Trophic models: What do we learn about Celtic Sea and Bay of Biscay ecosystems?

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Abstract :

Trophic models are key tools to go beyond the single-species approaches used in stock assessments to adopt a more holistic view and implement the Ecosystem Approach to Fisheries Management (EAFM). This study aims to: (i) analyse the trophic functioning of the Celtic Sea and the Bay of Biscay, (ii) investigate ecosystem changes over the 1980–2013 period and, (iii) explore the response to management measures at the food web scale. Ecopath models were built for each ecosystem for years 1980 and 2013, and Ecosim models were fitted to time series data of biomass and catches. EcoTroph diagnosis showed that in both ecosystems, fishing pressure focuses on high trophic levels (TLs) and, to a lesser extent, on intermediate TLs. However, the interplay between local environmental conditions, species composition and ecosystem functioning could explain the different responses to fisheries management observed between these two contiguous ecosystems. Indeed, over the study period, the ecosystem's exploitation status has improved in the Bay of Biscay but not in the Celtic Sea. This improvement does not seem to be sufficient to achieve the objectives of an EAFM, as high trophic levels were still overexploited in 2013 and simulations conducted with Ecosim in the Bay of Biscay indicate that at current fishing effort the biomass will not be rebuilt by 2030. The ecosystem's response to a reduction in fishing mortality depends on which trophic levels receive protection. Reducing fishing mortality on pelagic fish, instead of on demersal fish, appears more efficient at maximising catch and total biomass and at conserving both top-predator and intermediate TLs. Such advice-oriented trophic models should be used on a regular basis to monitor the health status of marine food webs and analyse the trade-offs between multiple objectives in an ecosystem-based fisheries management context.

Highlights

► Trophic models were built to analyze the functioning of ecosystems and changes over the 1980-2013 period. ► EcoTroph diagnoses showed that the ecosystem's exploitation status has improved in the Bay of Biscay but not in Celtic Sea. ► Changes in ecosystems result of the interplay between fisheries management and the occurrence of good recruitments. ► Reducing fishing mortality on small pelagics is the most efficient scenario to maximize catch and conserve predators. ► The fishing impact of every fleet on the food web was assessed using Ecosim, highlighting the large effect of trawling.

1 Introduction

Fishing activities do not only decrease the abundance of targeted species, they also affect their competitors, prey and predators (Olsen et al., 2004; Worm et al., 2006). The community structure and functioning could therefore be affected through trophic relationships (Daskalov et al., 2007; Tremblay-Boyer et al., 2011). Moreover, in a context of global change, direct and indirect impacts of fishing activities are cumulative and act in synergy to increase resource instability (Cheung et al., 2009; Pereira et al., 2010). In this context, implementing an Ecosystem Approach to Fisheries Management (EAFM) is an urgent necessity (FAO, 2003). EAFM aims to apply the principles of sustainable development to the fisheries sector and to move beyond the traditional single-species approaches in fisheries management (Collie and Gislason, 2001; Gascuel et al., 2011; Walters et al., 2005a) by accounting for interspecific interactions, habitat quality and global change in fisheries management. The ultimate goal is to maximise human welfare from an economic, social and environmental perspective (Garcia, 2003; Garcia and Cochrane, 2005). The necessity of this approach is now recognized as self-evident to all fishery scientists and stakeholders, but the main challenge lies in its implementation.

From this point of view, ecosystem modelling is an important tool for studying, evaluating and predicting the potential effects of fisheries on the exploited ecosystems and for exploring further the structure and trophic functioning of marine ecosystems (Plagányi, 2007). Among existing ecosystem models, trophic models like Ecopath with Ecosim (Christensen and Pauly, 1992; Polovina, 1984; Walters et al., 1997) have become widely used tools for EAFM (Christensen and Walters, 2004; Pauly et al., 2000). Ecopath provides a snapshot representation of the resources in the ecosystem and their interactions in a specific period. It is used to analyse interspecific relations and direct and indirect impacts of fishing activities on the whole food web (Christensen and Pauly, 1992). Ecosim is the time-dynamic version of Ecopath and uses mass-balance results from Ecopath for parameter estimation. The model is fitted to observed data and used to evaluate the relative effects of fishing, trophic relationships and environmental disturbances on observed dynamics (Christensen et al., 2005; Christensen and Walters, 2004). EcoTroph (Gascuel, 2005; Gascuel and Pauly, 2009) is a recent approach increasingly used for modelling aquatic ecosystems (e.g. Colléter et al., 2012; Gasche et al., 2013; Prato et al., 2016; Valls et al., 2012). It is based on a simple representation of ecosystems structure using trophic spectra that summarizes the trophic functioning as a continuous flow of

biomass surging up the food web, from low to high trophic levels due to predation and ontogeny processes.

In European Union waters, as a result of the overexploitation of some major stocks, yields began to decrease everywhere since the mid-1970s (Gascuel et al., 2016). Intensification of fishing effort and extension of exploitation to a wider part of the ecosystems were insufficient to compensate the decrease in abundance of exploited fish stocks and landings halved over the past 40 years (Ibid.). In the late 1990s, the overall fishing pressure reached its highest values and most stocks showed an alarming state of depletion. In addition, ecosystem indicators suggest a degradation of the health status in most of the European seas. Over the past decade, the fishing pressure decreased significantly, mainly due to more restrictive catch quotas, but no clear recovery in total biomass and ecosystem indicators is yet apparent (Gascuel et al., 2016).

The Bay of Biscay and the Celtic Sea, which are among the main European fishing zones in terms of landings, illustrate the situation described above. These ecosystems experienced a constant increase of fishing effort and an unprecedented increase in fishing capacity until the 1990s, reaching an excessive level in fishing power (Mesnil, 2008). As a consequence, several studies have shown a significant reduction of biomass with increasing impacts on all compartments of the ecosystem (e.g. Gascuel et al., 2012 and 2016; Guénette and Gascuel, 2012; Pinnegar et al., 2002; Rochet et al., 2005).

In previous studies dealing with trophic modelling (Guénette and Gascuel, 2009; Bentorcha 2014; Bentorcha et al., 2017), the Bay of Biscay and the Celtic Sea were considered as a single ecosystem. However, they are considered distinct ecosystems not only in the European Marine Strategy Framework Directive (European Commission, 2008), but also for the implementation of EAFM in European seas (STECF, 2012). Therefore, in this study, the two ecosystems were modelled separately, as case studies to improve ecosystem-based fisheries management in Europe. We show how these models can be used to (i) understand the trophic functioning of ecosystems and associated fishing-induced changes in the food web, (ii) build global diagnoses of the ecosystem impact of fishing and (iii) explore scenarios of ecosystem-based fisheries management. We compared the Bay of Biscay and the Celtic Sea in terms of changes in structure and trophic functioning. Ecopath models were built for 1980 and 2013 in a scientific advice-oriented approach and using all outputs of the International Council for the Exploration of the Sea (ICES) stock assessment and survey data as input. Then, indicators of fishing impacts on the food web were estimated using EcoTroph. In both ecosystems, Ecosim models were fitted to time series of biomass, abundance indices, catch and fishing mortalities over the 1980-2013 period. Several fisheries management scenarios were used with the best fitted model, namely the Bay of Biscay model, examining the impact on ecosystem

biomass and trophic indicators of the good environmental status of ecosystems as defined by the Marine Strategy Framework Directive (MSFD; European Commission, 2008).

2 Materials and Methods

2.1 Study sites

The two trophic models represent the continental shelves, from the coast to the 200 m isobaths, of the Celtic Sea and the Bay of Biscay ecosystems (Divisions VIIe-j and VIIIab, respectively, according to the classification of ICES) (Fig. 1). These two areas are characterized by distinct oceanographic and ecological features and by specific fish assemblages (Borja et al., 1998; Koutsikopoulos and Le Cann, 1996; Pingree et al., 1981; Planque et al., 2004; Varela, 1996). The total area is 232 360 km² for the "Celtic Sea" model and 83 466 km² for the "Bay of Biscay" model.

In the Bay of Biscay, catches amounted to about 105 000 tonnes in 1980 and 150 000 tonnes in 2013. The main exploited species (by weight) are sardine (21 %), hake (17 %), horse mackerel (10 %), anchovy (7 %), and mackerel (6 %). The Celtic Sea is characterized by greater catches with 320 000 tonnes reported in 1980, and 385 000 tonnes in 2013. The main targeted species are horse mackerel (15 %), hake (7 %), and anglerfish (6 %). Boarfish (*Capros aper*), one of the main by-catch, represents more than 15 % of total catches. The main countries fishing in this area are France, Spain, United Kingdom and, to a lesser extent, Ireland, Belgium and Germany.

2.2 The Ecopath with Ecosim model

2.2.1 Principles and equations

Ecopath is a mass-balanced model that represents the trophic functioning and structure of an aquatic ecosystem (Christensen and Pauly, 1992; Christensen and Walters, 2004; Polovina, 1984). The food web is modelled using functional groups, defined each as single species or group of species (i.e., grouped by similarities in size, food preferences, predators, habitats and life cycles). Ecopath is parameterized based on two master equations, the first one describes the production of each functional group, and the second the energy balance.

$$B_i \times \left(\frac{P}{B}\right)_i = \sum_{j=1}^{N} B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ji} + \left(\frac{P}{B}\right)_i \times B_i \times (1 - EE_i) + Y_i + E_i + BA_i \qquad \text{(Eq. 1)}$$

$$Q_i = P_i + R_i + UA_i \qquad \text{(Eq. 2)}$$

where B_i is the biomass of i (t·km⁻²), $\left(\frac{P}{B}\right)_i$ is the production rate (yr⁻¹), EE is the ecotrophic efficiency (i.e. the fraction of total production used in the system), $\left(\frac{Q}{B}\right)_j$ is the consumption rate (yr⁻¹), DC_{ji} is the fraction of prey i by weight in the average diet of predator j, Y_i is the catch (t·km⁻²·yr⁻¹), E_i is the

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net emigration, BA_i is the biomass accumulation , Q_i is the consumption, P_i is the production, R_i is the respiration and UA_i is the unassimilated food caused by excretion and egestion. Therefore, the model assumes that for each trophic group i, the production is equal to the sum of all predations, the biomass removed by other natural causes (non-predation), catches, exports (net migration), and biomass accumulation.

