Food-web interactions in a coastal ecosystem influenced by upwelling and terrestrial runoff off North-West Spain

Oriol Giralt Paradell[1,2], Bruno Díaz López[1], Séverine Methion[1], Emer Rogan[2]

Food-web interactions in a coastal ecosystem influenced by upwelling and terrestrial runoff off North-West Spain

Oriol Giralt Paradell[1,2], Bruno Díaz López[1], Séverine Methion[1], Emer Rogan[2]

1.   **The Bottlenose Dolphin Research Institute – BDRI. Address: Av Beiramar 192, 36980, O Grove, Pontevedra, Spain**
2. **2 School of Biological, Earth and Environmental Sciences, University College Cork. Address: Distillery Fields, North Mall, Cork, Ireland T23 N73K**

Corresponding author: Oriol Giralt Paradell. Email: oriol@thebdri.com

ABSTRACT:

Ecopath with Ecosim has been used to create mass-balance models of different type of ecosystems around the world to explore and analyse their functioning and structure. This modelling framework has become a key tool in the ecosystem approach to fisheries management, by providing a more comprehensive and holistic understanding of the interactions between the different species. Additionally, Ecopath with Ecosim has provided a useful framework to study ecosystem maturity, changes in the ecosystem functioning over time and the impact of fisheries and aquaculture on the ecosystem, among other aspects. The present work explores the ecosystem functioning and structure in an anthropogenically impacted coastal area, influenced by seasonal coastal upwelling and high input of nutrients from rias (ancient drowned tectonic valleys) off North-West Spain. A mass-balance model with 23 functional groups was created using Ecopath to study the trophic interactions in the ecosystem during the post-upwelling period (August to October) in 2017. The model described an immature, wasp-waist ecosystem, that shared characteristics of ecosystems found in upwelling areas and ecosystems found in fjords or coastal embayments. Deeper analyses highlighted the importance of small planktivorous pelagic fish as a keystone functional group, and of zooplankton, blue whiting (*Micromesistius poutassou*) and phytoplankton as structuring groups in the ecosystem. Additionally, the study revealed that the existing fishing pressure on species of intermediate-high trophic levels could alter ecosystem functioning and structure, and ultimately affect top predators in the area. Findings of this study provide baseline information in ecosystem functioning and structure in the area and highlight the need to deeper study the effects of fisheries and their potential impacts on top predators.

Keywords:

Ecopath; mass-balance model; upwelling; wasp-waist; North-West Spain; coastal waters; food web;

1. Introduction

Marine coastal ecosystems, particularly those close to densely populated areas, are heavily impacted by human activities (Halpern et al. 2008). Interestingly, some of the most productive marine ecosystems are located in coastal areas, typically linked to upwelling systems, estuaries or terrestrial runoff (Field et al. 1998; Jarre-Teichmann et al. 1998; Carr, 2001). These areas are of interest, not only due to their high biodiversity and production, but also because they provide important goods and services for coastal communities (Pauly and Christensen, 1995; Worm et al. 2006). Conservation and management strategies that consider the ecosystem as a whole, such as the ecosystem modelling approach, are needed to improve our knowledge of coastal marine ecosystem functioning, ensure their resilience, and make predictions about the effects of human activities (Coll et al. 2009a,b).

Ecopath with Ecosim (EwE) is a modelling software developed to create mass-balance models of exploited aquatic and marine ecosystems (Christensen and Walters, 2004; Heymans et al. 2016). Based on the work of Polovina (1984) and Ulanowicz (1986), EwE evolved to be a software capable of modelling complex ecosystems, considering not only the energy flows within the ecosystem, but also fisheries impact (Pauly et al. 2000). Since its development in the late 1980s, EwE has become a useful and crucial tool to create ecosystem mass-balance models that have been applied to a variety of scenarios in different ecosystems, ranging from oceanic to coastal regions, with emphasis on bays, fjords, estuaries and upwelling areas (Colléter et al. 2015). Although it has been mainly used as a tool for an ecosystem approach to fisheries management (Pauly et al. 2000), EwE has also been successfully applied to study ecosystem maturity (Christensen, 1995), compare similar ecosystems (Torres et al. 2013), analyse the temporal change of ecosystems (Shannon et al. 2003; Heymans et al. 2004; Ruzicka et al. 2012), evaluate the impact of environmental changes (Tam et al. 2008), and to assess the impact of fisheries or aquaculture on ecosystems (Sánchez and Olaso, 2004; Coll et al. 2006; Díaz López et al. 2008; Outeiro et al. 2018). The widespread use of EwE allows for comparisons between different marine ecosystems globally and

provides reference information for future mass-balance models (Heymans et al. 2014; Colléter et al. 2015). However, there is also a need to develop fine-scale mass-balance models describing specific productive coastal areas impacted by human activities at a regional scale. In this regard, studies providing baseline information on ecosystem functioning and structure are crucial to analyse changes in future scenarios and develop enhanced ecosystem management and conservation strategies.

The continental shelf off North-West Spain is a highly productive coastal area, heavily impacted by human activities, such as fisheries and aquaculture (López et al. 2003; Outeiro et al. 2018). Seasonal upwelling events coupled with terrestrial runoff bring nutrients to the photic layer in coastal waters, enhancing primary production (Alvarez et al. 2012). As a consequence, fisheries and aquaculture have become the main economic activities in the area, turning it into one of the most important regions for these activities in Europe (Rodríguez Rodríguez et al. 2011; Surís-Regueiro and Santiago, 2014). Despite the uniqueness of the area, and its influence in the local and regional economies, there is limited information regarding the ecosystem functioning and structure of the waters of the Galician continental shelf (Outeiro et al. 2018). The paucity of information on the ecosystem dynamics in this area poses great uncertainty around the likely responses (such as alteration in primary production and species distribution (Pérez et al. 2010; Casabella et al. 2014; Sousa et al. 2017)) of the studied ecosystem to changes in upwelling regimes triggered by climate change.

The present study aims to understand the functioning of the Rías Baixas shelf ecosystem, located in a coastal area influenced by coastal upwelling and high input of nutrients from rias (ancient drowned tectonic valleys) on the north-western coast of Spain, and to present a mass-balance model that could be used as baseline for future works. Special attention is given to marine top predators (i.e. cetaceans and seabirds) and to the fisheries impact on the ecosystem. The study offers a good opportunity to improve the scientific knowledge by creating the first EwE model of the Rías Baixas shelf ecosystem located in a highly

productive and impacted coastal area off North-West Spain, providing a new and powerful tool for ecosystem-based management strategies.

2. Material and methods

2.1. Study area and period

Galicia is an autonomous region in North-West Spain, located on the northern limit of the North-West Africa upwelling system (Gonzalez-Nuevo et al. 2014). The region is influenced by wind-driven seasonal coastal upwelling events, which carry deep, cold and nutrient-rich waters to the photic layer, enhancing primary production (Torres et al. 2003; Alvarez et al. 2012). Upwelling events are a consequence of sustained northerly winds (Torres et al. 2003) and typically occur during spring and summer, leading to peaks in chlorophyll a concentration in coastal waters of the continental shelf (Alvarez et al. 2012; Gonzalez-Nuevo et al. 2014). Additionally, terrestrial runoff enhances the production in the study area especially in winter, when rainfall is more important, and thus river discharge is higher (Pitcher et al. 2010; Alvarez et al. 2012).

The 1 498 km of Galician coastline is shaped by a series of drowned tectonic valleys, called rias, that influence the oceanic dynamics and enhance the coastal primary production (Prego et al. 1999; Alvarez et al. 2012). Previous studies emphasised the importance of this area for marine top predators (Pierce et al. 2010; Díaz López and Methion, 2018, 2019; Díaz López et al. 2019; Giralt Paradell et al. 2019) and fisheries (Surís-Regueiro and Santiago, 2014). The rias can be divided into Rías Altas, north of Cape Finisterre, and Rías Baixas, South of Cape Finisterre (Prego et al. 1999). The area considered in this study was located West of the entrance of Ría de Arousa, the biggest of the Rías Baixas (Prego et al. 1999) (Fig. 1). The study area covered 933.13 km^2, extending from the coast of Cape Corrubedo, Sálvora Island and Ons Island in the east (8° 56.69′ W), to the 300 metres bathymetry line in the west (9° 29.07′ W). The southern limit was set at the southern end of Ons island, at the entrance of the Ría de Pontevedra (42° 21.31′ N), and the area extended

north to the southern entrance of the Ría de Muros-Noia (42° 38.40′ N).

The study represents a scenario that corresponds to the post-upwelling period in 2017 (late summer: August – October), and was developed to study the dynamics of a coastal ecosystem influenced by coastal upwelling events and coastal primary production in the area.

2.2. Modelling framework

Ecopath with Ecosim (EwE) version 6.5.14040.0 (www.ecopath.org) was used to develop a mass-balance model of the study area using the Ecopath functionality of the software. Ecopath creates a model of a steady state ecosystem under the assumption of mass-balance over a specific period of time (Christensen and Walters, 2004). The software integrates routines that are used to estimate biomass, production/biomass ratios and consumption of the different functional groups, and makes them interact with routines that analyse the flows between functional groups based on the theory of Ulanowicz (1986). Ecopath works with two basic equations (Christensen and Pauly, 1992). The first equation explores the energy transfer in each functional group under the assumption that, in an ecosystem in a steady state, the inputs will equal the outputs.

$$Q = P + R + U \qquad (1)$$

or

$$Consumption = Production + Respiration + Unassimilated\ food \qquad (1)$$

The second equation explains the production in each functional group (i):

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + P_i \cdot (1 - EE_i) \qquad (2)$$

where P_i is the production rate of (i); Y_i is the total fishery catch rate of (i); B_i is the biomass of (i); $M2_i$ is the total predation rate for (i); E_i is the net migration rate (emigration − immigration) of (i); BA_i is the biomass accumulation rate of (i); EE_i is the ecotrophic efficiency of (i) and the product $P_i \cdot (1 - EE_i)$ is the other mortality rate of (i) or $M0_i$. This equation can also be expressed as:

$$B_i \cdot (P/B)_i - EE_i \sum_{j=1}^{n} B_j \cdot (Q/B)_j \cdot DC_{ji} - Y_i - E_i - BA_i = 0 \qquad (3)$$

where $(P/B)_i$ is the production/biomass ratio of (i); $(Q/B)_j$ is the consumption/biomass ratio of (j); DC_{ij} is the fraction of prey (i) in the average diet of a predator (j).

From equation 3, Ecopath establishes a modelling framework based on a set of linear functions, one per each functional group, to estimate 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 must be entered for each group. Additional information regarding the catch rate, the net migration rate, the biomass accumulation, the consumption rate and the diet composition of each group is also needed by the modelling package (Christensen and Walters, 2004). Further information on Ecopath working procedures and data requirements can be found in the scientific literature and in the Ecopath manual (Christensen and Pauly, 1992; Christensen and Walters, 2004; Christensen et al. 2005; Heymans et al. 2011).

2.3. Functional groups

To understand the trophic dynamics in this study area a total of 23 functional groups were included in the model. Special emphasis was given to top predator groups, especially cetaceans and seabirds as relative abundance data were obtained for these groups in the study area during the study period. Species with similar ecological roles were considered as functional groups. Additionally, the ecosystem was divided into two domains, the pelagic domain and the non-pelagic domain and each functional group was assigned to one of the domains (Table 1). In total, four groups of cetaceans, two of seabirds, ten of fish, three of invertebrates, a zooplankton group and a phytoplankton group were created. Detritus and discards were also included as separate functional groups.

2.3.1. Cetaceans

Systematic data collection on cetaceans since 2014 led to the identification of up to nine species of cetaceans in Galician waters (Díaz López and

Methion, 2017, 2018, 2019). Only species regularly found in the area were included in the model, including common dolphin (*Delphinus delphis*), harbour porpoise (*Phocoena phocoena*), bottlenose dolphin (*Tursiops truncatus*), and four species of baleen whales.

Common dolphin: Common dolphins are the most commonly seen cetacean in the north-western coast of Spain and are widely distributed in the study area (Saavedra et al. 2018), which includes optimal habitat for the species (Giralt Paradell et al. 2019). Data on relative abundance were calculated from direct observations at sea along 14 surveys carried out between August and October 2017. A total of 46 common dolphin groups with an average size of 49 ± 10 individuals were recorded and the relative abundance in the modelled area was estimated at 0.21 individuals/km^2. Information on the diet, mean body weight, daily food intake and mortality rates was obtained from previous studies conducted in the North-East Atlantic (Supplementary material, Table SM1).

Harbour porpoise: The smallest of the cetaceans species in the region, harbour porpoise, is commonly seen in the study area, mainly associated with coastal and continental shelf waters, where its relative abundance was estimated at 0.021 individuals/km^2 (Díaz López and Methion, 2018). Information on the diet of harbour porpoise, mean body weight and daily food intake was obtained from scientific literature (Supplementary material, Table SM2).

