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Combining quantitative and qualitative models to identify functional groups for monitoring changes in the Bay of Biscay continental shelf exploited foodweb

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Abstract:

To develop and implement ecosystem-based management, it is critical to monitor foodweb components or functional groups which are robust to uncertainty in ecosystem structure and functioning yet sensitive to changes. To select such functional groups for the Bay of Biscay continental shelf, both quantitative and qualitative foodweb models were developed. First, functional groups for which predictions of directions of change following an increase in primary productivity, prey or predators, or in fishing activities were identical across alternative qualitative model structures were identified. Second, the robustness to model type was assessed by comparing qualitative predictions with quantitative Ecopath model results. The demersal fish community was identified as a sensitive and robust indicator for monitoring foodweb ecological status in the Bay of Biscay. The present study also suggested the potential antagonistic effects of alternative management measures on small pelagic fish and highlighted the need for the joint management of all pressures.

Keywords: comparative studies ; ecosystem management ; foodweb ; loop analysis ; Northeast Atlantic continental shelf

1. Introduction

Human activities increasingly affect ecosystem processes (Millenium Ecosystem Assessment, 2005). Therefore the ability to predict the direct and indirect effects of human activities has become a priority (Jennings and Kaiser, 1998; Stevens *et al.*, 2000). For marine ecosystems, implementing the ecosystem approach to fisheries, also called ecosystem-based fisheries management (EBFM), has led to the development of a wide range of models dealing with fishing effects at ecosystem scale (Plagànyi, 2007). Ecosystem models that take into account several trophic levels are proposed as complements to conventional stock-assessment models, for example, for refining estimates of mortality and production of commercially important species (Gaichas *et al.*, 2010), or in a more holistic way, for providing information on the state of the whole system (Baltic Sea case study; ICES (2011b)). In parallel to the development of the ecosystem approach to fisheries, the European marine strategy framework directive (MSFD) provides a legislative and operational framework at the European scale. The main objective of the MSFD is to achieve or maintain "good environmental status" (GES) of marine ecosystems by 2020 at the latest (http://ec.europa.eu; Directive 2008/56/EC). Due to the complexity of ecosystems and their inherent spatial and temporal variability, model predictions based on a single model structure are highly uncertain. As marine food webs are difficult and costly to observe, variable amounts of information are gathered on different parts of them, leading to uncertainty in data and subsequently in model parameter estimates (Plagànyi and Butterworth, 2004; Hill *et al.*, 2007). The effects of model structure and parameter uncertainty can be considerably reduced by considering predictions from a suite of models of differing complexity; the approach is known as the "biological ensemble modelling approach, BEMA" (Gårdmark *et al.*, 2012).

Quantitative predictions of the magnitude of food web responses to natural perturbations or potential management measures are not always needed for management (Dambacher *et al.*, 2009). Instead, knowledge on directions of trends in food web components (Rochet *et al.*, 2010) and robust predictions from complementary models (Ortiz and Wolff, 2008; Metcalf, 2010) may be sufficient. In this study, robust model predictions are defined as those which are similar for different models. If a number of alternative plausible models with different structures and/or underlying functions and behaviours yield qualitatively similar predictions, this helps to gauge how much confidence can be placed in the predictions and provides a basis for selecting suitable management measures (Plagànyi and Butterworth, 2012). For the implementation of the MSFD, the GES of ecosystems should be translated into measurable environmental targets and associated indicators that can be monitored *in situ* in a cost-effective manner (Van Hoey *et al.*, 2010). In this context, a multiple comparative modelling approach could be useful for identifying reliable indicators of ecosystem changes (Samhouri *et al.*, 2009; Metcalf *et al.*, 2011).

In marine ecosystems worldwide, continental shelves and slopes are subject to both land-driven and marine anthropogenic pressures (Halpern *et al.*, 2008). The North-Eastern Atlantic shelf was identified by Halpern and collaborators as one of the areas suffering from high anthropogenic pressures. In the Bay of Biscay, fishing is the only human activity having widespread documented impacts on several ecosystem components (Lorance *et al.*, 2009). The present study used qualitative and quantitative food web models of the Bay of Biscay continental shelf ecosystem to predict the effects of two kinds of human and natural pressure changes: (i) increase in fishing pressure exerted by the different fleets operating in the area and, (ii) increase in primary productivity due to nutrient inputs and/or climate change. The main aims of the study were first to determine predicted ecosystem changes which were robust to model structure, i.e. identical for alternative qualitative models, and to model type (qualitative or quantitative models), and second to identify potential indicators for food web ecological status monitoring which are robust to model uncertainty but sensitive to changes in primary productivity or fishing pressure.

The paper is structured as follows. First, the two modelling approaches and the "Bay of Biscay" models are presented. Second, the methodology used to determine sensitive food web components are described. Third, a short description of Ecopath outputs is provided, followed by the identification of predictions robust to both model structure and model type. Lastly, the identification of suitable indicators of food web changes and management options that emerged from this study is discussed. The focus was generally on small pelagics given their large variability on an annual and decadal time scales and their role as a major natural resource and as key contributors to the functioning of marine ecosystems (see the review by Fréon *et al.* (2005)).

2. Material and Methods

2.1. Study area

The Bay of Biscay is a large gulf in the Northeast Atlantic located off the western coast of France and the northern coast of Spain, between 48°5 and 43°5'N and 8 and 3'W (Figure 1). It is part of the "Celtic-Biscay shelf" large marine ecosystem (LME; http://www.lme.noaa.gov/). The Bay of Biscay supports a multi-species, multi-fleet fishery with a large diversity of species exploited by a wide range of fishing gears primarily operated from French and Spanish ports. The French fleets can be characterized by 12 landing profiles each dominated by one or two species (Daurès *et al.*, 2009). Nine species characterized most profiles and 20 species contributed over 80% in volume and value of French landings during the period 2000 to 2006 (Daurès *et al.*, 2009). For the Spanish fleet, no equivalent information was found. Though French fleet capacity has decreased over the last two decades, the positive effects of this on the ecosystem are not (yet) detectable (Rochet *et al.*, 2012).

2.2. Quantitative modelling

2.2.1. Ecopath approach

The food web of the French continental shelf was modelled using Ecopath with Ecosim (Christensen and Walters, 2004; Christensen *et al.*, 2008). EwE is a tool to analyse organic matter and energy flows within a steady-state/static (Ecopath) and dynamic (Ecosim) mass-balance model. The Ecopath model parameterization is based on two “master” equations. The first equation decomposes the production term of each compartment (species or group of species with similar trophic role):

Production = fishery catch + predation mortality + net migration + biomass accumulation + other mortality

“Other mortality” includes natural mortality factors such as mortality due to senescence, diseases, etc.

The second equation describes the energy balance within each group:

Consumption = production + respiration + unassimilated food

More formally, the two equations can be written as follows for group *i* and its predator *j*:

$$B_i \times (P/B)_i = Y_i + \sum_j \left(B_j \times (Q/B)_j \times DC_{ij}\right) + Ex_i + Bacc_i + B_i(1 - EE_i) \times (P/B)_i \ (1)$$

and

$$B_i \times (Q/B)_i = B_i \times (P/B)_i + R_i + U_i \ (2)$$

where the main input parameters are biomass density (B, here in kg C·km^{-2}), production rate (P/B, year^{-1}), consumption rate (Q/B, year^{-1}), proportion of i in the diet of j (DC_{ij}; DC = diet composition), net migration rate (Ex, year^{-1}), biomass accumulation ($Bacc$, year^{-1}), total catch (Y; kg C·km^{-2}), respiration (R; kg C·km^{-2}·year^{-1}), unassimilated food fraction (U) and ecotrophic efficiency (EE).

Several indices can be derived from an Ecopath model. Niche overlap is calculated as the proportion of prey and predators shared among different functional groups. Niche overlap between two groups was assumed important if greater than 0.6. The mixed trophic impact (MTI) matrix quantifies the direct and indirect trophic impacts of each functional group on (the biomass of) all other functional groups (Ulanowicz and Puccia, 1990). It is calculated as the product of all net impacts. The MTI is based on the assumption that the overall trophic structure remains constant. The net impact of i on j, denoted q_{ij}, is given by the difference between positive effects d_{ji} (quantified by the fraction of prey i in the diet of predator j), and negative effects f_{ij} (evaluated as the fraction of total consumption of j used by predator i):

$$q_{ij} = d_{ji} - f_{ij} \quad (3)$$

The elements of the MTI matrix m_{ij} are then calculated as the product of the net impacts q_{ij} of all possible pathways in the food web that link the functional groups i and j. Negative m_{ij} values indicate prevalence of predator effects (top-down effects) while positive values indicate prevalence of prey effects (bottom-up effects). To evaluate the sensitivity of the signs of the m_{ij} values (referred to as the original MTI values) to small changes in the q_{ij} values, 5000 Q matrices were created by drawing q_{ij} values from independent uniform distributions defined by original q_{ij} ± 0.1. The sample of Q matrices was then used to calculate m_{ij} values, record their sign and estimate the percentage of m_{ij} values with the same sign as in the original MTI matrix (S_{MTI}) (Rochette *et al.*, 2009; Nelva Pasqual, 2013). This sensitivity analysis is not part of the distributed EwE 6 software package; further technical information can be found in Rochette *et al.* (2009) and be requested from the first author.

