

Contribution to the Theme Section 'Drivers of dynamics of small pelagic fish resources: biology, management and human factors'

First representation of the trophic structure and functioning of the Portuguese continental shelf ecosystem: insights into the role of sardine

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ABSTRACT: In this study, we analysed the structure and functioning of the Portuguese continental shelf ecosystem and investigated the role of sardine *Sardina pilchardus* using the Ecopath mass-balance approach. An Ecopath model was configured to represent the continental shelf waters in the period 2006–2009. The model showed that biomass was concentrated in low and intermediate trophic levels as in other upwelling areas. Several low- and medium-trophic-level groups were identified as dominant groups in the ecosystem (e.g. zooplankton, macrozoobenthos, sardine, chub mackerel *Scomber colias*, and demersal and benthopelagic invertivorous fish). Furthermore, low-trophic-level groups were responsible for the main energy flows, and overall higher impact on the ecosystem, emphasizing the importance of bottom-up control of the ecosystem structure. Our results are relevant to understand structure and functioning of this ecosystem and constitute an important step towards an ecosystem approach to fisheries management in the study area.

KEY WORDS: Sardine · Small pelagic fish · Upwelling ecosystem · Trophic interaction · Ecopath

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1. INTRODUCTION

The Portuguese coastal waters are at the northern limit of the Canary Current Upwelling System (Santos et al. 2007, Arístegui et al. 2009). As in other

upwelling areas, Portuguese waters have high primary and secondary productivity and are dominated by small and medium pelagic species such as sardine *Sardina pilchardus*, chub mackerel *Scomber colias* and horse mackerel *Trachurus trachurus* (Arístegui et al.

2009, Santos et al. 2013). Sardine is the dominant fish species in the ecosystem down to depths around 120 m (Gomes et al. 2001). Between 150 and 400 m, the ecosystem shifts to a dominance of benthopelagic and demersal species, such as blue whiting *Micro-mesistius poutassou*, snipefish *Macroramphosus* spp. and boarfish *Capros aper*. Other species, such as hake *Merluccius merluccius*, horse mackerel and chub mackerel have a ubiquitous distribution, with higher densities of younger individuals in shallower waters and older individuals in deeper waters (Sousa et al. 2005). Sardine is an important fishing resource in Portugal, being the target species of the purse-seine fleet and the main product of the fish canning industry (Silva et al. 2015). However, since 2006, sardine stock biomass has decreased by 75% and is currently around the lowest historical level in 30 yr (ICES 2016). The causes underlying this decrease are not clear and possibly result from a complex interplay between environmental variability, species interactions and fishing pressure (Malta et al. 2016). Improving the knowledge of the trophic relationships and trophic structure of the coastal western Iberian ecosystem is an important first step to assess the role of sardine in the ecosystem.

Ecosystem models are useful tools to identify the main energy flows within an ecosystem and to quantify the relative magnitude of such flows, providing insight into ecosystem structure and functioning (Murawski 2007, Plagányi 2007). Among such models, Ecopath with Ecosim (EwE), a mass-balance model of trophic interactions (Christensen & Pauly 1992, Christensen & Walters 2004), is one of the most common and widely used (Colléter et al. 2015). The ability to integrate fisheries in the analysis, evaluate their impacts on the ecosystem (Coll & Libralato 2012) and provide a set of ecological indicators are the important strengths of the EwE modelling approach (Fulton et al. 2003).

Mass-balance modelling has been widely used to quantitatively describe aquatic systems and to assess the role of small pelagic fish (SPF) in the upwelling regions around the world (Shannon et al. 2003, Moloney et al. 2005). However, there are still few examples of ecological modelling applied to the Portuguese coastal ecosystems, limited to modelling of the nearby estuaries of Ria Formosa (Gamito & Erzini 2005), Mondego (Patrício & Marques 2006, Baeta et al. 2011) and Aveiro (Bueno-Pardo et al. 2018). The present application is the first effort to study the Portuguese continental shelf upwelling ecosystem using a mass-balance model. In this study, we examine the structure and functioning of the Portuguese conti-

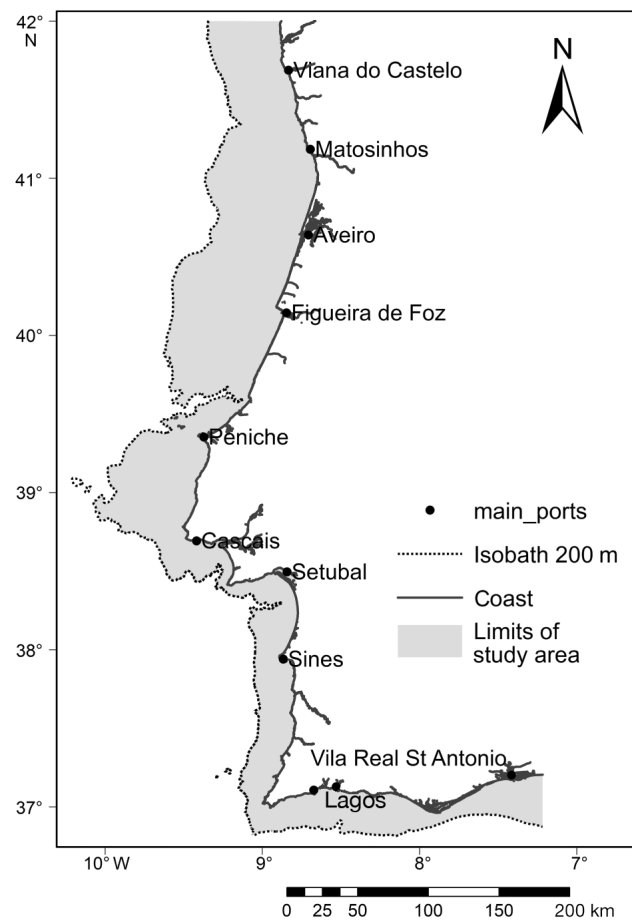


Fig. 1. Portuguese continental coast showing limits of the study area and main fishing ports

ental shelf ecosystem and investigate the role of sardine using the Ecopath mass-balance approach.

2. MATERIALS AND METHODS

2.1. Study area

The Portuguese continental shelf ecosystem (hereafter referred to as PCSE) food web model was developed for the area located in the northeast Atlantic between 36.5° and 42° N and between 10.5° and 7.5° W (Fig. 1). It covers an area of around 22 000 km² between the 30 and 200 m isobath. The continental shelf width varies along the coast, ranging from approximately 5 to 70 km, being wider on the northwest coast (Fig. 1), and having an average of 45 km (Aristegui et al. 2009, Martins et al. 2012). The Portuguese shelf sea surface temperature ranges from 18°C in the south to 16.5°C in the north with an overall average of 17°C.

2.2. Model structure

A mass-balance model was constructed using Ecopath with Ecosim version 6.5 (Christensen & Walters 2004, Christensen et al. 2008, www.ecopath.org). The static Ecopath model was applied to the period 2006–2009. The model had 33 functional groups including seabirds, cetaceans, fish, macroinvertebrates, zooplankton and phytoplankton (Table 1) and 2 types of detritus: discards and detritus. Groups were

formed based on criteria such as the similarity of ecological and/or biological features (e.g. habitat, feeding), amount of data available for the study area and period and potential relationships with the sardine. The most abundant pelagic fish species and their main predators were modelled as single species groups (e.g. sardine, anchovy, horse mackerel, blue jack mackerel, chub mackerel, Atlantic mackerel *Scomber scombrus*, hake and 5 species of marine mammals). This was not possible for tuna and cephalo-

Table 1. List of functional groups and species within each group included in the Portuguese continental shelf model. The relative abundance/biomass for each species within the respective functional group is shown in parentheses. When no relative abundance is given, such information was not available or was deemed unreliable (see explanation in 'Materials and methods')