Bottlenose dolphin: Bottlenose dolphins are the most commonly seen cetacean in inshore Galician waters, although they are also sighted in deeper waters above the continental shelf (López et al. 2004; Methion and Díaz López, 2018). Data on relative abundance were calculated from direct observations (number of sightings) at sea between August and October 2017. The average group size was estimated at 43 ± 10 individuals, and the relative abundance was 0.042 individuals/km^2. Information on the diet, average body weight, daily food intake and mortality rates was obtained from previous studies (Supplementary material, Table SM3).

Baleen whales: Four species of baleen whales have been recorded off the Galician coast, where feeding events occur, especially after the upwelling periods (Díaz López and Methion, 2019). This functional group included the four species of baleen whales most commonly seen in the area, namely fin whales (*Balaenoptera physalus*), blue whales (*B. musculus*), minke whales (*B. acutorostrata*) and humpback whales (*Megaptera novaeangliae*). Data on relative abundance were calculated from previous studies carried out in the area with data collected between August and October 2017 (Díaz López and Methion, 2019). Information to calculate the total biomass and the P/B and Q/B ratios was obtained from previous studies on diet, average weight, daily food intake and mortality rates (Supplementary material, Table SM4).

2.3.2. Seabirds

Systematic data collection on seabirds since 2014 led to the identification of up to 26 different species of seabirds in Galician waters (BDRI, 2018a). These include several species of seagulls, shearwaters, terns and skuas among others. Only the species commonly seen in the study area were included in the analysis and they were divided into two different groups depending on their feeding ecology and behaviours described by Camphuysen and Webb (1999). For each functional group, the most abundant species, based on the number of individuals, was selected as the representative of the group. The average weight for each seabird group was calculated taking into consideration the mean weight and the relative abundance of all the species included in the group. Information on the P/B and Q/B ratios was obtained from previous studies (Supplementary material, Table SM5 and SM6).

Seabirds I, pursuit and plunge divers: This functional group included species that used deep plunging, deep diving or pursuit diving as feeding techniques, mainly shags (*Phalacrocorax aristotelis*), great cormorants (*P. carbo*), northern gannets (*Morus bassanus*) and shearwaters (*Calonectris diomedea, Puffinus mauretanicus, P. gravis, P. griseus, P. puffinus*). Direct observations at sea were used to calculate the relative abundance of each species. Northern gannets were the most commonly seen species and consequently were selected as the representative of the group.

Seabirds II, surface and aerial pursuit feeders: This functional group included species that used surface feeding, shallow plunging and aerial pursuit as feeding techniques, mainly seagulls (*Larus fuscus, L. marinus, L. melanocephalus, L. michahellis, Xema sabini*), terns (*Sterna sandvicensis*) and skuas (*Stercorarius parasiticus, S. pomarinus, S. skua*). Direct observations at sea were used to calculate the relative abundance of each species. Yellow legged seagulls (*Larus michahellis*) were the most commonly seen species and consequently they were selected as the representative of the group.

2.3.3. Fish

To have a better understanding of the different fish species in the area, landings data from Ribeira harbour in 2017 provided by the Galician government (Xunta de Galicia, Consellería do mar, 2017) were examined. This data included only commercially exploited fish species, as these were the best locally available data. Ribeira harbour is located at the entrance of the Ría de Arousa, on its northern coast (Figure 1), and is considered the third most important European harbour for small-scale fisheries, in terms of landings (Cruz Pazos and Pizarro Alcalde, 2013). A total of 81 fish species caught within the area were landed, comprising species of Osteichthyes and Chondrichthyes. This information was used to create the different fish functional groups that were included in the model. Three species were considered as three separate functional groups, namely blue whiting (*Micromesistius poutassou*), sardine (*Sardina pilchardus*) and Atlantic horse mackerel (*Trachurus trachurus*), given their importance in terms of fishing (Xunta de Galicia, Consellería do mar, 2017). The other species were allocated to seven functional groups depending on their habitat and trophic ecology (Table 2).

Biomass values for each functional group were calculated by combining information on biomass and landings from ICCAT, ICES and information on landings in Ribeira harbour (Supplementary material, table SM24). P/B ratios were obtained from previous models in nearby areas, and Q/B ratios were obtained from either models created

in nearby areas or from previous studies (Supplementary material, tables SM7 to SM16).

Blue whiting: This species was allocated as a separate group due to its economic and ecological importance in the area (Villasante, 2012). The species is widely distributed in the North-East Atlantic, from the Barents Sea to the Strait of Gibraltar, and it plays an important ecological role as a predator of zooplankton and small fish, and as prey items for larger fish species and marine mammals (Villasante, 2012; ICES, 2018). Furthermore, this species is of great economic importance in the area, as it represents approximately 39% of the total landed fish biomass in Ribeira harbour (Xunta de Galicia, Consellería do mar, 2017) (Supplementary material, Table SM7).

Sardine: Despite the decreasing trend since the 1980s (Cabrero et al. 2019) sardine has historically been important for Galician fisheries (Vázquez-Rowe et al. 2014). Sardine is distributed along the North-East Atlantic Ocean, from the North Sea to Senegal and the Mediterranean Sea (Cabrero et al. 2019). This species plays an important ecological role in the area by feeding on lower trophic levels, mainly phytoplankton and zooplankton (Garrido et al. 2008), and is an important part of the diet of marine top predators (Santos et al. 2014). In 2017, sardine represented around 1.5% of the total fish biomass landed in Ribeira harbour (Xunta de Galicia, Consellería do mar, 2017) (Supplementary material, Table SM8).

Atlantic horse mackerel: The species is widely distributed along the North-East Atlantic, from the North Sea to the Strait of Gibraltar (Murta et al. 2008). Atlantic horse mackerel is an important species for local fisheries, comprising 25% of the total landed fish biomass in Ribeira harbour in 2017, becoming the second most landed species in that harbour (Xunta de Galicia, Consellería do mar, 2017) (Supplementary material, Table SM9).

Large piscivorous pelagic fish: This functional group was created to represent the different species of pelagic fish longer than 100 cm that feed predominantly on other fish. Several species of sharks, tuna and other pelagic fish have been recorded in the study area since 2014 (BDRI, 2018b). For instance, blue sharks (*Prionace glauca*) have been recorded year round in both inshore waters and waters above the continental shelf, and Atlantic bluefin tuna (*Thunnus thynnus*) have been recorded feeding on garfish (*Belone belone*) during the period of the year considered in this study (Supplementary material, Table SM10).

Other piscivorous pelagic fish: This functional group is mostly composed of piscivorous species of the family Scombridae, that are smaller than 100 cm, such as the Atlantic bonito (*Sarda sarda*) or the skipjack tuna (*Katsuwonus pelamis*). Additionally, other species such as John Dory (*Zeus faber*) or garfish were also included (Supplementary material, Table SM11).

Large planktivorous pelagic fish: Fish that mostly feed on plankton and measure more than 25 cm formed this functional group. Among others fish species, the group included several planktivorous species of the family Scombridae such as the Atlantic mackerel (*Scomber scombrus*) and the Atlantic chub mackerel (*Scomber colias*), which together represent around 25% of the landed fish biomass in Ribeira harbour (Xunta de Galicia, Consellería do mar, 2017) (Supplementary material, Table SM12).

Small planktivorous pelagic fish: Small species of pelagic planktivorous fish (less than 25 cm), such as sandeels (*Ammodytes* spp.) and European anchovy (*Engraulis encrasicolus*) are an important intermediate trophic level in upwelling ecosystems, that transfer energy from lower trophic levels (plankton) to top predators (Cury et al. 2000) (Supplementary material, Table SM13).

Benthopelagic fish: This functional group was composed mainly of fish species of the families Sparidae and Gadidae, and included species such as poor cod (*Trisopterus minutus*) and bogue (*Boops boops*), both relatively important commercial species in the area (Xunta de Galicia, Consellería do mar, 2017; Alonso-Fernández et al. 2008) (Supplementary material, Table SM14).

Bathydemersal piscivorous fish: Piscivorous fish species inhabiting bathydemersal habitats, such as angler fish (*Lophius piscatorius*), blackbellied angler (*Lophius budegassa*) or the alfonsino (*Beryx*

decadactylus) were included in this functional group (Supplementary material, Table SM15).

Demersal piscivorous fish: This was the most species rich functional group and included several species of importance in terms of fisheries, such as the European hake (*Merluccius merluccius*), the European conger (*Conger conger*), the white seabream (*Diplodus sargus*) and the European seabass (*Dicentrarchus labrax*), among others (Supplementary material, Table SM16).

2.3.4. Invertebrates

Cephalopods: These invertebrates play a crucial role in ecosystems, in which they act as links between different trophic levels and between different habitats (de la Chesnais et al. 2019). Squids and benthic cephalopods were included in the same group, as only very limited information about cephalopod distribution and abundance was available. The total cephalopod landings in Ribeira harbour during 2017 (Xunta de Galicia, Consellería do mar, 2017) were used to select the species that were included in the model. The group was mainly composed of neritic cephalopods such as lesser flying squid (*Todaropsis eblanae*) or European squid (*Loligo vulgaris*) (Supplementary material, Table SM17).

Non-planktivorous crustaceans: Information about non-commercial crustaceans in the area is scarce. Therefore, data on total crustaceans' landings in Ribeira harbour in 2017 were combined with data on demersal trawl surveys (Fariña et al. 1997) to determine the species composition that would be included in the functional group and to estimate their total biomass (Supplementary material, Table SM18).

Macrobenthos: Benthic communities in Galician waters are formed by a wide variety of species (Serrano et al. 2006). However, this functional group was conceived to represent the detritivorous communities and included mainly echinoderms such as the spiny star fish (*Marthasterias glacialis*) and sea urchins (*Spatangus purpureus*) among others (Supplementary material, Table SM19).

2.3.5. Zooplankton

The zooplankton biomass shows interannual and seasonal variation in the study area (Buttay et al. 2016). This variation is caused by a combination of several processes, such as seasonal upwelling events, oceanic currents and coastal runoff (Buttay et al. 2016). The highest abundance of zooplankton in the area typically occurs at the end of summer, coinciding with the upwelling season (Buttay et al. 2016). Copepods are the most abundant and persistent group in the zooplankton in the area, representing around 72% of the zooplankton community (Buttay et al. 2016). In the present study, P/B and Q/B ratios and the ecotrophic efficiencies were obtained from a similar, nearby area (Sánchez and Olaso, 2004) (Supplementary material, Table SM20).

2.3.6. Phytoplankton

Primary production peaks in the area have been linked to increased nutrients from both river runoff and seasonal upwelling events (Alvarez et al. 2012). The latter are especially important in late summer, a period in which they enhance primary production, causing the highest phytoplankton peaks of the year (Alvarez et al. 2012). Information on phytoplankton biomass and the P/B ratio was obtained from a similar, nearby area (Torres et al. 2013) (Supplementary material, Table SM21).

2.3.7. Detritus

Information on detritus was obtained from a nearby area on the western coast of Spain (Torres et al. 2013).

2.3.8. Landings and discards

Detailed information on fish, cephalopods and crustacean landings in Galician harbours was provided by the Galician government (Xunta de Galicia, Consellería do mar, 2017). An analysis of the marine species landed in the different harbours located in the area was conducted prior to creating the model and concluded that Ribeira harbour accounted for 94% of the total landings in the area. Therefore, only the landings reported for Ribeira harbour were included in the model. In total, 34,337 t of fish, 216 t of cephalopods and 98 t of crustaceans were landed in Ribeira harbour in 2017. These data were used to calculate the total

biomass caught per km^2 in the area (Supplementary material, Table SM24). To understand the combined effect of the different fishing techniques used in the area on the Rías Baixas shelf ecosystem, all fisheries were included as one group in the model. Additionally, recent studies estimated that 16.9% of the total fish caught by the Galician fishing fleet was discarded (Vázquez-Rowe et al. 2011). Hence, this value was applied to the study area to calculate the total amount of discards for each of the fish functional groups (Supplementary material, Tables SM22, SM24).

2.4. Diet

EwE requires quantitative diet information to calculate the consumption of the functional groups (Christensen et al. 2005). Several methodologies have been used to study the diet of marine species (Barrett et al. 2007; Ahlbeck et al. 2012; Bowen and Iverson, 2013). The diet of most of the marine mammals, fish and cephalopods groups included in the model (70% of the functional groups) was obtained from quantitative studies derived from stomach content analysis. The diet of both seabirds groups (10% of the functional groups) was obtained from studies that reconstructed diet using pellets. Scientific literature was used to obtain the diet of the remaining groups (20% of the functional groups). For groups containing more than one species, the diet of the most representative species was selected (See supplementary material). Diet variability among regions can be important for some marine species, thus quantitative diet studies carried out in Galicia were prioritised (Supplementary material, Table SM25). Indeed, the diet of 25% of the functional groups was obtained from studies carried out in Galician waters, and another 25% from studies conducted in Portugal. The diet of the remaining functional groups was obtained from studies that took place in the North-East Atlantic (20%), in the Mediterranean Sea (20%), in the North Atlantic (5%) and in other areas (5%).

