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Modelling ecosystem dynamics to assess the effect of coastal fisheries on cetacean species

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ABSTRACT

The expansion of fisheries and its increased efficiency are causing severe detrimental impacts on marine species and ecosystems, that can be categorised into operational and ecological effects. While impacts directly caused by fishing activities have been extensively documented, it is difficult to set an empirical link between fisheries and changes in predator biomass and abundance. Therefore, exploring the functioning of ecosystems as a whole, the interactions between the different species within them and the impact of human activities, is key to understanding the ecological effects of fisheries on top predators and ecosystems, and to develop effective conservation measures, while ensuring a more sustainable exploitation of fishing resources. For instance, mass balance models, such as Ecopath with Ecosim, have proven to be a useful tool to develop more holistic fisheries management and conservation strategies. In this study, Ecopath with Ecosim was used to investigate the temporal dynamics of the Rías Baixas shelf ecosystem (North-West Spain) between 2005 and 2017. Additionally, nine 30-year forward projecting simulations covering the period 2018-2047 were developed to examine the effects of differing fisheries management strategies on common dolphins (Delphinus delphis), bottlenose dolphins (Tursiops truncatus) and harbour porpoises (Phocoena phocoena). Results from these models suggest that when intense fishing increases it poses a major threat to the conservation of these top predators in the area, by reducing the variety of their available prey and potentially enhancing competition amongst them. The study highlights the applicability of Ecopath with Ecosim to develop cetacean conservation measures and despite its small spatial scale, it provides a general framework that can be used to assess cetacean conservation in larger and impacted areas.

1. Introduction

Technological improvements and the expansion of fisheries over the second half of the 20th century have led to an increase in the detrimental impacts of fishing activities on marine ecosystems (Pauly et al., 2005; Bell et al., 2017). This is particularly evident in marine mammals for which fisheries impacts can be divided into operational effects and ecological effects (Northridge, 2009). Operational effects are direct impacts from fisheries, that imply the dead, unintentional capture or the injury of marine mammals as a result of a physical contact with fishing gear (Matthiopoulus et al., 2008), and have been extensively documented (Bearzi, 2002; Díaz López, 2006; Read et al., 2006; Rogan and Mackey, 2007; Fernández-Contreras et al., 2010; Breen et al., 2017). Ecological effects include direct competition for the same resources, indirect competition for different resources that are linked through food

web dynamics, behaviour alteration, and habitat modification, degradation and loss (DeMaster, 2001; Bearzi, 2002; Plagányi and Butterworth, 2005; Díaz López et al., 2008; Matthiopoulus et al., 2008; Northridge, 2009; Northridge et al., 2017; Díaz López, 2019). As opposed to operational effects, ecological effects are more difficult to detect and evaluate accurately mainly due to insufficient knowledge of food-web dynamics of the affected ecosystems (Matthiopoulus et al., 2008; Moore, 2013). Despite these difficulties, recent studies have documented ecological effects of fisheries on a number of marine mammal species and have predicted an increase of such impacts in the future (DeMaster, 2001; Piroddi et al., 2010; Morissette et al., 2012). Owing to the indirect nature of ecological effects, it is crucial that studies that aim to elucidate the interactions between marine mammals, fisheries, shared resources and the ecosystem in general, include detailed biological information of all the groups in a given ecosystem

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(Matthiopoulus et al., 2008).

Mass-balance ecosystem modelling software packages, such as Ecopath with Ecosim (EwE), can be used to understand the nature of ecological effects and their impact on marine mammals. By integrating information from different sources, mass-balance ecosystem models offer an opportunity to have a better understanding of complex ecosystem dynamics (Christensen and Walters, 2004). EwE, in particular, combines information on the biomass and production of the different trophic groups in an ecosystem (including fisheries), the flows between them and the consumption among them (Christensen and Pauly, 1992), with dynamic, time-varying simulations of the prey-predator relationships among the trophic groups (Walters et al., 1997; Gascuel and Pauly, 2009). Due to these characteristics, it has been successfully applied not only to assess the impact of fisheries on the ecosystems under different fishing pressures (Sánchez and Olaso, 2004; Coll et al., 2006; Gascuel et al., 2011; Gasche and Gascuel, 2013; Torres et al., 2013; Bentorcha et al., 2017), but also to evaluate the impact of fishing activities on particular trophic groups, such as marine mammals and their prey, as well as the dynamics of top-down controls in the food-web (Díaz López et al., 2008; Piroddi et al., 2010; Lassalle et al., 2012; Morissette et al., 2012; Carlucci et al., 2020).

Several studies highlight that bycatch and interaction with fisheries represent a high risk on marine megafauna, specially cetaceans, in European waters (Díaz López, 2006; Rogan and Mackey, 2007; Fernández-Contreras et al., 2010; Breen et al., 2017; Díaz López et al., 2019). As a consequence, cetacean species such as the short-beaked common dolphin (Delphinus delphis, hereafter referred to as common dolphin), the common bottlenose dolphin (Tursiops truncatus, hereafter referred to as bottlenose dolphin), and the harbour porpoise (*Phocoena phocoena*) may suffer cumulative impacts derived from operational and ecological effects (Dolman et al., 2016; Murphy et al., 2019). This is particularly relevant in areas with intense fishing activity, such as the continental shelf off North-West Spain (Surís-Regueiro and Santiago, 2014), where the presence and distribution of these three cetacean species have been documented (Spyrakos et al., 2011; Díaz López and Methion, 2018; Methion and Díaz López, 2018; Saavedra et al., 2018; Giralt Paradell et al., 2019), result in the spatial and temporal overlap with different fishing operations (Díaz López et al., 2019). This overlap has been suggested to be as a consequence of cetaceans and purse-seine and trawl fisheries competing for the same resources (Díaz López et al., 2019; Giralt Paradell et al., 2020), and it can cause a dual impact on the cetacean species. Common dolphins, bottlenose dolphins and harbour porpoises are most frequently bycaught species in the region (López et al. 2002, 2003; Fernández-Contreras et al., 2010) and they are also susceptible to competition for resources with fisheries (Morissette et al., 2012). Even though operational effects on these species of cetaceans have been studied in the area (López et al. 2002, 2003; Fernández--Contreras et al., 2010; Goetz et al., 2015), the scarce information on ecosystem dynamics coupled with the difficulty in accurately detecting ecological effects has led to a lack of knowledge on the ecological effects of fisheries on dolphins and porpoises. Therefore, studies that combine information on ecosystem functioning and dynamics with fisheries information to better understand the ecological effects of fisheries on cetaceans in the area are key to formulating and promoting conservation strategies to help protect these vulnerable species.

This becomes increasingly important in areas where conservation measures are already in place, as new information on the ecological effects of fisheries on these species of cetaceans could result in improvements to these measures. In Europe, the Natura 2000 network is the largest coordinated network of protected areas and currently protects around 6% of the European marine territory (https://ec.europa.eu/environment/nature/natura2000/index_en.htm, last visited on February 18, 2020). This network is based on the Birds (Council Directive 79/409/EEC) and Habitats (Council Directive 92/43/EEC) Directives of the European Union, and aims to protect crucial areas for the species and habitats listed in both Directives. Three Natura 2000

network sites are located in the study area (information from EUNIS: https://eunis.eea.europa.eu/sites.jsp, last accessed on February 18th 2020). In this regard, studies that combine different sources of information to better understand the ecological effects of fisheries on these cetacean species could bring new perspectives to the conservation needs of the species in the area and could be an additional tool to improve the already existing protection measures.

The present work builds on previous studies that highlighted the spatial and resource overlap between cetaceans and fisheries in the coastal waters off North West Spain (Díaz López and Methion, 2018; Díaz López et al., 2019; Giralt Paradell et al. 2019, 2020). Based on a mass-balance model created to understand the Rías Baixas shelf ecosystem (Giralt Paradell et al., 2020), the present study develops dynamic simulations between 2005 and 2017 to explore the ecological effects of fisheries on common dolphins, bottlenose dolphins and harbour porpoises. Additionally, 30-years forward projecting simulations covering the period 2018-2047 were developed to examine the responses of the ecosystem, and more particularly these three species, to different fishing pressures. In total, nine scenarios were developed and divided into three categories: (1) two scenarios recreated the same trend in fishing effort and landings between 2005 and 2017; (2) two further scenarios recreated important fishing effort reductions, such as fishing at maximum sustainable yield (MSY) or a 30-year total fishing ban; (3) five scenarios recreated sustained annual increases in fishing effort between 5 and 25%. With these 30-year forward simulations the study aims to better understand the ecological effects of fisheries on cetacean species in the area. This better comprehension of the potential impacts caused by fishing activities could lead to the improvement of already existing conservation measures and management plans and to the proposal of new ones with the ultimate aim of protecting, not only the cetacean species present in these waters, but also the ecosystem they inhabit.