Functional group	Species
1 Seabirds	<i>Morus bassanus</i> (86.8%); <i>Calonectris borealis</i> (7.9%); <i>Alca torda</i> (2.7%); <i>Puffinus mauretanicus</i> (1.6%); <i>Uria aalge</i> (0.9%)
2 Minke whale	<i>Balaenoptera acutorostrata</i> (100%)
3 Common dolphin	<i>Delphinus delphis</i> (100%)
4 Striped dolphin	<i>Stenella coeruleoalba</i> (100%)
5 Bottlenose dolphin	<i>Tursiops truncatus</i> (100%)
6 Harbour porpoise	<i>Phocoena phocoena</i> (100%)
7 Tunas	<i>Sarda sarda</i> ; <i>Auxis rochei</i> ; <i>Thunnus thynnus</i>
8 Rays	<i>Raja clavata</i> ; <i>Raja brachyura</i> ; <i>Leucoraja naevus</i> ; <i>Raja montagui</i>
9 Hake	<i>Merluccius merluccius</i> (100%)
10 Squids	<i>Loligo vulgaris</i> ; <i>Illex coindetii</i> ; <i>Todaropsis eblanae</i> ; <i>Alloteuthis subulata</i> ; <i>Alloteuthis media</i>
11 Benthic cephalopods	<i>Octopus vulgaris</i> ; <i>Eledone cirrhosa</i> ; <i>Sepia officinalis</i> ; <i>Sepiola</i> spp.
12 Horse mackerel	<i>Trachurus trachurus</i> (100%)
13 Blue jack mackerel	<i>Trachurus picturatus</i> (100%)
14 Chub mackerel	<i>Scomber colias</i> (100%)
15 Mackerel	<i>Scomber scombrus</i> (100%)
16 Demersal piscivorous fish	<i>Conger conger</i> ; <i>Chelidonichthys lucernus</i> ; <i>Helicolenus dactylopterus</i> ; <i>Dicentrarchus labrax</i> ; <i>Lophius budegassa</i> ; <i>Lophius piscatorius</i>
17 Demersal invertivorous fish	<i>Trigla lyra</i> ; <i>Serranus hepatus</i> ; <i>Callionymus lyra</i> ; <i>Chelidonichthys cuculus</i> ; <i>Synchiropus phaeton</i> ; <i>Lepidotrigla cavillone</i> ; <i>Callanthias ruber</i> ; <i>Mullus surmuletus</i> ; <i>Mullus barbatus</i> ; <i>Cepola macrophthalmia</i> ; <i>Ammodytidae</i> ; <i>Gobiidae</i>
18 Benthopelagic piscivorous fish	<i>Zeus faber</i> ; <i>Lepidopus caudatus</i> ; <i>Belone belone</i> ; <i>Phycis blennoides</i> ; <i>Phycis phycis</i>
19 Benthopelagic invertivorous fish	<i>Trisopterus luscus</i> ; <i>Micromesistius poutassou</i> ; <i>Argentina sphyraena</i> ; <i>Macroramphosus</i> spp.; <i>Capros aper</i> ; <i>Gadiculus argenteus</i> ; <i>Anthias anthias</i>
20 Flatfish	<i>Solea solea</i> ; <i>Solea senegalensis</i> ; <i>Pegusa lascaris</i> ; <i>Microchirus azevia</i> ; <i>Microchirus variegatus</i> ; <i>Platichthys flesus</i> ; <i>Citharus linguatula</i> ; <i>Dicologlossa cuneata</i> ; <i>Scophthalmus maximus</i> ; <i>Scophthalmus rhombus</i> ; <i>Lepidorhombus boscii</i> ; <i>Lepidorhombus whiffiagonis</i> ; <i>Arnoglossus laterna</i>
21 Sparids	<i>Pagellus acarne</i> (55.9%); <i>Pagellus erythrinus</i> (3%); <i>Pagellus bogaraveo</i> (0.7%); <i>Spondylisoma cantharus</i> (12.5%); <i>Diplodus vulgaris</i> (26.4%); <i>Diplodus bellottii</i> (0.1%); <i>Diplodus annularis</i> (0.1%); <i>Diplodus sargus</i> (0.1%); <i>Pagrus pagrus</i> (1.1%); <i>Pagrus auriga</i> (0.2%)
22 Anchovy	<i>Engraulis encrasicolus</i> (100%)
23 Sardine	<i>Sardina pilchardus</i> (100%)
24 Bogue	<i>Boops boops</i> (100%)
25 Henslow's crab	<i>Polybius henslowii</i> (100%)
26 Shrimps	Unspecified Crustacea antantia
27 Macrozoobenthos	Starfishes; annelids; sea urchins; sea cucumbers; bivalves; crustaceans; sea anemone; other benthic invertebrates
28 Suprabenthic invertebrates	Euphausiids, mysids, isopods and amphipods
29 Macrozooplankton	Macrozooplankton (zooplankton length >3 mm, width >1 mm)
30 Meso- and microzooplankton	Mesozooplankton and microzooplankton (zooplankton length ≤3 mm, width ≤1 mm; including fish eggs)
31 Phytoplankton	Phytoplankton

Pods because of insufficient data. The fish species considered in the model were selected based on the results of monitoring surveys undertaken in the study area over the modelled period and include species that constituted 99% of total survey's biomass.

Benthopelagic and demersal fish were split into piscivorous and invertivorous based on the diet composition (Table S2 in the Supplement at www.int-res.com/articles/suppl/m12724_supp.pdf). Species with diets composed of more than 25% of weight or volume of fish were allocated to piscivorous groups, while the rest was allocated to invertivorous groups. Due to lack of data at species or genus level, invertebrates were aggregated into more broad functional groups (e.g. squids, benthic cephalopods, shrimps, suprabenthic invertebrates and macrozoobenthos). Henslow's swimming crab *Polybius henslowii* was modelled as an individual group owing to its high abundance and frequency of occurrence in the purse-seine fishery.

2.3. Parameter estimation

Data from the study period and area were given priority in the calculation of all input parameters stated in the following 5 subsections. If such data were not available, priority was given to data from the same species in nearby areas (Cantabrian Sea, Bay of Biscay and Gulf of Cadiz) followed by data from the same species or functional groups in a different ecosystem and, finally, data compiled from FishBase (www.fishbase.org). In the cases where, for a given functional group, the information available in nearby areas' models was different, the source of the information for each value was taken into account, and priority given to values that were obtained from experimental data and how similar the species within the functional groups were. If the uncertainty around those values was similar (e.g. same source type or values assumed), an average value was used. For functional groups that consisted of more than 1 species, input data (e.g. diet, production/biomass ratio and consumption/biomass ratio) were calculated as weighted averages of the species data using relative biomasses as weighting factors. When biomass data were not available, group data were simple averages of component species data (Tables 2 & S1 in the Supplement). Input parameters are presented in Table 2 and detailed information on data sources and estimation methods for each functional group are in Table S1.

2.4. Biomass data

Only biomasses within the coastal zone to 200 m depth were included in the model and were considered to be representative of the average biomass available throughout the year for each functional group. Abundance and density estimates for seabirds and marine mammals were obtained in aerial surveys covering the Portuguese continental shelf and adjacent oceanic waters (Araújo et al. 2014). For each species, density data were used to estimate total abundance and then biomass using mean weight (Table S1).

Biomass estimates for fish groups (pelagic, benthopelagic and demersal) were compiled from acoustic (AC) and bottom trawl (BT) surveys carried out annually in the Portuguese waters in spring and autumn, respectively (ICES 2012, 2013). Biomasses from BT surveys were estimated by the swept-area method. The fishing gear used in the BT survey is not in full contact with the ground because the ground-rope has rollers and it is not suitable for rocky bottoms. Thus, some species, such as flatfish (which can escape under the gear), demersal species that stay near the bottom and species that prefer rocky areas, may be highly underestimated. Therefore, catchability rates of 0.8 for hake (Huse et al. 2001) and 0.25 for other demersal and benthopelagic species (Harley & Myers 2001, Trenkel & Skaug 2005) were assumed. The model's initial inputs did not include the biomasses of 12 functional groups due to insufficient data (e.g. suprabenthic invertebrates, shrimps and benthic cephalopods) or because the estimated biomasses based on the BT surveys were too low even when assuming very low catchability rates (e.g. flatfish, squids, and the aggregated groups of benthopelagic and demersal fishes). Catchability rates lower than the recommended rates in the literature were tried for all species of these functional groups and the obtained biomasses for each species compared with the respective catches in the area. For the majority of the species, the catches were higher than the estimated biomasses; therefore, these estimates were considered unrealistically low. Furthermore, the abundance estimates were considered to be acceptable when considering each species individually, but when considering them within a functional group the relative abundances within each group were not considered to be representative. For all these 12 functional groups, the biomasses were estimated by the Ecopath model and for those groups ecotrophic efficiency (*EE*) was assumed to be 0.95, except for rays for which *EE* was assumed to be 0.85 based on *EE* values for the same group in nearby