Ecosim, the dynamic version of Ecopath, is based on a set of differential equations that predicts changes in biomass and biomass flow rates by taking into account modifications in predator-prey relationships, dietary preferences and changes in fishing mortality (detailed equations in Walters et al., 1997 and 2000; Pauly et al., 2000; Christensen et al., 2005). Thus, the biomass growth rate of a group i during a time t interval *(*derived from Eq. 1) is expressed as:

$$\frac{dB_i}{dt} = g_i \times \sum_{j=1}^{N} Q_{ji} - \sum_{j=1}^{N} Q_{ij} + I_i - (M0_i + F_i + e_i) \times B_i \qquad \text{(Eq. 3)}$$

where g_i is the net growth efficiency, $M0_i$ the non-predation natural mortality rate, Q_{ji} is the consumption of prey j by group i, Q_{ij} is the consumption of group i by predator j, I_i is the immigration flow (t·km⁻²·yr⁻¹), F_i is the annual fishing mortality rate, and e_i is the emigration rate. The Q_{ji} parameter, which is determined by predator-prey relationships, is based on the foraging arena theory, in which it is assumed that spatial and temporal restrictions in predator and prey activity cause partitioning of each prey population into vulnerable and invulnerable components (Ahrens et al., 2012; Walters and Kitchell, 2001).

2.2.2 Functional groups definition and data sources

A first Ecopath model of the whole Celtic Sea and the Bay of Biscay continental shelf was built by Guénette and Gascuel (2009) and updated by Bentorcha (2014) and Bentorcha et al. (2017). Here, using complementary and updated information, we derived distinct models for each ecosystem (i.e. the Bay of Biscay and the Celtic Sea) and for each 1980 and 2013. Exploited functional groups (e.g. demersal fish: seabass, blue whiting, hake, haddock, megrim, whiting, sole, plaice and boarfish and for small pelagic fish groups: horse mackerel, mackerel, herring, anchovy and sardine) were given special attention because of their economic importance which yields better parameters estimation (biomass, catch, natural mortality, fishing mortality). Hake and cod were split into two stanzas (adult and juvenile, with a transition age of 24 months, the age of recruitment to the fishery).

Other functional groups were defined on the basis of ecological criteria (trophic level, maximum length, feeding type etc.) and data availability. Ten functional groups were defined for other exploited species: two cartilaginous fish groups (large sharks and sharks/rays), five "multi-species" groups (large, medium and small demersal fish species; large and medium pelagic fish species), and three groups of exploited invertebrates (cephalopods, lobsters/crabs and shrimps). The two models

also included two seabirds groups (Lassalle et al., 2012; Lauria, 2012), five benthic invertebrates groups (Lassalle et al., 2012), three zooplankton groups (defined by their sizes) and three primary producers (Lassalle et al., 2012). Finally, a bacteria group and a box for discards from commercial fisheries were added to the previous model developed by Bentorcha et al. (2017), following other models developed in European seas (Lassalle et al., 2011 and 2012; Mackinson and Daskalov, 2008; Sánchez and Olaso, 2004).

Thus, the models include 43 trophic boxes (i.e. functional groups) for the Bay of Biscay and 48 trophic boxes for the Celtic Sea ecosystem. Among these, 7 and 14 groups respectively, in the Bay of Biscay and in the Celtic Sea, were fully assessed by ICES expert working groups. In addition, for 11 and 4 groups respectively, time series of relative biomass were available from surveys and data-limited assessments (Table 1, detailed composition of groups in Supplementary material S1).

2.2.3 Model input parameter (B, P/B, and Q/B EE), diet and fisheries data

Biomass estimates from ICES stock assessments were used as input parameters for all assessed fish groups (Table S2 in Supplementary material). A correction prorated with catch data was applied to groups whose distribution is wider than the modelled area (hake, boarfish, mackerel and horse mackerel). For juvenile cod and hake, biomass was determined according to specific growth and mortality parameters that were used to link the two stanzas. The marine mammal biomass estimations used by Guénette and Gascuel (2009) were retained and considered equal in both ecosystems. Seabird biomass data were obtained from Lassalle et al. (2012) and Lauria (2012), based on scientific surveys. For other groups, the biomass was estimated with the mass-balanced calculations of Ecopath by setting ecotrophic efficiency (EE). This also applies for non-assessed demersal groups for which biomass could be estimated directly from EVHOE surveys using an arbitrary value for catchability. We considered that it is more reliable to estimate these biomasses using Ecopath, and then check for consistency of such estimates with survey and catch data and verify that the resulting F=Y/B ratio is consistent with expert knowledge on fisheries. Similarly, the biomass of phytoplankton groups was estimated by the model and compared to values provided by the Sea Around Us Project (www.seaaroundus.org) for the large marine ecosystem based on SeaWifs data.

According to Allen (1971), the P/B ratio was estimated for each group using equation: P/B=F+M, where F is fishing mortality and M natural mortality. For assessed groups, fishing mortality is the ratio between catches (Y) and biomass (B). When it was possible, natural mortality rates were obtained from ICES. Otherwise, natural mortality was estimated from the empirical equation proposed by Hoenig (1983) or Pauly (1980). Q/B ratio was calculated based on the empirical equation described in Palomares and Pauly (1998). In the previous models (Bentorcha et al., 2017; Guénette and Gascuel,

2009), diet values were extracted from a large review of the scientific literature on the study area or on similar close ecosystems (Table S3 in Supplementary Material). In this study, four diet matrices were derived from previous models, one matrix for each year (1980 or 2013) and ecosystem. To reflect main changes in prey abundance between 1980 and 2013, initial matrices were corrected proportionally to biomasses. Diet for benthic invertebrates and zooplankton groups were based on the Ecopath model constructed by Lassalle et al. (2012, 2011) (Supplementary Materials S4).

For tuna (functional group of large pelagics), catch data came from ICCAT statistics database (https://www.iccat.int/en/accesingdb.htm). For all other exploited species, the fisheries landings from 1980 to 2013 were provided by the ICES stock assessment working groups and by the Statlant database compiled by ICES (http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx). Starting in 1980, most landings were recorded by ICES subdivision (for instance, VIIIa or VIIIb). The few landing data (less than 5%) reported at the division level were pro-rated based on surface area to obtain an estimate at the subdivision scale. In both ecosystems, discards are known to occur, mainly in demersal fisheries, so for assessed stocks, we used a 15% discard rate as estimated by ICES. Based on expert advice, the discard rate was set at 40% for pouts and at 15% for other exploited groups (excluding Large Sharks),

2.2.4 Balancing the Ecopath models and fitting Ecosim

The 2013 Ecopath models of each ecosystem, based on the most reliable and recent data, were balanced first. Thus, the balancing process ensured consistency between all available information. Balancing was conducted following a strategy called "top-down". First, the production/consumption (i.e. gross efficiency), the respiration/assimilation and the production/respiration ratios were controlled to fall within a realistic range of values (e.g. P/Q within 0.1 and 0.3 according to Christensen et al. (2005)). Then, when the EE parameter was greater than one, we corrected, with parsimony, the diet matrix, and/or P/B or Q/B ratios. For instance, the P/B ratio of pelagic species such as horse mackerel and mackerel were revised up while the P/B ratio for large sharks and anglerfish, which induces a significant top-down control, was revised downwards. Moreover, cannibalism within some groups (e.g. hake) was reduced. The P/B ratio of the bacteria group, initially taken from Lassalle et al. (2012), was increased to balance the model and to be consistent with the published literature (see for example, Mackinson and Daskalov, 2008). Finally, as the diets of some multi-specific groups was relatively uncertain (e.g. small, medium and large demersals or medium and large pelagics), balancing has consisted in adjusting their diet gradually and moderately. The model consistency was checked in three ways: 1. comparing the biomass estimates of non-assessed demersal fish groups with values we derived from EVHOE surveys data; 2. calculating the fishing mortality for all exploited groups; 3. using the Prebal tool of the EwE software, to check the

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consistency of B, P/B, and Q/P parameters, according to the "rules of thumb" defined by Link (2010) and Heymans et al. (2016). The 1980 models were derived from the balanced 2013 models, changing values of catches (Y), biomass (B) and productivity (P/B), according to the available stock assessment data. The balancing process led again to correcting the diet matrix to take into account changes in prey abundance.

Ecosim models were fitted to biomass and catch data over the 1980-2013 period, using time series of fishing mortality as an index of fishing effort (i.e. as forcing functions). The time series were built using biomass estimates and fishing mortalities provided by ICES working groups for all assessed stocks (Table 1). For all other demersal groups in the Bay of Biscay, biomass indices were derived from EVHOE surveys that started in 1988. Thus, the data set includes biomass time series (used as relative values) for 18 groups, both in the Bay of Biscay and the Celtic Sea. Time series of catches are available for all the exploited groups (30 and 34 groups in the Bay of Biscay and the Celtic Sea, respectively) from ICES working group reports for assessed stocks, and from the Statlant database for the others. Model fitting was achieved by estimating the vulnerability parameters that minimize the sum of squared deviations between logarithms of observed and predicted biomass and catches, for all groups for which time series were available. The model was fitted to abundance and/or catch time series data using an iterative fitting procedure as described in Christensen et al. (2008). The Akaike Information Criteria (AIC) and the sum of squared deviations were used to measure how well the models fit the data. Vulnerabilities vary from one (i.e. a bottom-up control) to infinity (i.e. a top-down control) and can be interpreted as a reaction coefficient of a predator group to a change in abundance of its prey. In this study, vulnerabilities were estimated "by predator" following the adjustment routines of the EwE software. In addition, we used recruitment anomalies as environmental variables to improve the fit. These anomalies are calculated as the ratio between a given annual recruitment and the recruitment of the starting year (Bentorcha et al., 2017). They were applied to all groups assumed to be highly dependent of the environment, namely blue whiting, horse mackerel, mackerel, anchovy, sardine, herring, juvenile hake and juvenile cod. Recruitment anomalies are used as forcing functions on prey consumption, thereby affecting the productivity of forced groups.