2. Methods

2.1. Study area, fisheries and period

The study area (hereafter referred to as "Rías Baixas shelf ecosystem", Giralt Paradell et al., 2020) is located in the continental shelf waters west from the entrance of the Ría de Arousa (North-West Spain), extending to the 300 m bathymetry line, and has a total area of 933.13 km² (Fig. 1). This coastal area exhibits a high marine primary productivity because of the combination of two factors; the seasonal upwelling events caused by northerly wind regimes that carry deep, nutrient-rich waters masses to the photic layer, and the terrestrial runoff caused by river discharge, that inputs nutrients into the coastal areas (Torres et al., 2003). Additionally, the study area includes the Atlantic Islands National Park, protecting an area of 75.82 km² and three Natura 2000 sites. Two of these cover approximately 130 km² of coastal marine waters, protecting, among other species, bottlenose dolphins and harbour porpoises. The third area covers 2219 km² of marine coastal waters and focuses exclusively on the protection of birds (Fig. 1).

There are predominantly two types of fishing fleets operating within the study area: (1) the artisanal fleet (88.87% of the total number of fishing boats in Galicia in 2017) is a mixed-gear fleet that targets different species depending on the season; (2) the coastal fleet (7.33% of the total number of fishing boats in Galicia in 2017) is the second largest fleet and uses several fishing techniques, such as trawling, purse-seine, gill-net and long-line, targeting several fish species, such as blue whiting (*Micromesistius poutassou*), sardine (*Sardina pilchardus*), Atlantic horse mackerel (*Trachurus trachurus*) and hake (*Merluccius merluccius*), among others (Surís-Regueiro et al., 2014; Xunta de Galicia, Consellería do Mar 2020). For the purposes of this study, only the fishing boats belonging to these two categories and that were registered in the fishing harbour of Ribeira were incorporated into the model. With a total of 240 boats (5.6% of the entire Galician fishing fleet), Ribeira harbour is the most important harbour in terms of landings, in the area (Xunta de

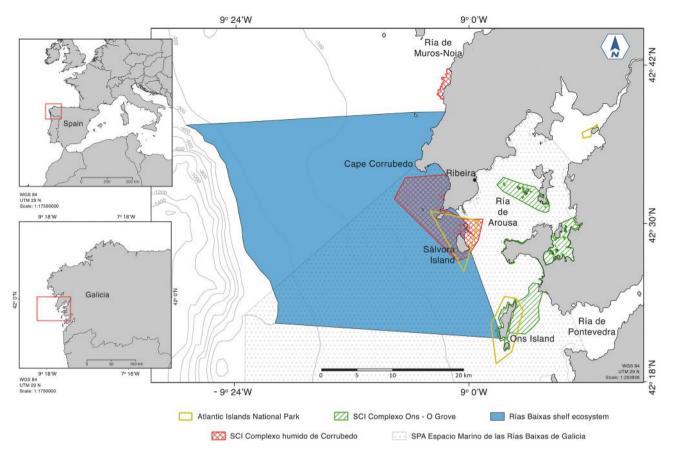


Fig. 1. Map of the study area, showing the Rías Baixas shelf ecosystem selected to create the Ecopath model, the Atlantic Islands National Park and the three Natura 2000 protected sites (SCI Complexo Ons – O Grove, SCI Complexo humido de Corrubedo and SPA Espacio Marino de las Rías Baixas de Galicia.

Galicia, Consellería do Mar, 2020). As seen in the rest of Galicia, the fishing fleet in Ribeira harbour and its aggregated fishing power have been steadily declining since 2005 (Supplementary Material, Figure SM1). Conversely, the volume of landings shows a positive trend since 2005 (Supplementary Material, Figure SM1).

The present study investigates the trophic dynamics in the Rías Baixas shelf ecosystem between 2005 and 2017. Although historical regional fisheries data would allow for a longer study period, a major oil spill affected the Galician coast in November 2002, causing severe alterations in all ecosystems (Penela-Arenaz et al., 2009). Significant recovery of shellfish, fish and marine birds were not reported until one to three years after the disaster (Martínez-Gómez et al., 2009; Viñas et al., 2009; Moreno et al., 2011). Therefore, the period between 2005 and 2017 was chosen, as it was the longest time period available to study of the trophic dynamics of the Rías Baixas shelf ecosystem, ruling out the effects of the oil spill, and thus focussing on the trophic dynamics and the effects of fisheries.

2.2. Modelling framework

Different components of the Ecopath with Ecosim (EwE) software version 6.6.16540.0 (www.ecopath.org) were used to create a mass balance representation of the Rías Baixas shelf ecosystem and to analyse its temporal dynamics between 2005 and 2017. The resulting model was then used to perform 30-years forward projecting simulations to analyse the response of the ecosystem, and more particularly that of common dolphins, bottlenose dolphins and harbour porpoises, to nine future scenarios simulating different fishing pressures.

2.2.1. Mass-balance model

A "Back to the Future" approach (Pitcher, 2001) was implemented to

create a new model of the Rías Baixas shelf ecosystem in 2005 based on the mass balance model created to represent the state of the ecosystem in 2017 (Giralt Paradell et al., 2020). The 2005 model was created with the Ecopath module, that ensures the energy balance between the functional groups by assuming that consumption of the functional group (i) equals the sum of its production, its respiration and the unassimilated food (Christensen and Walters, 2004). Ecopath takes into account several parameters, such as the fishery catch rate (Y_i) , biomass (B_i) , natural predation rate $(M2_i)$, net migration rate (E_i) , biomass accumulation rate (BA_i) , ecotrophic efficiency (EE_i) , and other mortality $(P_i \cdot (1\text{-}EE_i))$ to calculate the production rate (P_i) of each functional group (i) included in the model:

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + P_i \cdot (1 - EE_i)$$
 (1)

This equation can be re-expressed as:

$$B(P/B)_{i} = \sum_{j=1}^{n} B_{j}(Q/B)_{j}DC_{ij} + Y_{i} + E_{i} + BA_{j} + B_{i}(P/B)_{i}(1 - EE_{i})$$
 (2)

where $(P/B)_i$ is the production by biomass ratio of (i), $(Q/B)_j$ is the consumption by biomass ratio of (j), and DC_{ij} is the fraction of prey (i) in the average diet of a predator (j). From this second equation, a modelling framework based on a series of linear functions, one for each functional group, is developed and solved for one of the following parameters, biomass, production by biomass ratio, consumption by biomass ratio or ecotrophic efficiency (Christensen and Walters, 2004). The remaining three parameters need to be entered in the software for each of the functional groups. Detailed information on the Ecopath working procedures, capabilities and limitations has been extensively documented (Christensen and Pauly, 1992; Christensen and Walters, 2004; Plagányi and Butterworth, 2004; Heymans et al., 2011).

The 2005 Rías Baixas shelf ecosystem was formed by the same 23 functional groups that comprised the 2017 model from Giralt Paradell et al., (2020) (Table 1). The ecosystem was divided into the pelagic domain and the non-pelagic domain and each functional group was assigned to one of the domains. Species with similar ecological role were aggregated in the same functional group. Biomass was only calculated for the groups for which reliable information from the early 2000s was available. For the rest of the groups, biomass was assumed to be the same as in the 2017 model or was estimated by Ecopath (Supplementary material, Table SM1). Production by biomass ratio was calculated from abundance estimates for common dolphin (López et al., 2004) and harbour porpoise (Hammond et al., 2013). A precautionary approach was used when no reliable information was available to calculate production by biomass or consumption by biomass ratios, and these were assumed to be the same as in the 2017 model (Supplementary material, Table SM1). Information on landings, discards and fisheries was obtained using the same data sources and procedures as in the 2017 model from Giralt Paradell et al., (2020) (Supplementary material, Table SM2). The artisanal and the coastal fleet were included into a single group to better understand the combined effect of fisheries on the ecosystem. As no major changes of species have been reported in the area, diet of the different groups was also assumed to be the same as in 2017.