2.5. Model quality, balancing and analysis

The pedigree index was used to categorise the uncertainty of the inputs. This routine takes into account the origin of the data entered in the model to determine how well this is rooted in local data (Christensen and Walters, 2004). The index varies from 0, when data do not have a local origin, to 1, when inputs are fully rooted in local data (Christensen and Walters, 2004).

Using estimates of biomass, production/biomass ratios, consumption/biomass ratios and diet compositions as input parameters can result in unbalanced models in which ecotrophic efficiency values for some functional groups exceed unity (Kavanagh et al. 2004). The balancing process requires the modification of such input parameters in order to obtain a balanced model, in which the ecotrophic efficiencies of all groups do not exceed unity (Christensen and Walters, 2004). The PREBAL assessment technique (Link, 2010) checks several aspects on the biomass across groups, biomass ratios and vital rates, among others. This technique was used to analyse all the input parameters for each functional group, and to establish priorities during the balancing process.

Several of the ecological indicators described by Odum (1969), such as total net primary production, total primary production/total respiration, total primary production/biomass, biomass/total system throughput and net system production were used to evaluate the system's maturity (Christensen, 1995). The complexity and connectivity were evaluated using the system omnivory index, which is a measure of the variance of the prey's trophic level (Christensen and Pauly, 1993), and is calculated as a weighted average of the omnivory index of each functional group (Libralato, 2013). Another measure of system maturity and stability is the Finn's cycling index, which quantifies the proportion of cycling in a system compared to the total system throughput (Finn, 1976). This index ranges between 0, when there is no cycling in the system, and infinite, when there is no straight through flow. The Finn's cycling index has been linked to the recovery time after perturbations and thus, to the stability of ecosystems (Vasconcellos et al. 1997). Finally, ascendancy and overhead were used to evaluate the organisation and the "strength in reserve" of the food web respectively (Ulanowicz, 1986).

Network analysis was used to examine the relationship between the different functional groups and the importance of the different domains of the ecosystem using different parameters. One of these parameters was the trophic aggregation, a routine that aggregates the different functional groups in discrete trophic levels (Ulanowicz, 1995). This was displayed in the form of the Lindeman spine (Lindeman, 1942), a diagram that shows the flows and the transfer efficiency between discrete trophic levels. The transfer efficiency can be described as the proportion of the input trophic flows that are transferred to the next trophic level or that are exported (Lindeman, 1942; Christensen and Walters, 2004). Additionally, the flows between functional groups together with their consumption on other trophic levels were used to stablish the main flows in the ecosystem and to assess the importance of each domain in the modelled food web.

Keystone species and keystone functional groups have a disproportionately strong effect on the ecosystem despite their low biomass (Power et al. 1996) and have become crucial elements in the development of conservation strategies aiming to preserve ecosystems and their functioning (Valls et al. 2015). Therefore, identifying these crucial keystone species or keystone functional groups within the ecosystems is critical. In this regard, the keystoneness index (Libralato et al. 2006) was used to determine if there were any species or functional group that could be considered as a keystone species or keystone functional group.

3. Results and discussion

The model resulting from the balancing process had a pedigree index of 0.532, which is above the mean pedigree index value calculated from previously constructed models for which such information was available, and falls within the higher end of the variation range (Morissette, 2007; Colléter et al. 2015).

3.1. Balancing the model

The first model obtained was unbalanced, as nine groups had an ecotrophic efficiency greater than 1, meaning that their biomass was insufficient to sustain the trophic demand of their predators.

These groups included several high commercial valuable species such as blue whiting and sardine, but also other groups of fishes and invertebrates. Following Link (2010), a PREBAL assessment was conducted prior to balancing the model. The method detected several groups, the biomass of which was notably greater or notably smaller than the one expected for a group of a given trophic level in a balanced ecosystem. All the groups with a biomass higher than expected included highly commercially valuable species such as blue whiting, sardine, Atlantic horse mackerel and Atlantic mackerel. These high biomass values could be explained by the method used to estimate the biomass of the fish groups, which relied on the landings data from Ribeira harbour. Because these species are preferentially targeted in the area, this approach could have led to an overestimation of their biomass. In order to obtain a better estimate for the biomass, the ecotrophic efficiencies estimated for the same groups in other Ecopath models created in similar and nearby areas were used to modify the input parameters of these groups.

Once the biomass of all groups had been corrected, the subsequent balancing steps focussed on adjusting the diet of the different functional groups and especially the top predators. For instance, direct feeding observations recorded by researchers in the area since 2014 (Díaz López and Methion, 2017, 2019; Methion and Díaz López, 2019b) were used as complementary information to adjust the diet of cetacean species. Additionally, scientific literature was used to gather additional information to adjust the diet of several cetaceans, seabirds and fish groups. The final diet included in the model is shown in Table 3.

The input parameters obtained after the balancing process are shown in Table 4, together with basic parameters calculated by Ecopath. The respiration/assimilation, production/respiration and respiration/biomass ratios as well as the net efficiencies were within the expected values (Christensen et al. 2005).

3.2. Description of the balanced model and system maturity

The model obtained after the balancing process presents several characteristics of trophic models from upwelling areas (Table 5). These systems can be usually described as immature and are characterised by high nutrient inputs and a dependence on high system throughput (Christensen, 1995). The system modelled here had a total biomass excluding detritus of 268 t km^{-2}, 63% of which was contained in the pelagic domain and the remaining 37% in the non-pelagic domain. The total system throughput, a measure of the size of the ecosystem in terms of flows between functional groups, was 16025.89 t km^{-2} per year. Both total biomass and total system throughput values fell within the lower range of the values estimated for other upwelling systems around the world (Shannon et al. 2003; Heymans et al. 2004; Tam et al. 2008). Additionally, several other ecological indicators (Table 5) were used to assess the maturity of the ecosystem modelled here (following Odum, 1969; Christensen 1995). These included total net primary production, total primary production/total respiration, total primary production/biomass, biomass/total system throughput, net system production. The values found for each of the parameters confirmed that the Rías Baixas shelf ecosystem described here is in a low-intermediate developmental stage sensu Odum (1969) and that the ecosystem is immature.

This aspect was also confirmed by the system omnivory index, which was low-intermediate (Table 5) indicating that the system had moderate complexity and maturity (Libralato, 2013). These results are in line with what has been found in other upwelling regions (Tam et al. 2008), and are lower than the values of models created in nearby areas (Cantabrian Sea, Sánchez and Olaso, 2004; and Ría de Arousa, Outeiro et al. 2018). Additionally, system omnivory indices have been found to be sensitive to fishing activities, being lower in areas subjected to intensive fishing pressure (Libralato et al. 2010). Hence, the low values obtained in this study could indicate that the moderate complexity and maturity of the ecosystem was a consequence of intense fishing pressure in the area (Surís-Regueiro and Santiago, 2014).

The omnivory indices for each functional group show the variance of the prey's trophic level of a given consumer (Libralato, 2013). The index varies between 0, when consumers feed on just one trophic level and 1, when they feed on a variety of trophic levels. The results showed that the omnivory index for each functional group varied between 0 for Atlantic horse mackerel and small planktivorous pelagic fish and 0.905 for seabirds I (Table 4). In general, functional groups of the pelagic domain tended to have a higher omnivory index (mean = 0.30 ± 0.07) than those in the non-pelagic domain (mean = 0.14 ± 0.06). Similarly, pelagic top predators (dolphins, porpoises, seabirds and large pelagic pisicivorous fish) had higher omnivory indices (mean = 0.44 ± 0.12) than non-pelagic top predators (bathydemersal piscivorous fish and demersal piscivorous fish, mean = 0.07 ± 0.02).

The Finn's cycling index value for the present study was 19.4%, and indicated that the ecosystem had a shorter recovery time and a higher stability than other upwelling areas (Heymans et al. 2004; Tam et al. 2008), but a longer recovery time and lower stability than nearby, highly productive, inshore areas (Ría de Arousa, Outeiro et al. 2018). These results are in line with earlier studies, that showed that coastal lagoons and fjords have higher stability than upwelling systems (Vasconcellos et al. 1997), and that Finn's cycling index tends to decrease with increasing ecosystem size (Heymans et al. 2014). This would indicate that the study area has shared characteristics of upwelling and estuarine ecosystems.

In terms of general system homeostasis, ascendancy and overhead have been used as indices to explain the degree of organisation and the "strength in reserve" of food webs, respectively (Ulanowicz, 1986). These parameters provide insights on the organisation of the food web and the potential recovery of the system (Ulanowicz, 1986; Christensen, 1995). The low ascendancy (22.36%) and the high overhead (77.64%) of the system modelled here denoted a low organisational level and at the same time a high resilience. This is in line with findings in other upwelling systems, where overhead values tend to be high, indicating that the systems are capable of coping with external perturbations (Shannon et al. 2003; Heymans et al. 2004).

3.3. Flows and network analysis:

The functional groups in the model were organised into four integer trophic levels. In essence, the system could be organised into effective trophic levels (Field et al. 1989), such as primary producers (phytoplankton), primary consumers (zooplankton, macrobenthos, sardine and benthopelagic fish), secondary consumers (including the rest of the fish groups and the cephalopods), and top predators (including cetaceans and seabirds). Eight groups had a trophic level (TL) > 4, and among them, bottlenose dolphins, large piscivorous pelagic fish and common dolphins, had a TL close to 5. All cetaceans except for baleen whales had a TL > 4. Among the fish groups, large piscivorous pelagic, bathydemersal piscivorous, demersal piscivorous and other piscivorous pelagic had a TL > 4, whereas the rest of the fish groups had TL between 2.72 and 3.46. Both seabird groups had TL > 3, close to 4. Among the invertebrates, cephalopods was the group with the highest TL (4.25) and macrobenthos was the group with the lowest TL (2.12).

TLs of delphinids and porpoises, were slightly higher than those recorded by Pauly et al. (1998) and in other upwelling systems (Heymans et al. 2004; Tam et al. 2008), but were in accordance with previous models developed in the North-East Atlantic and in other upwelling regions (Shannon et al. 2003; Lassalle et al. 2011; Torres et al. 2013). These differences among models can be explained by differences in prey availability and in diet differences between populations. Baleen whales had similar TL than those previously reported (e.g. Pauly, et al. 1998, Morato et al. 2016). Conversely, both groups of seabirds had a slightly lower TL than those previously recorded (Lassalle et al. 2011; Outeiro et al. 2018). This difference might be due to a higher contribution of discards in the seabirds diet. The TL of the fish groups, invertebrates and zooplankton were in line with those found in the North-East Atlantic (Sánchez and Olaso, 2004; Lassalle et al. 2011; Torres et al. 2013).

The Lindeman spine (Figure 2) aggregates the different functional groups in discrete trophic levels and gives information about different aspects such as the flows between the trophic levels (Lindeman, 1942; Ulanowicz, 1995). The first trophic level is shared by both primary producers and detritus. The system here modelled shows that the majority of the flows (57.04% of the total system throughput) occurred between the TL I and TL II, and secondly between TL II and TL III (36.46% of the total system throughput). Conversely, flows from the TL III and above were insignificant (<7% of the total system throughput).

Figure 2 also provides information about the transfer efficiency between successive discrete trophic levels. These ranged between 11.7% (TL III) and 17% (TL IV). The highest values were found in TL IV (17%) and TL II (16.5%) and these might be explained by different factors. While the high transfer efficiency in TL II suggested a good link between phytoplanktivorous and detritivorous organisms and their predators (Coll et al. 2006), the high transfer efficiency in TL IV was determined by a higher contribution of the exports (Figure 3A). Indeed, the proportion of exports in relation to the total transfer efficiency increased with increasing TL. Two elements determine the exports of each TL, the emigration to adjacent ecosystems and the catches by fisheries (Christensen and Pauly, 1993). Since the emigration rate was considered 0 in the present model, the higher proportion of the export in the total transfer efficiency of TL IV could be directly linked to a more intense fishing pressure focussing on species of that trophic level, as it has been seen in other regions (Shannon et al. 2003; Coll et al. 2009b; Libralato et al. 2010).