2.2.2. Quantitative Bay of Biscay model

A full description of the Bay of Biscay Ecopath implementation, including the diet composition and parameter values, can be found in Lassalle *et al.* (2011). For Ecopath results to be meaningful, model parameters need to be based on information specific to the study area. For almost all groups, biomass (*B*), production/biomass ratio (*P/B*), consumption/biomass ratio (*Q/B*) as well as diet composition (*DC*) were derived from area and period specific raw data or stock assessment results. Thirty-two functional groups were included in the model: two seabirds groups, five marine mammal, nine fish, eight invertebrate, three zooplankton, two primary producer, and one bacteria group, as well as discards from commercial fisheries and pelagic detritus. The five main pelagic forage fish species were given their own group while demersal fish were divided into four multi-species groups on the basis of their diets. The model covered the central shelf of ICES divisions VIIIa and b between the 30-m and 150-m isobaths with a surface area of 102 585 km². Shallower and deeper parts were excluded for data availability reasons. The study area represented the core of the distribution range for most species included in the model. Nevertheless, those species were known to frequent the whole Northeast Atlantic (www.fishbase.org/). The model represented a typical year between 1994 and 2005, i.e. before the collapse of the European anchovy and the subsequent five-year closure of the fishery for this species.

The single fishery described in the original model by Lassalle *et al.* (2011) was split into three fleets targeting small pelagic fish, demersal fish and invertebrates respectively to be able to study the impacts of these fleets separately (Table 1). Regarding the main target species, anchovy and sardine were mainly captured by offshore pelagic trawlers and coastal seiners respectively, hake by offshore netters, sole by netters and *Nephrops* by trawlers, both operating from coastal to more offshore waters (Daurès *et al.*, 2009). Due to these changes in model structure, the model needed re-balancing, i.e. ecotrophic efficiency of piscivorous demersal fish and carnivorous invertebrates' compartments were slightly above one. Their biomasses were therefore increased by 4 and 10% respectively.

For parameterizing the three fishing fleets, for assessed stocks, international landings for divisions VIIIa and b were obtained from reports of the relevant ICES working groups (see Lassalle *et al.* (2011) for references). For multi-species fish groups, as well as mackerel and horse mackerel, landings were taken from the Eurostat/ICES catch database (ICES 2010 - Copenhagen). Annual landings were averaged over the period 1998-2003 for all compartments as most of the biomass data were gathered during this interval (see supplementary material 2 in Lassalle *et al.* (2011)). Due to lack of detailed spatial information, landings could not be limited to the central shelf area, so they might be somewhat overestimated.

Discards for each fishing fleet were obtained from the OBSMER programme for the year 2010 (Fauconnet *et al.*, 2011), stock assessment reports cited above and the scientific literature (Pierce *et al.*, 2010). For this, based on expert advice (L. Fauconnet, pers. comm.), each fishing gear was uniquely assigned to one of the three modelled fishing fleets (demersal, pelagic and invertebrates). Due to sparse discard sampling coverage (mostly 2010), observer bias, and non-random trip selection on a voluntary basis, discard estimates included in the present model should be considered as the best estimates available, though they are most likely underestimates.

Bycatch estimates for common dolphin and harbour porpoise were derived from observations of incidental captures of cetaceans and seabirds in European waters (data from national reports on the implementation of Regulation 812/2004); they were entered as discards in the model. These recent cetacean bycatch estimates and past scientific publications indicated that pelagic trawls were primarily responsible for common dolphins bycatch and set nets for harbour porpoises incidental captures (see Lassalle *et al.* (2012) for references). Hence, the estimates were assigned to the pelagic and demersal fleet respectively.

2.3. Qualitative modelling

2.3.1. Loop analysis

For qualitative system analysis, a food web can be represented by a graph, known as a signed digraph (Levins, 1974), which displays the interactions between variables (here functional groups and fleets) and is constructed using the signs of interactions (+, -, 0), not their magnitude. This means model parameter values are not specified, only their signs. A signed digraph has an equivalent representation in the community matrix (A) where each element a_{ij} represents the direct effect of variable j on variable i. For instance, the direct effect of a predator group on its prey, i.e. removal of biomass through predation, is represented by a negative link, and the direct effect of a prey group on its predators, i.e. biomass creation, gives rise to a positive link. Negative feedback connecting a population to it-self is termed a self-effect. It represents intra-specific competition for space and resources particularly for primary producers, intra-component predation, and links with the outside system as external recruitment or consumption of species from outside the system (Puccia and Levins, 1985). Dambacher (2001) showed that negative self-effects applied to all system components promoted the stability of the system and the results of associate inverse community matrix. Assuming the model system is at equilibrium, press perturbation analysis corresponds to investigating the expected direction of change (toward a new equilibrium) of each model variable, i.e. its abundance change, following sustained changes in the dynamics (birth or death rates) of one or more model variables. It is carried out by considering the signs of the adjoint of the negative community matrix (adj-A) (Dambacher *et al.*, 2002). In complex systems, a press perturbation may impact a given variable through multiple pathways, a pathway being a suite of direct (e.g. prey and predator) and indirect (e.g. prey of prey) effects that lead from the input (pressed) variable to the response variable. If multiple pathways exist, the resulting responses of a given variable may have opposing signs (increase, +, or decrease,

- in abundance). The opposing signs create ambiguity in the predicted responses to change (Dambacher *et al.*, 2002). Weights can be given to the predictions to provide an assessment of the level of ambiguity (Dambacher *et al.*, 2003). For a given response variable, the weight corresponds to the net number of pathways (difference between the number of positive and negative responses) divided by the total number of pathways. Weights range between 0 (complete sign indeterminacy of predictions; sign of overall effect will depend on interaction strength) and 1 (sign completely determined).

For investigating model stability, the sign of all feedback loops in the system are inspected. Negative feedback loops maintain a system's equilibrium. Conversely, positive feedbacks magnify changes in variables and drive runaway growth or collapse (refer to Dambacher *et al.* (2003) for a description of feedback cycles). A model system needs to be stable, at least under certain conditions, for the results of press perturbation analyses to be meaningful.

PowerPlay (version 2.0; http://esapubs.org/Archive/ecol/E083/022/suppl-1.htm) was used to draw signed digraph (Westfahl *et al.*, 2002) and the "Loop Analysis" facility provided on the "Loop Group" web page (http://www.ent.orst.edu/loop/) to perform qualitative and symbolic analysis of the community matrix, including press perturbation analyses corresponding to changes in primary productivity and fishing mortality. For further details on loop analysis, see Puccia and Levins (1985), Dambacher *et al.* (2002) and the web site of the "Loop Group".

2.3.2. Qualitative Bay of Biscay models

Rochet *et al.* (2013) proposed a simplified food web model for North-Atlantic temperate shelf fish communities, that was adapted in the present study to the specific case of the Bay of Biscay continental shelf (baseline model; Figure 2a). The model has seven functional groups or model nodes which were organized into two trophic chains, one pelagic chain and one bentho-demersal chain, coupled at different trophic levels and connected at the top by top predators. Pelagic piscivores include albacore (*Thunnus alalunga*) and bluefin (*Thunnus thynnus*) tunas which are highly migratory species caught off the shelf (but adjacent to the shelf break) in the Bay of Biscay (international commission for the conservation of Atlantic tunas (ICCAT); http://www.iccat.es/en/). As no reliable biomass estimates exist, pelagic piscivores were not included in the Ecopath model. Tunas were assumed to have no impact on pelagic planktivores given the low spatial and temporal overlap between these two groups. Benthos includes suspension and deposit feeders of dead plankton bodies, but because benthos is restricted to the sea floor, it is not expected to have a negative effect on living plankton. Other predator-prey links (benefiting the predator and detrimental to the prey) present in the original model of Rochet *et al.* (2013) were evaluated on the basis of the expertise gained with the Bay of Biscay Ecopath model, which led to the removal of several weak links. The modifications made to the original model of Rochet *et al.* (2013) were summarized in Figure 2b (both additions and removals of links).

Fisheries were grouped into three fleets as in the Ecopath model: a pelagic fleet which targets planktivores and pelagic piscivores, a demersal fleet targeting demersal piscivores, benthivores are targeted and/or taken as bycatch by this fleet, and benthos is negatively affected by the fishing gear. Some benthos species such as large crustaceans (e.g. Norway lobster (*Nephrops norvegicus*)) were specifically targeted by an invertebrates fishery.

Press perturbation analyses were carried out for two general scenarios representing changes in natural and anthropogenic pressures which correspond to a permanent increase or decrease in (i) primary productivity resulting in higher/lower birth rates of each functional group, (ii) the size of each fishing fleet due to fisheries management. As results of a permanent increase are symmetrical (reverse in signs) to those for a permanent decrease, press perturbation results are only presented for permanent increases.

The press perturbation of the baseline model and its three variants were compared to assess structural uncertainty. The model variants were obtained by modifying some of the links in the baseline model presented in Figure 2a. On the first hand, as the internal dynamics of a fishery are more driven by management rather than by economics or resource state (Rochet *et al.*, 2012), the positive links between targeted groups and fleets were removed from the baseline model leading to the variant 1. On the other hand, the positive effect of demersal benthivores on demersal piscivores was removed as it was questionable whether piscivores population dynamics really depend on benthivores abundance. Variants 2 and 3 were thus derived from the baseline model and the variant 1, respectively. Local conditions for stability of the baseline model and its three variants were evaluated using two Routh-Hurwitz criteria (Dambacher *et al.*, 2003).