To assess the ecological role of the different functional groups, the mixed trophic impact (MTI) routine and the keystoneness index were calculated. By quantifying the direct and indirect effects of each functional group on the rest of functional groups, the MTI routine provides information about the ecological role of each group within the ecosystem (Ulanowicz and Puccia, 1990). The keystoneness index (Libralato et al., 2006) relates the overall effect of a functional group in the food web to its biomass. This index was used to detect keystone functional groups (groups that have a strong impact on the ecosystem despite their small biomass (Power et al., 1996) and structuring functional groups (groups that have a strong impact on the ecosystem and a high biomass (Libralato et al., 2006)). Two methods were used to calculate this index. The first one, proposed by Libralato et al. (2006), is based on the overall effect and biomass of each functional group and focuses on finding the groups that have both low biomass and high effect. The second method is based on the impact of each functional group multiplied by the biomass in a descending order and focuses on highlighting the importance of top predators as keystone species (Valls et al.,

A PREBAL (Link, 2010) assessment was performed prior to the balancing process to detect the groups where modelled biomass diverged significantly from the expected biomass according to their trophic level. To address the anomalies detected by this process, the

Table 1
The 23 functional groups included in the 2005 model divided into pelagic and non-pelagic domains. Further details on the group composition are included in Supplementary material, Table SM1 and Tables SM5 to SM27.

Pelagic domain	Non-pelagic domain
Common dolphin (Delphinus delphis)	Blue whiting (Micromesistius poutassou)
Harbour porpoise (Phocoena	Atlantic horse mackerel (Trachurus
phocoena)	trachurus)
Bottlenose dolphin (Tursiops	Benthopelagic fish
truncatus)	Bathydemersal piscivorous fish
Baleen whales	Demersal piscivorous fish
Seabirds I, pursuit and plunge divers	Non-planktonic crustaceans
Seabirds II, surface and aerial	Macrobenthos
feeders	Detritus
Sardine (Sardina pilchardus)	Discards
Large piscivorous pelagic fish	
Other piscivorous pelagic fish	
Large planktivorous pelagic fish	
Small planktivorous pelagic fish	
Cephalopods	
Zooplankton	
Phytoplankton	

ecotrophic efficiency obtained in the 2017 model was used as an input parameter instead of the biomass for the functional groups with a higher than expected biomass.

2.2.2. Dynamic simulations

Once the 2005 model was balanced, the Ecosim module (Walters et al., 1997) of EwE was used to analyse and calibrate the temporal dynamics of the Rías Baixas shelf ecosystem between 2005 and 2017.

Ecosim takes the static ecosystem model generated by Ecopath and creates time-varying dynamic simulations of the same ecosystem (Walters et al. 1997, 2000), based on a set of differential equations derived from the Ecopath master equation (Equation (2)) and can be expressed as follows:

$$dB_{i} / dt = (P/Q)_{i} \sum_{j} Q_{ji} - \sum_{j} Q_{ij} + I_{i} - (M_{i} + F_{i} + e_{i})B_{i}$$
(3)

where dB_i/dt is the change in biomass of group (i) over time, $(P/Q)_i$ is the net growth efficiency, M_i is the non-predation mortality rate, F_i is the fishing mortality rate, e_i is the emigration rate, I_i is the immigration rate, B_i is the biomass of group (i), $\sum_j Q_{ji}$ is the total consumption rate by

group (i) and $\sum\limits_{i}Q_{ij}$ is the predation by all predators on the same group

(i). These dynamic simulations assume that prey and predator biomasses determine the flows between functional groups (Walters et al., 2000). This idea is based on the foraging arena theory (Walters and Korman, 1999) that states that prey alternates between a vulnerable and an invulnerable state with respect to predators. These concepts are incorporated in the model through the consumption rates (Q_{ij}) , which can be calculated as:

$$Q_{ij} = \frac{v_{ij} \cdot a_{ij} \cdot B_i \cdot B_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot M_{ij}/D_j}{v_{ij} + v'_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot B_j \cdot S_{ij} \cdot T_j/D_j}$$

$$\tag{4}$$

where v_{ij} is the rate at which prey move from the invulnerable to the vulnerable state or vulnerability, a_{ij} is the effective search rate for predator j feeding on prey type i, T_i and T_j are the prey and predator relative feeding times respectively, S_{ij} are the seasonal or long term forcing effects, M_{ij} are the mediation forcing effects and D_j are the effects of handling time as a limit to consumption rate. The vulnerabilities explain how a substantial increase of predator biomass impacts on the predation mortality and they determine the mechanism that controls the biomass of the different groups in the ecosystem (Christensen et al., 2005). In this regard, bottom-up control is expressed by low vulnerability values ($v_{ij} = 1$), top-down control is represented by high vulnerability values ($v_{ij} \gg 1$), and mixed flow control is achieved when $v_{ij} = 2$. Detailed information on the Ecosim assumptions and working procedures has been documented extensively (Walters et al. 1997, 2000; Christensen and Walters, 2004).

2.2.3. Time series data and fitting

To adjust the model to the ecosystem historical dynamics, a time series on biomass, catches, fishing effort and mortality for different functional groups were incorporated (Supplementary material, Table SM3). Partial biomass time series were calculated for common dolphins, harbour porpoises and two groups of seabirds from relative abundances derived from direct observations at sea (BDRI 2018a, b; Giralt Paradell et al., 2020). Bottlenose dolphin was the only odontocete species not included in the fitting process, as there are no reliable historical biomass data. Time series on absolute biomass, catches and fishing mortalities for most fish groups, cephalopods and non-planktonic crustaceans, were obtained by combining regional landing statistics (Xunta de Galicia, Consellería do Mar, 2020) with information from pelagic surveys (ICES, 2018a,b, 2019a,b,c,d,e). Aggregated engine horsepower (expressed as HP) of the small-scale and coastal fleets

operating in Ribeira harbour was obtained from regional statistics (Xunta de Galicia, Consellería do Mar, 2020), and was used as a proxy for fishing effort. To do so, the number of boats in 2005 was used to set the starting relative fishing effort value (1). Then this value was changed by calculating the percentage of variation in the number of fishing boats from one year to the next. Daily time series on chlorophyll *a* concentration in waters above the Rías Baixas continental shelf (Beca-Carretero et al., 2019) were used as a proxy to recreate historical changes in primary production in the area.

Once the time series data are included in the model, a measure of goodness of fit consisting of a weighted sum of squared (SS) deviations of log observed biomasses from log predicted biomasses is calculated for each model run (Christensen et al., 2005). Changes in fishing impact, vulnerability settings, primary productivity, will alter the fit of the model to the time series and thus several hypothetical models need to be tested in order to find the best fit (Heymans et al., 2016). To consider all the possible hypothetical models, the "fit to time series" procedure (Tomczak et al., 2012) was applied. This method consists of systematically changing the number of vulnerabilities and primary productivity anomalies (historical shifts in primary productivity that could impact the biomasses across the ecosystem) used to fit the model to the time series (Tomczak et al., 2012). To reduce human error in this critical process the automated "stepwise fitting" procedure of Ecosim was used (Scott et al., 2016). Vulnerability parameters were searched by predator for all iterations. Eight different groups of hypothetical models were tested (Table 3). The SS and the Akaike Information Criterion (AIC), which penalises for overparameterisation (Akaike, 1974), were used to find the model with the best fit for each group of hypothetical models. In this regard, the models with the lowest SS, AIC and AICc, which corrects for small sample sizes (Burnham et al., 2004), were considered the best fits for each group of hypothetical models.

2.2.4. Assessing model uncertainty

Monte-Carlo simulations can be used to evaluate the uncertainty of Ecopath input parameters on Ecosim simulations (Heymans et al., 2016). The model that showed the best fit to the time series data after the automated stepwise fitting procedure was used to run 100 Monte-Carlo simulations. Ecopath input parameters (biomass, production by biomass and consumption by biomass ratios and ecotrophic efficiency) were randomly selected with a coefficient of variation of 0.1 around them giving 100 different outcomes. These results were used to assess the uncertainty of the input data and to plot the 5th and 95th percentile confidence intervals for the fitted biomass (Corrales et al., 2017).

