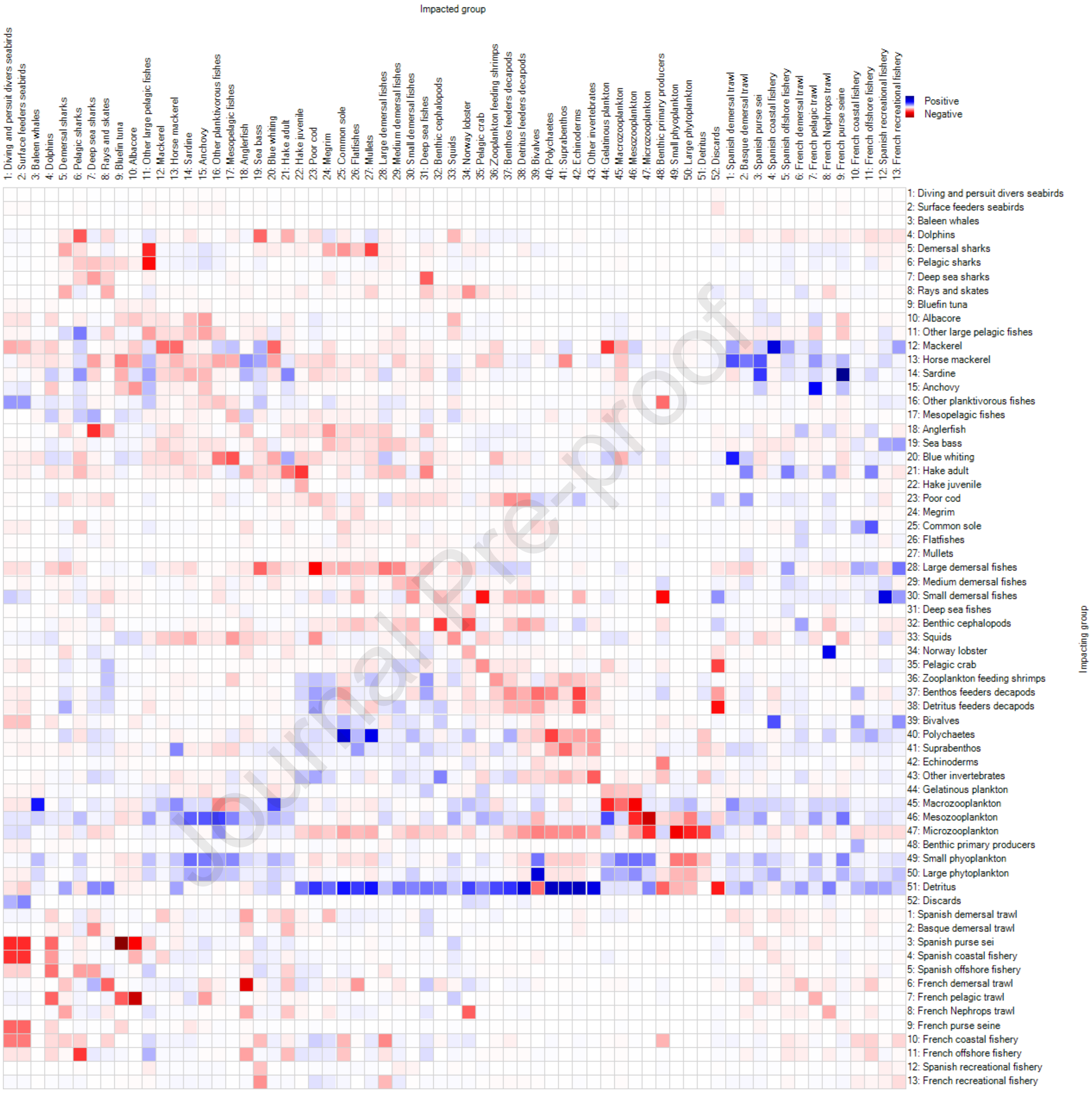

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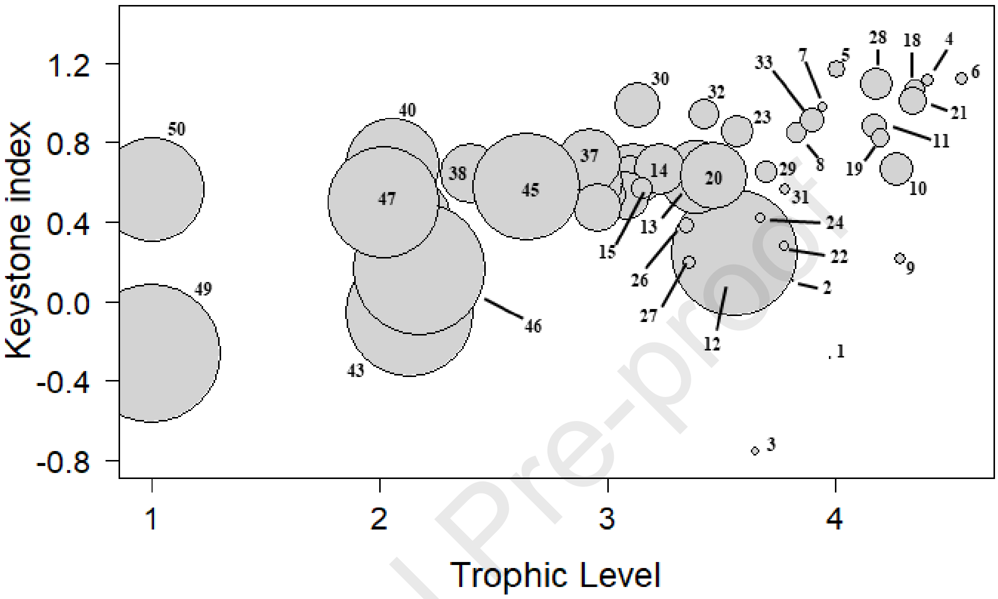
Fig. 6. Functional groups plotted against keystone index (Valls et al., 2015) and trophic level (a) and relative total impact (RTI) (b) for the Bay of Biscay ecosystem in early 2000s. The numbers identify the functional groups of the model (listed in Table 1). The size of each circle is proportional to the biomass of the functional group.

a)



b)