2.4 Comparability of the qualitative and quantitative models

Studying potential system changes using loop analysis or the MTI matrix of an Ecopath model both aim at taking into account direct (e.g. prey and predator) and indirect (e.g. prey of prey) ecosystem interactions and depend on matrix algebra. Therefore, the results are often interpreted in a similar way, that is as providing the likely system response to sustained small positive or negative inputs (e.g. Metcalf (2010)). This interpretation was retained in the present study but other alternatives exist (Nelva Pasqual, 2013). Metcalf (2010) asserted that if model structure is the same when using MTI and qualitative modelling, and if no ambiguity of flows or predictions occurs, the results obtained with the two methods will be of the same sign. However, there is an important difference in the resolution at which the two model types function the best and as such are generally constructed. A typical Ecopath model has between 24 and 40 functional groups, and should include at least 12 groups in order to cover the entire ecosystem, from detritus to top predators (Christensen *et al.*, 2008). A qualitative model with so many variables would provide highly ambiguous press perturbation results and thus bring little insights into the dynamics of the system following perturbation. For example, weights of most predictions were zero for a qualitative model with 35 functional groups as in the Ecopath model. In contrast, in qualitative modelling, it is easy to use multiple simple model structures and thus assess the effects of structural uncertainty on press perturbation results. As Ecopath models with different number of groups can have different total impact matrices in which the signs of relationships can be reversed, differences between MTI predictions and press perturbation analyses should be interpreted with care (Nelva Pasqual, 2013). Briefly, loop analysis is a qualitative analysis of the community matrix (Levins, 1974). Each element of the community matrix represents the direct effect (+, -, 0) of one variable on the growth rate of another variable at equilibrium (Puccia and Levins, 1985). In the case of MTI, the direct impact matrix is calculated from flow transfers (Ulanowicz and Puccia, 1990). Therefore, the community matrix and the MTI matrix can only be related when the flow intensity reflects the strength of the dynamic effects between two variables. High flow transfers can potentially be associated with a high dynamic effect, but it is not always the case especially when considering interactions between populations.

2.5. Identifying functional groups sensitive to food web changes

Functional groups sensitive to natural or anthropogenic pressure changes are suitable as indicators for monitoring changes in the food web dynamics. When identifying sensitive functional groups, particular attention was paid to MTI and press perturbation results for scenarios corresponding to an increase in fleets or a functional group, in particular plankton; responses to a decrease are strictly reverse in signs. Indeed, in both approaches, the qualitative nature of any indirect effect is determined by the sign of the product of the sequential actions along the pathway by which such influence is exerted (Ulanowicz and Puccia, 1990). The consequences of several perturbations happening concomitantly were not assessed as it greatly increases model prediction ambiguity and such complex simulations (multiple pressure scenarios) could not be performed using the available tools in Ecopath.

The identification of indicator functional groups was carried out in several steps. First, qualitative (press perturbation) model predictions which had weighted predictions ≥ 0.5 and were consistent over the baseline model and its three variants were selected. They were termed robust qualitative predictions. Dambacher *et al.* (2002) had demonstrated that weighted-prediction values >0.5 were found to exhibit high (near 95%) sign determinacy. Second, their robustness to model type was investigated by comparing the qualitative predictions to the niche overlap and MTI matrices from the Ecopath model. Further, the predator and prey overlap indices were combined on the same graph to quantitatively identify which species, or groups of species, were strongly linked by trophic interactions. Third, functional groups (and species) with robust qualitative predictions and quantitative MTI predictions with the same sign were identified. Fourth, among those groups, functional groups which change (increase or decrease) when fleet size or another functional group is increased, i.e. perturbed, were selected as suitable indicators of food web changes. They are three important criteria for suitable ecosystem indicators: they should be sensitive to perturbations, have an overall influence on the ecosystem and be currently monitored (Fulton *et al.*, 2005). The modelling approach applied here ensures the first two criteria are fulfilled, the third criteria is evaluated using additional information.

3. Results

3.1. Robust predictions determined from qualitative models

The baseline model and its three variants had local conditions for stability based on the metrics of Dambacher *et al.* (2003). Press perturbation results for single pressure changes are summarised in Table 2. The percentage of concordant predictions was low but allowed the identification of robust conclusions which could be compared with the quantitative Ecopath outputs. Most robust predictions corresponded to a top-down control exerted by higher trophic level groups which was transmitted down the food web. Given the general structure of the considered models, plankton (Plkt) was never influenced by any of the other functional groups in any of the press perturbation analyses.

Regarding fishing activities, none of the qualitative predictions for an increase in the invertebrate fleet (Inv Fleet) were consistent across alternative model structures. In contrast, predictions regarding the impact of the pelagic fleet (Pel Fleet) presented high consistency in terms of the groups impacted and the directions of responses. In all cases, the functional group “top predators” (TopP) was predicted to decrease in abundance following a press perturbation (increase) in the pelagic fleet. This decrease was associated with a concomitant response of the demersal food chain, i.e. an increase of demersal piscivores and a decrease in demersal benthivores. An increase in the demersal fleet (Dem Fleet) was always predicted to lead to an increase of pelagic planktivores (Plv). Plv were predicted to also increase in response to an increase in primary productivity (Plkt).

Permanent changes in top predators and demersal piscivores led to robust qualitative predictions of changes for themselves and other functional groups. An increase in top predators was predicted to have a negative effect on demersal piscivores and a positive one on demersal benthivores. An increase in demersal piscivores was predicted to have a negative impact on their benthic, demersal and pelagic prey, namely demersal benthivores and pelagic planktivores.

3.2 Ecopath outputs

The combination of predator and prey diet overlap indices highlighted two groups occupying the same trophic niche within the Bay of Biscay food web and as such being susceptible to respond similarly or conjointly to perturbations. The two groups consist of the small pelagics which have both similar prey and predators among the five species, and the suprabenthivorous demersal fish which share a large part of their prey, and have the same predators (Figure 3a). Considering the MTI of each functional group, the largest impacts were positive and due to phytoplankton, mesozooplankton and detritus (Figure 3b). Among the three fishing fleets, only the invertebrate fleet had a positive MTI. Discards, which were caused by the invertebrate fleet, were predicted to induce a positive response of the system in the MTI assessment as well. Top predators and demersal fish compartments presented a homogeneous overall negative impact on the system while the effects of small pelagics differed. A small increase of anchovy, sardine and sprat was predicted to provoke a positive response of the food web as a whole, in contrast to a negative impact for mackerel and horse mackerel (Figure 3b).

3.3. Concordant predictions

Robust qualitative predictions were found to be largely but not always consistent with the quantitative Ecopath outputs (Table 3). In the Ecopath model, suprabenthivorous demersal fish shared the same predators with all five modelled forage fish species (predator overlap index ≥ 0.8) (Figure 3a). This quantitative result was consistent with the predicted identical qualitative response of Btv and Plv to an increase in demersal piscivores (Table 3). However, when considering the MTI matrix, a negative impact of piscivorous demersal fish was predicted only for prey pertaining to the bentho-demersal food chain, thus the equivalent of Btv (Figure 4). S_{MTI} values ranged from 91 to 100 depending on the functional groups which indicated that the signs of the MTI matrix were insensitive to small changes in net impacts.

The small pelagic species shared the highest percentage of common prey, mostly composed of zooplankton (prey overlap index ≥ 0.75) (Figure 3a). A slight increase in large phytoplankton was predicted by the MTI to result in a common positive response of all small pelagic species, with the value of S_{MTI} being smallest for sprat (65%). This shared pattern was even clearer when mesozooplankton was the impacting group (Figure 4), *i.e.* MTI values were higher and sign stable (S_{MTI} 100%). These two quantitative results were in accordance with the robust qualitative prediction of a positive response of the Plv group to a persistent increase of primary production (Plkt) (Table 3).

Prey overlap was found to be high between seabirds, marine mammals and piscivorous demersal fish. In the MTI it translated only into significant negative impacts between bottlenose dolphins and piscivorous demersal fish which constituted the sole major effect of top predators on the food web (Figure 4) (S_{MTI} 100%). As such, the Ecopath model was able to take the analysis one step further in suggesting that the negative impact of top predators (TopP) on Dpis identified through press perturbation analysis was more likely related to competition for food resources rather than to predation, i.e. the two groups feed largely on the same prey.

In contrast, quantitative and qualitative findings did not agree regarding a positive impact of an increase of top predators for benthivores (Table 3). This was due to some extent to the diet regime of top predators differing between the two modelling approaches. In the Ecopath model, marine mammals were feeding on piscivorous and benthivorous, suprabenthivorous, and benthivorous demersal fish. No such trophic link existed between TopP and Btv in the qualitative baseline model (Figure 2a).

Common dolphins and harbour porpoises, which are bycaught by the pelagic and demersal fleets respectively (Table 1), were predicted by the Ecopath model to be negatively (S_{MTI} 100%) impacted by a slight increase of fishing activities (Figure 4). Nevertheless, prey overlap between top predators and fishing fleets was low to moderate (values ≥ 0.6 only for common dolphins) and did not suggest strong competition between these two predator groups for the same resources. Thus, the negative impacts were a result of direct effects of fishing. These quantitative findings again strengthened the predictions obtained from the qualitative models (Table 3).

Finally, conclusions derived from qualitative modelling regarding the impacts of the pelagic fleet on functional groups in the bentho-demersal food chain and the effects of the demersal fleet on zooplanktivorous pelagic fish were not confirmed by quantitative model outputs (Table 3).

3.4 Potential indicators of food web changes

The predictions which were robust to model structure and model type concerned benthivores (corresponding to several demersal fish compartments in the Ecopath model) and planktivores (corresponding to anchovy, sardine, sprat, mackerel and horse mackerel in the Ecopath model) (Table 3). Benthivores are predicted to decrease when their demersal piscivores predators increase, while planktivores increase when primary productivity increases. Thus benthivores and planktivores are potential indicator groups as together they are sensitive to two types of food web changes, in the abundance of demersal piscivores and in primary productivity, respectively.

Though all demersal fish had a negative MTI, the relative magnitude varied between Ecopath demersal compartments (Figure 3b). The two groups with the strongest negative impact on the ecosystem (MTI) were the suprabenthivorous demersal fish and the benthivorous and piscivorous demersal fish (see supplementary material for their detailed composition). Blue whiting (*Micromesistius poutassou*) represented 80% of the biomass of suprabenthivorous demersal fish. Half of the biomass of benthivorous and piscivorous demersal fish was composed of Gadidae, i.e. bib (*Trisopterus luscus*) and sand goby (*T. minutus*). The remaining half comprised several other species.