2.3. Future scenarios

The model with the best fit was used to perform the 30-year forward projecting simulations after the time-series period to predict the impact of fishing on the ecosystem in general, and, more particularly, on common dolphins, bottlenose dolphins and harbour porpoises. To do so, nine scenarios representing different plausible fishing effort levels were examined and are detailed below. To prioritise the effects of fishing pressure and minimize the influence of seasonal and annual primary production fluctuations, the forcing function was left constant throughout the 30-year forward projecting simulations.

- a. Base scenario: This scenario was conceived to assess the impact of fishing if the 2017 conditions were kept throughout the forward simulation. To do so, the 2017 fishing effort and fishing mortalities for the different functional groups were kept constant throughout the 30-year forward projecting simulation.
- b. Same trend scenario: The times series used to fit the model showed a 2.6% annual decrease in fishing effort and a 3% increase in landings between 2005 and 2017. This scenario reproduces those trends throughout the 30 year forward simulation.

- c. Fisheries ban scenario: A temporal 30-year fisheries closure was considered in this scenario. To simulate this closure, both fishing effort and fishing mortalities were set to 0 throughout the 30 year forward simulation.
- d. Fishing mortality at maximum sustainable yield (F_{MSY}) scenario: According to the United Nations Convention on the Law of the Sea, coastal states should manage fisheries aiming to achieve maximum sustainable yield (UNCLOS, 1982). The Member States of the European Union agreed to achieve this goal for all depleted stocks by 2015, at the World Summit on Sustainable Development held in Johannesburg in 2002 (WSSD, 2002). This agreement was then further regulated within the Common Fisheries Policy (CFP) of the European Union that extended the deadline to 2020 (EC, 2013). The fishing mortality at maximum sustainable yield (F_{MSY}) for each functional group was calculated for 2017 (Supplementary Material, Table SM3). Fishing effort was set at the same value as in 2017. Both fishing mortalities at MSY and fishing effort were kept constant throughout the forward simulation.
- e. Increased fishing effort scenarios: Five additional scenarios (e $_1$, e $_2$, e $_3$, e $_4$, e $_5$) were conceived to evaluate the effects of a sustained annual increase in fishing effort on the ecosystem. Five different annual increases (e $_1=5\%$ increase, e $_2=10\%$ increase, e $_3=15\%$ increase, e $_4=20\%$ increase and e $_5=25\%$ increase) were considered. Fishing mortality was increased accordingly for each scenario.

3. Results

3.1. Balancing the mass-balance model

The Ecopath model resulting from the "Back to the Future" approach had a pedigree index of 0.532, which was above the mean pedigree index calculated for other studies (Morissette et al., 2007; Colléter et al., 2015). The model was unbalanced and had to be readjusted. Six groups, including blue whiting, Atlantic horse mackerel, large piscivorous pelagic fish, other piscivorous pelagic fish, small planktivorous pelagic and demersal piscivorous fish, showed an ecotrophic efficiency higher than one. The PREBAL assessment (Supplementary material Figure SM2) showed that these species had a biomass notably higher than the one expected from a group of their trophic level. In addition, six groups showed cannibalism within their diets, although this represented less than 5% of their diets, except for the zooplankton. Although cannibalism can constitute a problem, especially if it represents more than 10% of a groups diet (Christensen et al., 2005), no adjustments were made as percentages for most groups were lower than 5% (Heymans et al., 2016). The same precautionary approach as in Giralt Paradell et al., (2020) was applied to balance the model. The results of the balanced model are shown in Table 2.

Similar to what was found in the 2017 ecosystem model (Giralt Paradell et al., 2020), the method proposed by Libralato et al. (2006) showed that the functional group with the highest keystoneness index was small planktivorous pelagic fish (Fig. 2 and Supplementary Material Table SM4). Other groups such as zooplankton, phytoplankton and blue whiting had a high keystoneness index, but they showed a higher biomass, especially zooplankton. Hence, these groups could be considered as important structuring groups of the ecosystem (Libralato et al., 2006). Common dolphins and harbour porpoises had a lower keystoneness index than bottlenose dolphins, suggesting that their impact on the ecosystem was lower (Fig. 2 and Supplementary Material, Table SM4). The second method used to assess the keystone species (Valls et al., 2015) ranked three species of top predators (large piscivorous pelagic fish, bathydemersal piscivorous fish and bottlenose dolphin) and small planktivorous pelagic fish among the four functional groups with a higher keystoneness. This method confirmed small planktivorous pelagic fish as a key functional group, and highlighted the importance of top predators in the Rias Baixas shelf ecosystem. In contrast, both methods ranked other top predators such as common

Table 2Results of the balanced Ecopath 2005 model using the "Back to the Future" approach. Input parameters are shown in bold letters and stars show Ecotrophic Efficiencies taken from the 2017 model to balance the model.

Group	TL	В	P/B	Q/B	EE	P/Q
Common dolphin	4.58	0.036	0.05	23	0	0
Harbour porpoise	4.37	0.001	0.11	28.08	0	0
Bottlenose dolphin	4.73	0.076	0.05	19.08	0	0
Baleen whales	3.52	0.061	0.06	6.46	0	0.01
Seabirds 1: Pursuit and plunge divers	3.89	0.001	0.32	82.79	0	0
Seabirds 2: Surface and aerial pursuit feeders	3.56	0.001	0.25	182.12	0	0
Blue whiting	3.46	29.892	1.06	6.52	0.99*	0.16
Sardine	2.96	78.695	0.58	8.8	0.24	0.07
Atlantic horse mackerel	3.37	27.434	0.64	6.47	0.80*	0.1
Large piscivorous pelagic fish	4.68	0.502	0.82	7.8	0.45*	0.11
Other piscivorous pelagic fish	4.3	2.357	0.82	6.5	0.43*	0.13
Large planktivorous pelagic fish	3.57	9.349	1.14	6.28	0.85	0.18
Small planktivorous pelagic fish	3.37	25.185	1.98	9.13	0.83*	0.22
Benthopelagic fish	2.72	4.868	0.68	3.62	0.71*	0.19
Bathydemersal piscivorous fish	4.41	3.269	1.09	4.04	0.82*	0.27
Demersal piscivorous fish	4.34	4.224	0.67	3.81	0.99*	0.18
Cephalopods	4.25	1.906	3.2	7.5	0.92*	0.43
Non-Planktonic Crustaceans	3.24	21.849	2.35	6.33	0.02*	0.37
Macrobenthos	2.12	15.14	2.5	6.5	0.24*	0.38
Zooplankton	2.37	128.32	39.08	80	0.80*	0.49
Phytoplankton	1	47.246	158.04	0	0.83*	0
Discards	1	5.062	0	0	0	0
Detritus	1	70	0	0	0.34	0

dolphins, harbour porpoise and both groups of seabirds among the groups with lower keystoneness.

The MTI routine showed that the functional groups with high key-stoneness indices were also crucial groups in supporting the ecosystem (Fig. 3). For instance, small pelagic fish, zooplankton and phytoplankton had a positive impact on most functional groups, whereas blue whiting had a negative impact. This highlights the importance of these groups in the ecosystem, and suggests a mix of top-down and bottom-up ecosystem control, as seen in the 2017 ecosystem model (Giralt Paradell et al., 2020). Therefore, the 2005 Rías Baixas shelf ecosystem could be described as a wasp-waist ecosystem (Cury et al., 2000). Additionally, small planktivorous pelagic fish, zooplankton and phytoplankton, together with blue whiting, Atlantic horse mackerel and to a lesser extent benthopelagic fish, had positive effects on common dolphins, harbour porpoises and bottlenose dolphins.

The routine also allowed the identification of the impact of the coastal fisheries on the different functional groups. The results show that the largest negative impacts were exerted on demersal piscivorous fish

and large planktivorous fish. However, lower impacts were caused to Atlantic horse mackerel, sardine and bathydemersal piscivorous fish. These functional groups included species that are components of common dolphin, harbour porpoise and bottlenose dolphin diet. In addition, coastal fisheries showed an indirect impact on the three species of cetaceans, in particular on common and bottlenose dolphins.

3.2. Fitting the model to time series

The automated stepwise fitting procedure analysed 398 hypothetical models (Table 3). This process was used to choose the model with the lowest AICc and the lowest SS for each group of hypothetical models, which corresponded to the best fit for that particular group. The model with the best fit (lowest AICc = 16.6) was achieved when trophic effects and forcing function were included in the stepwise fitting procedure. This model included 11 trophic effects and 4 spline points in the environmental forcing function, and improved the fit by 58.7% compared to the baseline model (AICc = 59).