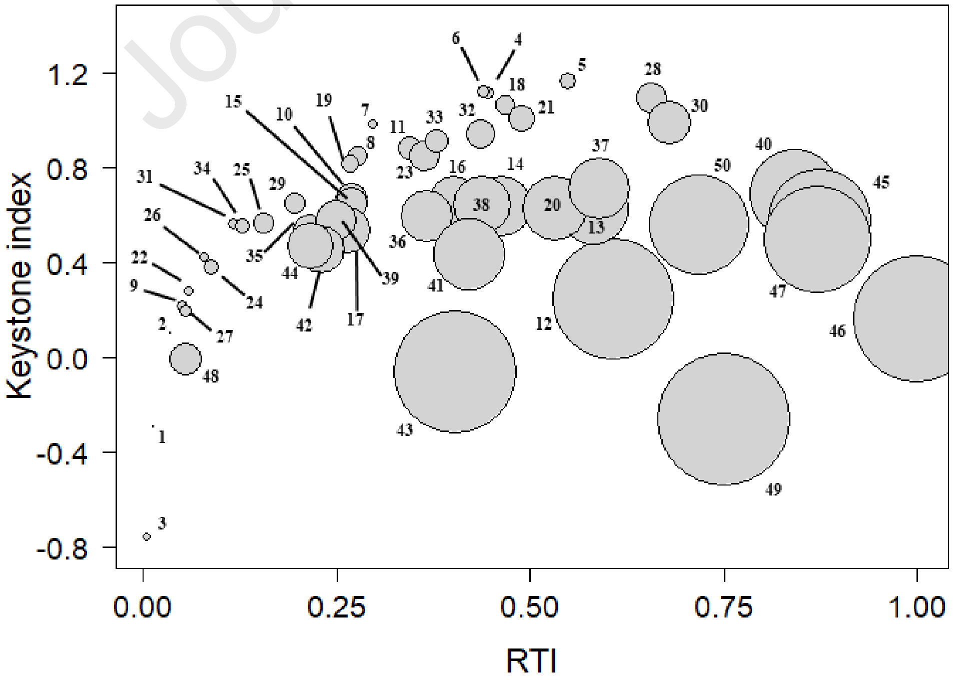


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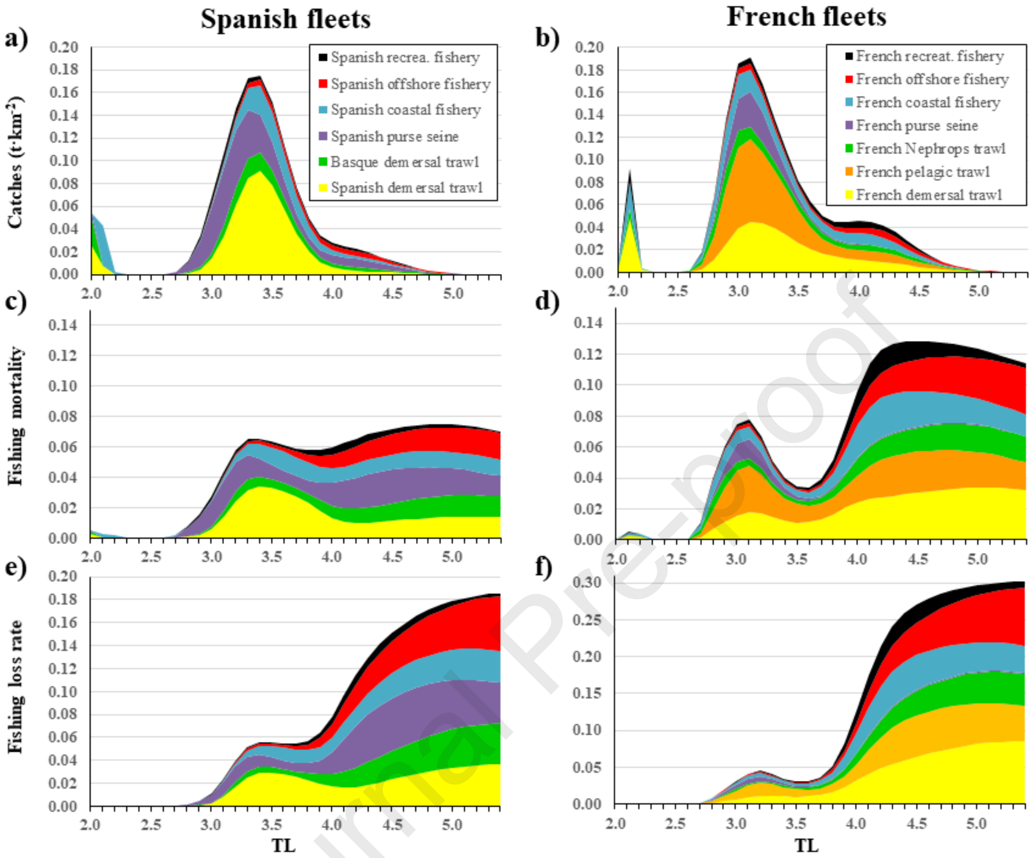
Fig. 7. The trophic spectrum of the ecosystem for the Spanish (a, c and e) and French fleets (b, d and f): spectrum of catches (a and b), fishing mortality (c and d) and fishing loss rate (e and f).



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- We characterize the structure and functioning of the whole Bay of Biscay with a food web model.
- The model highlights the dominance of the pelagic domain and the importance of the detritivore pathway.
- Forage fish play a key role in fostering the connectivity between the benthic and pelagic domains.
- The results show an intense exploitation by fisheries in early 2000s.
- The model highlight different strategies between Spanish and French fleets.

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Declaration of interests

☒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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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