Availability of survey data series is the third criteria for suitable indicator groups. In the Bay of Biscay, a regular bottom trawl survey started in 1987, while pelagic planktivores have been surveyed annually since 2000 using fisheries acoustics.

4. Discussion

In this study, benthivores and planktivores were identified as functional groups sensitive to food web changes, independent of model structure and type. For planktivores, commonly referred to as small pelagics, two robust predictions were identified: a high risk of decline associated with an increase in demersal piscivorous fish abundance and a potential increase following a rise in primary productivity, the reverse being also true. The first pressure change, for which predictions were only partially robust to model type, is very likely to take place during phases of demersal fish stock rebuilding, such as occurred in the recent years for the European hake (*Merluccius merluccius*) stocks (ICES, 2011a). The European hake is an abundant piscivorous species with a substantial part of its diet composed of small pelagics (Guichet, 1995; Cabral and Murta, 2002; Le Loc'h, 2004). The second result is relevant in the context of decreasing eutrophication in coastal areas, but also climate variability (Beaugrand and Reid, 2003). A temporary or permanent diminution in system fertility and thus primary production could follow and as such constrain to a certain degree the abundance of zooplanktivorous fish populations (Malzahn *et al.*, 2007). In the Bay of Biscay, several coastal areas with eutrophication problems have been identified (AAMP and Ifremer, 2011). Recently, balanced harvesting, which is defined as applying fishing mortality in proportion to natural productivity, has been advocated as a way to maintain relative size and species compositions of exploited ecosystems (Garcia *et al.*, 2012). However, indirect effects might complicate the picture. The qualitative model analyses results indicated that a given fishery could affect the opposite food chain, e.g. pelagic fleets could change the abundance of functional groups in the bentho-demersal food chain. This cross-effect is in line with the findings of Rochet *et al.* (2013) regarding the way anthropogenic and natural pressures propagate within food webs. Indeed, these authors stated that the multi-species fisheries operating in the northeast Atlantic are characterised since decades by a low fishing selectivity across and within functional groups. Using qualitative models, the same authors demonstrated that these less selective fisheries might create antagonistic pressures, the impacts of which being less predictable. Nevertheless, quantitative outputs of the present work (MTI and overlap index) did not confirm propagation of fishing pressure. A possible explanation for this discrepancy is that direct impacts of individual fishing fleets on their targeted stocks were not strong and consequently indirect impacts on opposite food chain components were even less detectable.

A four step approach was proposed in the present study to determine indicator functional groups suitable to evaluate food web effects of pressure changes, particularly fishing. In a previous study of the Bay of Biscay ecosystem, functional groups were also found to be a relevant level at which to seek impacts of fishing pressures and other changes (Rochet *et al.*, 2010). The indicator groups of the current study being robust to model structure and type, they can provide support for the definition of management options robust to model uncertainty. However, multiple impacts were not analysed in the present work as they increase ambiguity in qualitative predictions and are difficult to perform with EwE. However, it should be acknowledged that applying several pressures concomitantly is an important step in selecting and interpreting ecological indicators, particularly when ambiguities can be overcome by accounting for the relative strength of positive and negative effects.

During the selection process of indicators suitable to describe GES under the European MSFD, the “large fish indicator” (LFI) has been identified as an indicator of “food web” structure (Rogers *et al.*, 2010) and was more particularly viewed as an indicator of the general “health” of the demersal fish community (Greenstreet *et al.*, 2009). In the North Sea, LFI is defined as the proportion by weight of fish greater than 40 cm in length and is notably sensitive to variations in fishing pressure. Others have derived expected directions of changes under the impact of fishing (Shin *et al.*, 2005), i.e. a decrease in the proportion of large fish with increasing fishing pressure. However, concrete applications to demersal communities have highlighted that the actual processes that link changes in the LFI to changes in fishing pressure still remain to be properly understood (Rochet *et al.*, 2007; Greenstreet *et al.*, 2011; Shephard *et al.*, 2011).

Propositions were made to convert the LFI index into an indicator of “food web” status (MSFD descriptor 4) (Rombouts *et al.*, 2013): the use of species-specific thresholds to define large individuals rather than a single cut-off point, e.g. 40 cm, and coupling of this indicator with the maximum asymptotic length (L_∞) to take into account changes in species composition. From this perspective, the two demersal compartments in the Ecopath model with the greatest overall impact on the ecosystem corresponded to 48 species, among which five dominated the biomass and included most of the evaluated stocks (see supplementary material). This information could help to define the species to be included in the suite of species to be monitored within the demersal fish functional groups in the Bay of Biscay continental shelf ecosystem.

In conclusions, an easy-to-implement modelling approach combining two types of ecosystem models was applied to draw robust conclusions regarding the functioning of the Bay of Biscay continental shelf food web and its expected responses to single perturbations. The approach offers a structured way towards the selection of indicators for monitoring food web status and responses to perturbations.

Acknowledgement

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Supplementary material

Supplementary material is available at the ICESJMS online version of the paper. It includes the species composition of the four demersal fish compartments in the Bay of Biscay continental shelf ecosystem model.

Figure captions

Figure 1. Study area of the Bay of Biscay continental shelf and locations of the main rivers flowing into it. The shaded area corresponded to the French part of the continental shelf. For clarification, ICES divisions VIIIa and b are also added in bold line.

Figure 2. (a) Baseline qualitative model of the Bay of Biscay continental shelf food web. System variables include trophic groups (circles) and fishing fleets (squares). Arrows represent positive links, circles negative links. Closed circles starting and ending at the same variable represent self-effect (density-dependence). TopP: Top Predators; Ppis: Pelagic Piscivores; Plv: Pelagic Planktivores; Plkt: Plankton; Dpis: Demersal Piscivores; Btv: Demersal Benthivores; Bthos: benthos; Dem fleet: Demersal fleet; Pel fleet: Pelagic fleet; Inv fleet: Invertebrate fleet. Dashed links were those that were altered for creating model variants. (b) Summary of modifications made to adapt the generic qualitative model proposed by Rochet *et al.* (2013) to the Bay of Biscay case study. Added links are in bold and removed links dashed.

Figure 3. (a) Prey versus predator niche overlap index derived from an Ecopath model. Groups in the upper left corner have a very high overlap of prey; groups in the upper right corner have a high overlap of both predators and prey. (b) Total mixed trophic impacts of each functional group on the ecosystem (sum over the remaining groups). Compartments were ordered by qualitative model groups, e.g. mackerel, horse mackerel, anchovy, sardine and sprat pertained to the planktivorous fish category (Plv) and as such they were more closely grouped together in the graph. The names corresponding to the numbers of functional groups are given in Table 1. 33 pelagic fleet; 34 demersal fleet; 35 invertebrate fleet.

Figure 4. Combined direct and indirect trophic impacts that a functional group (impacting group) had on each of the remaining groups (impacted groups) in the Ecopath model. Black circles indicate potential positive impacts and white circles potential negative impacts.

References

AAMP and Ifremer 2011. DCSMM - Rapport de l'atelier de synthèse de l'évaluation initiale. Agence des Aires Marines Protégées and Ifremer. 86 pp.

Beaugrand, G., and Reid, P. C. 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. Global Change Biology, 9: 801-817.

Cabral, H. N., and Murta, A. G. 2002. The diet of blue whiting, hake, horse mackerel and mackerel off Portugal. Journal of Applied Ichthyology, 18: 14-23.

Christensen, V., and Walters, C. J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling, 172: 109-139.

Christensen, V., Walters, C. J., Pauly, D., and Forrest, R. 2008. Ecopath with Ecosim version 6. User guide - November 2008. Lenfest Ocean Futures Project 2008. Fisheries Centre, The University of British Columbia, Vancouver, Canada. 235 pp.

Dambacher, J. M. 2001. Qualitative analysis of the community matrix. PhD Thesis, Oregon State University, Corvallis.

Dambacher, J. M., Gaughan, D. J., Rochet, M. J., Rossignol, P. A., and Trenkel, V. M. 2009. Qualitative modelling and indicators of exploited ecosystems. Fish and Fisheries, 10: 305-322.

Dambacher, J. M., Li, H. W., and Rossignol, P. A. 2002. Relevance of community structure in assessing indeterminacy of ecological predictions. Ecology, 83: 1372-1385.

Dambacher, J. M., Luh, H. K., Li, H. W., and Rossignol, P. A. 2003. Qualitative stability and ambiguity in model ecosystems. American Naturalist, 161: 876-888.

Daurès, F., Rochet, M. J., Van Iseghem, S., and Trenkel, V. M. 2009. Fishing fleet typology, economic dependence, and species landing profiles of the French fleets in the Bay of Biscay, 2000-2006. Aquatic Living Resources, 22: 535-547.

Fauconnet, L., Badts, V., Biseau, A., Diméet, J., Dintheer, C., Dubé, B., Gaudou, O., *et al.* 2011. Observations à bord des navires de pêche - Bilan de l'échantillonnage 2010. Ifremer, Nantes, France. 214 pp.

Fréon, P., Cury, P., Shannon, L., and Roy, C. 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. Bulletin of Marine Science, 76: 385-462.

Fulton, E. A., Smith, A. D. M., and Punt, A. E. 2005. Which ecological indicators can robustly detect effects of fishing? ICES Journal of Marine Science, 62: 540-551.

Gaichas, S. K., Aydin, K. Y., and Francis, R. C. 2010. Using food web model results to inform stock assessment estimates of mortality and production for ecosystem-based fisheries management. Canadian Journal of Fisheries and Aquatic Sciences, 67: 1490-1506.

Garcia, S. M., Kolding, J., Rice, J., Rochet, M. J., Zhou, S., Arimoto, T., Beyer, J. E., *et al.* 2012. Reconsidering the consequences of selective fisheries. Science, 335: 1045-1047.