The mean transfer efficiency, calculated as the geometric mean for TL II, III and IV (Christensen et al. 2005) was 14.89%, and was higher than the mean transfer efficiency found in other upwelling systems (Baird et al. 1991; Jarre-Teichmann et al. 1998; Heymans et al. 2004). Higher than usual efficiencies in the transfer of biomass have been explained by several factors, such as anomalous performances of key species (Baird et al. 1991), bottleneck effect and food limitation (Shannon et al. 2003). However, the high transfer efficiency in the present model could be explained by two main factors, the importance of catches in TL III and above (Shannon et al. 2003; Coll et al. 2009b; Libralato et al. 2010) and the good coupling between zooplankton and its predators (Baird et al. 1991; Coll et al. 2006). Regarding the first

factor, 94% of the total biomass landed in Ribeira harbour in 2017 was represented by eight species of fish: European conger, sardine, bogue, European hake, Atlantic mackerel, Atlantic chub mackerel, Atlantic horse mackerel and blue whiting (Xunta de Galicia, Consellería do mar, 2017). Seven of these species were classified by the model in TL III and IV. As a consequence, the high fishing pressure on these species doubled the TE for TL III and IV, and contributed to an increase of the mean transfer efficiency of the system (Figure 3A). With regard to the second factor, the transfer efficiency of TL II was mainly determined by predation (Figure 3). The zooplankton was the main component of the TL II in terms of biomass and it was efficiently predated by a series of groups, namely small planktivorous pelagic fish, blue whiting, Atlantic horse mackerel and sardine, which control the transfer of energy into higher trophic levels. These aspects were reinforced by the fate of the total system throughput (Figure 3B), which showed the importance of predation in TL I and II, as well as an increasing importance of the exports in higher trophic levels (III and above).

The modelled system showed that most of the biomass excluding detritus (63%) was contained within the pelagic domain, whereas the remaining 37% was held in the non-pelagic domain. Additionally, the model revealed the importance of the pelagic domain in the system as well as some differences between domains (Figure 4). For instance, most of the consumption (86%) of the functional groups in the pelagic domain originated within the same domain, phytoplankton and zooplankton being the most important groups (Supplementary material, Table SM26). The remaining 14% originated in the non-pelagic domain, where detritus was the most important group. Conversely, 85% of the consumption in the non-pelagic domain originated in the pelagic domain, in which zooplankton was the most important group. The remaining 15% originated within the same domain.

Zooplankton played an important role in the system by linking the lower levels with the higher levels from the pelagic and the non-pelagic domains, as the main flows from the lower levels towards higher levels passed through it. For instance, blue whiting, Atlantic horse mackerel and, to a lesser extent, non-planktonic

crustaceans, fed on zooplankton and determined the energy transfer from the lower to the higher trophic levels in the non-pelagic domain. Similarly, sardine, small planktivorous pelagic fish and large planktivorous pelagic fish were the main predators of zooplankton in the pelagic domain and determined the energy transfer from the lower to the higher trophic levels in that domain.

A deeper analysis shows that most of the flows in the pelagic domain were determined by the interactions between zooplankton, phytoplankton, and planktivorous pelagic fish (Supplementary material, Table SM26). Some functional groups exclusively fed within the pelagic domain (baleen whales, sardine, large planktivorous pelagic fish and small planktivorous pelagic fish), others primarily fed on functional groups of the pelagic domain (seabirds I, large piscivorous pelagic fish, other piscivorous pelagic fish, cephalopods and zooplankton) and the remaining groups primarily fed on functional groups of the non-pelagic domain (common dolphins, harbour porpoises, bottlenose dolphins and seabirds II). The non-pelagic domain was especially dominated by the interactions between zooplankton, detritus and blue whiting. Some functional groups in the non-pelagic domain mainly fed on functional groups of the same domain (bathydemersal piscivorous fish, demersal piscivorous fish and macrobenthos), while others primarily or exclusively fed on groups of the pelagic domain (blue whiting, Atlantic horse mackerel, benthopelagic fish, and non-planktonic crustaceans). Both domains were connected at low levels through the zooplankton, which was consumed by a wide variety of fish and invertebrate groups of both domains. At intermediate levels, several functional groups, such as the blue whiting, the Atlantic horse mackerel and the benthopelagic fish of the non-pelagic domain and the small planktivorous pelagic fish of the pelagic domain, connected the lower and upper levels of both domains. At higher levels, small cetaceans, seabirds II and large piscivorous pelagic fish connected the pelagic domain with the non-pelagic domain.

3.4. Keystoneness Index

The functional group with a highest keystoneness was small planktivorous pelagic fish (group 20 in

Figure 5). Additional functional groups that ranked high in this index were zooplankton, blue whiting and phytoplankton, however, their biomass was higher than the small planktivorous pelagic fish biomass (Table 6). These results indicate that the small planktivorous pelagic fish played a crucial role in the ecosystem structure and functioning, despite its relative low biomass, thus it could be considered as a keystone group (Libralato et al. 2006). Conversely, the dominant role in the ecosystem of the remaining three groups derived from their higher biomass, especially the zooplankton biomass, and therefore they could be considered important structuring groups (Libralato et al. 2006; Heymans et al. 2011). Furthermore, the results show that the keystone and the structuring functional groups had intermediate trophic levels and variable top-down effects (Table 6), suggesting that the Rías Baixas shelf ecosystem is regulated by a mix of top-down and bottom-up controls, and could be described as a wasp-waist ecosystem (Cury et al. 2000; Bakun, 2006; Hunt and McKinnell, 2006; Libralato et al. 2006).

These findings are reinforced by the flows between functional groups, which show two main energy transfer pathways from lower to higher trophic levels (Figure 4). Both pathways originate in the zooplankton, and transfer the energy to higher trophic levels through the small planktivorous pelagic fish (group 13 in Figure 4) on one hand, and the blue whiting (group 7 in Figure 4)on the other hand. Indeed, small planktivorous pelagic fish have been found to play an important role for predators, becoming an energy-rich source to their diet (Spitz et al. 2018). In North-West Spain, small planktivorous pelagic fish are subjected to recurrent changes in recruitment and biomass that are mostly driven by environmental changes (Santos et al. 2007; Garrido et al. 2017; Cabrero et al. 2019). Furthermore, blue whiting is primarily targeted by Galician fisheries and represented the higher landings biomass in Ribeira harbour in 2017 (Xunta de Galicia, Consellería do mar, 2017). Consequently, changes in environmental regimes, coupled with fishing pressure of both small planktivorous fish and blue whiting, could have drastic effects on the ecosystem structure and functioning (Santos et al. 2007; Coll et al. 2009c; Valls et al. 2015).

4. Conclusions

This study presents the first comprehensive mass-balance model of the Rías Baixas shelf ecosystem, a coastal ecosystem located in a highly productive area influenced by coastal upwelling and terrestrial runoff, and heavily impacted by human activities off North-West Spain. EwE proved to be a useful tool to create a mass-balance model describing the trophic interactions among the different functional groups and species in the area which could be used as baseline information for future work focused on coastal management and conservation. Local and detailed information was available for marine top predators, such as cetaceans and seabirds, providing high reliability to the results obtained for these specific functional groups. Data on the fish and cephalopod functional groups were calculated from regional fisheries landing statistics, assuming that the fishing vessels operated within the limits of the study area. These assumptions could have led to an underrepresentation of the non-commercial species in the model. However, since biomass estimates of non-commercial species are not available in the area, landing statistics were considered the best locally available data in order to create the fish functional groups. Additionally, findings for these groups should be considered carefully, as official landing statistics might underrepresent the real catches in the area (Pauly and Zeller, 2016), leading to an underestimation of the fisheries impacts. Parameter estimates for benthic invertebrates in the area were scarce, highlighting the need to further study these communities if more detailed ecosystem models were to be created. In summary, this study presents a realistic mass-balance model with higher reliability for the results obtained on marine top predators.

In general terms, the Rías Baixas shelf ecosystem shows a wasp-waist control and can be described as immature, moderately complex, stable, with a low organisational level and high resilience, characteristics that apply to upwelling systems worldwide (Christensen, 1995; Jarre-Teichmann and Christensen, 1998 ; Heymans et al. 2004). However, some of the parameters of the model suggest that the ecosystem includes some attributes of ecosystems typically found in fjords or coastal embayments (Vasconcellos et al. 1997).

The adjacent rias (Ría de Pontevedra, Ría de Arousa and Ría de Muros-Noia) seem to play an important role in influencing the dynamics of the studied continental shelf ecosystem.

Some of the parameters and indicators used in the model, such as the transfer efficiency and system omnivory index, suggest that the ecosystem functioning and structure could be impacted by the fisheries operating in the area. Indeed, several studies have linked intense fishing pressure to drastic changes in species abundance, evolutionary characteristics of the populations and ultimately alterations in the ecosystem structure and functioning (Pauly et al. 2002; Spitz et al. 2018). Higher than usual transfer efficiencies found in the ecosystem modelled here suggested that fisheries were mainly targeting fish species with a trophic level higher than III. These findings agree with regional catch statistics that state that 94% of the fish biomass caught and landed in the area included fish species of trophic level III or higher (Xunta de Galicia, Concelleria do Mar, 2017). These landings included mostly three species, blue whiting, Atlantic horse mackerel and Atlantic chub mackerel, which respectively accounted for 38%, 24% and 20% of the total landed biomass (Xunta de Galicia, Concelleria do Mar, 2017), and are mainly targeted by pair-trawlers operating in the area (Fernandez-Contreras et al. 2010)

The fishing pressure on blue whiting, coupled with the fluctuations in small pelagic fish biomass, might have caused a dual impact on the ecosystem functioning. On one hand, blue whiting was found to have a crucial structuring role by feeding on zooplankton and serving as prey for top predators of both the pelagic and the non-pelagic domains, thus linking the lower and higher trophic levels. Similarly, small planktivorous pelagic fish, were considered a keystone functional group, linking lower with higher trophic levels. On the other hand, both functional groups were abundant prey items in the diet of top predators such as common dolphins, bottlenose dolphins and harbour porpoises. Additionally, the wasp-waist nature of the Rías Baixas shelf ecosystem makes it particularly vulnerable to climate variability and to drastic changes in the trophic groups that link lower and higher trophic levels (Cury et al. 2000). Consequently, the fishing pressure, especially on

blue whiting, and environmental changes could lead to drastic changes in the ecosystem structure and in the energy flows, ultimately affecting top predators.

Indeed, the study area has been found to be important for some of the marine top predators included in this model, such as common dolphins, bottlenose dolphins, harbour porpoises (Díaz López and Methion, 2018; Giralt Paradell et al. 2019) or Atlantic blue fin tuna. For instance, Atlantic bluefin tuna, is listed as endangered by the IUCN, as a consequence of intensive fishing (Collette et al. 2011). Harbour porpoise commonly seen in the area belong to a distinct ecotype, which is already affected by vessel traffic in the area (Fontaine et al. 2014; Díaz López and Methion, 2018). Bottlenose and common dolphins are regularly observed in the area, where they face several threats such as fisheries bycatch, water pollution, and microplastics (López et al. 2002; Hernandez-Gonzalez et al. 2018; Methion and Díaz López, 2019b). As a consequence, drastic changes in the ecosystem functioning and structure could imply an added stress on these and other top predator species, compromising their conservation in the area.

Results of this study provide baseline information on the Rías Baixas shelf ecosystem structure and functioning, locaed in a coastal area influenced by coastal upwelling and the presence of rias. Moreover, this study provides insights on the potential impacts of intense fishing pressure on the ecosystem in the region. However, given the unique characteristics of the area and its importance for marine top predators, deeper and comprehensive understanding of the effects of fisheries is needed to ensure the ecosystem conservation. The combination of this holistic approach with previous studies focused on marine top predator distribution could lead to the development of management plans that ensured sustainable exploitation of fishery resources and conservation strategies focused on these vulnerable species.

6. *References*

Ahlbeck, I., Hansson, S., Hjerne, O., 2012. Evaluating fish diet analysis methods by individual-based modelling. Can. J. Fish. Aquat. Sci. 69, 1184–1201. https://doi.org/10.1139/f2012-051

Alonso-Fernández, A., Domínguez-Petit, R., Bao, M., Rivas, C., Saborido-Rey, F., 2008. Spawning pattern and reproductive strategy of female pouting *Trisopterus luscus* (Gadidae) on the Galician shelf of north-western Spain. Aquat. Living Resour. 21, 383–393. https://doi.org/10.1051/alr:2008059

Alvarez, I., Lorenzo, M.N., DeCastro, M., 2012. Analysis of chlorophyll a concentration along the Galician coast: seasonal variability and trends. ICES J. Mar. Sci. 69, 728–738. https://doi.org/10.1093/icesjms/fss045

Baird, D., McGlade, J.M., Ulanowicz, R.E., 1991. The comparative ecology of six marine ecosystems. Philos. Trans. R. Soc. London. Ser. B Biol. Sci. 333, 15–29. https://doi.org/10.1098/rstb.1991.0058

Bakun, A., 2006. Wasp-waist populations and marine ecosystem dynamics: Navigating the "predator pit" topographies. Prog. Oceanogr. 68, 271–288. https://doi.org/10.1016/j.pocean.2006.02.004

Barrett, R.T., Camphuysen, K. (C. J.., Anker-Nilssen, T., Chardine, J.W., Furness, R.W., Garthe, S., Hüppop, O., Leopold, M.F., Montevecchi, W.A., Veit, R.R., 2007. Diet studies of seabirds: a review and recommendations. ICES J. Mar. Sci. 64, 1675–1691. https://doi.org/10.1093/icesjms/fsm152

BDRI. 2018a. Marine birds in Galician waters in 2017. Report of the Bottlenose Dolphin Research Institute, O Grove, Spain

BDRI. 2018b. Fish species in Galician waters in 2017. Report of the Bottlenose Dolphin Research Institute, O Grove, Spain

Bowen, W.D., Iverson, S.J., 2013. Methods of estimating marine mammal diets: A review of validation experiments and sources of bias and uncertainty. Mar. Mammal Sci. 29, 719–754.