Table 2. Main inputs of the Portuguese continental shelf Ecopath model. Functional groups that include commercially exploited species are shown in bold. Biomass and ecotrophic efficiency values estimated by the model are shown underlined. *B*: biomass; *P*: production; *Q*: consumption; *EE*: ecotrophic efficiency; *BA*: biomass accumulation; –: not applicable

Functional group	<i>B</i> (t km ⁻²)	<i>EE</i>	<i>P/B</i> (yr ⁻¹)	<i>Q/B</i> (yr ⁻¹)	<i>BA</i> rate (yr ⁻¹)	Landings (t km ⁻²)	Discards (t km ⁻²)
1 Seabirds	0.01	<u>0.00</u>	0.10	57.64	–	–	–
2 Minke whale	0.06	<u>0.37</u>	0.03	35.11	–	0.001	–
3 Common dolphin	0.04	<u>0.20</u>	0.08	31.29	–	0.001	–
4 Striped dolphin	0.01	<u>0.11</u>	0.08	30.98	–	4.0×10 ⁻⁵	–
5 Bottlenose dolphin	0.01	<u>0.03</u>	0.08	32.06	–	1.6×10 ⁻⁵	–
6 Harbour porpoise	0.00	<u>0.33</u>	0.08	14.17	–	1.1×10 ⁻⁴	–
7 Tunas	0.20	<u>0.10</u>	0.42	4.21	–	0.008	–
8 Rays	<u>0.14</u>	0.85	0.73	4.83	–	0.067	0.017
9 Hake	0.39	<u>0.93</u>	1.30	6.07	–	0.090	0.050
10 Squids	<u>0.96</u>	0.95	2.80	8.00	–	0.012	0.006
11 Benthic cephalopods	<u>1.15</u>	0.95	2.30	6.50	–	0.340	0.081
12 Horse mackerel	2.84	<u>0.93</u>	0.51	7.61	–	0.508	0.001
13 Blue jack mackerel	0.78	<u>0.90</u>	0.54	7.21	–	0.115	0.012
14 Chub mackerel	6.58	<u>0.92</u>	0.65	6.82	–	0.601	0.470
15 Mackerel	0.45	<u>0.94</u>	0.80	7.14	–	0.105	0.013
16 Demersal piscivorous fish	<u>0.53</u>	0.95	0.64	3.57	–	0.106	0.024
17 Demersal invertivorous fish	<u>5.77</u>	0.95	1.22	6.68	–	0.027	0.005
18 Benthopelagic piscivorous fish	<u>0.34</u>	0.95	0.83	4.10	–	0.033	0.007
19 Benthopelagic invertivorous fish	<u>6.62</u>	0.95	0.95	7.10	–	0.268	0.107
20 Flatfish	<u>0.91</u>	0.95	0.94	5.69	–	0.046	0.009
21 Sparids	0.60	<u>0.86</u>	0.73	5.42	–	0.104	0.021
22 Anchovy	0.31	<u>0.92</u>	1.17	12.22	–	0.016	–
23 Sardine	14.76	<u>0.72</u>	0.89	9.68	–0.21	2.838	0.156
24 Bogue	<u>0.79</u>	0.95	1.25	6.20	–	0.009	0.019
25 Henslow's crab	<u>0.53</u>	0.95	2.10	10.64	–	0.001	–
26 Shrimps	<u>3.62</u>	0.95	4.20	11.67	–	–	–
27 Macrozoobenthos	14.54	<u>0.84</u>	3.55	9.73	–	0.023	0.005
28 Suprabenthic invertebrates	<u>3.60</u>	0.95	16.00	42.00	–	–	–
29 Macrozooplankton	5.25	<u>0.78</u>	17.00	44.00	–	–	–
30 Meso- and microzooplankton	25.29	<u>0.47</u>	30.10	152.52	–	–	–
31 Phytoplankton	18.72	<u>0.58</u>	350.78	–	–	–	–
32 Discards	1.00	<u>0.93</u>	–	–	0.13	–	–
33 Detritus	45.23	<u>0.08</u>	–	–	–	–	–

areas (Sánchez & Olaso 2004, Torres et al. 2013). Biomass estimates from AC surveys were assumed to be absolute (i.e. catchability = 1; ICES 2011).

Macro- and mesozooplankton biomass estimations were based on samples collected with a continuous underway fish eggs sampler (CUFES) (mesh size of 335 µm) during AC surveys, chosen because of their high spatial resolution along a large geographical coverage. To approximate near-surface (3 m depth) zooplankton biomass estimates sampled by CUFES to the whole water column and correct for the effect of the comparatively larger mesh size (335 µm), an extensive research of localized paired comparisons between CUFES samples and net-hauled vertically integrated samples (Bongo 200 and 335 µm, Wp2 200 µm, Calvet 150 µm) was performed (L. Sobrinho-Gonçalves unpubl. data). As a result, a factor of 3.5 was found and biomass values, obtained from

CUFES samples, were multiplied by this factor. Microzooplankton biomass data was available for coastal waters and for offshore waters it was corrected by a factor of 2 in the productive season (April–October) based on the study in the nearby region of the Bay of Biscay (Marquis et al. 2011).

Phytoplankton biomass was estimated using chlorophyll *a* satellite data from the Globcolour project (www.globcolour.info; Table S1). Detritus biomass was estimated based on the empirical equation proposed by Pauly et al. (1993):

$$\text{Log}(D) = -2.41 + 0.954 \times \text{log}(PP) + 0.863 \times \text{log}(E)$$

where *D* is the detritus biomass in g m⁻², *PP* is the annual primary production of the area in g C m⁻² yr⁻¹ and *E* is the average euphotic depth in m.

Due to the well-documented decreasing trend in sardine biomass observed in recent decades, and the

significant change in its biomass between 2006 and 2009 for which the model was parametrized, a negative annual average rate of sardine biomass accumulation (BA) of -0.21% , was applied. This value was calculated based on the acoustic data. As no clear changes in biomass were observed for the other functional groups, in their case, BA and other export terms were assumed equal to zero.

2.5. Diet composition

For the vast majority of the species considered in the model, diet composition was compiled from studies on stomach content analysis of individuals caught within the PCSE. Cetacean stomach contents analyses were performed on stranded dead animals; thus, the identified prey likely came from within the PCSE. More detailed information regarding the sources for the different species' diet composition can be found in Table S1.

The diet composition matrix (Table S2) was constructed taking into account the following steps: (1) in case unidentified species were present in the diet, data were rescaled to 100% for the respective taxonomic groups; (2) when diet composition from areas other than the PCSE was used, the proportion of the elements in the diet was adapted to the species composition of the PCSE (e.g. species from the same genus or family and similar function in the ecosystem); (3) for mackerels *Scomber* spp. and horse mackerels *Trachurus* spp. whose older individuals are distributed beyond the shelf and show ontogenetic variation in the feeding habits, diets were adjusted to the continental shelf life stage based on the literature (e.g. Garrido et al. 2015), and to the average length size caught within the shelf for each species; (4) species' migratory behaviour (e.g. seabirds and minke whale *Balaenoptera acutorostrata*) was taken into account by adjusting a portion of their diet as import to the ecosystem proportionally to the time they spent outside the area (Christensen & Walters 2004, Coll et al. 2006); and (5) for the 4 small cetacean species considered in the model, prey that is distributed outside the continental shelf or estuaries were considered as import.