2.2.5 Simulation of fishing scenarios

Using Ecosim, simulations were performed to assess the effect of various fishing mortality levels on the Bay of Biscay ecosystem. The Ecosim model previously fitted to past time series was used in forecast mode over the 2014 to 2030 period which was assumed sufficient to reach equilibrium. All simulations assumed constant recruitment at the 2013 level.

A first group of scenarios considers different values of F proposed in the literature from actual management targets to more ecosystem-based considerations (Table 2). The first simulation uses the status quo value (F=F_{2013}), and is considered as a baseline. The second scenario uses an F equal or lower than F_{MSY} when F_{msy} is known. The third scenario applied F≤0.25 (e.g. Worm et al 2009) and the fourth F≤M (e.g. MacCall, 2009). The last two scenarios investigate the effect of a more important reduction in F for demersal fish (F≤0.8*M, Walter and Martell, 2004) and pelagic fish (F≤0.6*M, Patterson, 1992).

A second group of scenarios simulates a reduction in F through the removal of fishing fleets. Although such scenarios are unrealistic, it is an interesting theoretical exercise to assess the specific impact of each fleet and to investigate the consequences of the removal of different species assemblages on the food web structure. Fishing fleets are defined according to the definition found in the French Observer at Sea Program (OBSMER, Cornou et al., 2015). Partial mortalities by fleet segment and by group were prorated with the relative catches in the last available year (2013). Each scenario simulates the removal of one of the following fishing fleets: the nephrops trawlers, the bottom trawlers, the pelagic trawlers, the small (<15 meters) and large gillnetters (>15 meters), and the long liners-hand liners.

Trends from all Ecosim scenarios were compared to the status quo scenario using trophic spectra (see next section). Then, the ecosystem effects and trade-offs between scenarios were analysed based on a set of indicators including: the mean trophic level (TL) of the biomass that reflects the impact of fishing on the entire network (MTL$_B$, Pauly et al. (1998)), the marine trophic index that measures the impact of fishing on high TLs (MTI, Pauly and Watson, 2005), the mean trophic level of the catch (MTLy, Pauly et al., 1998), the primary production required to support fisheries (PPR, Pauly and Christensen (1995)) and the total biomass and catches. We also used two new indicators proposed by Bourdaud et al. (2016): the high trophic level indicator (HTI) which is the ratio of the biomass of apex predators (TL>4) on the total biomass of consumers (TL>2) present in the ecosystem, and the apex predator indicator (API), the ratio of apex predators biomass on the biomass of all groups whose trophic level is greater than 3.25.

2.3 The EcoTroph model

2.3.1 Principles and equations of EcoTroph

EcoTroph (ET; Gascuel, 2005; Gascuel and Pauly, 2009) represents the continuous distribution of the ecosystem biomass B (or production P, or catch Y, etc.) across TLs, and can simulate the distribution changes induced by fishing. This distribution is called the biomass (or production, or catch, etc.) trophic spectrum (Gascuel et al., 2005). Moreover, trophic spectra can be calculated for fishing mortalities (Fτ=Yτ/Bτ) and fishing loss rate (φτ =Yτ/Pτ) which give two different images of the

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exploitation situation of the ecosystem: the fishing mortality spectrum reflects which TLs are currently targeted, whereas the fishing loss rate spectrum reflects the level of impact of fishing on each TL (Gasche et al., 2012).

Conventionally, the continuous distribution is approximated in the ET model by a discrete distribution, using trophic classes whose width is Δτ = 0.1 TL (Gascuel, 2005). The biomass enters the food web at TL=1, generated by the photosynthetic activity of primary producers and recycled by the microbial loop. There is usually no biomass between TLs 1 and 2, herbivores and detritivores being at TL 2. At TLs >2, the biomass is distributed along a continuum of values of TL, the diet variability of the various consumers resulting in all fractional TLs being filled (Gascuel, 2005; Gascuel and Pauly, 2009). Biomass moves from one class to the next according to predation and ontogenic processes. From a given secondary production occurring at trophic level 2, the ecosystem biomass distribution can therefore be expressed as the result of the biomass flow passing through the ecosystem, from low to high trophic levels (Gascuel, 2005). Thus, the model is constructed from two major equations derived from fluid mechanics. In steady-state conditions, the biomass at TL τ is calculated as:

$$B_\tau = \frac{\Phi_\tau}{K_\tau} \times \Delta\tau \qquad\qquad\qquad (Eq.\ 4)$$

where B_τ is the biomass present in the trophic class [τ, τ+Δτ[, K_τ is the flow kinetics and Φ_τ is the mean flow of biomass passing through trophic classes.

Because natural losses occur during trophic transfer (natural processes of respiration, excretion and egestion, non-predation mortality and removals by fisheries), the biomass flow is a decreasing function of TL:

$$\Phi_{\tau+\Delta\tau} = \Phi_\tau \times exp(-(\mu_\tau + \varphi_\tau) \times \Delta\tau) \qquad\qquad (Eq.\ 5)$$

where μ_τ and φ_τ are the natural loss rate and the fishing loss rate over a [τ, τ+Δτ[interval, respectively.

The last version of EcoTroph distinguishes two compartments, one accessible to the fishery and the other not (Gascuel et al., 2011). The accessibility to fisheries parameter corresponds to the proportion of a species or group that would be caught under the hypothesis of an infinite fishing effort. The same ET equations are used for both compartments, but their parameters differ since they take into account the fact that exploited species usually do not have the same characteristics as the unexploited ones, especially at low or intermediate trophic levels (Colléter et al., 2015; Gasche et al., 2012; Gascuel et al., 2011). Thus, parameters of the accessible part of the biomass are noted B_τ^*, φ_τ^* or F_τ^*. For each trophic group in the Ecopath model, a fishing accessibility coefficient, which varies from 0 to 1, is defined according to the selectivity that protects juveniles, the refuge effect in areas inaccessible to fishing operations, the presence of non-fished species within distinct Ecopath multispecific groups and the permanent arrival of fish via dispersal or migration for species whose

distribution range is larger than the study area (Bentorcha et al., 2017; Gascuel et al., 2011). Additional details for EcoTroph can be found in a number of papers (see e.g. Gascuel et al., 2011; Halouani et al., 2015), and the software is freely available either as an R package (Colléter et al., 2013), or as a plug-in module for EwE version 6.

2.3.2 EcoTroph parametrization and use

In the present study, analyses were performed with the R-EcoTroph package. Using the ET-Transpose sub-routine, biomass and catches of each functional group from Ecopath were distributed over a range of trophic classes around the mean TL of the group (estimated by Ecopath model), thus providing trophic spectra of biomass, catch, and fishing mortalities. This approach allows for a comparison of the 1980 and 2013 Ecopath models.

The ET-diagnosis sub-routine was used to establish a diagnosis of the fishing impact on the food web in both ecosystems in 2013. To do this, the accessibility parameter was fixed to zero for trophic boxes that are not exploited and determined following the available literature (ICES working group publications) or expert knowledge for groups targeted or caught as bycatch in fisheries (Tables S2 and S3). Then, the effects of increasing or decreasing fishing pressure on ecosystem functioning were simulated using effort multipliers varying between 0 (simulation of a no fishing scenario) and 3, applied to the 2013 fishing mortality F_τ. The ET-Diagnosis routine takes as input two parameters affecting ecosystem functioning: the top-down parameter α which specifies the magnitude of the control of predators on the abundance of their prey, and the shape parameter γ which defines the functional relationship between prey and predators (Gascuel and Pauly, 2009). Default values for α and γ were fixed in EcoTroph to 0.4 and 0.5, respectively.

EcoTroph also calculates two fishing indicators to evaluate the exploitation state of the food web (Gasche et al., 2012): $mF_{MSY,\tau}$, the fishing mortality multiplier giving the highest catch for each trophic level (thus overfishing occurs at level τ when $mF_{MSY,\tau} < 1$) and $mF_{0.1,\tau}$, the fishing mortality multiplier for which the slope of the catch per trophic level as a function of effort becomes inferior to a tenth (0.1) of the slope at the origin. By convention, the value $mF_{0.1,\tau} = 1$ defines the lower limit of the full exploitation (Gasche et al., 2012). Fishing indicators $mF_{0.1}$ and mF_{MSY} are commonly used in single species assessment and we used them to establish an overall ecosystem-scale diagnosis.

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3   Results

3.1   *Results of the Ecopath models and EcoTroph diagnostics*

3.1.1   *Current state of ecosystems*

Based on the 2013 Ecopath models, the total biomass of the Bay of Biscay ecosystem is 229.6 t·km^{-2} including trophic level 1 and 85.6 t·km^{-2} for animals only (TLs ≥ 2) (Table S2 in the supplementary material). The Celtic Sea ecosystem displays a higher biomass of 461.6 t·km^{-2} for all trophic levels, and 118.4 t·km^{-2} for animals only (Table S2). The accessible biomass (B*), the fraction of ecosystem biomass accessible to fisheries, is 7.3 and 8.3 t·km^{-2} for the Bay of Biscay and the Celtic Sea respectively, and catches amount to 1.9 and 2.1 t·km^{-2} year^{-1} respectively.