Buttay, L., Miranda, A., Casas, G., González-quirós, R., Nogueira, E., 2016. Long-term and seasonal zooplankton dynamics in the northwest Iberian shelf and its relationship with meteo-climatic and hydrographic variability. J. Plankton Res. 38, 106–121. https://doi.org/10.1093/plankt/fbv100

Cabrero, Á., González-Nuevo, G., Gago, J., Cabanas, J.M., 2019. Study of sardine (*Sardina pilchardus*) regime shifts in the Iberian Atlantic shelf waters. Fish. Oceanogr. 28, 305–316. https://doi.org/10.1111/fog.12410

Camphuysen, C.J., Webb, A., 1999. Multi-species feeding associations in North Sea seabirds - Jointly exploiting a patchy environment. Ardea 87, 177–198.

Carr, M.-E., 2001. Estimation of potential productivity in Eastern Boundary Currents using remote sensing. Deep Sea Res. Part II Top. Stud. Oceanogr. 49, 59–80. https://doi.org/10.1016/S0967-0645(01)00094-7

Casabella, N., Lorenzo, M.N., Taboada, J.J., 2014. Trends of the Galician upwelling in the context of climate change. J. Sea Res. 93, 23–27. https://doi.org/10.1016/j.seares.2014.01.013

Christensen, V., 1995. Ecosystem maturity — towards quantification. Ecol. Modell. 77, 3–32. https://doi.org/10.1016/0304-3800(93)E0073-C

Christensen, V., Pauly, D., 1993. Trophic Models of Aquatic Ecosystems, in: Christensen, V., Pauly, D. (Eds.), ICLARM Conference Proceedings 26. Manila, p. 390.

Christensen, V., Pauly, D., 1992. ECOPATH II — a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Modell. 61, 169–185. https://doi.org/10.1016/0304-3800(92)90016-8

Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecol. Modell. 172, 109–139. https://doi.org/10.1016/j.ecolmodel.2003.09.003

Christensen, V., Walters, C.J., Pauly, D., 2005. Ecopath with Ecosim: A user's guide. Fisheries Centre. University of Columbia

Coll, Marta, Bundy, A., Shannon, L.J., 2009a. Ecosystem Modelling Using the Ecopath with Ecosim Approach, in: Megrey, B.A., Moksness, E. (Eds.), Computers in Fisheries Research. Springer Netherlands, Dordrecht, pp. 225–291. https://doi.org/10.1007/978-1-4020-8636-6_8

Coll, Marta, Palomera, I., Tudela, S., 2009b. Decadal changes in a NW Mediterranean Sea food web in relation to fishing exploitation. Ecol. Modell. 220, 2088–2102. https://doi.org/10.1016/j.ecolmodel.2009.04.049

Coll, M., Palomera, I., Tudela, S., Sardà, F., 2006. Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. J. Mar. Syst. 59, 63–96. https://doi.org/10.1016/j.jmarsys.2005.09.001

Coll, M, Santojanni, A., Palomera, I., Arneri, E., 2009c. Food-web changes in the Adriatic Sea over the last three decades. Mar. Ecol. Prog. Ser. 381, 17–37. https://doi.org/10.3354/meps07944

Colléter, M., Valls, A., Guitton, J., Gascuel, D., Pauly, D., Christensen, V., 2015. Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. Ecol. Modell. 302, 42–53. https://doi.org/10.1016/j.ecolmodel.2015.01.025

Collette, B., Amorim, A.F., Boustany, A., Carpenter, K.E., de Oliveira Leite Jr., N., Di Natale, A., Die, D.,

Fox, W., Fredou, F.L., Graves, J., Viera Hazin, F.H., Hinton, M., Juan Jorda, M., Kada, O., Minte Vera, C., Miyabe, N., Nelson, R., Oxenford, H., Pollard, D., Restrepo, V., Schratwieser, J., Teixeira Lessa, R.P., Pires Ferreira Travassos, P.E., Uozumi, Y., 2011. *Thunnus thynnus* [WWW Document]. IUCN Red List Threat. Species 2011

Cruz Pazos, P., Pizarro Alcalde, F., 2013. La pesca de bajura en España. Un caso práctico: la lonja Gallega de Ribeira como recurso didáctico. Clio 39, 1–21.

Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñones, R.A., Shannon, L.J., Verheye, H.M., 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES J. Mar. Sci. 57, 603–618. https://doi.org/10.1006/jmsc.2000.0712

de la Chesnais, T., Fulton, E.A., Tracey, S.R., Pecl, G.T., 2019. The ecological role of cephalopods and their representation in ecosystem models. Rev. Fish Biol. Fish. 29, 313–334. https://doi.org/10.1007/s11160-019-09554-2

Díaz López, B., Bunke, M., Bernal Shirai, J.A., 2008. Marine aquaculture off Sardinia Island (Italy): Ecosystem effects evaluated through a trophic mass-balance model. Ecol. Modell. 212, 292–303. https://doi.org/10.1016/j.ecolmodel.2007.10.028

Díaz López, B., Methion, S., 2019. Habitat drivers of endangered rorqual whales in a highly impacted upwelling region. Ecol. Indic. 103, 610–616. https://doi.org/10.1016/j.ecolind.2019.04.038

Díaz López, B., Methion, S., 2018. Does interspecific competition drive patterns of habitat use and relative density in harbour porpoises? Mar. Biol. 165, 92. https://doi.org/10.1007/s00227-018-3345-8

Díaz López, B., Methion, S., 2017. The impact of shellfish farming on common bottlenose dolphins' use of habitat. Mar. Biol. 164, 83. https://doi.org/10.1007/s00227-017-3125-x

Díaz López, B., Methion, S., Giralt Paradell, O., 2019. Living on the edge: Overlap between a marine predator's habitat use and fisheries in the Northeast Atlantic waters (NW Spain). Prog.

Oceanogr. 175, 115–123. https://doi.org/10.1016/j.pocean.2019.04.004

Fariña, A.C., Freire, J., González-Gurriarán, E., 1997. Megabenthic decapod crustacean assemblages on the Galician continental shelf and upper slope (north-west Spain). Mar. Biol. 127, 419–434. https://doi.org/10.1007/s002270050029

Fernandez-Contreras, M.M., Cardona, L., Lockyer, C.H., Aguilar, A., 2010. Incidental bycatch of short-beaked common dolphins (*Delphinus delphis*) by pairtrawlers off northwestern Spain. ICES J. Mar. Sci. 67, 1732–1738. https://doi.org/10.1093/icesjms/fsq077

Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkowski, P., 1998. Primary Production of the Biosphere: Integrating Terrestrial and Oceanic Components. Science. 281, 237–240. https://doi.org/10.1126/science.281.5374.237

Field, John G., Wulf, F., Mann, Kenneth H., 1989. The need to analyze ecological networks, in: Wulff, F., Field, J.G., Mann, K.H. (Eds.), Network Analysis in Marine Ecology: Methods and Applications. Coastal and Estuarine Studies. Springer Verlag, Berlin, pp. 3–12. https://doi.org/10.1029/CE032p0001

Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. J. Theor. Biol. 56, 363–380. https://doi.org/10.1016/S0022-5193(76)80080-X

Fontaine, M.C., Roland, K., Calves, I., Austerlitz, F., Palstra, F.P., Tolley, K.A., Ryan, S., Ferreira, M., Jauniaux, T., Llavona, A., Öztürk, B., Öztürk, A.A., Ridoux, V., Rogan, E., Sequeira, M., Siebert, U., Vikingsson, G.A., Borrell, A., Michaux, J.R., Aguilar, A., 2014. Postglacial climate changes and rise of three ecotypes of harbour porpoises, *Phocoena phocoena*, in western Palearctic waters. Mol. Ecol. 23, 3306–3321. https://doi.org/10.1111/mec.12817

Garrido, S., Ben-Hamadou, R., Oliveira, P., Cunha, M., Chícharo, M., van der Lingen, C., 2008. Diet and feeding intensity of sardine *Sardina pilchardus*: correlation with satellite-derived chlorophyll data. Mar. Ecol. Prog. Ser. 354, 245–256. https://doi.org/10.3354/meps07201

Garrido, S., Silva, A., Marques, V., Figueiredo, I., Bryère, P., Mangin, A., Santos, A.M.P., 2017. Temperature and food-mediated variability of European Atlantic sardine recruitment. Prog. Oceanogr. 159, 267–275. https://doi.org/10.1016/j.pocean.2017.10.006

Giralt Paradell, O., Díaz López, B., Methion, S., 2019. Modelling common dolphin (*Delphinus delphis*) coastal distribution and habitat use: Insights for conservation. Ocean Coast. Manag. 179, 104836. https://doi.org/10.1016/j.ocecoaman.2019.104836

Gonzalez-Nuevo, G., Gago, J., Cabanas, J.M., 2014. Upwelling index: a powerful tool for marine research in the NW Iberian upwelling system. J. Oper. Oceanogr. 7, 47–57. https://doi.org/10.1080/1755876X.2014.11020152

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A Global Map of Human Impact on Marine Ecosystems. Science . 319, 948–952. https://doi.org/10.1126/science.1149345

Hernandez-Gonzalez, A., Saavedra, C., Gago, J., Covelo, P., Santos, M.B., Pierce, G.J., 2018. Microplastics in the stomach contents of common dolphin (*Delphinus delphis*) stranded on the Galician coasts (NW Spain, 2005–2010). Mar. Pollut. Bull. 137, 526–532. https://doi.org/10.1016/j.marpolbul.2018.10.026

Heymans, J.J., Coll, M., Libralato, S., Christensen, V., 2011. Ecopath Theory, Modeling, and Application to Coastal Ecosystems, in: Wolanski, E., McLusky, D.S. (Eds.), Treatise on Estuarine and Coastal Science. Elsevier, pp. 93–113. https://doi.org/10.1016/B978-0-12-374711-2.00905-0

Heymans, J.J., Coll, M., Libralato, S., Morissette, L., Christensen, V., 2014. Global Patterns in Ecological Indicators of Marine Food Webs: A Modelling Approach. PLoS One 9, e95845. https://doi.org/10.1371/journal.pone.0095845

Heymans, J.J., Coll, M., Link, J.S., Mackinson, S., Steenbeek, J., Walters, C., Christensen, V., 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. Ecol. Modell. 331, 173–184. https://doi.org/10.1016/j.ecolmodel.2015.12.007

Heymans, J.J., Shannon, L.J., Jarre, A., 2004. Changes in the northern Benguela ecosystem over three decades: 1970s, 1980s, and 1990s. Ecol. Modell. 172, 175–195. https://doi.org/10.1016/j.ecolmodel.2003.09.006

Hunt, G.L., McKinnell, S., 2006. Interplay between top-down, bottom-up, and wasp-waist control in marine ecosystems. Prog. Oceanogr. 68, 115–124. https://doi.org/10.1016/j.pocean.2006.02.008

ICES, 2018. Stock Annex: Blue whiting (*Micromesistius poutassou*) in subareas 1 – 9, 12 and 14 (Northeast Atlantic and adjacent waters). 40 pp

Jarre-Teichmann, A., Christensen, V., 1998. Comparative modelling of trophic flows in four large upwelling ecosys- tems: global vs. local effects, in: Durant, M.H., Cury, P., Mendelssohn, R., Roy, C., Bakun, A., Pauly, D. (Eds.), From Local to Global Changes in Upwelling Systems. ORSTOM, Paris, pp. 423–433

Jarre-Teichmann, A., Shannon, L.J., Moloney, C.L., Wickens, P.A., 1998. Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems. South African J. Mar. Sci. 19, 391–414. https://doi.org/10.2989/025776198784127024

Kavanagh, P., Newlands, N., Christensen, V., Pauly, D., 2004. Automated parameter optimization for Ecopath ecosystem models. Ecol. Modell. 172, 141–149. https://doi.org/10.1016/j.ecolmodel.2003.09.004

Lassalle, G., Lobry, J., Le Loc'h, F., Bustamante, P., Certain, G., Delmas, D., Dupuy, C., Hily, C., Labry, C., Le Pape, O., Marquis, E., Petitgas, P., Pusineri, C., Ridoux, V., Spitz, J., Niquil, N., 2011. Lower trophic levels and detrital biomass control the Bay of Biscay continental shelf food web: Implications for ecosystem management. Prog. Oceanogr. 91, 561–575. https://doi.org/10.1016/j.pocean.2011.09.002

Libralato, S., 2013. System Omnivory Index, in: Fath, B. (Ed.), Encyclopedia of Ecology. Elsevier, pp. 481–486. https://doi.org/10.1016/B978-0-12-409548-9.00605-9