2.6. Production/biomass ratio (P/B)

Production/biomass (P/B) data for seabirds and marine mammals were compiled from Christensen et al. (2009) since these values were an average of similar groups in exploited areas around the world. Consider-

ing no active fishery for marine mammals, fishing mortality was replaced by bycatch mortality from 2010 to 2012. For fish groups, P/B was estimated using the assumption that, in steady-state conditions, it is equivalent to total mortality (Z) where Z is equal to natural mortality (M) plus fishing mortality (F) in accordance with Allen (1971). To calculate M , the empirical equation by Pauly (1980) (Appendix 1) was used while F was calculated as catch/biomass. When no biomass estimates were available, a mean F for the group was assumed based on literature and expert knowledge. For invertebrate and zooplankton groups, values were compiled from the literature (e.g. squids, meso- and microzooplankton) or adapted based on data from models of nearby areas (e.g. benthic cephalopods, Henslow's crab, shrimps, macrozoobenthos, suprabenthic invertebrates; Table S1). Phytoplankton P/B was calculated by dividing the annual primary production by the annual mean biomass. Phytoplankton primary production was estimated using a vertically generalized production model (VGPM; Behrenfeld & Falkowski 1997; Table S1) that based the product on the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and moderate resolution imaging spectroradiometer (MODIS) satellite sensors.

2.7. Consumption/biomass ratio (Q/B)

Daily ration for seabirds (DR) in g d^{-1} was calculated using the empirical equation from Nilsson & Nilsson (1976) (Appendix 2). Values for marine mammals were calculated using daily food consumption estimates (kg d^{-1}) in Iberian Atlantic waters (Santos et al. 2014), except for minke whale estimates, which were for the Northeast Atlantic (Markussen et al. 1992). For fish groups, Q/B was calculated with the empirical equation from Pauly et al. (1990) (Appendix 2).

For Henslow's swimming crab, Q/B was calculated using the empirical equation for the daily consumption rate of invertebrates (Cammen 1979) (Appendix 2).

For other groups of invertebrates and zooplankton, Q/B values were compiled from literature or from Ecopath models from nearby areas (Table S2).

2.8. Fisheries data

Average landings in 2006–2009 were calculated for purse-seine, BT and polyvalent fleets, the last of these referring to the (artisanal) multi-gear fleet. BT and purse-seine discards were compiled from literature (Feijó 2013, Fernandes et al. 2015). For the purse-

seine fleet, slipping estimates were also included assuming a mortality of one-third of the slipped biomass for all species and included as discards in the model (Huse & Vold 2010, Marçalo et al. 2010, Tenningen et al. 2012). Similar assumptions were made for discards of SPF in the polyvalent fleet since those species are mainly caught using purse seine. For all other groups caught by the polyvalent fleet, 20% of the catch was assumed to be discarded based on local studies (Borges et al. 2008, Batista et al. 2009). Marine mammal bycatch estimates were derived from unpublished data of the MarPro strandings and bycatch evaluation databases (Ferreira et al. 2012).

2.9. Pre-balance, model balancing and analysis

To ensure that the model parameters followed the general ecological principles, a pre-balance (PREBAL) diagnostic (Link 2010) was performed, including the slopes of biomass ratios, vital rates, total production and consumption based on trophic levels. The results of this diagnostic were used as a guide for the balancing procedure and to check the integrity of the input data. Furthermore, pedigree level (Christensen & Walters 2004, Christensen et al. 2008) was attributed to input data and used as a guideline to select the parameters more suitable for adjustment during model balancing. Pedigree values vary between 0 for highly uncertain inputs, such as guesstimates, and 1 for precise estimates, i.e. well-sampled and high-precision local data (Christensen & Walters 2004). The process of model balancing was carried out following the best practice guidelines provided in the literature (Christensen et al. 2008, Heymans et al. 2016). The model was considered balanced when the following requirements were met: (1) *EE* estimates were lower than 1; (2) estimated values of gross food conversion efficiency (*GE* or *P/Q*) were within the range 0.05–0.35 considered physiologically realistic for most species; top predators and fast-growing species can have lower and higher values, respectively; (3) estimates of net efficiency of food conversion were below 1 for all functional groups.

The sensitivity of the model input parameters was examined by changing each parameter from –50% to 50% of its original value in 10% steps and re-running the model. This was carried out for either *B* or *EE*, *P/B* and *Q/B* per functional group. The impact that each step change has on the output parameters was recorded for all functional groups. An index of sensitivity was calculated as the number of impacts, of one given functional group, equal to or above 30%

on the output parameters of other functional groups (Olson & Watters 2003).

Ecopath built-in ecological indices and network analysis tools were used to summarise the ecosystem status in terms of biomasses, flows, maturity and resistance to external perturbations (Christensen et al. 2008). Trophic level (TL) and transfer efficiency (TE) were calculated for each functional group. Flows and biomasses were aggregated by TL to provide a quantitative description of the ecosystem structure (Lindeman spine analysis; Lindeman 1942, Libralato et al. 2002). Keystone groups, relatively low biomass groups with high overall effect in the trophic network, and dominant groups, with both relatively high biomass and high overall effect, were identified (Libralato et al. 2006). The quantification of total trophic impacts (direct and indirect, positive and negative) of a hypothetical increase in biomass of one group in all other groups in the ecosystem was carried out using mixed trophic impact (MTI) analysis (Ulanowicz & Puccia 1990).

3. RESULTS

3.1. PREBAL, pedigree and uncertainty routines

The PREBAL procedure revealed that for some functional groups, *B*, *P/B* and *Q/B* values were low (underestimated, below slope line) or high (overestimated, above slope line; Fig. S1 in the Supplement). These values were checked for data integrity before initiating mass balance of the model.

The pedigree index obtained for the PCSE model was 0.54, placing the model in the upper range (0.16–0.68) of 50 balanced Ecopath models analysed by Morissette (2007). This value implies a reasonable quality of data, but also highlights room for improvement.

The sensitivity analysis routine showed that by altering the input parameters of a functional group, the model is mainly sensitive to both cephalopod groups and, to a lesser extent, demersal piscivorous and invertivorous fish, benthopelagic invertivorous fish, flatfish, and meso- and microzooplankton groups (Table 3).

3.2. Model balancing

The initial model presented *EE* values higher than 1 for horse mackerel, mackerel, macrozoobenthos and hake. For horse mackerel and mackerel, the balance

Table 3. Main outputs of the Portuguese continental shelf Ecopath model. Functional groups that include commercially exploited species are shown in bold. TL: trophic level; *B*: biomass; *P*: production; *Q*: consumption; *F*: fishing mortality; *M2*: predation mortality; *M0*: other mortality; *Z*: total mortality; *NE*: net efficiency; *OI*: omnivory index; *SI*: sensitivity index; –: not applicable

Functional group	TL	<i>F</i> (yr ⁻¹)	<i>M2</i> (yr ⁻¹)	<i>M0</i> (yr ⁻¹)	<i>F/Z</i>	<i>P/Q</i>	<i>NE</i>	<i>OI</i>	<i>SI</i>
1 Seabirds	4.3	0.000	0.00	0.10	0.00	0.002	0.002	0.224	0
2 Minke whale	4.2	0.011	0.00	0.02	0.37	0.001	0.001	0.125	0
3 Common dolphin	4.3	0.016	0.00	0.06	0.20	0.003	0.003	0.176	0
4 Striped dolphin	4.5	0.008	0.00	0.07	0.11	0.003	0.003	0.278	0
5 Bottlenose dolphin	5.3	0.003	0.00	0.08	0.03	0.002	0.003	0.489	0
6 Harbor porpoise	4.9	0.027	0.00	0.05	0.33	0.006	0.007	2.064	0
7 Tunas	4.0	0.040	0.00	0.38	0.10	0.100	0.125	1.165	0
8 Rays	4.2	0.619	0.00	0.11	0.85	0.151	0.189	0.309	0
9 Hake	4.3	0.360	0.85	0.09	0.28	0.214	0.268	0.129	0
10 Squids	4.2	0.018	2.64	0.14	0.01	0.350	0.438	0.212	24
11 Benthic cephalopods	4.1	0.364	1.82	0.11	0.16	0.354	0.442	0.220	24
12 Horse mackerel	3.5	0.179	0.30	0.03	0.35	0.067	0.084	0.069	0
13 Blue jack mackerel	3.3	0.162	0.32	0.05	0.30	0.074	0.093	0.118	0
14 Chub mackerel	3.4	0.163	0.44	0.06	0.25	0.096	0.120	0.290	4
15 Mackerel	3.3	0.264	0.49	0.05	0.33	0.113	0.141	0.248	0
16 Demersal piscivorous fish	4.3	0.245	0.37	0.03	0.38	0.180	0.225	0.248	8
17 Demersal invertivorous fish	3.4	0.005	1.15	0.06	0.00	0.183	0.229	0.125	15
18 Benthopelagic piscivorous fish	4.1	0.120	0.67	0.04	0.14	0.203	0.254	0.303	0
19 Benthopelagic invertivorous fish	3.4	0.057	0.85	0.05	0.06	0.134	0.168	0.111	10
20 Flatfish	3.9	0.061	0.83	0.05	0.06	0.165	0.207	0.430	6
21 Sparids	3.6	0.210	0.41	0.10	0.29	0.134	0.167	0.334	0
22 Anchovy	3.0	0.051	1.02	0.09	0.04	0.096	0.120	0.013	0
23 Sardine	2.8	0.203	0.65	0.04	0.05	0.092	0.115	0.139	0
24 Bogue	3.5	0.035	1.15	0.06	0.03	0.201	0.251	0.051	0
25 Henslow's crab	3.3	0.002	1.99	0.11	0.00	0.197	0.329	0.361	0
26 Shrimps	2.7	–	3.99	0.21	–	0.360	0.600	0.421	0
27 Macrozoobenthos	2.3	–	2.99	0.56	–	0.365	0.609	0.355	0
28 Suprabenthic invertebrates	2.3	–	15.20	0.80	–	0.381	0.635	0.244	0
29 Macrozooplankton	2.7	–	13.27	3.73	–	0.386	0.644	0.210	0
30 Meso- and microzooplankton	2.0	–	14.16	15.94	–	0.197	0.329	–	8
31 Phytoplankton	1.0	–	202.10	148.70	–	–	–	–	0
32 Discards	1.0	–	–	–	–	–	–	–	–
33 Detritus	1.0	–	–	–	–	–	–	0.334	–