Gårdmark, A., Lindegren, M., Neuenfeldt, S., Blenckner, T., Heikinheimo, O., Müller-Karulis, B., Niiranen, S., *et al.* 2012. Biological ensemble modelling to evaluate potential futures of living marine resources. Ecological Applications.

Greenstreet, S., Fraser, H., Cotter, J., and Pinnegar, J. 2009. Assessment of the “state” of the demersal fish communities in OSPAR regions II, III, IV and V. Monitoring and Assessment Series, OSPAR Commission, London, U.K. 88 pp.

Greenstreet, S. P. R., Rogers, S. I., Rice, J. C., Piet, G. J., Guirey, E. J., Fraser, H. M., and Fryer, R. J. 2011. Development of the EcoQO for the North Sea fish community. ICES Journal of Marine Science, 68: 1-11.

Guichet, R. 1995. The diet of European hake (*Merluccius merluccius*) in the northern part of the Bay of Biscay. ICES Journal of Marine Science, 52: 21-31.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., *et al.* 2008. A global map of human impact on marine ecosystems. Science, 319: 948-952.

Hill, S. L., Watters, G. M., Punt, A. E., McAllister, M. K., Quéré, C., and Turner, J. 2007. Model uncertainty in the ecosystem approach to fisheries. Fish and Fisheries, 8: 315-336.

ICES 2011a. Report of the ICES Advisory Committee, 2011 - Book 7: Bay of Biscay and Atlantic Iberian waters. ICES Advice 2011. 118 pp.

ICES 2011b. Report of the ICES/HELCOM working group on integrated assessments of the Baltic Sea (WGIAB). ICES CM 2011/SSGRSP:03. 139 pp.

Jennings, S., and Kaiser, M. J. 1998. The effects of fishing on marine ecosystems. *In* Advances in marine biology, pp. 201-352. Ed. by J. H. S. Blaxter, A. J. Southward, and P. A. Tyler. Academic Press.

Lassalle, G., Gascuel, D., Le Loc'h, F., Lobry, J., Pierce, G. J., Ridoux, V., Santos, M. B., *et al.* 2012. An ecosystem approach for the assessment of fisheries impacts on marine top-predators: the Bay of Biscay case study. ICES Journal of Marine Science, 69: 925-938.

Lassalle, G., Lobry, J., Le Loc'h, F., Bustamante, P., Certain, G., Delmas, D., Dupuy, C., *et al.* 2011. Lower trophic levels and detrital biomass control the Bay of Biscay continental shelf food web: implications for ecosystem management. Progress In Oceanography, 91: 61-75.

Le Loc'h, F. 2004. Structure, fonctionnement, évolution des communautés benthiques des fonds meubles exploités du plateau continental Nord-Gascogne. Thèse de Doctorat, Océanographie Biologique, Université de Bretagne Occidentale, Brest, France. 326 pp.

Levins, R. 1974. The qualitative analysis of partially specified systems. Annals of the New York Academy of Sciences, 231: 123-138.

Lorance, P., Bertrand, J. A., Brind'Amour, A., Rochet, M. J., and Trenkel, V. M. 2009. Assessment of impacts from human activities on ecosystem components in the Bay of Biscay in the early 1990s. Aquatic Living Resources, 22: 409-431.

Malzahn, A., Aberle, N., Clemmesen, C., and Boersma, M. 2007. Nutrient limitation of primary producers affects planktivorous fish condition. Limnology and Oceanography, 52: 2062-2071.

Metcalf, S. J. 2010. Qualitative models to complement quantitative ecosystem models for the analysis of data-limited marine ecosystems and fisheries. Reviews in Fisheries Science, 18: 248-265.

Metcalf, S. J., Pember, M. B., and Bellchambers, L. M. 2011. Identifying indicators of the effects of fishing using alternative models, uncertainty, and aggregation error. ICES Journal of Marine Science, 68: 1417-1425.

Millenium Ecosystem Assessment 2005. Ecosystems and human well-being: current state and trends, volume 1.

Nelva Pasqual, J. S. 2013. Exploring estuarine ecological networks: from structure to dynamics. A synthesis and comparison of matrix approaches. PhD Thesis, University of Bordeaux 1, Bordeaux, France.

Ortiz, M., and Wolff, M. 2008. Mass-balanced trophic and loop models of complex benthic systems in northern Chile (SE Pacific) to improve sustainable interventions: a comparative analysis. Hydrobiologia, 605: 1-10.

Pierce, G. J., Allcock, L., Bruno, I., Bustamante, P., González, A., Guerra, A., Jereb, P., *et al.* 2010. Cephalopod biology and fisheries in Europe. ICES Cooperative Research Report, 303. 175 pp.

Plagànyi, E. E. 2007. Models for an ecosystem approach to fisheries. FAO Fisheries Technical Paper, FAO, Rome, Italy, 477. 107 pp.

Plagànyi, E. E., and Butterworth, D. S. 2004. A critical look at the potential of Ecopath with Ecosim to assist in practical fisheries management. African Journal of Marine Science, 26: 261-287.

Plagànyi, E. E., and Butterworth, D. S. 2012. The Scotia Sea krill fishery and its possible impacts on dependent predators - modelling localized depletion of prey. Ecological Applications, 22: 748-761.

Puccia, C. J., and Levins, R. 1985. Qualitative modeling of complex systems: an introduction to loop analysis and time averaging, Harvard University Press.

Rochet, M. J., Collie, J. S., and Trenkel, V. M. 2013. How do fishing and environmental effects propagate among and within functional groups? Bulletin of Marine Science, 89: 285-315.

Rochet, M. J., Daurès, F., and Trenkel, V. M. 2012. Capacity management, not stock status or economics, drives fleet dynamics in the Bay of Biscay ecosystem on a decadal time scale. Canadian Journal of Fisheries and Aquatic Sciences, 69: 695-710.

Rochet, M. J., Trenkel, V., Gil de Sola, L., Politou, C. Y., Tserpes, G., and Bertrand, A. 2007. Do population and community metrics tell the same story about recent changes in Northern Mediterranean fish communities? : ICES CM 2007 / D:16.

Rochet, M. J., Trenkel, V. M., Carpentier, A., Coppin, F., Gil de Sola, L., Leaute, J. P., Mahe, J. C., *et al.* 2010. Do changes in environmental pressures impact marine communities? An empirical assessment. Journal of Applied Ecology, 47: 741-750.

Rochette, S., Lobry, J., Lepage, M., and Boët, P. 2009. Dealing with uncertainty in qualitative models with a semi-quantitative approach based on simulations. Application to the Gironde estuarine food web (France). Ecological Modelling, 220: 122-132.

Rogers, S., Casini, M., Cury, P., Heath, M., Irigoien, X., Kuosa, H., Scheidat, M., *et al.* 2010. Marine Strategy Framework Directive - Task group 4 report food webs. EUR - Scientific and Technical Research series, Joint Research Centre, Luxembourg: EUR 24343 EN. 55 pp.

Rombouts, I., Beaugrand, G., Fizzala, X., Gaill, F., Greenstreet, S., Lamare, S., Le Loc'h, F., *et al.* 2013. Food web indicators under the Marine Strategy Framework Directive: from complexity to simplicity? Ecological Indicators, 29: 246-254.

Samhouri, J., Levin, P., and Harvey, C. 2009. Quantitative evaluation of marine ecosystem indicator performance using food web models. Ecosystems, 12: 1283-1298.

Shephard, S., Reid, D. G., and Greenstreet, S. P. R. 2011. Interpreting the large fish indicator for the Celtic Sea. ICES Journal of Marine Science, 68: 1963-1972.

Shin, Y. J., Rochet, M. J., Jennings, S., Field, J. G., and Gislason, H. 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. ICES Journal of Marine Science, 62: 384-396.

Stevens, J. D., Bonfil, R., Dulvy, N. K., and Walker, P. A. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science, 57: 476-494.

Ulanowicz, R. E., and Puccia, C. J. 1990. Mixed trophic impacts in ecosystems. Coenoses, 5: 7-16.

Van Hoey, G., Borja, A., Birchenough, S., Buhl-Mortensen, L., Degraer, S., Fleischer, D., Kerckhof, F., *et al.* 2010. The use of benthic indicators in Europe: from the Water Framework Directive to the Marine Strategy Framework Directive. Marine Pollution Bulletin, 60: 2187-2196.

Westfahl, P., Heath, Z., and Woodrow, C. 2002. PowerPlay Digraph Editor. Version 2.0 GNU General Public License (GPL).

Table 1. Landings and discards (kg C·km^{-2}·year^{-1}) of the three fishing fleets included in the Ecopath model of the continental shelf of the Bay of Biscay.

	Pelagic fleet (Pel Fleet)		Demersal fleet (Dem Fleet)		Invertebrates fleet (Inv Fleet)	
	Y	Discards	*Y*	Discards	*Y*	Discards
1. Plunge and pursuit divers seabirds						
2. Surface feeders seabirds						
3. Striped dolphins *Stenella coeruleoalba*						
4. Bottlenose dolphins *Tursiops truncatus*						
5. Common dolphins *Delphinus delphis*		0.101*				
6. Long-finned pilot whale *Globicephala melas*						
7. Harbour porpoise *Phocoena phocoena*				0.0078*		
8. Piscivorous demersal fish			8.86	0.43	1.56	0.38
9. Piscivorous and benthivorous demersal fish	0.64		5.45	2.43	4.59	1.22
10. Suprabenthivorous demersal fish					0.64	26.79
11. Benthivorous demersal fish			4.63		0.37	
12. Mackerel *Scomber scombrus*	1.69	0.49	4.55	0.90		0.34
13. Horse mackerel *Trachurus trachurus*	15.13				1.68	
14. Anchovy *Engraulis encrasicolus*	16.80	0.10				
15. Sardine *Sardina pilchardus*	10.82					
16. Sprat *Sprattus sprattus*						
17. Benthic cephalopods			3.53			
18. Pelagic cephalopods			1.99			
19. Carnivorous benthic invertebrates				1.24	2.91	0.84
20. Necrophagous benthic invertebrates						
21. Sub-surface deposit feeders invertebrates						
22. Surface suspension and deposit feeders inv.						
23. Benthic meiofauna						
24. Suprabenthic invertebrates						
25. Macrozooplankton (≥ 2 mm)						

26. Mesozooplankton (0.2-2 mm)
27. Microzooplankton (≤ 0.2 mm)
28. Bacteria
29. Large phytoplankton (≥ 3 µm)
30. Small phytoplankton (< 3 µm)
31. Discards
32. Pelagic detritus

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[*] Bycatch of toothed cetaceans (common dolphins and harbour porpoises).