In both ecosystems, a decrease in total biomass was observed from the lower to higher TLs (Fig. 2). The biomass at trophic levels close to 2.3 is composed of various groups of zooplankton (i.e. micro and mesozooplankton groups) and benthic invertebrates such as subsurface deposit feeders and suprabenthic invertebrates. In both systems, a peak in biomass was observed between TLs 3 and 3.5 which are composed of pelagic fish (e.g. anchovy, herring, sardine) and various demersal fish (e.g. sole, plaice and other demersal groups). Predatory species such as hake, cod, anglerfish, seabass and large sharks have a trophic level around 4.5. The observed gap in the biomass spectrum at around TL 2.7 is mainly due to the small number of trophic groups present (e.g. macrozooplankton group). In both ecosystems, the larger accessible biomass is observed between TL 3 and 4.5, with more exploited species (or groups) in higher trophic levels. At around TL 4.7, selectivity (B*/B ratio) reaches a maximum of 0.75 (Table S2).

In both Bay of Biscay and Celtic Sea, the fishery targets a variety of ecological groups with TLs ranging from 3 to 5 (Fig 2). Fishing mortality for high TLs is slightly higher in the Bay of Biscay (at around 0.3 year^{-1}) because the fisheries target predatory species such as hake or seabass. Trophic levels between 3.5 and 4.0 (mainly pelagics and small to medium various demersals) are less targeted (F<0.2 year^{-1}). Nevertheless, in both ecosystems, a peak of catches was observed at TL 3.5 corresponding to horse mackerel, mackerel, and other small pelagic fish like sardine, herring and sprat. These catches represent approximately 25% of the accessible biomass at TL 3.5. The fishing loss rate, which measures the proportion of the production caught each year, increases with trophic level (Fig 2). TLs between 2 and 2.8 (benthic invertebrates such as bivalves and small crustaceans) were lightly exploited (fishing loss of 5-15%), while catches of intermediate TLs (small pelagics) amount to 30 % of their annual production and that of TLs higher than 4 (hake, anglerfish, megrim, cod, seabass, large sharks, etc.) amount to 60-70 %. The 2013 Bay of Biscay and the Celtic Sea ecosystems appear to have similar trophic structure with trophic spectra of biomass, catches and fishing mortalities roughly exhibiting the same shape.

3.1.2 Changes observed between 1980 and 2013

In the Bay of Biscay, trophic levels higher than 4.2 (mainly demersal species such as hake, whiting, anglerfish and large demersal) appeared to be less targeted in 2013, compared to 1980, with a fishing mortality reduced by more than 5 % at TL 4.7 (Fig. 3). However, this decrease is rather small, given the management measures adopted by the European Union in the late 1990s (precautionary approach) and then in the late 2000s (MSY management). For instance, fishing mortality decreased by about 20 % for hake, whiting and large pelagics, but remained almost unchanged for anglerfish or megrim and more than doubled for seabass. The biomass of high TLs classes increased by over 10 % as a result of the fishing mortality reduction and the occurrence of good recruitments. In particular, hake spawning stock biomass reached 200 000 t in 2013 from 100 000 t in 1980. Despite the fishing mortality reduction, the increase in biomass allowed the 2013 catches to increase to the 1980 level for these high TLs.

At intermediate trophic levels (mainly pelagic fish), successful recruitments led to a 20% increase in biomass, and up to 30 % for TL 3.5. Fishing mortalities increased by 31 % on average for TLs between 3 and 4. For instance, fishing mortality increased from 0.04 to 0.19 year^{-1} for horse mackerel. The increase in effort resulted in a 2-fold increase in catches at TL 3.5 between 1980 and 2013 (from 0.11 to 0.21 t km^{-2}, respectively).

In the Celtic Sea, the comparison between the 1980 and 2013 Ecopath models tells a different story. Fishing mortalities for high TLs (between 4.2 and 5) remained at a rather low level (around 0.24 year^{-1}, Figure 3). Their biomass increased by 58 %, likely due to favourable environmental conditions (with a growing biomass for large sharks, rays, hake, cod, whiting, megrim), while catches increased in the same proportion (+53%). At intermediate TLs, fishing pressure strongly increased (F was doubled at TL 3.6), while biomass declined (-13% on average between TL 3.5 and 4.0, mainly due to horse mackerel and mackerel). However, at TL 3.6, the decline is partly compensated by boarfish, an emerging species whose stock biomass was boosted by successive good recruitments. Total catch between TL 3.5 and 4.0 increased by 55 %, mainly driven by boarfish and horse mackerel. Additionally, the trophic flow kinetic (which quantifies the velocity of biomass transfers in the food web) has increased by 47 % at TL 3.6 as a result of change in species composition.

3.1.3 Diagnosis of the Exploitation status of ecosystems

In the Bay of Biscay, EcoTroph simulations showed a clear improvement of the exploitation status in 2013 compared to 1980 (Fig. 4). In 1980, all trophic classes greater than 4.4 were overfished (F_{msy} <1) (these trophic levels include some of the ecosystem's most economically important predator species

such as hake, seabass, anglerfish, large pelagic fish) whereas nowadays, overexploitation starts at TL 4.7 (mainly large sharks). Thus, trophic classes between 4.4 and 4.6 shifted from overfishing in 1980 to sustainable fishing in 2013. Moreover, F_{msy} for TL above 4.8 are closer to one in 2013 than in 1980, which suggests less overexploitation. Indeed in 1980, fishing effort at TL 5.0 would have had to be reduced by 40% to shift from overfishing to full exploitation (mF_{MSY}=0.6), while in 2013 the reduction required to reach full exploitation is only 10% (mF_{MSY}=0.9). This improvement in the status of high TL classes is partly the result of fishing effort reduction initiated in the early 2000s, which enabled the (slow) recovery of some stocks, and of some good recruitments (e.g. hake) due to favourable environmental conditions.

In the Celtic Sea ecosystem, EcoTroph simulations showed no clear improvement between 1980 and 2013 (Figure 4). In both years, the full exploitation is reached for trophic classes between TL 4.1 and 4.4 (cod, juvenile hake, whiting, sharks and rays) with overfishing for trophic levels higher than TL 4.4 (large sharks, large pelagics, anglerfish, seabass, hake, megrim). Furthermore, in 2013, fishing effort at TL 5.0 should be reduced by 40% to reach the full exploitation state.

In both ecosystems, values of mF_{MSY} and $mF_{0.1}$ suggest that trophic levels lower that 4.0 are moderately exploited. These overly optimistic results are due, in part, to the fact that some groups (such as sole at TL 3.2) are aggregated with other very abundant groups (as carnivorous and necrophagous benthic invertebrates), lightly fished, that could support a strong increase in fishing effort before being overfished.

3.2 Ecosim results and simulation of fishing scenarios

3.2.1 Biomass and catch trends over the 1980-2013 period

In both ecosystems, the best fit of the Ecosim model was obtained using both fishing mortalities and recruitment anomalies as forcing functions (see Table S5.1 in Supplementary Material, for AIC and SS results). Recruitment anomalies, assumed to be a proxy of the effects of environmental conditions, appeared especially important for the fit of stanza groups and monospecific pelagic groups such as anchovy, sardine (mediocre fit), herring, mackerel (still not very good fit), and, to a lesser extent horse mackerel. Trends in hake predicted biomass, in the Bay of Biscay, were close to the observed values, with a decrease until the 2000s mainly due to high fishing pressure, and a sharp increase since 2008 which can only be obtained by taking into account the occurrence of good recruitment over the last decade (Fig. S5.2). In both ecosystems, we note that fishing mortalities on demersals show similar temporal trends with an increase between 1980 and 1990, a plateau between 1990 and 2005, followed with a decrease between 2005 and 2010. Thus, since 2010, fishing mortalities remain stable and close to the 1980 assessed level (Fig. 5). In contrast with pelagic catches, fluctuations of observed demersals catches are not well reproduced by the models in both ecosystems.

In the Bay of Biscay, the biomass of demersal fish estimated from Ecosim increased since the mid-1990s, and reached a level 28% higher in 2013 than in 1980 (Fig. 5). This is especially the case for groups such as small and medium demersal fish and hake. Small demersals benefited from a release of predation, due to the decrease in horse mackerel biomass, while medium demersals and hake benefited from a release of the fishing pressure and from an increase in prey abundance. The biomass of pelagics decreased as the demersal biomass increased. This decline is mainly caused by horse mackerel, while in contrast, the sardine biomass increased slightly over the study period, due to good recruitments. According to the Ecosim model, the predation mortality of hake on horse mackerel rose from 0.04 to around 0.14 year^{-1} between 2000 and 2013, and is a significant driver of the downward trend observed for horse mackerel biomass. The model reproduces pretty well the peak of pelagics catches in the early 2000s and the following decline associated with the decrease in fishing pressure and biomass. This change is mainly driven by two groups: anchovy, for which there has been a fishery closure between 2006 and 2010, and horse mackerel for which fishing mortality decreased after 1996 (Fig. 5). Thus, the predicted trends (and the trophic functioning) for the Bay of Biscay ecosystem appear to be controlled by two main groups: hake and horse mackerel.

In the Celtic Sea, the recovery of demersal biomass occurs earlier than in the Bay of Biscay but is less pronounced (+15% in 2013 compared to 1980). The predicted increase in predation was mainly caused by two groups (result not shown) who's fishing mortalities decreased over the period: anglerfish (biomass from 0.44 t·km^{-2} in 1980 to 1.12 t·km^{-2} in 2013) and haddock (from 0.31 to 0.86 t·km^{-2}). The recent increase in hake biomass is not well captured by the Ecosim model due to an increase of anglerfish (potential predator) in the same period. Overall, the rising demersal biomass led to an increase in catches despite the reduction in fishing mortality in the last decade. In contrast with the Bay of Biscay, pelagics biomass declined continuously since the mid-1990s, mainly due to horse mackerel (-12% in 2013 compared to 1980), strongly impacted by an increase in fishing mortality and predation by anglerfish and whiting. On the contrary, mackerel would have benefited from a decrease in fishing pressure since 2003, a general decline in predation until 2007, and large recruitments over the last years (but biomass did not increase according to Fig. S5.3). Overall, the increase in fishing pressure on pelagic fish in the late 2000s led to very substantial catches but at the cost of a decrease in biomass for some groups such as horse mackerel.