was achieved by a small adjustment (less than 5%) of the predatory pressure, redirecting it to similar small pelagic groups. For macrozoobenthos, the initial percentage of cannibalism was high (around 10%) and the balance was achieved by setting cannibalism to 2%. Hake had an *EE* over 1.5 in the initial model. Since the assumed catchability (0.8) had a higher pedigree score than *P/B*, the latter was adjusted, the value obtained from empirical equations (Allen 1971, Pauly 1980) was replaced by total mortality estimated in stock assessment for the age groups predominant in the Portuguese continental shelf (1–3 yr). The final output parameters for the 33 functional groups are shown in Table 3.

3.3. Summary statistics

The summary statistics and ecological network analysis indicators (for more details see Heymans

et al. 2014) describing the PCSE are presented in Table 4. Total flow of detritus and total exports represented about one-third of total system throughput (TST—defined as total ecosystem size), total consumption represented around 25% of TST and the remaining fraction of the TST was total respiration. Furthermore, ecosystem indices that describe the ecosystem's maturity state *sensu* Odum (1969), such as total primary production/total respiration, connectance index, system omnivory index, Finn's mean path length, ascendancy and overhead (for more details see Heymans et al. 2014; Table 4), suggested that the PCSE was an immature ecosystem.

Total ecosystem biomass was 162.0 t km⁻². Producers, consumers and detritus represented 11.6, 59.9 and 27.9% of the total biomass, respectively. Discards represented a negligible parcel of the total biomass (0.6%). In terms of consumers' biomass (i.e. excluding detritus, discards and phytoplankton), the

ecosystem was dominated by SPF (27.3%), invertebrates (23.0%) and zooplankton (31.5%). Marine mammals and seabirds represented a negligible fraction of consumers' biomass (0.1%). Sardine presented the second highest fraction of consumers' biomass (15.2%), after the group of meso- and microzooplankton, and 35.1% of the total biomass of the fish groups. Moreover, sardine was the dominant small pelagic species in the PCSE, representing 55.7% of their biomass, followed by chub mackerel (24.8%).

3.4. Mortalities

EE values estimated for fish and macroinvertebrate groups showed a broad range, from 0.10 (tunas) to 0.96 (sardine), but were generally high (mean \pm SD = 0.78 ± 0.33 ; Table 2). The exploitation rates (F/Z), where F is fishing mortality and Z is the total mortality (Table 2), suggest that fishing mortality was not the main cause of mortality in the PCSE, except for rays. Among commercially exploited groups, the highest F estimates were registered for rays, benthic cephalopods and hake (0.62, 0.36 and 0.36 yr^{-1} , respectively) and the lowest for demersal invertivorous fish and squids (0.005 and 0.01 yr^{-1} , respectively). Sardine fishing mortality (0.20 yr^{-1}) was slightly above the average for the commercially exploited groups (0.18 yr^{-1}). Accidental mortality of cetaceans in fisheries ranged from 0.003 yr^{-1} for bottlenose dolphin to 0.027 yr^{-1} for harbour porpoise. There was no obvious relationship between TL and either fishing mortality or exploitation rate.

3.5. Trophic levels and flows

The mean TL of the PCSE was 3.5 (Table 3). Trophic levels ranged from 1.0 (phytoplankton) to 5.3 (bottlenose dolphin). Trophic levels of catch (TLc) for the purse-seine fleet was 2.97, while for BT and polyvalent fleets TLc was 3.53 and 3.56, respectively. Among fish groups, demersal piscivorous fish and hake showed the highest TL (both 4.3), while sardine showed the lowest, 2.8. Among invertebrates, cephalopods showed the highest TL (higher than 4 for both groups). The trophic flows diagram of the PCSE reveals the complexity of trophic connections between and within the pelagic and benthic domains (Fig. 2). The link between the 2 domains appears to be made through dolphins, hake and squid groups. The Lindeman spine analysis shows an ecosystem

divided into 11 TLs, which may be represented by only the first 5 levels due to the low biomasses and flow values in the other levels (Fig. 3). TEs were similar between trophic levels, being the highest from TL III to TL IV (0.20). The majority of the flows in the ecosystem (99%) originate from TL I to TL III. The integration of results from the diet and the trophic flows diagram showed that a high proportion of catches, consumption and predation originate from TL III, where SPF, particularly sardine, are the main components.

3.6. Consumption

Fisheries consumed 22.8% of sardine annual production and 19 of the 30 consumer groups consumed 72.8% within the PCSE, the most important being fish (31.5%) and cephalopods (30.9%), whilst cetaceans and seabirds had a comparatively lower importance, 9.4% and 1%, respectively. Furthermore, sardine is exclusively planktivorous, preying on meso/microzooplankton and phytoplankton (83% and 17% of the diet composition, respectively). Among fish groups, sardine consumed the highest fraction of phytoplankton and meso/microzooplankton production (0.4% and 21.1%, respectively).

3.7. Mixed trophic impact

The MTI analysis (Fig. 4) showed that in general, fishing fleets have a negative impact on their target species with the substantially stronger and more widespread impact of the polyvalent fleet. As expected, predator groups have negative impacts on their prey while lower-trophic-level groups had generally positive effects on corresponding predators. Sardine showed the second highest overall impact on the ecosystem after polyvalent fleet, owing both to the positive and the negative overall impacts and the number of functional groups that were impacted (Fig. 5). As expected, an increase in sardine biomass positively affects some of its main predators (seabirds, minke whale, cephalopods and hake), and negatively impacts its main prey (meso- and microzooplankton) (Fig. 4). However, sardine also had a positive impact on its other prey, phytoplankton, while having negative impacts on some top predators, such as the common dolphin, striped dolphin and tunas. Moreover, a negative effect of sardine biomass increase on other small pelagic species was observed (Fig. 4).