Table 2. Expected directions of change[*] of the abundance of different functional groups and fishing fleets based on press perturbation analysis of Bay of Biscay continental shelf food web models. Only predictions which were consistent (same direction) across a baseline model and its three variants and had weights ≥ 0.5 were retained. Corresponding Ecopath compartment numbers from Table 1 are given in brackets. Blank cells indicate ambiguous predictions.

Impacted	Impacting group (increase)									
group (Ecopath)	TopP	Ppis	Dpis	Plv	Btv	Plkt	Bthos	Dem fleet	Pel Fleet	Inv fleet
Top predators (1-7)	+							-[†]	-	
Pelagic piscivores										
Demersal piscivores (8)	-		+						+	
Planktivores (12-16)			-	+		+		+		
Benthivores (9-11)	+		-						-	
Plankton (25-27, 29, 30)	0	0	0	0	0		0	0	0	0
Benthos (19-24)										
Demersal fleet (33)								+		
Pelagic fleet (34)									+[†]	
Invertebrates fleet (35)										

[*] + (increase), – (decrease) or 0 (no trend) indicates the direction of the response in group *i* (impacted group in rows) resulting from a sustained positive input into group *j* (impacting groups in columns); e.g. the predicted response of a sustained increase in top predators is predicted to have a positive effect on demersal benthivorous fish.

[†] Signs vary with the inclusion (or not) of the positive effect of Btv on Dpis in model variants.

Table 3. Concordance between robust qualitative model predictions (press perturbation analyses in Table 2) and quantitative Ecopath outputs. Ecopath outputs were compared with qualitative predictions in terms of ecosystem components impacted and directions of change.

Robust qualitative predictions	Quantitative outputs	
	Diet overlap	MTI
Increase in demersal piscivores (Dpis) has negative effect on their bentho-demersal (Btv) and pelagic prey (Plv).	Yes	Yes, only for demersal prey
Increase in primary productivity (Plkt) has positive effect on Plv.	Yes	Yes
Increase in top predators (TopP) has negative effect on Dpis and positive effect on Btv	Yes	Yes, only bottlenose dolphins No
Increase in Pel Fleet has negative effect on TopP and Btv and positive effect on Dpis	Yes* No*	Yes, on common dolphins No
Increase in Dem Fleet has positive effect on Plv	No	No

*Prey overlap indices between ecosystem components and pelagic fishery were calculated using the modified Pianka index proposed in Ecopath which is based on proportions of the different prey consumed: pursuit diver seabirds (0.64), common dolphins (0.73) and piscivorous demersal fish (0.66).

The species composition of the four demersal fish compartments in the Bay of Biscay continental shelf ecosystem model. In bold are those with the greatest impact on the ecosystem based on the overall Mixed Trophic Impact calculated in Ecopath and * corresponded to species with the highest biomass.

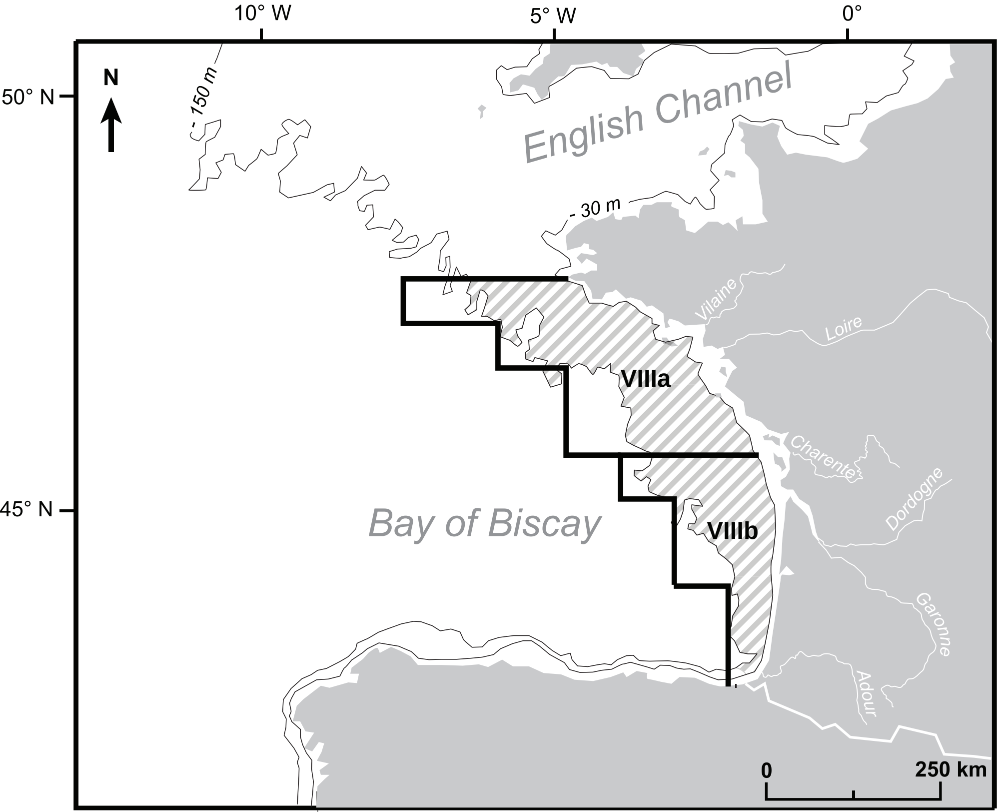
Benthivorous demersal fish
Arnoglossus laterna
Arnoglossus imperialis
Arnoglossus thori
Callionymus lyra
Microchirus variegatus
Solea solea
Chelidonichthys cuculus
Liza ramada
Balistes carolinensis
Enchelyopus cimbrius
Mullus surmuletus
Raja clavata
Raja montagui
Sparus auratus
Microstomus kitt
Callionymus maculatus
Buglossidium luteum
Chelidonichthys obscurus
Dicologlossa cuneata
Lesueurigobius friesii
Leucoraja circularis
Pomatoschistus minutus
Syngnathus acus
Umbrina canariensis

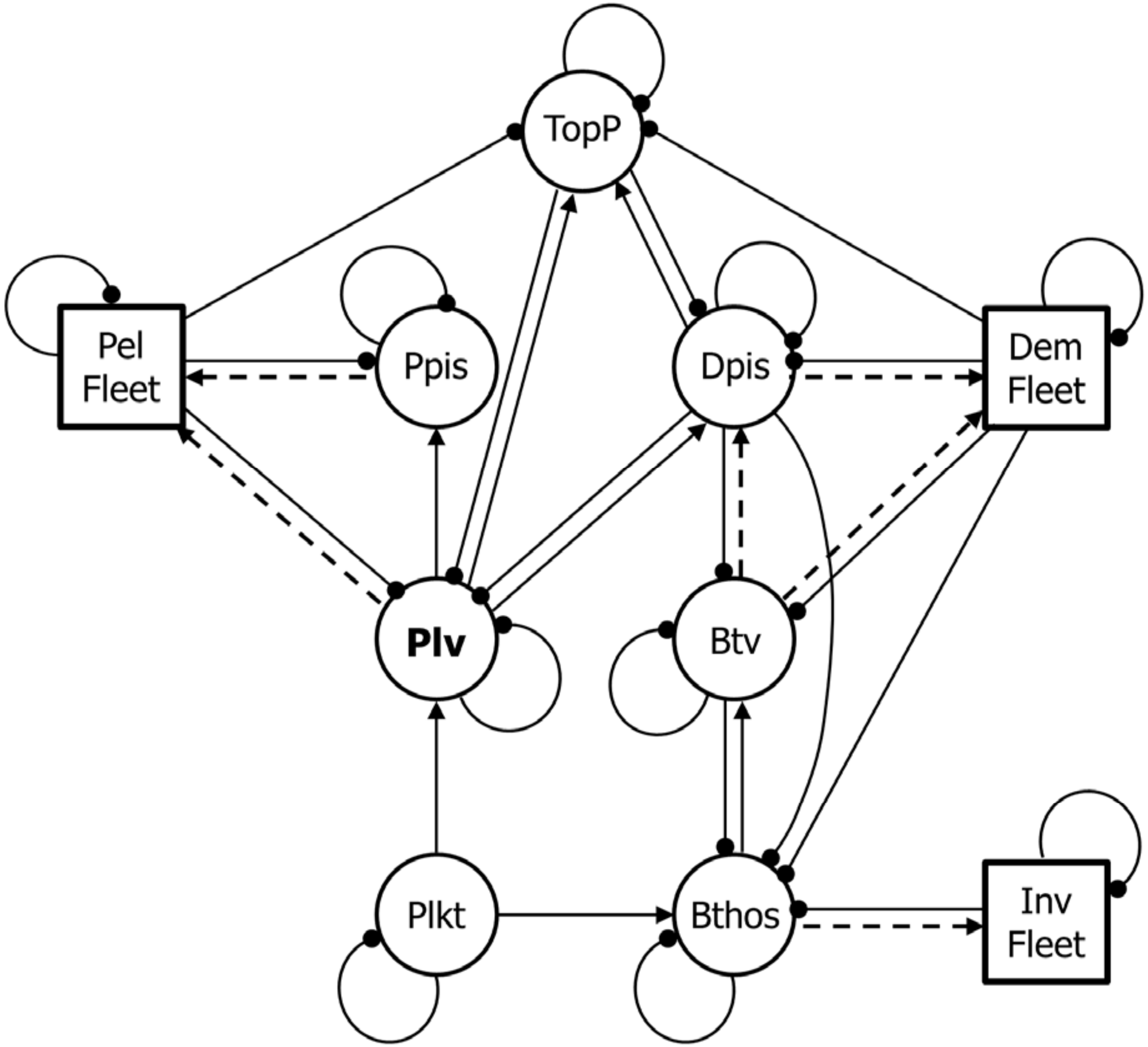
Suprabenthivorous demersal fish
Capros aper*
Micromesistius poutassou*
Argentina silus
Boops boops
Cepola macrophthalma
Ammodytes tobianus
Aphia minuta
***Merluccius merluccius* (juveniles)**