Libralato, S., Christensen, V., Pauly, D., 2006. A method for identifying keystone species in food web models. Ecol. Modell. 195, 153–171. https://doi.org/10.1016/j.ecolmodel.2005.11.029

Libralato, S., Coll, M., Tempesta, M., Santojanni, A., Spoto, M., Palomera, I., Arneri, E., Solidoro, C., 2010. Food-web traits of protected and exploited areas of the Adriatic Sea. Biol. Conserv. 143, 2182–2194. https://doi.org/10.1016/j.biocon.2010.06.002

Lindeman, R.L., 1942. The Trophic-Dynamic Aspect of Ecology. Ecology 23, 399–417. https://doi.org/10.2307/1930126

Link, J.S., 2010. Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: A plea for PREBAL. Ecol. Modell. 221, 1580–1591. https://doi.org/10.1016/j.ecolmodel.2010.03.012

López, A., Pierce, G.J., Santos, M.B., Gracia, J., Guerra, A., 2003. Fishery by-catches of marine mammals in Galician waters: results from on-board observations and an interview survey of fishermen. Biol. Conserv. 111, 25–40. https://doi.org/10.1016/S0006-3207(02)00244-6

López, A., Pierce, G.J., Valeiras, X., Santos, M.B., Guerra, A., 2004. Distribution patterns of small cetaceans in Galician waters. J. Mar. Biol. Assoc. United Kingdom 84, 1–13. https://doi.org/10.1017/S0025315404009166h

López, A., Santos, M.B., Pierce, G.J., González, A.F., Valeiras, X., Guerra, A., 2002. Trends in strandings and by-catch of marine mammals in northwest Spain during the 1990s. J. Mar. Biol. Assoc. United Kingdom 82, 1–9. https://doi.org/10.1017/S0025315402005805

Methion, S., Díaz López, B., 2019a. First record of atypical pigmentation pattern in fin whale *Balaenoptera physalus* in the Atlantic Ocean. Dis. Aquat. Organ. 135, 121–125. https://doi.org/10.3354/dao03385

Methion, S., Díaz López, B., 2019b. Natural and anthropogenic drivers of foraging behaviour in bottlenose dolphins: Influence of shellfish aquaculture. Aquat. Conserv. Mar. Freshw. Ecosyst. 29, 927–937. https://doi.org/10.1002/aqc.3116

Methion, S., Díaz López, B., 2018. Abundance and demographic parameters of bottlenose dolphins in a highly affected coastal ecosystem. Mar. Freshw. Res. 69, 1355. https://doi.org/10.1071/MF17346

Morato, T., Lemey, E., Menezes, G., Pham, C.K., Brito, J., Soszynski, A., Pitcher, T.J., Heymans, J.J., 2016. Food-Web and Ecosystem Structure of the Open-Ocean and Deep-Sea Environments of the Azores, NE Atlantic. Front. Mar. Sci. 3. https://doi.org/10.3389/fmars.2016.00245

Morissette, L., 2007. Complexity, cost and quality of ecosystem models and their impact on resilience: a comparative analysis, with emphasis on marine mammals and the Gulf of St. Lawrence. University of British Columbia. https://doi.org/10.14288/1.0074903

Murta, A.G., Pinto, A.L., Abaunza, P., 2008. Stock identification of horse mackerel (*Trachurus trachurus*) through the analysis of body shape. Fish. Res. 89, 152–158. https://doi.org/10.1016/j.fishres.2007.09.026

Odum, E.P., 1969. The Strategy of Ecosystem Development. Science. 164, 262–270. https://doi.org/10.1126/science.164.3877.262

Outeiro, L., Byron, C., Angelini, R., 2018. Ecosystem maturity as a proxy of mussel aquaculture carrying capacity in Ria de Arousa (NW Spain): A food web modeling perspective. Aquaculture 496, 270–284. https://doi.org/10.1016/j.aquaculture.2018.06.043

Pauly, D., Christensen, V., 1995. Primary production required to sustain global fisheries. Nature 374, 255–257. https://doi.org/10.1038/374255a0

Pauly, D., Zeller, D., 2016. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. Nat. Commun. 7, 10244. https://doi.org/10.1038/ncomms10244

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. Nature 418, 689–695. https://doi.org/10.1038/nature01017

Pauly, D., Christensen, V., Walters, C.J., 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J. Mar. Sci. 57, 697–706. https://doi.org/10.1006/jmsc.2000.0726

Pauly, D., Trites, A.W., Capuli, E., Christensen, V., 1998. Diet composition and trophic levels of marine mammals. ICES J. Mar. Sci. 55, 467–481. https://doi.org/10.1006/jmsc.1997.0280

Pérez, F.F., Padín, X.A., Pazos, Y., Gilcoto, M., Cabanas, M., Pardo, P.C., Doval, M.D., Farina-Busto, L., 2010. Plankton response to weakening of the Iberian coastal upwelling. Glob. Chang. Biol. 16, 1258–1267. https://doi.org/10.1111/j.1365-2486.2009.02125.x

Pierce, G.J., Caldas, M., Cedeira, J., Santos, M.B., Llavona, Á., Covelo, P., Martinez, G., Torres, J., Sacau, M., López, A., 2010. Trends in cetacean sightings along the Galician coast, north-west Spain, 2003–2007, and inferences about cetacean habitat preferences. J. Mar. Biol. Assoc. United Kingdom 90, 1547–1560. https://doi.org/10.1017/S0025315410000664

Pitcher, G.C., Figueiras, F.G., Hickey, B.M., Moita, M.T., 2010. The physical oceanography of upwelling systems and the development of harmful algal blooms. Prog. Oceanogr. 85, 5–32. https://doi.org/10.1016/j.pocean.2010.02.002

Polovina, J.J., 1984. Model of a coral reef ecosystem. Coral Reefs 3, 1–11. https://doi.org/10.1007/BF00306135

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the Quest for Keystones. Bioscience 46, 609–620. https://doi.org/10.2307/1312990

Prego, R., Barciela, M. del C., Varela, M., 1999. Nutrient dynamics in the Galician coastal area (Northwestern Iberian Peninsula): Do the Rias

Bajas receive more nutrient salts than the Rias Altas? Cont. Shelf Res. 19, 317–334. https://doi.org/10.1016/S0278-4343(98)00099-5

Rodríguez Rodríguez, G., Villasante, S., Carme García-Negro, M. do, 2011. Are red tides affecting economically the commercialization of the Galician (NW Spain) mussel farming? Mar. Policy 35, 252–257. https://doi.org/10.1016/j.marpol.2010.08.008

Ruzicka, J.J., Brodeur, R.D., Emmett, R.L., Steele, J.H., Zamon, J.E., Morgan, C.A., Thomas, A.C., Wainwright, T.C., 2012. Interannual variability in the Northern California Current food web structure: Changes in energy flow pathways and the role of forage fish, euphausiids, and jellyfish. Prog. Oceanogr. 102, 19–41. https://doi.org/10.1016/j.pocean.2012.02.002

Saavedra, C., Gerrodette, T., Louzao, M., Valeiras, J., García, S., Cerviño, S., Pierce, G.J., Santos, M.B., 2018. Assessing the environmental status of the short-beaked common dolphin (*Delphinus delphis*) in North-western Spanish waters using abundance trends and safe removal limits. Prog. Oceanogr. 166, 66–75. https://doi.org/10.1016/j.pocean.2017.08.006

Sánchez, F., Olaso, I., 2004. Effects of fisheries on the Cantabrian Sea shelf ecosystem. Ecol. Modell. 172, 151–174. https://doi.org/10.1016/j.ecolmodel.2003.09.005

Santos, A.M.P., Chícharo, A., Dos Santos, A., Moita, T., Oliveira, P.B., Peliz, Á., Ré, P., 2007. Physical–biological interactions in the life history of small pelagic fish in the Western Iberia Upwelling Ecosystem. Prog. Oceanogr. 74, 192–209. https://doi.org/10.1016/j.pocean.2007.04.008

Santos, M., Saavedra, C., Pierce, G.J., 2014. Quantifying the predation on sardine and hake by cetaceans in the Atlantic waters of the Iberian peninsula. Deep Sea Res. Part II Top. Stud. Oceanogr. 106, 232–244. https://doi.org/10.1016/j.dsr2.2013.09.040

Serrano, A., Sánchez, F., Preciado, I., Parra, S., Frutos, I., 2006. Spatial and temporal changes in benthic communities of the Galician continental shelf after the Prestige oil spill. Mar. Pollut. Bull. 53, 315–331. https://doi.org/10.1016/j.marpolbul.2005.09.030

Shannon, L.J., Moloney, C.L., Jarre, A., Field, J.G., 2003. Trophic flows in the southern Benguela during the 1980s and 1990s. J. Mar. Syst. 39, 83–116. https://doi.org/10.1016/S0924-7963(02)00250-6

Sousa, M.C., DeCastro, M., Alvarez, I., Gomez-Gesteira, M., Dias, J.M., 2017. Why coastal upwelling is expected to increase along the western Iberian Peninsula over the next century? Sci. Total Environ. 592, 243–251. https://doi.org/10.1016/j.scitotenv.2017.03.046

Spitz, J., Ridoux, V., Trites, A.W., Laran, S., Authier, M., 2018. Prey consumption by cetaceans reveals the importance of energy-rich food webs in the Bay of Biscay. Prog. Oceanogr. 166, 148–158. https://doi.org/10.1016/j.pocean.2017.09.013

Surís-Regueiro, J.C., Santiago, J.L., 2014. Characterization of fisheries dependence in Galicia (Spain). Mar. Policy 47, 99–109. https://doi.org/10.1016/j.marpol.2014.02.006

Tam, J., Taylor, M.H., Blaskovic, V., Espinoza, P., Michael Ballón, R., Díaz, E., Wosnitza-Mendo, C., Argüelles, J., Purca, S., Ayón, P., Quipuzcoa, L., Gutiérrez, D., Goya, E., Ochoa, N., Wolff, M., 2008. Trophic modeling of the Northern Humboldt Current Ecosystem, Part I: Comparing trophic linkages under La Niña and El Niño conditions. Prog. Oceanogr. 79, 352–365. https://doi.org/10.1016/j.pocean.2008.10.007

Torres, M.Á., Coll, M., Heymans, J.J., Christensen, V., Sobrino, I., 2013. Food-web structure of and fishing impacts on the Gulf of Cadiz ecosystem (South-western Spain). Ecol. Modell. 265, 26–44. https://doi.org/10.1016/j.ecolmodel.2013.05.019

Torres, R., Barton, E.D., Miller, P., Fanjul, E., 2003. Spatial patterns of wind and sea surface temperature in the Galician upwelling region. J. Geophys. Res. 108, 3130. https://doi.org/10.1029/2002JC001361

Ulanowicz, R.E., 1995. Ecosystem trophic foundations: Lindeman Exonerata, in: Patten, B.C., Jorgensen, S.E. (Eds.), Complex Ecology: The Part-

Whole Relation in Ecosystems. Prentice Hall, Englewood Cliffs, New Jersey, pp. 549–560.

Ulanowicz, R.E., 1986. Growth and Development. Springer New York, New York, NY. 203 pp. https://doi.org/10.1007/978-1-4612-4916-0

Valls, A., Coll, M., Christensen, V., 2015. Keystone species: toward an operational concept for marine biodiversity conservation. Ecol. Monogr. 85, 29–47. https://doi.org/10.1890/14-0306.1

Vasconcellos, M., Mackinson, S., Sloman, K., Pauly, D., 1997. The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. Ecol. Modell. 100, 125–134. https://doi.org/10.1016/S0304-3800(97)00150-6

Vázquez-Rowe, I., Moreira, M.T., Feijoo, G., 2011. Estimating global discards and their potential reduction for the Galician fishing fleet (NW Spain). Mar. Policy 35, 140–147. https://doi.org/10.1016/j.marpol.2010.08.012

Vázquez-Rowe, I., Villanueva-Rey, P., Hospido, A., Moreira, M.T., Feijoo, G., 2014. Life cycle assessment of European pilchard (*Sardina pilchardus*) consumption. A case study for Galicia (NW Spain). Sci. Total Environ. 475, 48–60. https://doi.org/10.1016/j.scitotenv.2013.12.099

Villasante, S., 2012. The management of the blue whiting fishery as complex social-ecological system: The Galician case. Mar. Policy 36, 1301–1308.
https://doi.org/10.1016/j.marpol.2012.02.013

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of Biodiversity Loss on Ocean Ecosystem Services. Science (80-.). 314, 787 LP – 790. https://doi.org/10.1126/science.1132294

Xunta de Galicia, Consellería do mar. 2017. Online statistics (www.pescadegalicia.gal). (Last accessed 1 October 2019

Table 1: The 23 functional groups included in the model and their distribution in the pelagic and non-pelagic domains.