Table 4. Comparisons of the Portuguese continental shelf with models of the global large upwelling ecosystems. TL: trophic level; TST: total system throughput; na: data not available; *: dimensionless indices

	Portuguese continental shelf ecosystem	Southern Benguela current		Northern Benguela current		
Characteristics of the model						
Modelled period	2006–2009	1980	1990	1971–1977	1980–1989	1990–1995
Area (km ²)	22209	220000	220000	179000	179000	179000
Number of groups	33	31	31	17	17	17
Depth range (m)	15–200	0–500	0–500	0–500	0–500	0–500
Longitude range	7.5°–10.5° W	15°–28° E	15°–28° E	11°–17° E	11°–17° E	11°–17° E
Latitude range	36.6°–42° N	29°–35° S	29°–35° S	15°–29° S	15°–29° S	15°–29° S
Ecosystem theory indices (t km⁻² yr⁻¹)						
Total system throughput	16412	37975	39304	17443	23495	16252
Sum of all consumption	4776	17230	18831	3214	11743	4477
Sum of all exports	4654	2559	1698	6124	1221	4452
Sum of all respiratory flows	1917	9416	10279	1550	6070	1731
Sum of all flows into detritus	5066	8771	8496	8264	4461	5591
Sum of all production	7585	16233	16638	8264	10036	7479
Calculated total net primary production	6566	11974	11977	7675	7319	6183
Total primary production/total respiration *	3.4	1.3	1.0	5.0	1.2	3.6
Net system production	4649	2559	1698	6124	1249	4452
Total primary production/total biomass *	56.7	54.1	51.8	27.0	20.0	16.0
Total biomass/total throughput *	0.01	0.01	0.01	0.02	0.02	0.02
Total biomass (excluding detritus)	116	221	231	282	361	381
Connectance index *	0.29	0.23	0.24	0.26	0.29	0.30
System omnivory index *	0.22	0.23	0.24	0.15	0.17	0.12
Fishery status indices						
Total catch (t km ⁻² yr ⁻¹)	6.3	3.0	2.5	6.6	6.7	3.4
Mean trophic level of the catch	3.25	4.74	4.80	2.85	3.25	3.10
Gross efficiency (catch/net PP)	0.001	0.0003	0.0002	0.0009	0.0009	0.0006
PPR (%)	17.0	4.4	4.5	5.0	5.9	4.3
Transfer efficiencies — all flows (%)						
TL II	11.0	6.5	6.5	7.8	3.0	6.8
TL III	20.1	24.3	24.3	6.0	6.5	3.5
TL IV	16.4	22.0	22.0	2.5	4.5	1.5
TL V	15.5	11.3	11.2	0.5	1.5	1.0
TL VI	14.4	12.1	11.9	na	na	na
Mean TL II–IV	15.3	15.1	15.1	na	na	na
Proportion of flow originated from detritus	18.3	45.0	45.0	na	na	na
Keystone index						
Libralato et al. (2006) (first 6 with the highest relative total impact > 0.5)	Phytoplankton, benthic cephalopods, meso- and microzooplankton, sardine, chub mackerel, minke whale	na	na	na	na	na
Role of small pelagics						
Biomass	High sardine but decreasing	High anchovy, low sardine	Low anchovy, sardine increasing	High sardine, moderate anchovy	Low sardine, low anchovy, increase in other small pelagics	Low sardine, low anchovy
Presence in keystone index	Yes — sardine and chub mackerel	na	na	na	na	na
Cycling indices						
Predatory cycling index (PCI, % of TST without detritus)	0.07	na	na	6.3	12.1	11.2
Throughput cycled (excluding detritus)	5.82	na	na	na	na	na
Finn's cycling index (FCI, % of TST)	1.94	na	na	2.8	22.1	9.5
Finn's mean path length (MPL)	3.58	3.17	3.28	2.3	3.2	2.6
Information indices						
Ascendency (%)	27.2	21.0	20.0	41.7	23.9	31.7
Overhead (%)	72.8	79.0	80.0	58.3	76.1	68.3
Publication						
	Present study	Shannon et al. (2003)		Heymans et al. (2004)		

3.8. Keystone and dominant species

Minke whale, demersal piscivorous fish, squids and benthic cephalopods were identified as keystone groups in the ecosystem (Fig. 5). Moreover, 8 functional groups were pointed out as dominant: phytoplankton, meso- and microzooplankton, macrozooplankton, macrozoobenthos, sardine, chub mackerel, benthopelagic invertivorous fish and demersal invertivorous fish. Groups that showed little or no impact on the ecosystem in the MTI analysis were also identified as low-impact functional groups by the keystone analysis.

4. DISCUSSION

The present study indicated that the ecosystem of the Portuguese continental shelf is regulated by low- and intermediate-trophic-level species, mainly plankton and SPF. These groups made up the bulk of the biomass, generated most of the flows and had the highest relative impact on other groups, including fisheries, pointing to the importance of bottom-up control in the ecosystem. Similar bottom-up structures have been described for other areas of the Atlantic Iberian Peninsula (Lassalle et al. 2011, Santos et al. 2013). Moreover, SPF were shown to be a key link between lower and higher trophic levels, as in nearby ecosystems: the Bay of Biscay and the Cantabrian Sea located north, and the Gulf of Cadiz located south of the Portuguese coast (Sánchez & Olaso 2004, Lassalle et al. 2011, Torres et al. 2013). Also, in terms of system maturity, the PCSE ecosystem resembles nearby ecosystems: the Cantabrian Sea and the Gulf of Cadiz, which were also described as immature ecosystems (Sánchez & Olaso 2004,

Northwest Africa Canary current	Northern Humboldt current			Northern California current
1987	1953	1960	1973	1990
3561029	780000	780000	780000	70000
27	20	20	20	65
na	0-2000	0-2001	0-2002	0-1280
6.5°–30° W	67°–83° W	67°–83° W	67°–83° W	123°–127° W
8.5°–36° N	3°–18° S	3°–18° S	3°–18° S	40°–47° N
26556	59638	59677	53101	15993
10617	23127	23601	19661	4331
1	12754	11985	10186	4180
6526	9774	10075	9895	2442
9413	13982	14016	13359	5040
14433	26996	26606	49540	7636
12461	22528	22060	47235	6620
1.9	2.3	2.2	4.8	2.7
5935	12754	11985	37340	4178
43.2	76.3	69.2	117.0	25.6
0.01	0.00	0.01	0.01	0.02
288	295	319	404	259
0.15	0.25	0.25	0.26	0.19
0.15	0.12	0.11	0.14	0.16
0.5	6.5	91.7	32.2	4.7
2.80	2.35	2.22	2.61	3.52
0.0000	0.0003	0.0042	0.0007	0.0007
0.4	5.2	7.2	17.8	18.1
8.2	2.6	2.9	5.1	19.5
6.2	9.8	10.6	11.5	16.1
4.0	1.8	1.9	5.6	13.3
0.9	0.9	0.1	1.9	9.4
0.1	0.6	0.0	1.1	6.7
5.9	3.6	3.9	6.9	16.1
4.3	0.3	0.3	0.3	0.4
Cephalopods, coastal demersal fish, phytoplankton, zooplankton, clupeids, mesopelagic predators	Anchovy, horse mackerel, phytoplankton	Anchovy, phytoplankton, cormorant, zooplankton, horse mackerel	Horse mackerel, anchoveta, phytoplankton, sardine, zooplankton, hake	Orcas, euphisidis, forage fish, phytoplankton, copepods, gulls
High clupeids	High anchovy, smaller sardine	High anchovy, small sardine	High anchovy and sardine	Low sardine, forage fish high
Yes — clupeids	Yes — anchovy	Yes — anchovy	Yes — anchovy and sardine	Yes — forage fish
0.60	3.42	3.41	0.62	na
81.5	1082	1080	164.7	na
7.65	4.35	6.13	6.67	1.13
4.07	2.65	2.71	2.64	2.42
32.4	44.4	40.6	36.4	31.6
67.6	55.6	59.4	63.6	68.4
Morissette et al. (2010)	Jarre-Teichmann & Pauly (1993)			Field (2004)