3.2.2 Simulations of fishing scenario in the Bay of Biscay up to 2030

Bearing in mind the poor Ecosim fits for the recent years in the Celtic Sea ecosystem, simulations were performed for the Bay of Biscay only. Ecosim simulation using the status quo scenario suggests that most exploited groups require 6 to 7 years to reach their equilibrium values (not shown). Maintaining fishing pressure at the 2013 level is predicted to cause a 10% decrease in the abundance

of higher trophic levels such as whiting, toothed whales, seabass, hake, anglerfish, large demersals and large pelagics, while the biomass of intermediate trophic levels such as mackerel, horse mackerel and sardine is predicted to decrease by 18%. Thus, under status quo, the main exploited groups of the Bay of Biscay would likely not recover.

Three of the scenarios, F≤F_{MSY}, F≤M and F≤0.25, show similar patterns regarding predicted biomass trends (Fig. 6) although the groups affected vary. For example, fishing mortalities are reduced for sole, hake, megrim, anglerfish and Norway lobster in the F≤0.25 scenario, and for blue whiting, sole, hake, mackerel and horse mackerel in the F≤F_{MSY} scenario. The three scenarios predict that high TLs (>4.2) would be positively impacted by the reduction in fishing pressure (+5% in biomass), while the biomass of intermediate trophic levels would decrease (-3%) due to top-down controls which are not compensated by the reduction in fishing pressure. The total biomass would decrease (Table 3) because the higher biomass of high TLs does not compensate for losses at intermediate TLs. Also, reducing fishing mortality would likely result in a lower catch than that of the status quo and in an increase in the trophic level of both catches and biomass, as expressed by the ecological indicators API, HTI and MTI.

The last two fishing scenarios aim to protect demersals (F demersal) or pelagics (F pelagic) (Table 2). The F demersal scenario is predicted to result in a 5% increase in biomass for high trophic levels (seabass, anglerfish, sharks and rays) and in an indirect negative impact induced by predation on intermediate trophic levels (mainly on horse mackerel, mackerel, medium and small demersals). This scenario would maximise ecological indicators related to the ecosystem trophic structure and especially to high trophic level (MTI, HTI and API), minimise the primary production required (PPR), and result in the lowest biomass and catch. The mean trophic level of the catch (MTL_Y) would be low, due to smaller catches at high TLs, while those of lower TLs would be maintained. The F pelagic scenario results in a decrease in fishing mortality by half for mackerel and horse mackerel and would benefit all higher TLs (hake, seabass, megrim and various seabirds) through prey-predator relationships (i.e. bottom-up controls). Compared to the others, this scenario exhibits the highest values of total biomass, total catches and MTL_B. Nevertheless, there is no discernible improvement of the trophic structure of the Bay of Biscay ecosystem, as all other indicators (MTI, HTI, PPR and MTL_Y) are similar to that of the status quo scenario. This scenario also exhibits the smallest API value.

In practice, a reduction in fishing intensity could be achieved in many ways. Figure 7 illustrates that the removal of different fleets would result in very different effects on the food web structure. Indeed, the removal of the two most important fishing fleets, the bottom trawlers and the large gillnetters (> 15 m), would have a large impact on the entire trophic structure (Fig. 7). Bottom trawlers induce a reduction in biomass at the higher trophic levels (around 9%) and cause a release of the predation pressure (by top-down control) on intermediate trophic levels (approximately +9%

of biomass at TL=3.5). Large gillnetters have a negative impact on the higher trophic levels, especially on hake, and cause a decrease of about 5% on the biomass of trophic class TL=5, resulting in a top-down induced increase for intermediate TLs (such as mackerel and horse mackerel). Thus, through cascading effect, bottom trawlers and large gillnetters impact all TLs between 2 and 5, inducing changes in species composition and benefiting intermediate and low trophic levels characterised by high turnover rates (e.g. small pelagic fish, benthic invertebrates, etc.). The impacts of other fleets operating in the Bay of Biscay are less pronounced, due to the small landings and/or the reduced spatial coverage (e.g. Nephrops trawlers). However, pelagic trawlers, which target mainly anchovy, sardine and to a lesser extent mackerel and the medium pelagics, have a larger impact on high trophic levels than on the targeted trophic levels. The effect of pelagic trawlers, although weak, due to limited fishing effort, highlights the bottom-up control of prey on their predators and thus, the ecosystem effects of prey exploitation.

4   Discussion

4.1   Models limitations and perspectives

Ecosystem models, especially trophic models, have a key role to play in improving scientific knowledge on exploited marine ecosystems, and in the development of management scenarios for an ecosystem approach to fisheries (Coll et al., 2015). Despite the many uncertainties inherent to their uses, EwE and EcoTroph models provide an opportunity to represent marine ecosystems in a simplified form, to test the consistency of the available data and to explore the long-term development of complex systems (Christensen and Walters, 2004).

According to Fulton et al. (2003), the structure and complexity of models have a strong influence on the ability to capture the complexity and real properties of an ecosystem. In this study, we chose to focus on commercially important species in the perspective of developing an ecosystem-based fisheries management. The structure of our models (composed of 43 and 48 functional groups, for the Bay of Biscay and the Celtic Sea respectively) follows the trend observed in the scientific community to increase complexity and number of compartments in Ecopath models (Colléter et al., 2015b). For example, the "North Sea" model developed by Mackinson and Daskalov (2008) is composed of 68 functional groups, and the "Celtic Sea" model built by Lauria (2012) to study seabirds includes 64 functional groups.

The comparison of structure and diagnosis of the Bay of Biscay and the Celtic Sea confirms the need to consider them separately. However, splitting the initial model of Bentorcha et al. (2017) led to empirical adjustments of some parameters and especially of the diet matrix. Thus, although the initial diet matrix was based on published stomach content analysis from studies performed mainly in

close or similar ecosystems, it undoubtedly remains the main weakness of our models. To this end, the Eatme project, currently conducted by IFREMER, is collecting stomach contents and isotopic measurements of the main commercial species, and should provide more robust information for the implementation of future trophic models.

In this work, we used reliable estimates of biomass and catch, issued from ICES working groups. Corrections of catch statistics that were necessary to make up for incomplete time series and geographical distribution were based on the strong assumption that the catch distribution is related to the stock distribution. Indeed, in spite of potential biases linked to fishing strategies, the distribution of commercial catches usually reflects, at least in the same order of magnitude, those of the underlying populations (Klyashtorin, 1998; Pauly et al., 1998). Furthermore, this type of correction only affects a limited part of the ecosystem biomass and is relatively common in Ecopath approaches (see for example Ainsworth et al., 2001; Sánchez and Olaso, 2004).

The diagnosis of the ecosystems status (1980 and 2013) using EcoTroph is sensitive to the accessibility coefficients (Colleter et al., 2012; Halouani et al., 2015; Gasche et al., 2012). Nevertheless, changing the accessibilities does not affect the qualitative differences observed between ecosystems and time periods. In other words, the contrast we showed between the Bay of Biscay and the Celtic Sea, as well as the improvement in ecosystem status observed in the Bay of Biscay should be considered as robust results.

The Ecosim models we developed suffer from a lack of contrast in the time series and a lack of data on fishing effort. Thus, they were not able to properly reproduce some demersals catches fluctuations over the period 1980-2013, which weakens our results both in terms of diagnostics and projections. According to Guénette and Gascuel (2012), the largest changes in biomasses and catches took place after World War II, between 1950 and 1980, while the following period is marked by relative stability in abundances and catches. The next step to disentangle fishing and environmental impacts on these ecosystems would be to rebuild historical time series of catch and fishing effort, over the 1950 to 1980 period, and to update Ecopath and Ecosim models.

Simulations in forecast mode were conducted assuming a constant recruitment, which is the usual assumption in many approaches related to fisheries management, although it is probably unrealistic in the perspective of global change, especially knowing that Ecosim fits were better when including recruitment anomaly indices. However, our goal is not to predict the future, but rather to compare contrasted theoretical scenarios of fisheries management, all other things being equal. In the same way, removing an entire fleet is a theoretical but unrealistic management scenario in an ecosystem-based approach to fisheries where socio-economical aspects have to be taken into account (Garcia and Cochrane, 2005).

The use of ecological indicators provides additional information on the diversity and the complexity of interactions between ecosystem compartments. Even if it is difficult to interpret absolute values of such indicators, they are convenient to compare scenarios (Shannon et al., 2014). It is noteworthy that some indicators used, such as MTLs, are insensitive to change in F, while the two indicators HTI and API proposed by Bourdaud et al. (2016) appear more informative. Moreover, additional indicators related to habitats, for instance, are also required and deserve to be further developed (Cury et al., 2005; Jennings, 2005).

4.2 EwE to understand trophic interactions and monitor food web health

Several EwE models have been published regarding the north eastern Atlantic ecosystems, with a large diversity of objectives. Trophic models are dedicated to analyse food web interactions and ecosystems properties *sensu* Odum (e.g. Araújo et al., 2005; Lassalle et al., 2011; Lees and Mackinson, 2007; Mackinson and Daskalov, 2008), to assess fisheries and environmental impacts on ecosystems (Ainsworth et al., 2011; Araújo et al., 2006; Lassalle et al., 2012; Sánchez and Olaso, 2004), to explore fisheries strategies (Araújo et al., 2008; Lynam and Mackinson, 2015), or to assess economic or ecological impacts of Marine Protected Areas (Beattie et al., 2002; Guénette et al., 2014; Valls et al., 2012). Our models were built specifically to explore the impact of fishing and analyse various fishing scenarios for their impact on catch, and food web structure and dynamics.