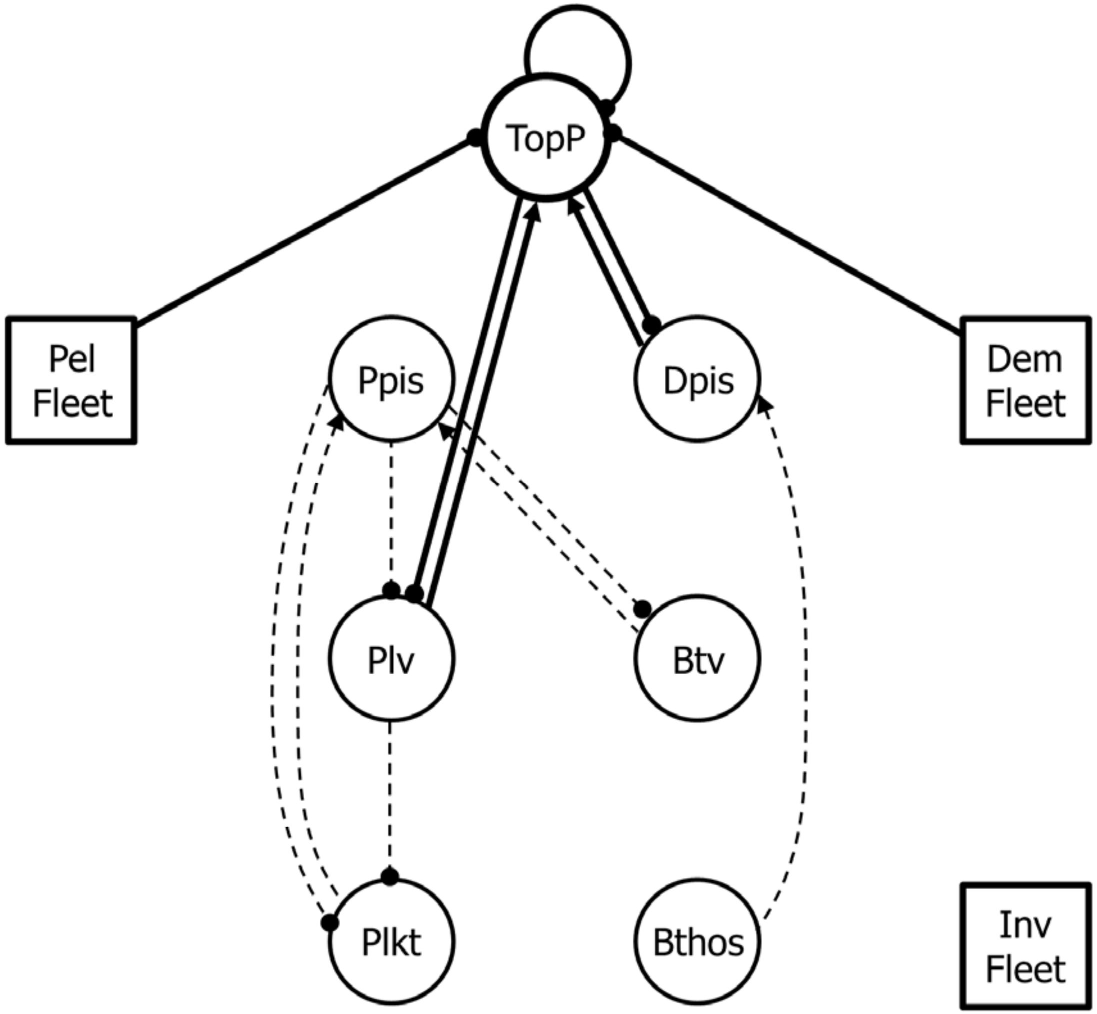
Piscivorous and benthivorous demersal fish
Scyliorhinus canicula*
Conger conger
Gaidropsarus vulgaris
Lepidorhombus boscii
Lepidorhombus whiffiagonis
Lophius budegassa
Lophius piscatorius
Merlangius merlangus

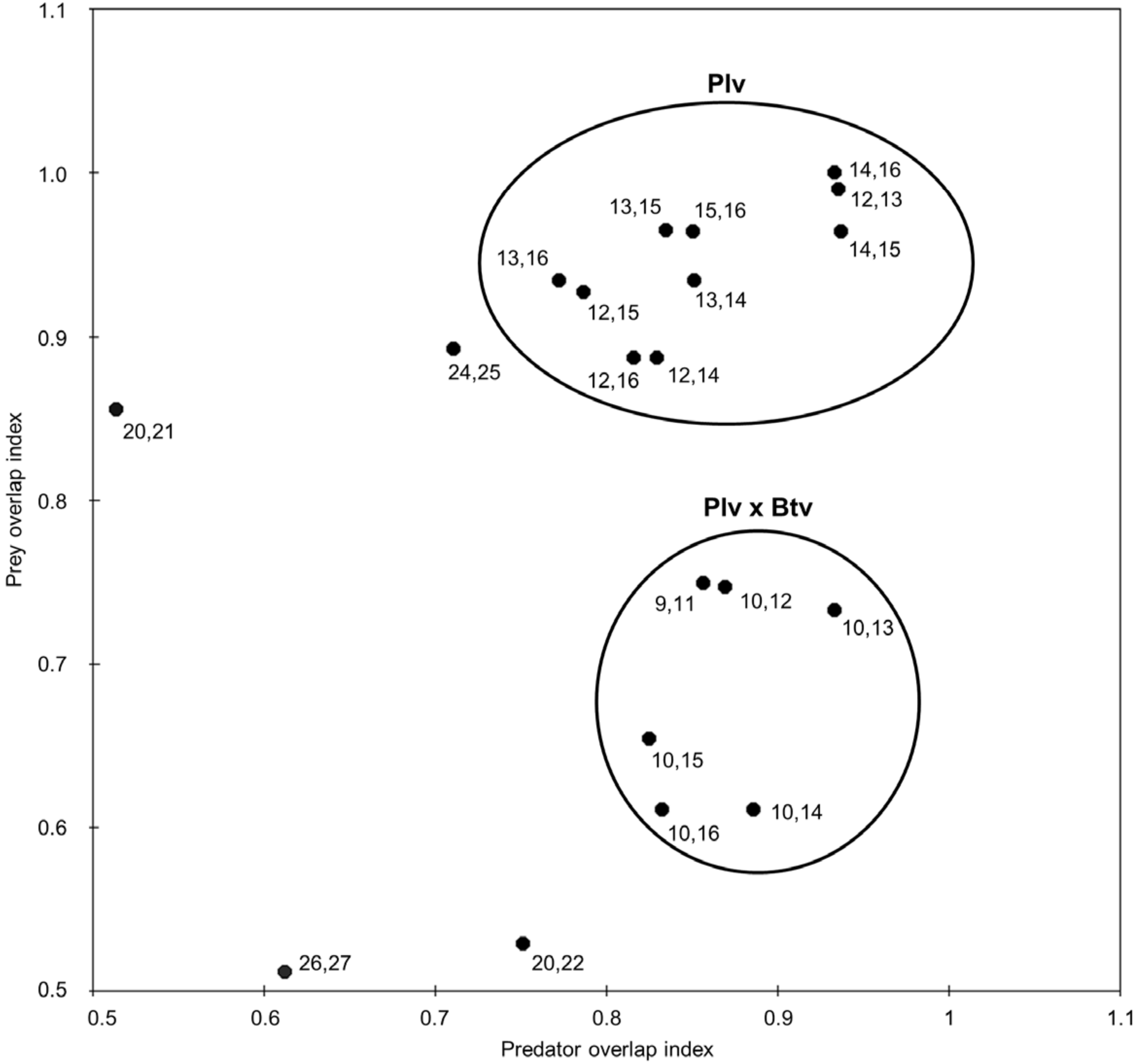
Trisopterus luscus*
Trisopterus minutus*
Argentina sphyraena
Dicentrarchus labrax
Galeorhinus galeus
Leucoraja naevus
Myliobatis aquila
Zeus faber
Spondyliosoma cantharus
Squalus acanthias
Torpedo marmorata
Trachinus draco
Molva molva
Molva dypterygia
Chelidonichthys gurnardus
Mustelus asterias
Pollachius pollachius
Melanogrammus aeglefinus
Chelidonichthys lucerna
Mustelus mustelus
Galeus melastomus
Dasyatis pastinaca
Dicentrarchus punctatus
Diplodus vulgaris
Echiichthys vipera
Helicolenus dactylopterus dactylopterus
Hyperoplus lanceolatus
Labrus mixtus
Lithognathus mormyrus
Pagellus acarne
Pagellus bogaraveo
Phycis blennoides
Scophthalmus maximus