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

Table 2: Description of the fish functional groups included in the Rías Baixas shelf ecosystem model

Functional group	Definition
Large piscivorous pelagic fish	Fish whose diet mainly consists of other fish species, feed in the top 200 metres of the water column and are more than 100 cm long.
Other piscivorous pelagic fish	Fish whose diet mainly consists of other fish species, feed in the top 200 metres of the water column and are less than 100 cm long.
Large planktivorous pelagic fish	Fish whose diet mainly consists of zoo- and/or phytoplankton and feed in the top 200 metres of the water column and are more than 25 cm long.
Small planktivorous pelagic fish	Fish whose diet mainly consists of zoo- and/or phytoplankton and feed in the top 200 metres of the water column and are less than 25 cm long.
Benthopelagic fish	Fish whose diet consists mainly of fish and feed in the benthopelagic zone.
Bathydemersal planktivorous fish	Fish whose diet consists mainly of fish and feed in the bathydemersal zone.
Demersal piscivorous fish	Fish whose diet consists mainly of fish and feed in the demersal zone.

Table 3: Diet composition (% of prey biomass) of the different functional groups. Columns show the predators and rows show the preys.

	1 Common dolphin	2 Harbour porpoise	3 Bottlenose dolphin	4 Baleen whales	5 Seabirds I	6 Seabirds II	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 Cephalopdos	18 Non-Planktonic crustaceans	19 Macrobenthos	20 Zooplankton	21 Phytoplankton	22 Discards	23 Detritus
1																							
2																							
3																							
4																							
5																							
6																							
7	0.309		0.337			0.055	0.01								0.46	0.656							
8	0.114	0.029				0.029					0.239					0.151							
9	0.071	0.355	0.025			0.023					0.002				0.44	0.043							
10			0.05							0.027													
11	0.051		0.143		0.004	0.006				0.025	0.031												
12	0.112		0.152		0.016	0.007				0.261													
13	0.11	0.254	0.012	0.15	0.772		0.04			0.093	0.727	0.158				0.064	0.805						
14	0.04	0.208	0.102		0.008	0.016				0.063					0.05	0.054							
15	0.059	0.063	0.004				0.01			0.103						0.011							
16	0.059	0.001	0.1							0.012							0.03						
17	0.075	0.09	0.075				0.01			0.214		0.026			0.04	0.011	0.014						
18					0.462					0.155	0.001				0.01	0.005							
19					0.185					0.004							0.0162	0.028	0.05				
20				0.85			0.93	0.7	1	0.043		0.816	1	0.527		0.005	0.135	0.886	0.05	0.268			
21								0.3						0.273						0.583			
22					0.2	0.217													0.003				
23														0.2				0.086	0.897	0.149			
Total	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	-	-	-

Table 4: Modified input and output parameters of the Rías Baixas shelf ecosystem model. Values in bold show the modified input parameters, whereas the rest of the values were calculated by Ecopath. Header abbreviations are defined as: Dom: Domain (PL: Pelagic; NPL: Non-Pelagic); TL: Trophic Level; B: Biomass (t km^{-2}); P/B: Production/Biomass ratio (year^{-1}); Q/B: Consumption/Biomass ratio (year^{-1}); EE: Ecotrophic Efficiency; P/Q: Production/Consumption ratio (year^{-1}); F: Instantaneous fishing mortality rate (year^{-1}); M2: Instantaneous predation rate (year^{-1}); M0: Instantaneous "other mortality" rate (year^{-1}); F/Z: Instantaneous fishing mortality/Total mortality ratio (year^{-1}); R: Respiration (t km^{-2} year^{-1}); A: Assimilation (t km^{-2} year^{-1}); R/A: Respiration/Assimilation ratio; P/R: Production/Respiration ratio; R/B: Respiration/Biomass ratio; FTD: Flow to detritus (t km^{-2} year^{-11}); NE: Net Efficiency; OI: Omnivory Index; Q: Consumption (t km^{-2} year^{-1}).

Functional Group	Dom	TL	B	P/B	Q/B	EE	P/Q	F	M2	M0	F/Z	R	A	R/A	P/R	R/B	FTD	NE	OI	Q
Common dolphin	PL	4.58	**0.019**	**0.09**	**23**	0	0	0	0	0.09	0	0.36	0.36	1	0	18.31	0.09	0	0.22	0.45
Harbour porpoise	PL	4.37	**0.001**	**0.11**	**28.08**	0	0	0	0	0.11	0	0.02	0.02	0.99	0.01	22.35	0.01	0.01	0.23	0.03
Bottlenose dolphin	PL	4.73	**0.076**	**0.05**	**19.08**	0	0	0	0	0.05	0	0.12	0.12	1	0	15.21	0.03	0	0.29	0.14
Baleen whales	PL	3.52	**0.061**	**0.06**	**6.46**	0	0.01	0	0	0.06	0	0.31	0.31	0.99	0.01	5.11	0.08	0.01	0.13	0.39
Seabirds I: Pursuit and plunge divers	PL	3.89	**0.001**	**0.32**	**82.79**	0	0	0	0	0.32	0	0.07	0.07	1	0	65.92	0.01	0	0.91	0.09
Seabirds II: Surface and aerial pursuit feeders	PL	3.56	**0.001**	**0.25**	**182.12**	0	0	0	0	0.25	0	0.19	0.19	1	0	145.45	0.01	0	0.87	0.24
Blue whiting	NPL	3.46	34.346	**1.06**	**6.52**	**0.99**	0.16	0.5	0.55	0.01	0.47	142.74	179.15	0.8	0.26	4.16	45.15	0.2	0.12	223.94
Sardine	PL	2.96	14.089	**0.58**	**8.8**	**0.61**	0.07	0.09	0.27	0.23	0.15	91.02	99.19	0.92	0.09	6.46	27.98	0.08	0.39	123.98
Atlantic horse mackerel	NPL	3.37	33.3	**0.64**	**6.47**	**0.8**	0.1	0.33	0.18	0.13	0.52	151.05	172.37	0.88	0.14	4.54	47.35	0.12	0	215.46
Large piscivorous pelagic fish	PL	4.68	**0.085**	**0.82**	**7.8**	0.45	0.11	0.07	0.3	0.45	0.09	0.46	0.53	0.87	0.15	5.42	0.17	0.13	0.35	0.66
Other piscivorous pelagic fish	PL	4.3	**0.745**	**0.82**	**6.5**	0.43	0.13	0.06	0.29	0.47	0.08	3.26	3.87	0.84	0.19	4.38	1.32	0.16	0.06	4.84
Large planktivorous pelagic fish	PL	3.57	11.903	**1.14**	**6.28**	**0.85**	0.18	0.95	0.02	0.17	0.83	46.23	59.8	0.77	0.29	3.88	16.99	0.23	0.21	74.75
Small planktivorous pelagic fish	PL	3.37	22.364	**1.98**	**9.13**	**0.83**	0.22	0.01	1.63	0.34	0.01	119.07	163.35	0.73	0.37	5.32	48.36	0.27	0	204.18
Benthopelagic fish	NPL	2.72	5.931	**0.68**	**3.62**	**0.71**	0.19	0.21	0.27	0.2	0.31	13.14	17.18	0.77	0.31	2.22	5.46	0.23	0.47	21.47
Bathydemersal piscivorous fish	NPL	4.41	2.936	**1.09**	**4.04**	**0.82**	0.27	0.03	0.86	0.2	0.03	6.29	9.49	0.66	0.51	2.14	2.95	0.34	0.05	11.86
Demersal piscivorous fish	NPL	4.34	**4.458**	**0.67**	**3.81**	1	0.18	0.57	0.1	0	0.84	10.6	13.59	0.78	0.28	2.38	3.41	0.22	0.08	16.98
Cephalopods	PL	4.25	1.794	**3.2**	**7.5**	**0.95**	0.43	0.13	2.91	0.16	0.04	5.02	10.76	0.47	1.14	2.8	2.98	0.53	0.19	13.46
Non-Planktonic Crustaceans	NPL	3.24	**10.221**	**2.35**	**6.33**	0.02	0.37	0.01	0.04	2.3	0	27.74	51.76	0.54	0.87	2.71	36.43	0.46	0.15	64.7
Macrobenthos	NPL	2.12	**7.845**	**2.5**	**6.5**	0.24	0.38	0	0.59	1.91	0	21.18	40.79	0.52	0.93	2.7	25.19	0.48	0.14	50.99
Zooplankton	PL	2.37	86.435	**39.08**	**80**	**0.8**	0.49	0	31.26	7.82	0	2153.97	5531.86	0.39	1.57	24.92	2058.54	0.61	0.37	6914.82

Phytoplankton	PL	1	31.061	**158.04**	0	**0.83**	0	0	131.17	26.87	0	0	0	0	0	0	834.52	0	0	0
Discards		1	**7.608**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Detritus		1	**70**	0	0	0.34	0	0	0	0	0	0	0	0	0	0	0	0	0.49	3157.04

Table 5: Summary statistics of the model.

Parameter	Value	Units
Statistics and flows		
Sum of all consumption	7943.450	t km^{-2} year^{-1}
Sum of all exports	2124.402	t km^{-2} year^{-1}
Sum of all respiratory flows	2792.846	t km^{-2} year^{-1}
Sum of all flows into detritus	3165.196	t km^{-2} year^{-1}
Total system throughput	16025.890	t km^{-2} year^{-1}
Sum of all production	8470.828	t km^{-2} year^{-1}
Mean trophic level of the catch	3.485	
Gross efficiency (catch/net p.p)	0.009	
System energetics		
Calculated total net primary production	4908.915	t km^{-2} year^{-1}
Total primary production/total respiration	1.758	
Net system production	2116.069	t km^{-2} year^{-1}
Total primary production/total biomass	18.344	
Total biomass/total throughput	0.017	Year
Total biomass (excluding detritus)	267.607	t km^{-2}
Total catch	45.113	t km^{-2} year^{-1}
Network flow indices		
Connectance index	0.234	
System Omnivory Index	0.205	
Throughput cycled (excluding detritus)	1860	t km^{-2} year^{-1}
Predatory Cycling Index (PCI)	19.18	% of throughput without detritus
Throughput cycled (including detritus)	3107	t km^{-2} year^{-1}
Finn's cycling index	19.4	% of total throughput
Finn's mean path length	3.257	-
System thermodynamics sensu Ulanowicz (1986)		
Ascendency (Total)	12318	Flowbits
Ascendency	22.36	%
Overhead (Total)	42763	Flowbits
Overhead	77.64	%
Capacity (Total)	55081	Flowbits
Quality of the model		
Ecopath pedigree index	0.532	
Measure of fit, t*	2.738	
Shannon diversity index	2.125	

Table 6: The first four functional groups ranked in decreasing order of keystoneness index. Top-down effects (TD), biomass and trophic level are also shown for each functional group .