Using models built in a consistent way we showed that exploitation patterns at the ecosystem scale are quite similar in both the Bay of Biscay and Celtic Sea ecosystems. However, in the Bay of Biscay, fisheries management resulted in a decrease in fishing pressure on the highest TLs, while the diagnosis for the Celtic Sea remained almost unchanged. Two factors may explain this difference. First, even if high TLs species benefited from some good recruitment years in the Celtic Sea (e.g. cod, hake), catches increased proportionally to biomass and thus fishing mortalities remained high. Second, biomass of prey fishes increased in the Bay of Biscay while it decreased in the Celtic Sea. In addition, the species composition at intermediate TLs changed with the increase in boarfish abundance, which seems to lead to faster trophic transfers, and to a less efficient food web with potential detrimental effects for predators (Bentorcha et al., 2017; Smith et al., 2011). Our results suggest that the observed changes at the stock and the ecosystem (species composition) level, can be explained by the interplay between anthropogenic impact and changes in environmental conditions.

The results tend to confirm the beneficial effect of the management measures implemented at the European scale since the late 1990s. First, using B_{pa} and F_{pa} as thresholds to calculate the Total Allowable Catch (TAC), and the precautionary approach implemented since 1998 (ICES, 1997) in

European waters, led to restrictive quotas and contributed to the relative stabilisation or the decrease in fishing mortality rates recorded in the late 1990s. Then, in the context of the Common Fishery Policy, the MSY approach (ICES, 2009) adopted in 2008 and based on more precautionary thresholds (F_{MSY}) has led to a more pronounced decrease in fishing mortality rates at ecosystems scales, which enabled a partial recovery for several fish stocks. However, in some cases, the improvement in biomass and reduction in F result from serendipitous good recruitment years (e.g. hake). In the Bay of Biscay, the overall decrease in fishing pressure only led to a slight increase in total biomass.

Our results suggest that both ecosystems returned more or less to exploitation levels of the early eighties. However, according to Guénette and Gascuel (2012), looking back only 20-30 years would lead to believe that the situation is stable and that the ecosystem has not changed in a typical case of "shifting baseline" syndrome (Pauly, 1995). In fact, fishing impacts are still high at the ecosystem scale and the progression towards a sustainable exploitation is too slow to meet the Common Fisheries Policy objective, i.e., all stocks fished at F_{MSY} by 2020 at the latest. Additionally, the primary production required to sustain fisheries in 2013, 32% in the Bay of Biscay and 22% in the Celtic Sea, is similar to those of the 1980 models. These high PPR values suggest that fisheries use a high proportion of the productive capacity of the continental shelves, and are similar to heavily exploited ecosystems studied by Pauly and Christensen (1995). Regarding patterns of exploitation, some of our results suggest a combination of fishing down (Pauly et al., 1998) and fishing through marine food web (Essington et al., 2006), in agreement with previous studies (Gascuel et al., 2016). This appears to be especially the case in the Bay of Biscay where changes in exploitation patterns were partly caused by an increase in abundance of lower trophic levels such as horse mackerel, and by economic considerations which encouraged fishing fleets to replace high value groundfish by large volumes of lower value fish (Guénette and Gascuel, 2012; Steinmetz et al., 2008).

4.3   EwE to analyse various scenarios of an ecosystem-based fisheries management

The Ecosim simulations used in forecast mode for the 2014-2030 period sheds new light on the exploitation status of the Bay of Biscay, and on the fishing scenarios that would maintain forage fish communities and conserve or restore top predator populations. This largely depends on the respective importance of top-down vs. bottom-up controls in trophic interactions (Power, 1992; Rosemond et al., 2001; Walters et al., 2005b). Our results, supported by the analysis of vulnerability parameters (not shown), suggest that top-down controls are of great importance in both ecosystems. In the scenarios reducing the fishing mortalities on high TLs (F≤M, F demersal, F≤0.25 and F≤F_{MSY}), top-down controls resulted in a decrease in the biomass of intermediate trophic levels following the

high TLs rise in biomass. For instance, fishing at F_{MSY} has a positive impact for demersal species such as hake, but at the cost of a decrease of intermediate trophic levels such as horse mackerel. Walters et al. (2005a) have shown that applying F_{MSY} (calculated from single-species assessments) at the scale of the ecosystem might results in widespread degradation in ecosystem function, and in considerably smaller overall yield and value than would be predicted from the sum of corresponding single-species yields. This is partly what the model predicted with the F_{MSY} scenario under which total catch and total biomass are lower than in the status quo scenario. Thus, biological interactions may prevent achieving current single-species-based thresholds simultaneously for all stocks (Gascuel et al., 2016; Piet and Rice, 2004). We therefore have to accept that there will be "winners" and losers" in each fishing scenario, as Lynam and Mackinson (2015) have shown in the North Sea.

The F≤0.25 scenario is derived from simulations developed by Worm et al. (2009) demonstrating that a low fishing mortality can be considered an appropriate trade-off between conservation and exploitation objectives. However, applying the same fishing mortality to all trophic levels is a simplistic approach, clearly not optimal in a practical fisheries management perspective and for minimising the impact of fishing on ecosystems (Froese et al., 2016). Among the various scenarios we tested, managing to protect intermediate trophic levels (F pelagic), demersals' prey, emerges as a possible strategy to maintain forage fish stocks and rebuild the biomass of higher-trophic levels. The impact of abundant groups such as mackerel and horse mackerel on other trophic groups suggests that bottom-up controls also play a key role in the ecosystem, partly confirming the conclusions drawn by Lassalle et al. (2011) for the Bay of Biscay and by Smith et al. (2011) in a worldwide meta-analysis.

It is now recognized that fleet-based approach is a pathway to implement an effective ecosystem approach to fisheries management, especially in European seas (Gascuel et al., 2012; Lynam and Mackinson, 2015). Mixed fisheries models are now used routinely to inform managers on the influence of technical interactions on operational implementation of management options calculated on a single stock basis. Also, long-term management plans are often developed to assess socio-economic impacts of various management options at the scale of fleets and metiers. Our analysis demonstrated that trophic models can also be useful to examine the direct and indirect consequences of fleet-based management options on ecosystem compartments. Due to a lack of data, our results should be considered as preliminary and interpreted qualitatively rather than quantitatively. Nevertheless, the fleet-based scenarios utilized in the Bay of Biscay clearly suggest that the highest ecological impacts on fish communities are caused by the most important fleets in terms of landings, i.e. bottom trawlers and large gillnetters. Here, simulations suggest that trawl impacts a large part of the food web by removing a large range of predators and, through predation release, induces an increase of lower trophic levels abundance, eventually leading to large changes in

all species assemblages. Combining trophic models and model-based indicators to assess the ecological, economic and social performances of the various fleets operating within an ecosystem, appears as a key step for the effective implementation of EAFM. The impacts of bottom trawling on habitats and associated communities have been well described (De Groot, 1984; Kaiser et al., 2006; Palanques et al., 2001) and would add to the impacts described in the present study.

Conclusion

In the present study, we showed how trophic models, especially Ecopath with Ecosim as well as EcoTroph, are key tools to implement EAFM. In particular, they make it possible to establish diagnoses of the exploitation status at the scale of the entire food web. They provide insights into how trends in biomass and catch depend on the fishing impacts, environmental changes and predator-prey interactions. Moreover, Ecosim simulations enable the assessment of the impact of every fleet on the food web.

These models do not replace single-species approaches of stock assessment. However, they can complement them and inform the decision-making in fisheries management by testing various fishing scenarios to identify "winners" and losers", which cannot be identified with single-species models. To conclude, we suggest that such advice-oriented trophic models should be developed within each European marine ecosystem and routinely used in order to monitor ecosystems health and to analyse trade-offs between various objectives and scenarios of an ecosystem-based fisheries management.

Acknowledgements

Supplementary material

S1 – List of species included in the trophic groups of the Ecopath model

S2 – Parameters of the Ecopath models (Bay of Biscay and Celtic Sea, 1980 and 2013)

S3 - Diet information: sources by species

S4 – Diet matrix (Bay of Biscay and Celtic Sea, 1980)

S5 – Fit of the Ecosim models (AIC and trends in biomass and catch for the two models)

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Table 1 - Functional groups, and data sources used to build Ecopath models, and time series used in fitting Ecosim, in the Celtic Sea (CS) and the Bay of Biscay (BB) ecosystems.

Number of groups	Group types	ECOPATH		ECOSIM time series		
		Biomass	Catches	Biomass	Catches	Fishing mortality
2	Marine mammals	Literature	0	n.a.	0	0
2	Seabirds	Surveys	0	n.a.	0	0
7 (BB) 14 (CS)	Fully assessed stocks : hake (juv+ad), sole, mackerel, horse mackerel, anchovy, sardine, seabass(CS), cod (CS, juv+ad), haddock (CS), whiting (CS), boarfish (CS), plaice (CS)	ICES working group	ICES working group	ICES working group	ICES working group	ICES working group
11 (BB) 4 (CS)	Partially assessed groups : anglerfish, blue whiting, megrim, Norway lobster (CS), rays (BB), seabass (BB), demersal L, M & S (BB), pouts (BB), cephalopods (BB)	Estimated according to survey data	ICES & Statlant database	EVHOE survey	Statlant database	ICES (4 goups only)
7 (BB) 12 (CS)	Other exploited groups: sharks L, pelagic L & M, crabs, shrimps, whiting (BB), plaice (BB), rays (CS), demersal L, M & S (CS), sprat (CS), pouts (CS), cephalopods (CS)	Estimated by the model	ICES & Statlant database	n.a.	Statlant database	n.a.
5	Other benthic invertebrates	Estimated by the model	0 or Statlant (molluscs)	--		
3	Zooplankton	Estimated by the model	0	--		
3	Primary producers	Estimated according to SeaWifs data	0 or Stadland (algae)	--		
3	Bacteria, Detritus and Discards	Literature or estimated by the model	0	--		