The best model was used to fit the data to the time series covering the period from 2005 to 2017. In general, the historical biomass trends for most of the functional groups included in the time series were well reproduced by the model (Fig. 4). Comparing the observed biomass data with the model predictions, the functional groups with the best fit were sardine, Atlantic horse mackerel and bathydemersal piscivorous fish. The uncertainty addressed with the Monte-Carlo simulations was lowest for Atlantic horse mackerel, small planktivorous pelagic fish and bathydemersal piscivorous fish, which showed very narrow confidence intervals throughout the time series period, and highest for demersal piscivorous fish (Fig. 4). The best fitting model reproduced catch trends differently depending on the functional group. For instance, benthopelagic fish, bathydemersal piscivorous fish and cephalopods were the functional groups for which the predicted catches better replicated the observed trends, whereas catches were underestimated or overestimated for other functional groups (Supplementary material, Figure SM3).

3.3. Analysing the forward simulations

The results of the 30-year forward projecting simulations, created to assess the impact of different fishing efforts on common dolphins, bottlenose dolphins and harbour porpoises, showed different results for the different species. The evolution of the relative biomass over the modelled period was assessed for these species under the nine scenarios (Fig. 5). In general, all three species showed a decreasing biomass trend in the simulations in which fishing effort was increased and a steady increasing trend in the FMSY scenario. Some particularities were found for each species.

3.3.1. Forward simulations for common dolphins

In general terms, the common dolphin's biomass was predicted to increase steadily in the base, same trend, no fishing and FMSY scenarios. However, this increase was lower if conditions were kept at a similar

Table 3
Results of the automated "stepwise fitting" procedure, showing the best fit for each of the eight groups of hypothetical models tested. The model with the best overall fit is highlighted in bold letters. N shows the number of hypothetical models tested in each group. The number of parameters (K) equals the number of vulnerability parameters (TE) plus the number of primary production spline points (PP). The fit improvement shows the percentage of reduction of SS compared to the baseline hypothetical model.

Group	Hypothetical models	N	TE	PP	K	Min SS	AICc	Fit improvement
1	Baseline	1	0	0	0	323.4	59	_
2	Baseline + trophic effects	22	7	0	7	275	32.2	45.4%
3	Baseline + primary productivity anomalies	11	0	3	3	318.7	61.5	-4.2%
4	Baseline + trophic effects and primary productivity anomalies	165	11	4	15	240.4	16.6	58.7%
5	Fishing	1	0	0	0	339.9	71.9	-21.9%
6	Fishing + trophic effects	22	6	0	6	292.5	45.8	22.4%
7	Fishing + primary productivity anomalies	11	0	2	2	339.9	75.9	-28.6%
8	$Fishing + trophic \ effects \ and \ primary \ productivity \ anomalies$	165	6	2	8	266.5	26.4	55.3%

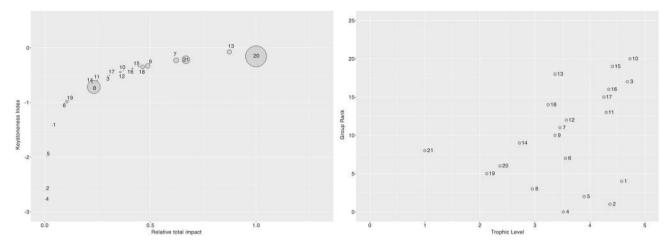


Fig. 2. Results of the two methods used to calculate the Keystoneness (left, Libralato et al., 2006; right, Valls et al., 2015) of the 2005 Rías Baixas ecosystem model. Circles on the left plot are scaled to the biomass of the group. Functional groups on the right are ranked according to their keystoneness in ascending order. The functional groups are: 1: Common dolphin; 2: Harbour porpoise; 3: Bottlenose dolphin; 4: Baleen whales; 5: Seabirds 1; 6: Seabirds 2; 7: Blue whiting; 8: Sardine; 9: Atlantic horse mackerel; 10: Large piscivorous pelagic fish; 11: Other piscivorous pelagic fish; 12: Large planktivorous pelagic fish; 13: Small planktivorous pelagic fish; 14: Benthopelagic fish; 15: Bathydemersal piscivorous fish; 16: Demersal piscivorous fish; 17: Cephalopods; 18: Non-Planktonic crustaceans; 19: Macrobenthos; 20: Zooplankton; 21: Phytoplankton.

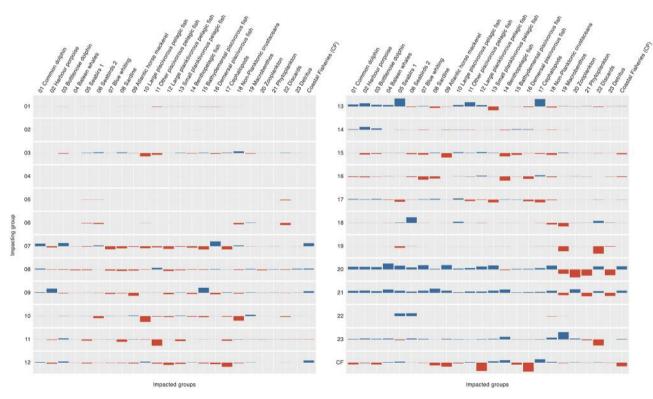


Fig. 3. Mixed Trophic Impact (MTI) plot of the 2005 Rías Baixas shelf ecosystem. The plot indicates the relative impacts caused by the impacting functional groups (rows) on the impacted functional groups (columns). Blue boxes indicate positive impacts whereas red boxes show negative impacts. The size of the box shows the degree of the impact with bigger boxes showing more important impacts. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

level to those found in 2017. Conversely, scenarios that simulated an increase in fishing effort, predicted mostly a decrease in common dolphin's biomass throughout the 30-year forward projecting simulation. In these cases, biomass was predicted to have halved by 2043 compared to the start of the simulation.

3.3.2. Forward simulations for harbour porpoises

Predicted biomass trends for harbour porpoises showed a similar pattern for most scenarios. With the exception of the FMSY scenario, which exhibited a steady increase in biomass throughout the 30-year forward projecting simulation, the predictions for this species showed an increasing trend until 2025–2030 followed by a decrease until the end of the forward simulation. Harbour porpoise relative biomass was predicted to be less than 1 at the end of the forward simulation in all scenarios except for the FMSY. The biggest decreases in biomass were shown by the no fishing, the same trend scenarios and when fishing effort was increased by at least 15%, for which relative biomass would be lower than 0.5 by 2043.

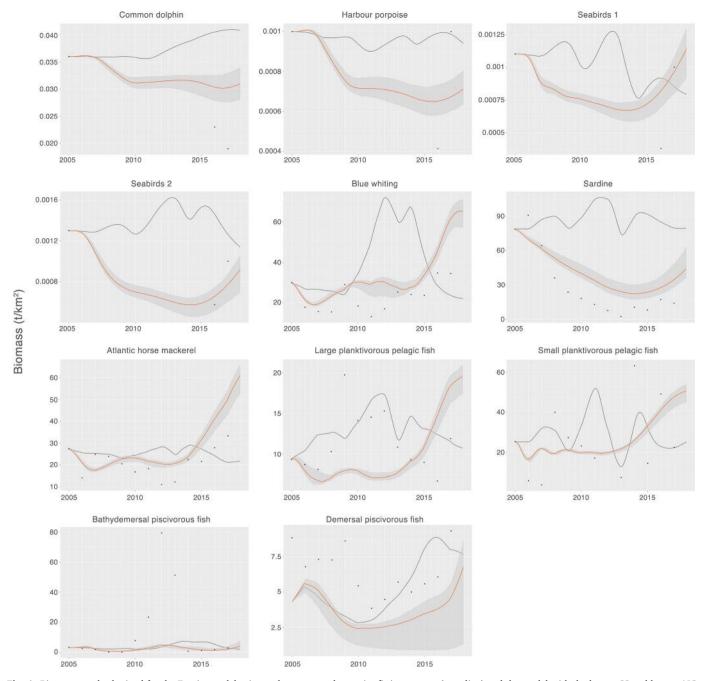


Fig. 4. Biomass trends obtained for the Ecosim model prior to the automated stepwise fitting process (grey line) and the model with the lowest SS and lowest AICc (orange line). The grey shaded area represents the 5th and 95th percentiles obtained during the Monte-Carlo simulations. Black dots show the observed biomass. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.3.3. Forward simulations for bottlenose dolphins

Two contrasted general trends in bottlenose dolphin relative biomass could be identified throughout the nine 30-year forward projecting simulations. On the one hand, biomass was predicted to increase at different rates in the four scenarios that simulated similar conditions to 2017 or a reduction in fishing effort. The most optimistic scenario, predicted a 4-fold biomass increase by 2043. On the other hand, the biomass was predicted to decrease in the scenarios with a more intense fishing effort, dropping to less than half the biomass of 2005.