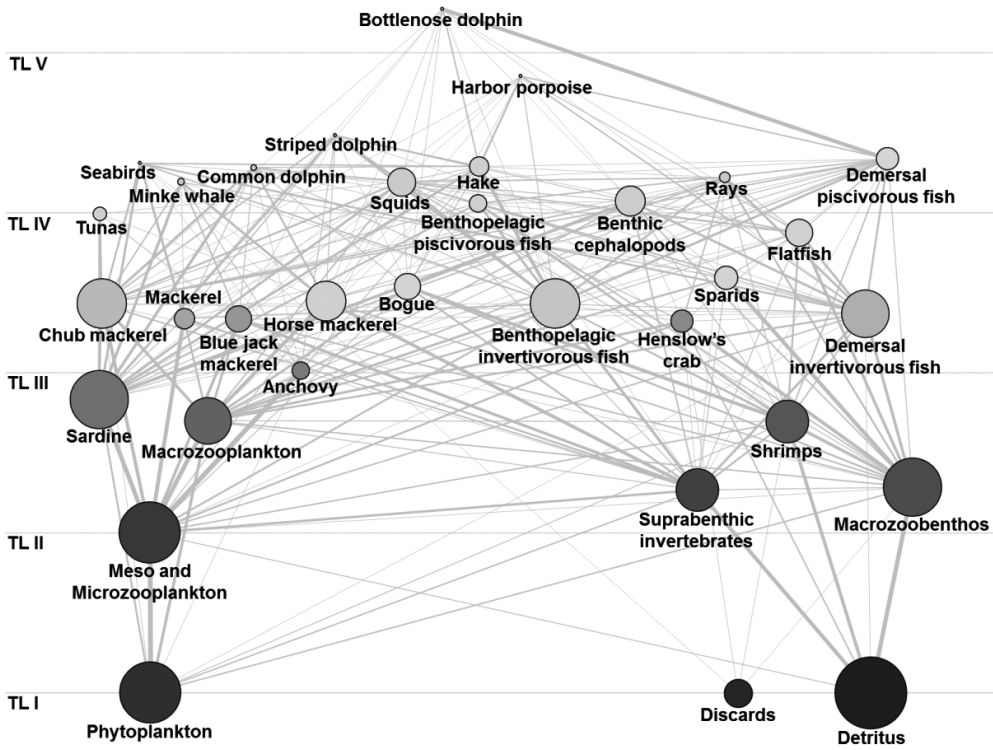


Fig. 2. Flow diagram of the food web of the Portuguese continental shelf in 2006–2009. The size of each circle is proportional to the biomass of the functional group. All the functional groups are represented according to their trophic levels on the y axis (TL). Light grey lines connecting the groups represent prey–predator relationships. The thickness of the lines indicates the proportion of the prey in the predator diet (thicker lines, higher proportion)

Torres et al. 2013). Although, in contrast to the other nearby areas, the French Bay of Biscay was described as a mature ecosystem (Lassalle et al. 2011).

The Portuguese fisheries showed higher catches of lower-trophic-level species than fisheries in other areas of the Iberian Peninsula, particularly the Cantabrian Sea (Sánchez & Olaso 2004), as reflected by the mean trophic level of the catches obtained in the present study. This is due to the high contribution of the purse-seine fishery to the total catches. The high overall impact of the polyvalent fleet in the ecosystem is due to targeting high-trophic-level species, which are highly sensitive to increases in fishing effort, such as rays and benthopelagic and demersal piscivorous fishes (Gascuel et al. 2008, Shannon et al. 2014). The higher bycatch rates of marine mammals in this fishery compared with other fisheries may have also contributed to the overall high impact in the PCSE.

Sardine was identified as a dominant species in the PCSE, with particularly strong dominance of the pelagic component of the ecosystem. This was due to its high biomass, the second highest after multi-specific zooplankton groups, and more than 2 times the biomass of any other consumer group, and due to

showing one of the highest relative impacts on the ecosystem. Furthermore, the large number of functional groups preying on sardine and the fact that sardine was one of the main predators of the lower-trophic-level groups highlights its importance as a link between the lower and the higher trophic levels. This role of sardine in the ecosystem has also been described for other areas of the Iberian Peninsula (Sánchez & Olaso 2004, Torres et al. 2013). The proportion of sardine total biomass production captured in the fishery concurs with the mean exploitation level estimated in the assessment of the Iberian stock during the study period (0.30 yr^{-1} ; ICES 2016). Fur-

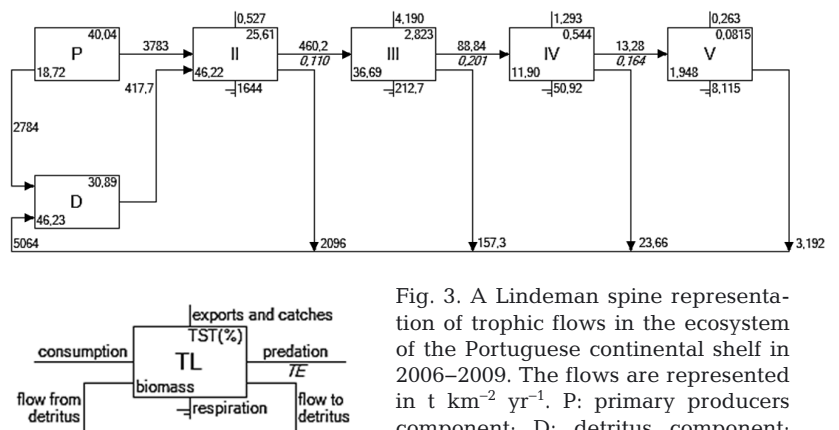


Fig. 3. A Lindeman spine representation of trophic flows in the ecosystem of the Portuguese continental shelf in 2006–2009. The flows are represented in $\text{t km}^{-2} \text{ yr}^{-1}$. P: primary producers component; D: detritus component; TL: trophic level; TE: trophic efficiency

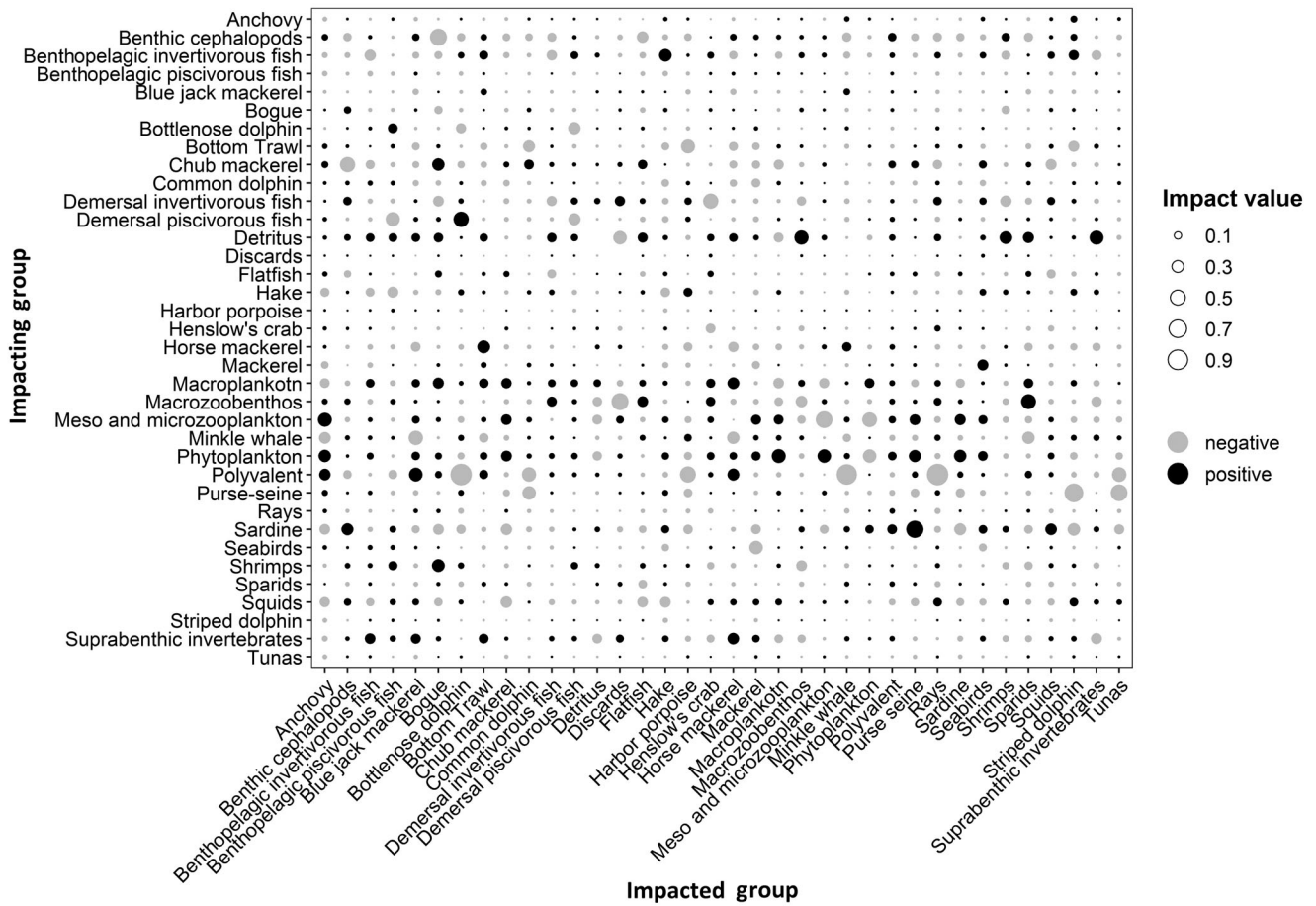


Fig. 4. Mixed trophic impact analysis of the Portuguese continental shelf Ecopath model in 2006–2009

thermore, the high percentage of sardine caught by the purse-seine fleet emphasizes the dependency of this fleet on the sardine. The polyvalent fleet also showed a considerable portion of sardine in its catches. This is mainly because some of the vessels in this fleet use purse seine and target sardine in some periods of the year.