Table 2 - Fishing scenarios 2014-2030 simulated in the Bay of Biscay with Ecosim

Scenario	Observations	Sources
F = status quo	Fishing mortality maintained at its 2013 level for all fished groups (baseline scenario)	
F ≤ F$_{MSY}$	Blue whiting, sole, horse mackerel, mackerel and hake harvested at Fs set to achieve Maximum Sustainable Yield (MSY). All other species harvested at F status quo (Fsq lower than F$_{MSY}$ or F$_{MSY}$ unknown).	F$_{MSY}$ are taken from ICES single species assessments and advice (ICES, 2013).
F ≤ 0.25	F = 0.25 for all exploited groups whose F$_{2013}$ > 0.25. This concerned sole, hake, megrim, anglerfish and Norway lobster. All other species harvested at F status quo.	According to Worm et al. (2009), reducing exploitation rates (here F = Y/B) to 0.25 is predicted to rebuild total biomass, increase average body size and strongly reduce species collapses with little loss in long-term yield.
F ≤ M	F = Natural mortality (M) for all groups for which F$_{2013}$ is higher than the corresponding natural mortality. All other species harvested at F status quo.	M has long been used in fisheries science as a proxy for the upper limit of the instantaneous rate of sustainable fishing mortality F$_{MSY}$ (Froese et al., 2016; MacCall, 2009)
F demersal	F = 0.8 x M for all demersal groups for which F$_{2013}$ is higher than this threshold value. All other species harvested at F status quo.	Threshold of fishing mortality recommended by Walters and Martell (2004) for demersal species.
F pelagic	F = 0.6 x M for all pelagic groups for which F$_{2013}$ is higher than this threshold value. All other species harvested at F status quo.	According to Patterson (1992), pelagic stocks appeared to be in equilibrium for an exploitation rate F/Z=0.4, which may be used as a guideline for the appropriate exploitation of pelagic stocks.

Table 3 - Values of ecological indicators in 2030 for the six fishing scenarios simulated in the Bay of Biscay (see table 2). Mean trophic level of the ecosystem biomass (MTL$_B$), marine trophic index (MTI), high trophic level indicator (HTI), apex predator indicator (API), total biomass and catches, primary production required to sustain fisheries (PPR, in % of the primary production), and mean trophic level of the catch (MTL$_Y$)

	Status quo	F=F$_{MSY}$	F≤0.25	F≤M	F demersal	F pelagic
MTL$_B$	2.39	2.39	2.39	2.39	2.38	2.39
MTI	3.70	3.71	3.71	3.71	3.73	3.70
HTI (%)	2.7	2.8	2.8	2.8	2.9	2.7
API (%)	21.4	22.6	22.8	22.8	24.6	20.9
Total biomass (t/km²)	89.2	88.8	88.8	88.9	88.5	89.4
Total catch (t/km²)	1.36	1.29	1.26	1.26	1.19	1.35
PPR	10.1	9.1	9.0	9.1	8.1	10.2
MTL$_Y$	3.74	3.72	3.72	3.73	3.70	3.74

Figure captions

Figure 1 - Map of the continental shelves (hatched area) of the Celtic Sea (ICES divisions VIIe-j) and the Bay of Biscay (ICES divisions VIIIab).

Figure 2 - Trophic spectra of biomass (B), accessible biomass (B*), catches, fishing mortalities (F) and accessible fishing losses (φ*) in the Bay of Biscay (grey) and the Celtic Sea (black) in 2013.

Figure 3 - Changes in trophic spectra derived from Ecopath models, between 1980 (dotted line) and 2013 (solid line), for the Bay of Biscay (left) and the Celtic Sea (right). Top: biomass (t/km²) in log scale. Middle: fishing mortalities (year^{-1}). Bottom: catches (t/km²/year).

Figure 4 - Indicators of the exploitation status of ecosystems obtained using EcoTroph simulations: fishing mortality multipliers $mF_{0.1}$ and mF_{MSY} per trophic level in the Bay of Biscay (left) and the Celtic Sea (right), in 1980 (top) and 2013 (bottom).

Figure 5 - Changes over the 1980 to 2013 period for: relative biomass (standardized to the 1980 value), observed and predicted (from Ecosim) catches, and fishing mortalities, for demersal fish, pelagic fish and miscellaneous invertebrates (such as cephalopods, Norway lobster or benthic invertebrates).

Figure 6 - Biomass ratio per trophic class (2030 simulated / 2030 status quo) according to 5 fishing management scenarios run with Ecosim (see table 3)