3.3.4. Changes in diet composition

When comparing the evolution of the predicted diet composition between the different scenarios of common dolphin, harbour porpoise and bottlenose dolphins, three main patterns could be identified (Fig. 6,

Table 4 and Supplementary material Figures SM4 – SM6). First, in those scenarios that kept conditions similar to 2017 or that simulated a decrease in fishing effort, the three species tended to show more diverse diets. In these cases, the predominant group were predicted to be demersal piscivorous fish for both dolphin species and Atlantic horse mackerel for harbour porpoises, although they were never predicted to exceed 60% of the diet composition. Secondly, diets tended to be less varied when the fishing effort was increased. In the most extreme cases, common and harbour porpoises were predicted to feed only on one functional group. Thirdly, increasing the fishing effort resulted in common dolphins and harbour porpoises, and to a lesser extent, bottlenose dolphins, feeding almost exclusively on small pelagic planktivorous fish.

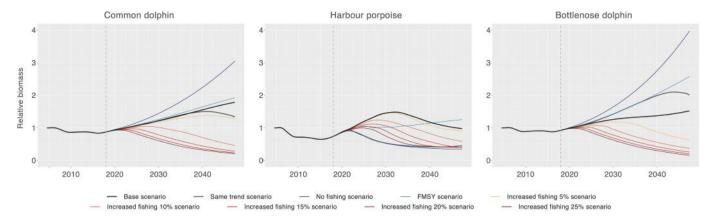


Fig. 5. Common dolphin, harbour porpoise and bottlenose dolphin relative biomass evolution between 2005 and 2043 under the nine future scenarios. The grey vertical dashed line represents the end of the time series period and the start of the 30-year forward projecting simulations. The black line to the left of the grey vertical dashed line represents the model with the best fit to the time series. The lines to the right of the dashed line represent the predicted relative biomasses under the different scenarios.

4. Discussion

Food-web dynamics models can help elucidate the extent of operational and ecological impacts of fisheries on cetaceans, as a first step towards more effective ecosystem conservation and management plans. In this regard, findings of this study provide insights on the ecological effects of fisheries on common dolphins, bottlenose dolphins and harbour porpoises in a coastal area, impacted by fishing activities, and highlight the applicability of EwE models to cetacean conservation. This work could serve as a starting point to develop comprehensive tools that could be used to better realise an ecosystem approach to fisheries management, while ensuring the conservation of top predators.

4.1. Assumptions and limitations of the model

The 2005 and 2017 Ecopath models and the time series used in this study were built prioritising the best available local data. High resolution abundance data were obtained for common dolphins, harbour porpoises and both seabird functional groups for the last two years of the simulation. However, a complete biomass time series for these species could not be obtained due to the lack of regular biomass and population trend assessments in the area prior to 2015. Similarly, bottlenose dolphins were not included in the time series due to the lack of data on the species abundance in the area between 2005 and 2017. Another limitation of the models was that 70% of the fish functional groups resulted from aggregating several species with similar trophic ecology, which could have led to an underrepresentation of species interactions (Alexander et al., 2015). Additionally, biomass estimates and catches for the fish and cephalopods functional groups were obtained from official regional landing statistics, potentially leading to an underrepresentation of the non-commercial species. However, commercial species comprised 98% and 90% of the demersal and pelagic fish communities' biomass, respectively (Fariña et al., 1997; Santos et al., 2013), confirming the representativeness of the fish and cephalopod functional groups used in this study. A further potential side effect of using official landing statistics is that they tend to underrepresent real catches (Coll et al., 2014), and therefore, findings for the fish and cephalopod functional groups should be considered carefully. However, in the absence of more reliable data, regional landing statistics were the best local available data to use as input parameters for both Ecopath models and Ecosim time series.

Another constraint relates to the Ecosim dynamic simulations. These simulations did not address the potential real diet variations over time. However, since the dynamic simulations covered 13 years, local, quantitative diet studies conducted in a similar time frame to the present study were prioritised (Giralt Paradell et al., 2020), and assumed to be

representative for the whole period. Despite these limitations and pitfalls, Ecopath with Ecosim proved to be a useful tool to represent the time-dynamic variations of the Rías Baixas shelf ecosystem and to assess the impact of fishing activities on marine top predators.

4.2. Time series fitting

The duration of the time series period was determined by the Prestige oil spill, that occurred in November 2002. The starting point of the dynamic simulations was set to 2005, to minimize the influence of the oil spill in the ecosystem dynamics and to focus on the effects of fishing activities on common and bottlenose dolphins, harbour porpoises and the ecosystem.

The best model explained 59% of the variability of the data and suggested that trophic interactions were the main driver influencing the Rías Baixas shelf ecosystem. These results are in line with what have been seen in other areas (Coll et al., 2008; Corrales et al., 2017). The trophodynamic model captured the overall biomass and catches variations over time for most functional groups. However, it was unable to reproduce the fluctuating biomass trend or the observed catches of small and large planktivorous pelagic fish. This could be explained because these functional groups included species such as the European anchovy (Engraulis encrasicolus) and the Atlantic mackerel (Scomber scombrus), which may be subjected to migratory and seasonal patterns that extend beyond the scope of the area studied here (Uriarte et al., 1996; Murta et al., 2008). Additionally, yearly fluctuations have been documented for small pelagic fish in other areas (Coll et al., 2006; Lindegren et al., 2013; Van Beveren et al., 2016). These have been linked to recruitment variability determined by environmental factors such as upwelling intensity and density-dependent processes (Borja et al., 2008; Lindegren et al., 2013; Bakun et al., 2015), ultimately affecting fisheries (Uriarte et al., 1996; Van Beveren et al., 2016). The uncertainties addressed with the Monte-Carlo simulations showed a narrow confidence interval around the model predictions with a slight increase at the end of the time series period for most groups, giving strength to the prediction outcomes.

4.3. Analysing the scenarios

The 30-year forward projecting simulations highlighted the vulnerability of common dolphins, bottlenose dolphins and harbour porpoises to fishing activities. The model drew different general predictions for harbour porpoises and both dolphin species, dividing the three cetacean species into two groups. In this regard, harbour porpoise biomass was predicted to decrease in all scenarios except when fishing effort was set

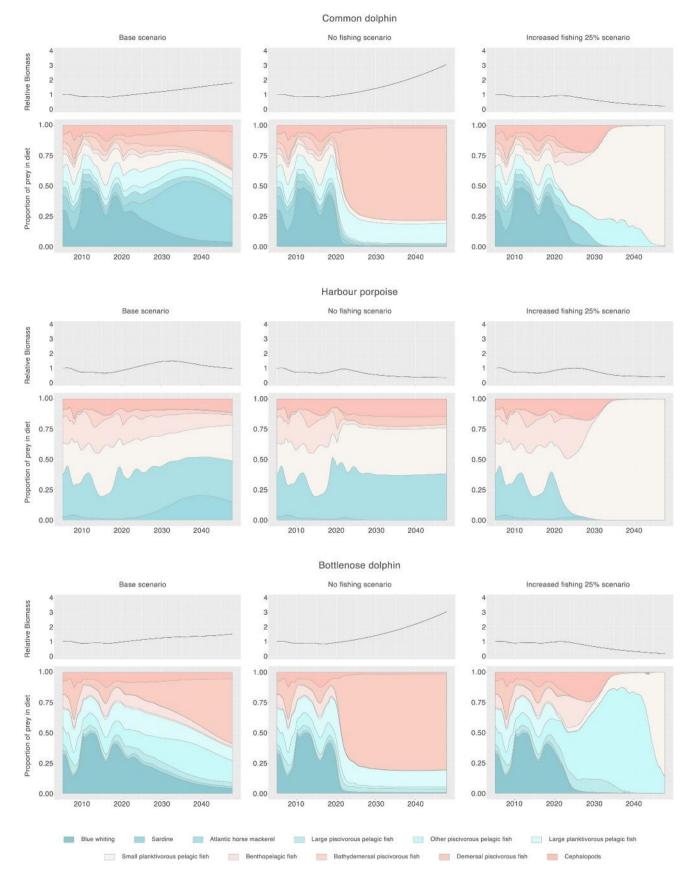


Fig. 6. Evolution of the contribution of the different functional groups in the diet of common dolphins, harbour porpoises and bottlenose dolphins for the base, no fishing and increased fishing 25% scenarios. The black lines on the graphs above show the common dolphin's relative biomass trends for each scenario.