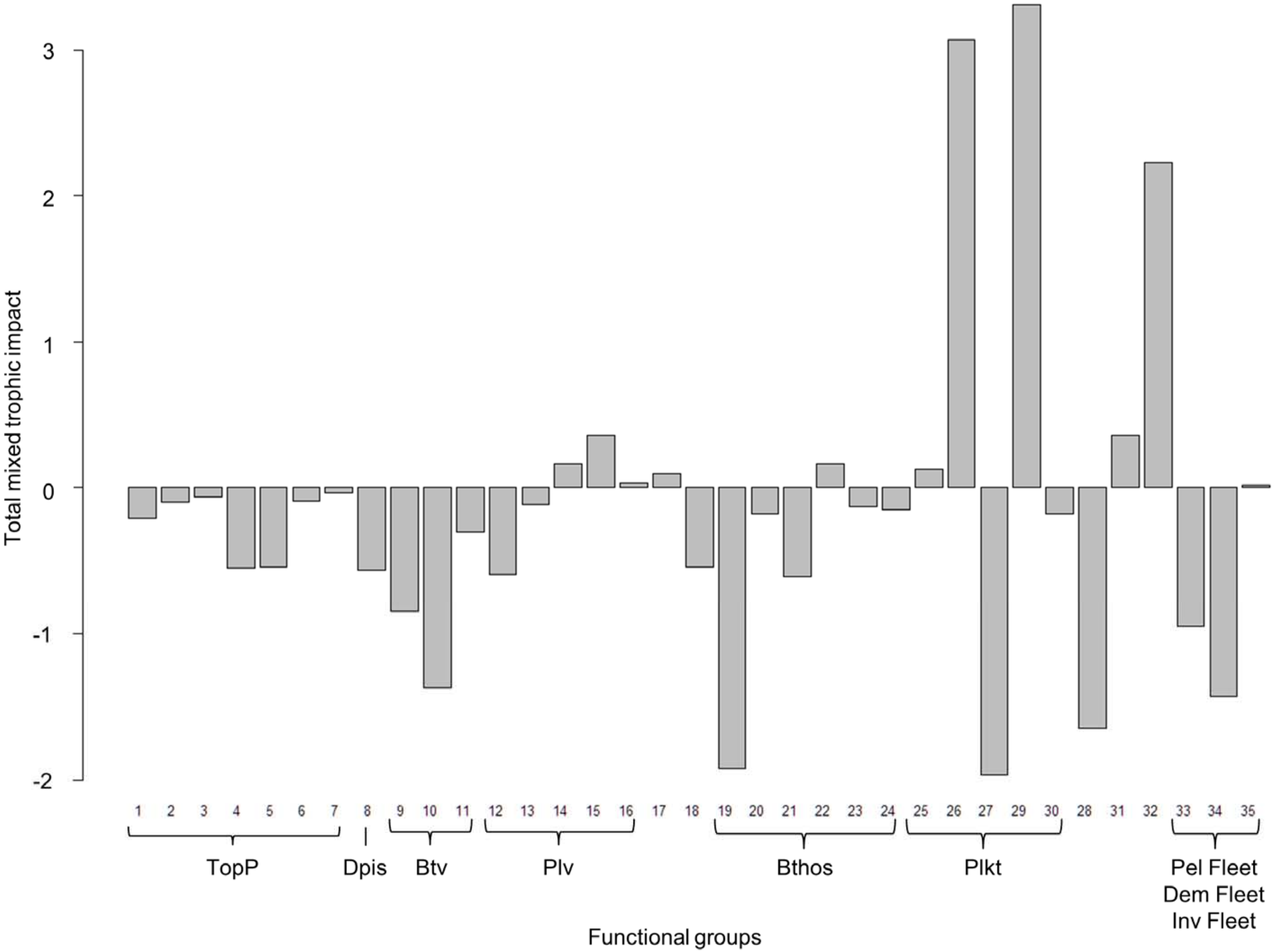
Piscivorous demersal fish
Merluccius merluccius
Argyrosomus regius
Torpedo nobiliana
Hexanchus griseus

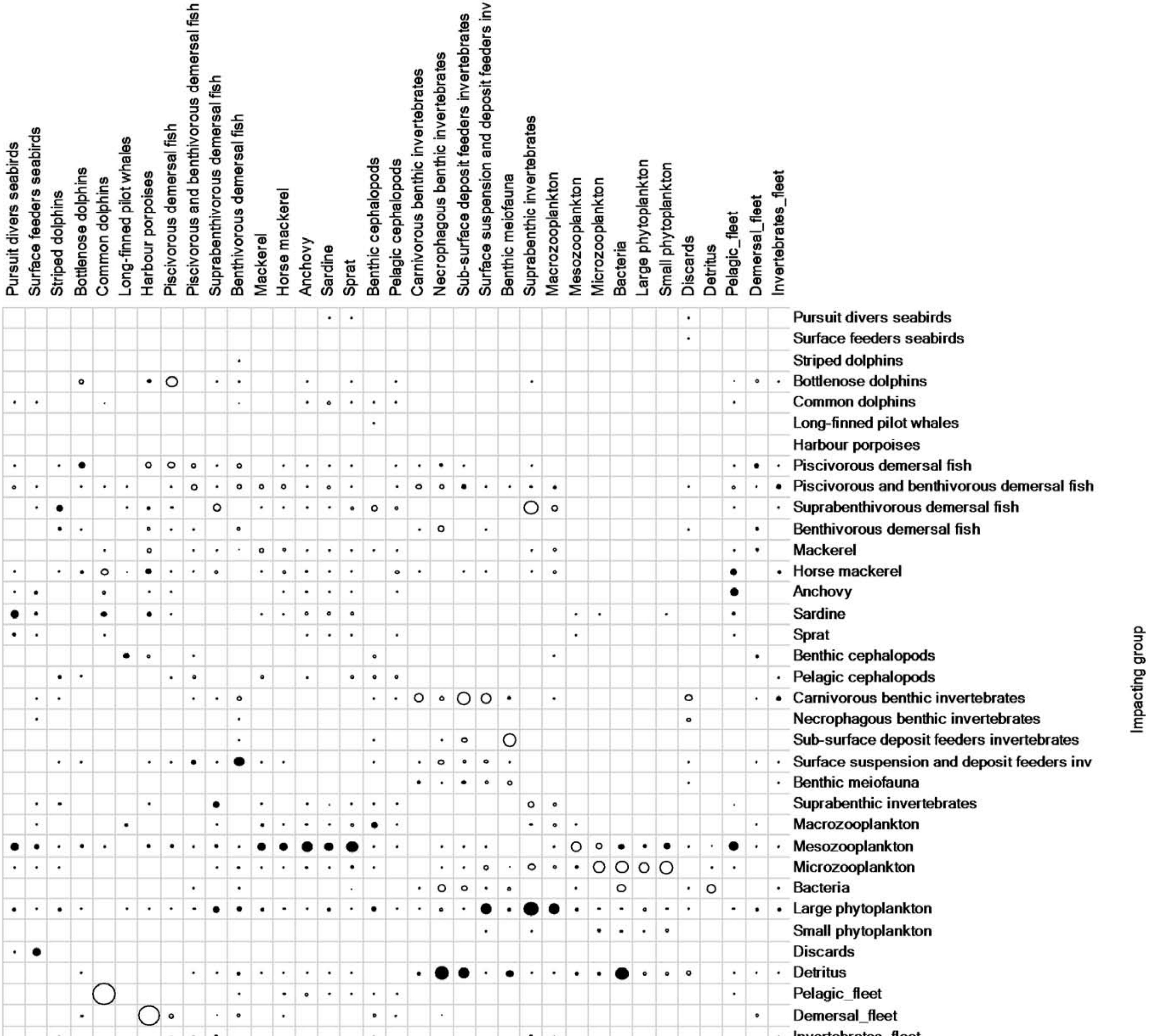

10° W
5° W
0°
50° N
45° N
N
150 m
30 m
English Channel
Bay of Biscay
VIIIa
VIIIb
Vilaine
Loire
Charente
Dordogne
Garonne
Adour
0
250 km


TopP
Pel Fleet
Ppis
Dpis
Dem Fleet
Plv
Btv
Plkt
Bthos
Inv Fleet


TopP
Pel
Fleet
Ppis
Dpis
Dem
Fleet
Plv
Btv
Plkt
Bthos
Inv
Fleet


Plv
Plv x Btv
14,16
12,13
13,15
15,16
14,15
13,16
13,14
12,15
24,25
12,16
12,14
20,21
9,11
10,12
10,13
10,15
10,16
10,14
26,27
20,22
Prey overlap index
Predator overlap index
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.5
0.6
0.7
0.8
0.9
1
1.1


Total mixed trophic impact
3
2
1
0
-1
-2
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
29
30
28
31
32
33
34
35
TopP
Dpis
Btv
Plv
Bthos
Plkt
Pel Fleet
Dem Fleet
Inv Fleet
Functional groups


Pursuit divers seabirds
Surface feeders seabirds
Striped dolphins
Bottlenose dolphins
Common dolphins
Long-finned pilot whales
Harbour porpoises
Piscivorous demersal fish
Piscivorous and benthivorous demersal fish
Suprabenthivorous demersal fish
Benthivorous demersal fish
Mackerel
Horse mackerel
Anchovy
Sardine
Sprat
Benthic cephalopods
Pelagic cephalopods
Carnivorous benthic invertebrates
Necrophagous benthic invertebrates
Sub-surface deposit feeders invertebrates
Surface suspension and deposit feeders inv
Benthic meiofauna
Suprabenthic invertebrates
Macrozooplankton
Mesozooplankton
Microzooplankton
Bacteria
Large phytoplankton
Small phytoplankton
Discards
Detritus
Pelagic_fleet
Demersal_fleet
Invertebrates_fleet
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Surface feeders seabirds
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Bottlenose dolphins
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Mesozooplankton
Microzooplankton
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Small phytoplankton
Discards
Detritus
Pelagic_fleet
Demersal_fleet
Invertebrates_fleet
Impacting group