Functional group	Keystoneness	TD	Biomass	Trophic level
Small planktivorous pelagic fish	-0.0717	28.51%	22.36	3.37
Zooplankton	-0.18	70.85%	86.44	2.37
Blue whiting	-0.192	82.03%	34.35	3.46
Phytoplankton	-0.212	47.87%	31.06	1
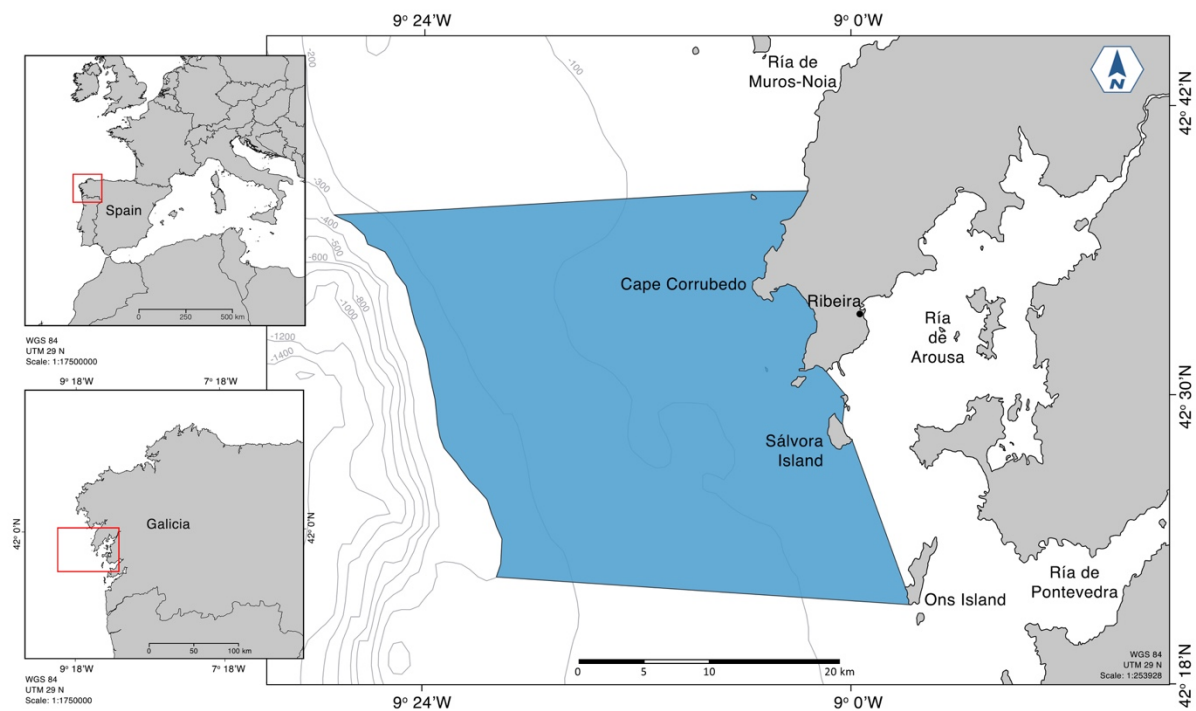
Figure 1. Map showing the Rías Baixas shelf ecosystem selected to create the Ecopath model. This included waters above the continental shelf, to the West of the entrance of Ría de Arousa; Ría de Pontevedra and Ría de Muros-Noia (North-West Spain).
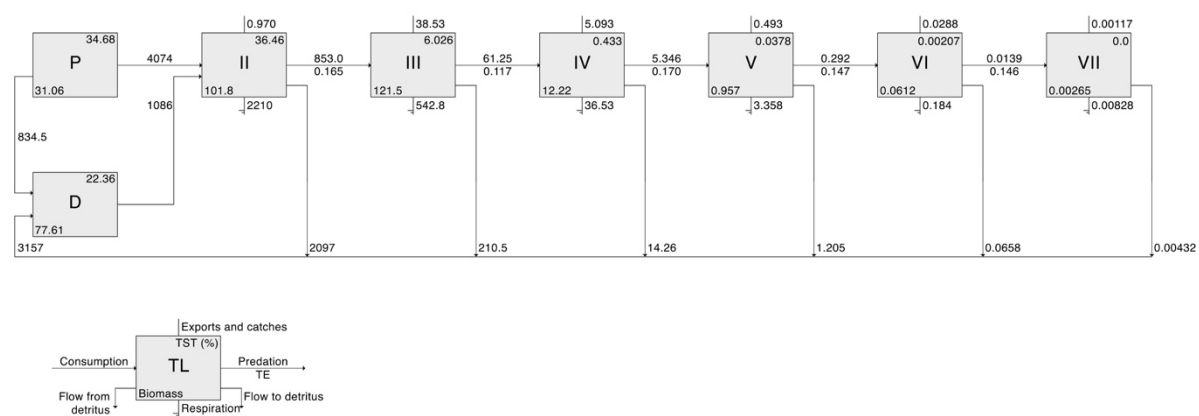
Figure 2. Trophic aggregation showing the different integer trophic levels of the Rías Baixas shelf ecosystem, their transfer efficiencies and the flows between them. D denotes detritus, and P denotes phytoplankton.
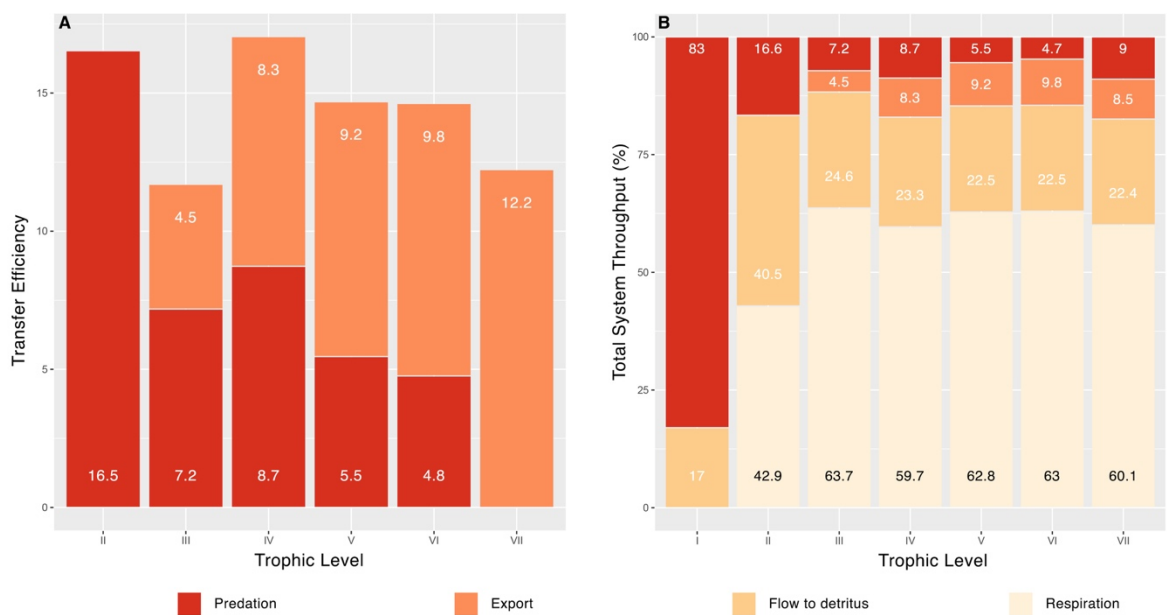

Figure 3. Shows the contribution of the exports and predation on the indicated trophic level to the Transfer Efficiency for each trophic level (A), and the contribution of the exports, predation on the indicated trophic level, flow to detritus and respiration, to the total system throughput (B).
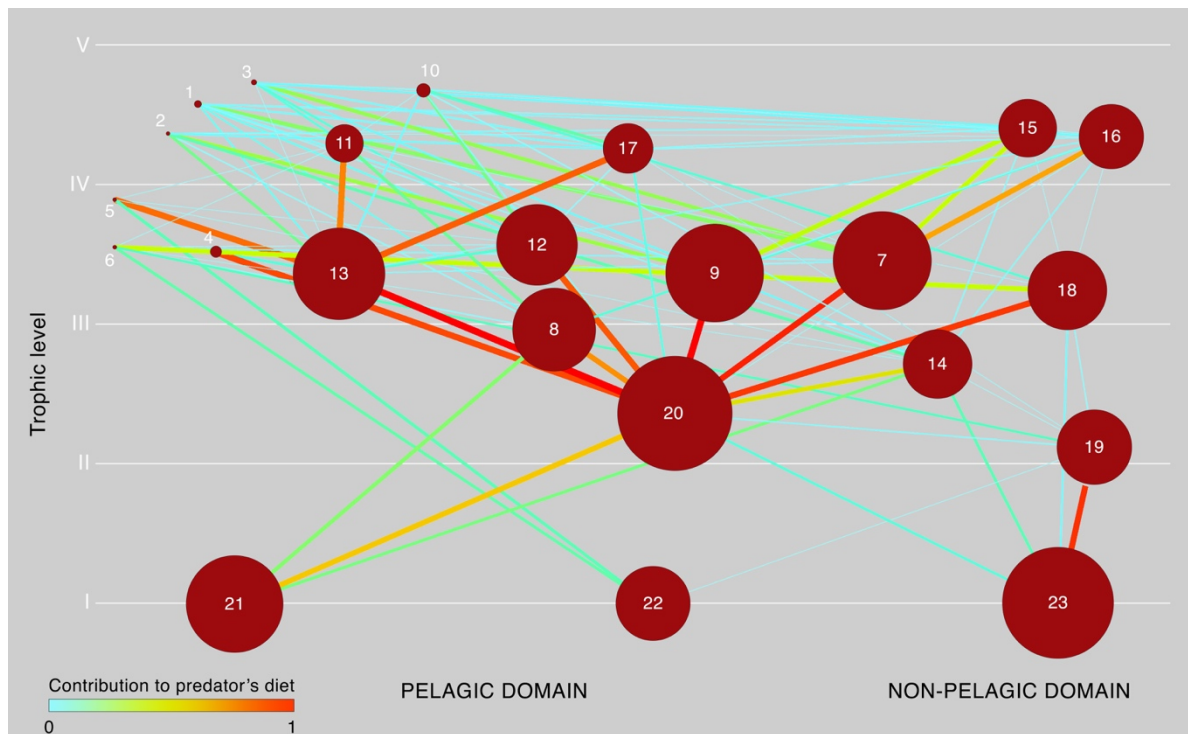
Figure 4: Flow diagram showing the main flows between the functional groups of the ecosystem. Circles represent the different functional groups (scaled to their biomass) and lines the flows between them (colours representing the contribution of each prey to the predator's diet). The functional groups are: 1. Common dolphin; 2: Harbour porpoise; 3: Bottlenose dolphin; 4: Baleen whales; 5: Seabirds I: Pursuit and plunge divers; 6: Seabirds II: Surface and aerial pursuit feeders; 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; 22: Discards; 23: Detritus.
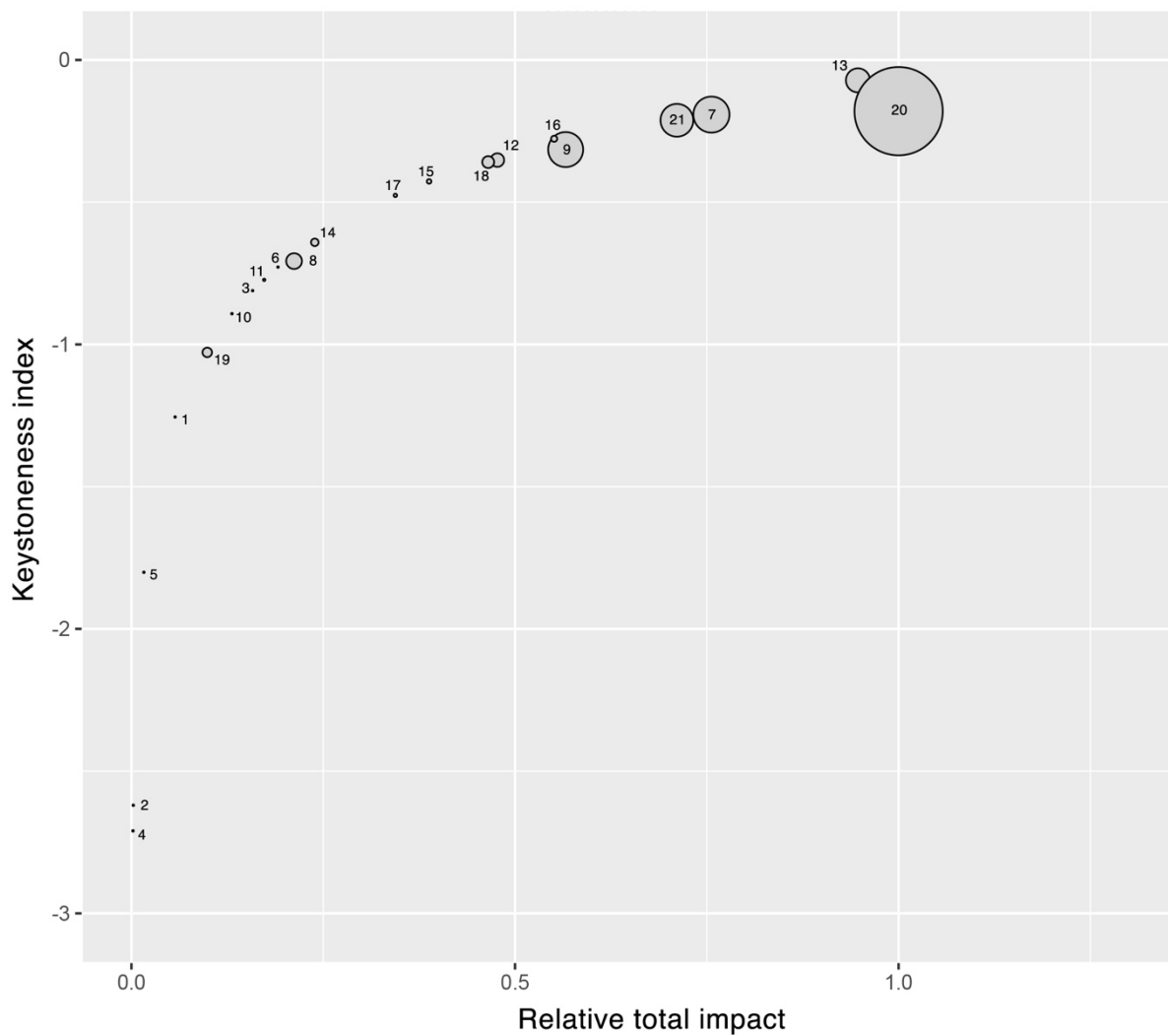
Figure 5: Keystoneness index of the food web modelled in this study sensu Libralato et al. (2006). The size of the circles is scaled according to the biomass of each functional group. The functional groups are: 1. Common dolphin; 2: Harbour porpoise; 3: Bottlenose dolphin; 4: Baleen whales; 5: Seabirds I: Pursuit and plunge divers; 6: Seabirds II: Surface and aerial pursuit feeders; 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; 22: Discards; 23: Detritus.