Table 4

Percentage of contribution of the different functional groups (only the most relevant functional groups are shown) to the diet of common dolphin, harbour porpoise and bottlenose dolphin at the end of each scenario. The group with a higher percentage is shown in bold letters. Abbreviations can be understood as follows: S: Sardine; AHM: Atlantic horse mackerel; LPPF: Large piscivorous pelagic fish; OPP: Other piscivorous pelagic fish; LPLP: Large piscivorous pelagic fish; SPLP: Small piscivorous pelagic fish; BP: Benthopelagic fish; BDP: Bathydemersal piscivorous fish; C: Cephalopods.

Scenario	Common dolphin						Harbour porpoise				Bottlenose dolphin							
	S	OPP	LPLP	SPLP	DP	С	S	AHM	SPLP	BP	С	LPPF	OPP	LPLP	SPLP	BP	DP	С
Base	33.8	6.2	7.6	7.3	30.5	5.2	14.9	34.0	29.4	8.5	10.8	3.5	17.9	10.7	0.8	2.5	53.4	5.4
Same trend	0.0	10.3	1.0	22.4	48.4	15.0	0.0	1.6	63.4	12.4	21.7	6.0	19.9	0.9	1.7	2.8	57.6	10.3
No Fishing	0.0	0.8	16.6	2.7	75.9	2.0	0.0	38.4	37.9	2.5	14.4	3.1	1.4	13.9	0.2	0.1	79.3	1.3
FMSY	0.0	2.0	28.8	8.2	44.0	5.5	0.0	57.4	28.2	3.2	9.8	4.3	4.1	28.1	0.6	0.8	53.6	4.0
Increased Fishing 5	57.3	11.0	0.2	14.2	0.0	9.3	16.0	0.7	35.1	36.2	12.0	6.3	48.1	0.4	2.4	25.8	0.0	14.5
Increased Fishing 10	0.7	19.7	0.1	58.3	0.0	20.0	0.1	0.0	83.4	1.4	15.0	11.0	58.4	0.2	6.7	1.2	0.0	21.5
Increased Fishing 15	0.0	20.3	0.0	78.4	0.0	1.0	0.0	0.0	99.3	0.0	0.7	2.6	83.0	0.0	12.4	0.0	0.0	1.5
Increased Fishing 20	0.0	10.9	0.0	88.8	0.0	0.2	0.0	0.0	99.9	0.0	0.1	0.3	75.7	0.0	23.5	0.0	0.0	0.6
Increased Fishing 25	0.0	0.6	0.0	99.4	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.1	13.6	0.0	86.2	0.0	0.0	0.0

to ensure MSY, whereas common and bottlenose dolphins showed increasing trends for all scenarios in which fishing effort was not increased. This became especially apparent in the no fishing scenario, which predicted a biomass increase for both dolphin species, but forecasted the biggest decrease in harbour porpoise biomass. With no fishing boats operating in the area and an increase in bottlenose dolphin biomass, other mechanisms such as interference competition or trophic competition between these species could take place (Spitz et al., 2006; Fernández et al., 2013; Méndez-Fernandez et al., 2013), despite the spatial separation that both species show in the area (Díaz López and Methion, 2018), and cause the decrease of this small cetacean species.

Similarly, both same trend and base scenarios predicted an increase in common and bottlenose dolphin biomass but a decrease for harbour porpoise. Accurate data on fishing effort and catches in Galicia are difficult to obtain (Villasante et al., 2010). As a result of the CFP, the European Union urged Member States to adjust their fishing capacity to the fishing opportunities over time by decommissioning specific types of fishing vessels (EC, 2002). However, these measures have been proven insufficient due to inadequate methods to calculate the real fishing effort and capacity of the fleets, ineffective implementation of the measures to reduce the fishing effort, and misreporting of fishing power (European Court of Auditors, 2011; European Union, 2019). These aspects could explain inconsistencies found in the regional statistics (Xunta de Galicia, Conselleria do Mar, 2020) that showed an increasing trend for landings between 2005 and 2017, while the number of boats and the fishing power decreased steadily (Supplementary Material, Figure SM1). Additionally, illegal, unreported and unregulated (IUU) fishing has been estimated at around 40% in North-West Spain (Villasante et al., 2015), hampering the understanding of the effects of fisheries on the ecosystem (Coll et al., 2014). Since fishing effort and catches included in this study come from official statistics, IUU fisheries were not accounted for, and as a consequence, these two scenarios might be overly optimistic when predicting cetacean biomass throughout the simulation(s).

Only the FMSY scenario suggested that achieving the CFP objective of exploitation at MSY level would also benefit the small cetaceans in the Rías Baixas shelf ecosystem. However, a number of assumptions were made here. First, MSY was assumed to be constant throughout the simulation and therefore, a constant fishing mortality value was applied to this scenario, not accounting for probable future changes that may occur as a result of fluctuating environmental conditions or management decisions, which could result in substantially different results (Serpetti et al., 2017). Second, although it seems that adopting an MSY approach to fisheries management would be a first step in the right direction, this would not necessarily ensure the conservation of the species and the ecosystem (Moore, 2013; Prellezo and Curtin, 2015). Traditional MSY approaches build on single stock fisheries management methods and aim to obtain the maximum sustainable yield of different fish stocks. However, they do not consider fish stocks as part of an ecosystem, failing to capture the multispecific nature of ecosystems, and the relationships among the different trophic groups (Walters et al., 2005). Recently, multispecies MSY approaches have been developed to account for the interactions between different fish species in mixed fisheries (Stäbler et al., 2016; Thorpe, 2019). However, these might not be sufficient to ensure both sustainable fishing and ecosystem conservation (Legović et al., 2010; Smith et al., 2011).

4.4. Ecological effects of fisheries

Competition for resources between fisheries has been suggested to be one of the main drivers of cetacean disappearance in some areas (Bearzi et al., 2008; Piroddi et al., 2011), and has been suggested to occur in the North-East Atlantic (Lassalle et al., 2012; Santos et al., 2014). Additionally, spatial overlap between cetaceans and fishing activities targeting shared resources (Díaz López and Methion, 2018; Díaz López et al., 2019; Giralt Paradell et al., 2019) and operational effects (López et al. 2002, 2003; Goetz et al., 2015) have been documented previously in the Rías Baixas shelf ecosystem. However, resource overlap is not a sufficient condition for interactions between cetaceans and fisheries, unless negative or positive impacts can be proven (Santos et al., 2014). In this regard, the MTI routine showed that fisheries had negative impacts on common dolphins, harbour porpoise and bottlenose dolphins. Fisheries also had a negative impact on functional groups that included key components of the cetaceans' diet, such as demersal piscivorous fish, large planktivorous pelagic fish and to a lesser extent, Atlantic horse mackerel and sardine. These results would support the idea that, indeed detrimental effects of fisheries on common dolphins, harbour porpoises and bottlenose dolphins are occurring in the area, as has been reported in other regions (Piroddi et al., 2011).

Although the MTI routine refers to a specific moment in time (in this case, the 2005 Rías Baixas shelf ecosystem, Valls et al., 2015), the scenarios with increased fishing effort, further explored the effects of the impacts of the fishing activities on the different cetacean species. These analyses involved two main aspects, decreasing cetacean biomass trends and a tendency towards less varied diets with increased fishing effort, suggesting an indirect effect of fisheries on all three cetacean species included in the model through their diet (Walters et al., 2005).