Figure 7 – Impact of the French fishing fleets operating in the Bay of Biscay: biomass ratio per trophic class (2030 simulated / 2030 status quo) resulting from the removal of each fleet.
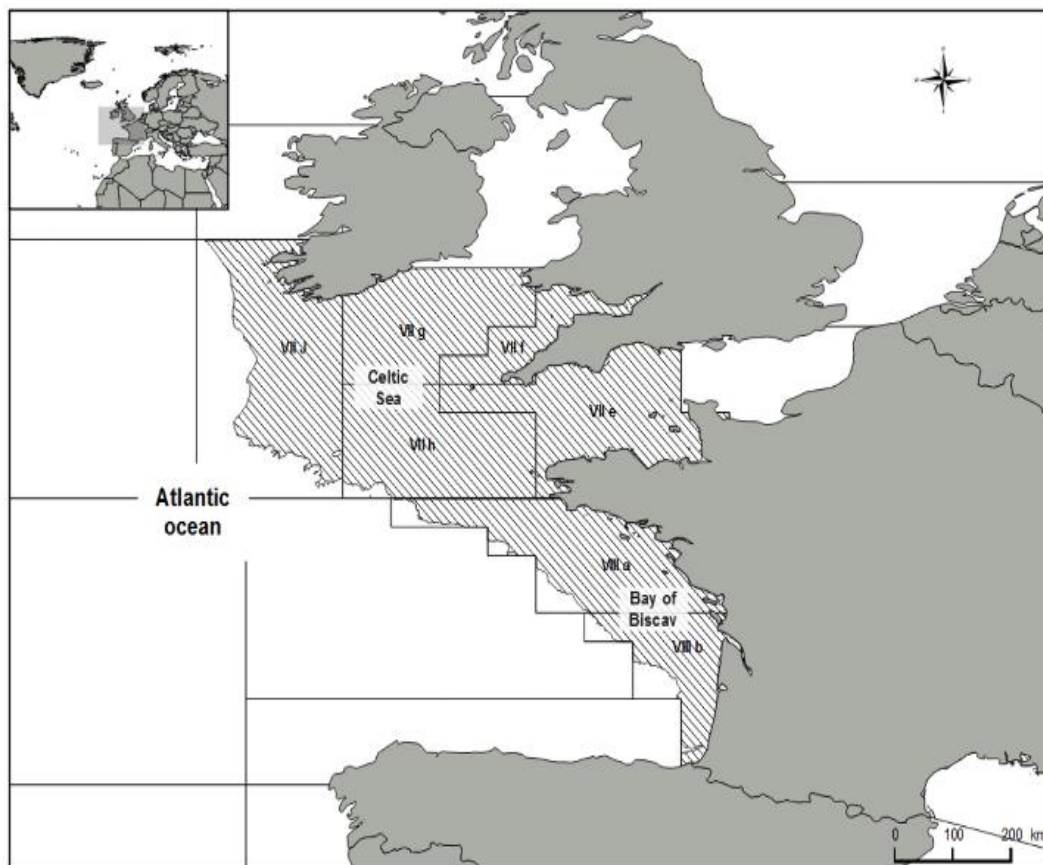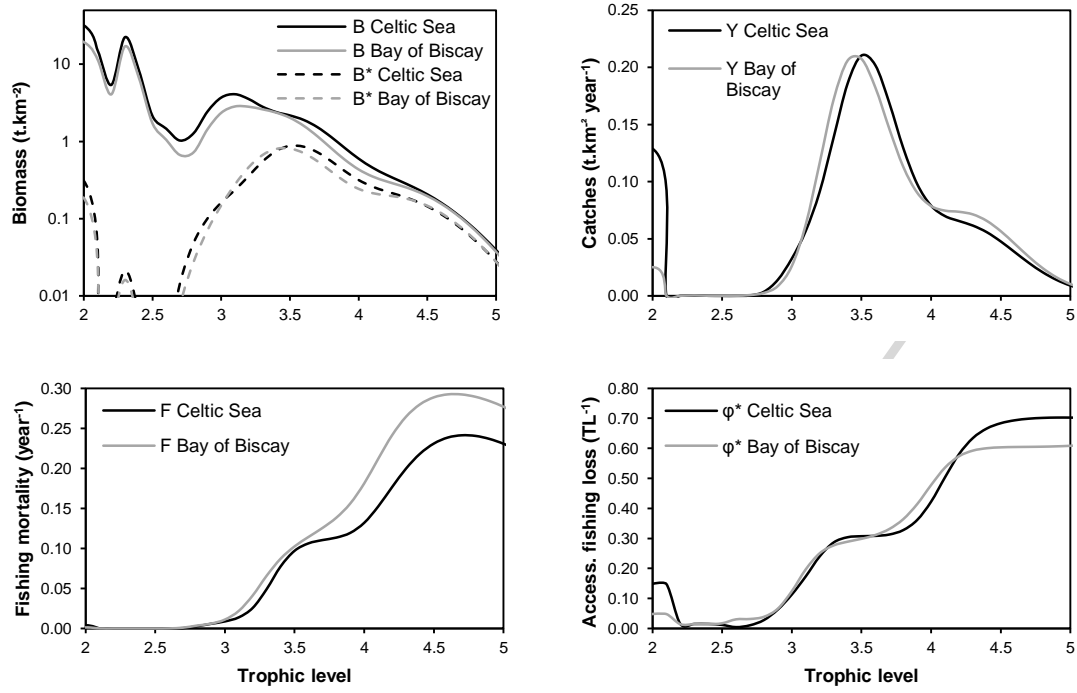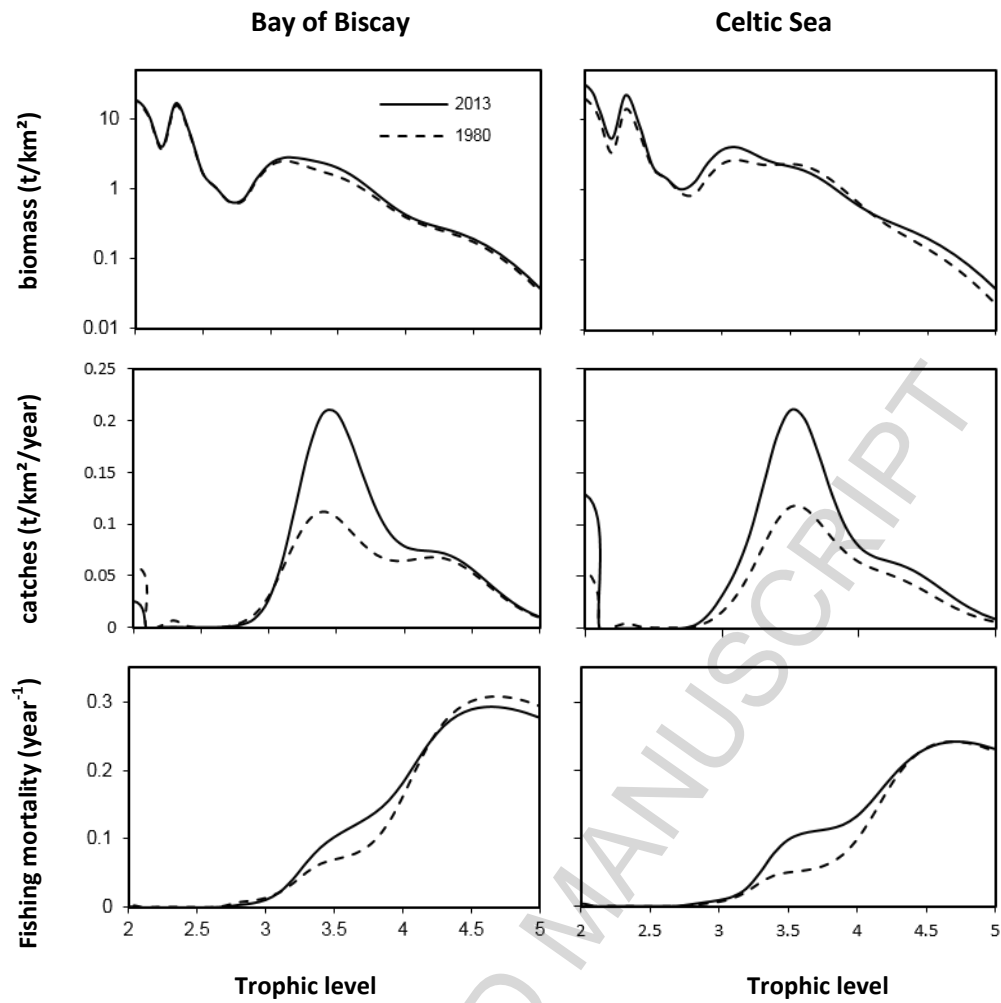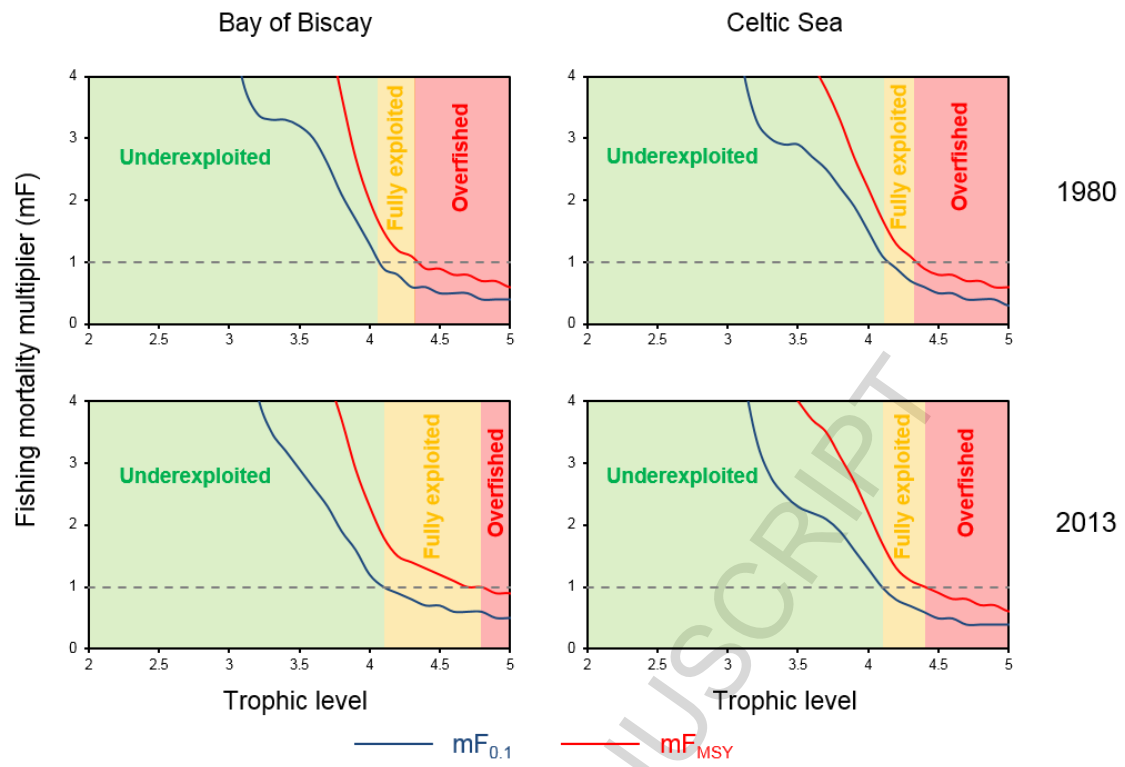
Figure 1 .

Figure 2.

Figure 3.

Figure 4.

Bay of Biscay

Celtic Sea
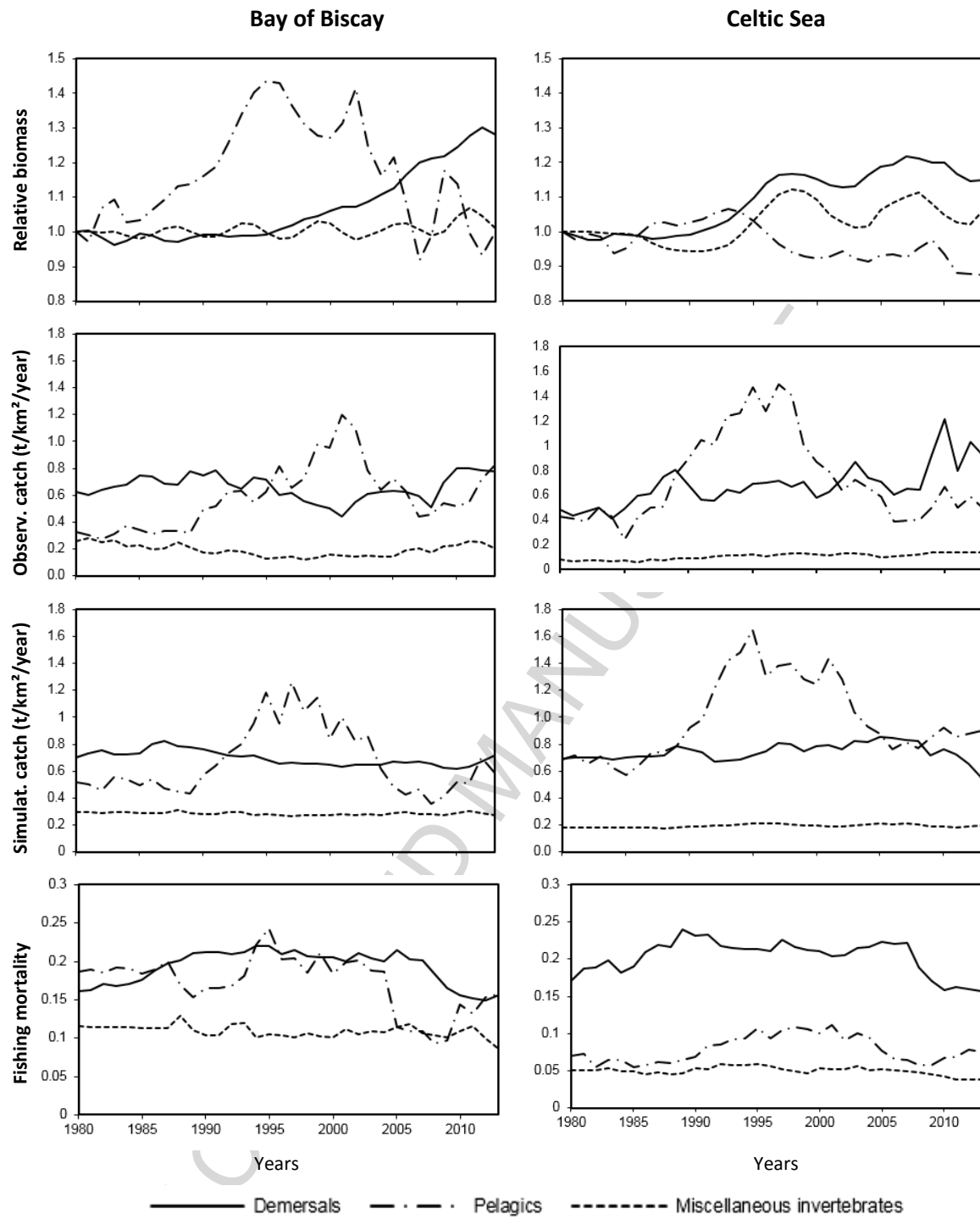
Figure 5.

Figure 6.

Figure 7.

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