The predicted generalised collapse of most fish stocks caused by higher fishing effort would result in a trend towards less varied diets for the three cetacean species, especially in the scenarios with higher fishing effort. In these cases, their diet would be almost exclusively composed by small pelagic planktivorous fish, which is one of the keystone functional groups of the Rías Baixas shelf ecosystem (Giralt Paradell et al., 2020). Small pelagic fish are energy rich species, capable of meeting the energetic requirements of common dolphins, harbour porpoises and bottlenose dolphins (Spitz et al., 2010). However, collapses in multiple fish stocks could hinder the ability of generalist cetacean species, such as the ones studied here, to switch to another prey if their preferred prey becomes unavailable (Jennings et al., 2001). As a result, they would

depend upon a reduced group of fish species the recruitment and biomass of which have shown important fluctuations in the past, and are highly determined by environmental changes that influence primary production (Cabrero et al., 2019). Indeed, climate change makes the evolution of primary productivity in shelf waters off North-West Spain in the coming years unclear, and some studies predict an important decrease (Pérez et al., 2010), while others predict an increase (Casabella et al., 2014). Therefore, these fluctuations, which were not considered in the 30-year forward projecting simulations, could strongly influence small pelagic fish, ultimately determining the presence of common dolphins, harbour porpoises and bottlenose dolphins in the area.

4.5. Fishing pressure, an additional threat on cetacean species

Currently, bycatch and marine traffic are major threats for cetacean populations in Galicia (Díaz López and Methion, 2018; Murphy et al., 2019). Bycatch, for instance, has been estimated to kill around 1623 dolphins annually in Galicia (López et al., 2003). Of those, 3% are bottlenose dolphins, and 97% are small cetaceans, mostly common dolphins and, to a much lesser extent, harbour porpoises. These high bycatch numbers are already likely to exceed the limits set to achieve Good Environmental Status for common dolphins in Galician waters (Fernández-Contreras et al., 2010; Saavedra et al., 2018), and could have a similar impact on bottlenose dolphins and harbour porpoises (Llavona Vallina, 2018). Additionally, concerns raised about the increase in bycatch of common dolphins in the Bay of Biscay and adjacent areas, suggest that real bycatch mortality could be underestimated (Peltier et al., 2019; ICES, 2020), and led the European Commission to urge Spain to implement effective bycatch control measures (European Commission, 2020). However, these previous studies focussed only on the effects of bycatch and did not consider other aspects. Recently, fisheries were found to target fish species of intermediate-high trophic levels in the Rías Baixas shelf ecosystem, potentially altering ecosystem functioning and ultimately affecting top predators (Giralt Paradell et al., 2020). This aspect was further investigated in the present study, showing that the ecological effects of fisheries on common dolphins, bottlenose dolphins and harbour porpoises probably pose the major threat to these species, adding to already existing threats and seriously endangering their conservation.

The situation would be especially critical for harbour porpoise, as the 30-year forward projecting simulations predicted a decrease in the species biomass in almost all scenarios. Harbour porpoises in the Iberian coast form a distinct ecotype and population (Fontaine et al., 2014). Despite a significant gene flow, genetic characteristics and habitat preferences differentiate the Iberian ecotype from other North-East Atlantic populations (Fontaine et al., 2014; Llavona Vallina, 2018). Additionally, the seasonality and the relatively small extension of the upwelling region along the Iberian coast, may reduce available food resources for the species and trigger emigration from the area (Fontaine et al., 2014). Although no competition between bottlenose dolphins and harbour porpoise has been reported in the Rías Baixas (Méndez-Fernandez et al., 2013; Díaz López and Methion, 2018), the present study predicts a reduction in fish resources due to fishing activities, which could ultimately lead to competition for prey, particularly among these two top predators. Harbour porpoise conservation status in the area is already delicate due to their reduced population size and the impact of boat traffic (Díaz López and Methion, 2018). The combination of previous findings with results of the present study pose a very pessimistic future for the species, in which the cumulative effect of boat traffic, intrinsic characteristics of the species, competition with other top predators and ecological effects caused by fisheries seriously threaten harbour porpoise conservation in the short term.

4.6. Implications for conservation and management

Several measures have been proposed to improve cetacean

conservation in Galicia, including seasonal closures, operational changes, spatial redistribution of certain fisheries, the designation of Special Areas of Conservation or the development of improved legislative frameworks (López et al., 2003; Fernández-Contreras et al., 2010; Díaz López et al., 2019; Giralt Paradell et al., 2019; Methion and Díaz López, 2019; Methion, 2019). Most of these measures were suggested as a response to one threat to a particular species, and the reduction of fishing effort had never been seen as a priority. However, given the global impact of fishing on the Rías Baixas shelf ecosystem and the cumulative nature of the impacts caused by human activities on cetaceans, efforts to understand the functioning of ecosystems as a whole, the interactions between the different species within them and the impact of human activities, should be prioritised to develop effective conservation measures for both species and ecosystems (Jennings and Rice, 2011). In this regard, different measures are suggested to improve the conservation of common dolphins, harbour porpoises and bottlenose dolphins in

First, this study shows that exploitation of fish resources is altering the entire Rías Baixas shelf ecosystem in an unsustainable manner and this is already threatening top predator conservation. Therefore, immediate action should be taken to reduce fishing effort in the area. This could be done by developing methods to accurately calculate the real fishing capacity of the fleet and by improving fishing effort monitoring (McCluskey and Lewison, 2008). This would lead to a more accurate estimation of the real fishing pressure exerted on the ecosystem and could be used to better monitor and reduce the fishing effort where needed. Second, the study highlights the need to go beyond single stock management strategies in fisheries management. Fisheries play a major role in ecosystem dynamics, directly affecting the exploited stocks, but also indirectly impacting the rest of the species (Pauly et al., 2005). Therefore, future management strategies should focus on prioritising the conservation of the ecosystem and the species within it while ensuring the sustainability of fisheries. Understanding this also implies acknowledging the fact that all affected parties should be involved in the development of any management strategy or conservation measure in order to ensure their effectiveness. Third, the use of ecosystem based approaches, such as the one presented in this study, requires accurate and extensive datasets on the different interacting actors within the ecosystem (Plagányi and Butterwoth, 2004; Heymans et al., 2016). In this regard, efforts should be focused on obtaining regular scientific data on abundance and biomass of the different functional groups within an ecosystem and on obtaining accurate, reliable, and objective fisheries data, to develop comprehensive and effective conservation decisions and management plans. Fourth, as proposed in other studies (e.g. Cámara and Santero-Sánchez, 2019), a combination of compensation schemes and legal enforcement measures should be applied by the different administrations to help fishermen affected by any of the proposed measures and to encourage good practices in fishing activities. Fifth, global measures, such as the expansion of the first two Natura 2000 network sites and the marine area of the National Park to protect larger areas in coastal waters (Giralt Paradell et al., 2019; Methion, 2019) and waters above the continental shelf, should be considered in order to favour the protection of the ecosystem as a whole. Last, the conservation measures suggested in this study should be considered as an addition to the strategies already in place and to the ones proposed previously.

5. Conclusions

Although this work is restricted to a relatively small area, it provides a framework that could be extended to other impacted regions and species. Additionally, the scientific understanding of ecosystem dynamics has significantly improved due to the development of software packages such as EwE, and these can be used to enhance management and conservation decisions (Coll et al., 2015; Villasante et al., 2016). For instance, the present study is an example of how ecosystem information

can be used to work towards cetacean conservation, and it provides a general framework that can be extended to other species, trophic groups or areas. However, extensive scientific data and accurate and reliable fisheries data are not always available, although they are critical to the understanding of ecosystem functioning, assessing the extent of the impact of human activities on the different species and ecosystems, and creating effective conservation and management frameworks. Findings of the study also show that fishing probably poses the most critical threat to common dolphins, bottlenose dolphins and especially harbour porpoises conservation in the Rías Baixas shelf ecosystem. The situation for these three species is critical and urges the different affected parties to find consensual global solutions to improve both ecosystem and species conservation while developing real sustainable fisheries.

Author contribution

B.D.L. and O.G.P. conceived and designed this study. B.D.L., S.M. and O.G.P. collected the data. O.G.P. developed the model with input from B. D.L. and E.R. O.G.P. wrote the manuscript with significant input from B. D.L., S.M. and E.R. All authors contributed critically to the manuscript and gave final approval for publication

Declaration of competing interest

The authors of this study declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2021.112175.

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