The low *EE* of sardine suggests that other mortality, besides predation and fisheries, is important in explaining sardine consumption within the ecosystem. High sardine other mortality might be related to environmental variability, as SPF are documented to be considerably affected by environmental changes (Fréon 2005).

Direct and indirect interactions within the PCSE were observed. As expected, the MTI analysis showed that most of the groups had a negative impact on their prey and on themselves. Also, indirect impacts within the system could be detected; for example, the negative effect of sardine on the common dolphin, the striped dolphin and the tunas. This may be a result of the overall negative impact that sardine has

on the other small pelagic species, which are also prey for top predator groups. Another example of indirect impacts was the negative effect of sardine on anchovy and other SPF that can be explained by overlap between their niches and consequently increased competition for food (Garrido et al. 2015). However, the negative impact of sardine on the other SPF may be overestimated due to the aggregation of meso- and microzooplankton into one functional group. Garrido et al. (2015) showed that sardine prey on considerably smaller prey sizes than the other small pelagic species.

The PCSE has several structural features in common with the main large upwelling ecosystems (the Northern Humboldt current, the Northern Benguela current, the Southern Benguela current, the Southern Canary current and the California current). These shared characteristics are (1) general species composition, (2) major flow patterns, (3) important role of small pelagics as a basis of the food web, (4) total fraction of primary production required to sustain fish groups in the ecosystem and (5) overall low

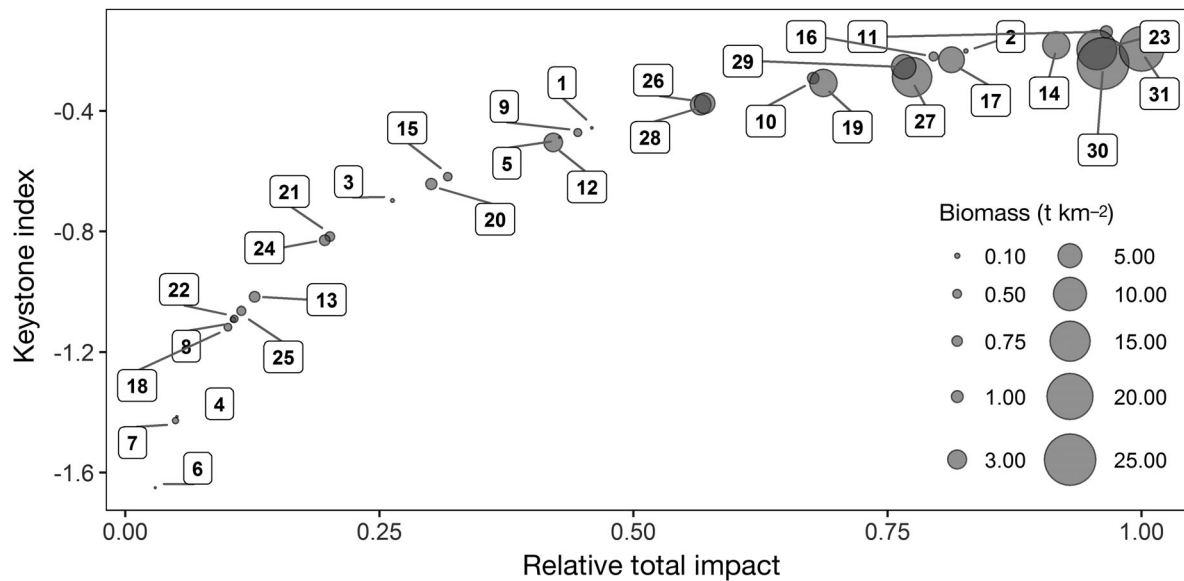


Fig. 5. Keystone index (Libralato et al. 2006) and relative total impact of each of the functional groups in the ecosystem of the Portuguese continental shelf in 2006–2009. Numbers in labels represent the different functional groups in the model (see Table 1 for identification)

system maturity (Jarre-Teichmann & Christensen 1998). In terms of the system's size (TST, catch, biomass and net primary production), the PCSE is similar to the Northern California current upwelling system (Field 2004, Jarre-Teichmann & Christensen 1998). The productivity of small pelagics in the PCSE (anchovy and sardine) falls in the range of other upwelling systems and also their natural mortality appears to be considerably higher than their fishing mortality, the same as in other upwelling systems (Jarre-Teichmann & Christensen 1998). In addition, the primary production required to sustain the fishery (PPR) in the Portuguese upwelling system is similar to large global upwelling systems, especially those of the Northern Benguela (Jarre-Teichmann & Christensen 1998) and Northern Humboldt (Jarre-Teichmann & Pauly 1993) currents. In terms of TEs, the PCSE is similar to the Southern Benguela ecosystem (Shannon et al. 2003). However, these values are generally higher than in the majority of upwelling systems (Pauly & Christensen 1995, Jarre-Teichmann & Christensen 1998). This indicates that the PCSE system may be food limited much like the Southern Benguela (Shannon et al. 2003) or Northwest Mediterranean (Coll et al. 2006) systems.

Another common characteristic shared by upwelling ecosystems is large decadal fluctuations in abundance and species replacement between small pelagics (Cury et al. 2000). Based on the modelling studies of upwelling systems where these fluctuations have been observed (Cury & Shannon 2004,

Heymans et al. 2004), it can be concluded that changes in SPF might inflict significant changes in the ecosystem structure and function, defined as regime shifts, as was the case for the Northern Benguela system (Heymans et al. 2004). However, it is not a rule and replacement between 2 pelagic species in upwelling ecosystems might occur, without causing shift to a new ecosystem state (Cury & Shannon 2004). The Ecopath model developed in this study provides a basis to further develop dynamic simulations to understand the cause and impact of sardine decrease on the ecosystem.

4.1. Model quality, uncertainties and knowledge gaps

The pedigree index obtained for this Ecopath model implies moderate data quality, although lower than similar models of nearby areas (Sánchez & Olaso 2004, Bănaru et al. 2013, Torres et al. 2013). If the production/biomass and consumption/biomass ratios were based on local estimates (since local data is incorporated in the empirical formula) instead of estimated from empirical equations, the model pedigree would improve to 0.65 and consequently show values similar to those of the models mentioned above. Nevertheless, the present model pedigree points to a need to improve knowledge within the PCSE. In particular, the information required for several input parameters of the model was not avail-

able for some of the cephalopods, most invertebrate species and local microzooplankton offshore biomass data. Moreover, the top 5 functional groups indicated by the sensitivity analysis are groups where 2 or more of the input parameters showed data deficiency. This adds uncertainty to the model as the outputs from these groups can considerably affect the outputs of other groups where data were available. However, it also can be used as a guide for allocation of future research effort. Furthermore, biomass information on demersal and benthic fish species obtained from BT surveys is usually in the form of relative biomass indices, highlighting the importance of future studies on research surveys catchability for the different species. Also, even though data regarding diet composition came mainly from the analysed ecosystem, the time period when it was obtained was highly variable.

The present model is to our knowledge, the first representation of the trophic structure and functioning of the ecosystem of the Portuguese continental shelf. A large effort was required to compile, standardize and adapt the best-available data and information for a large number of functional groups within the ecosystem. We believe that our results provide a broad understanding of the ecosystem functioning and deepen the knowledge of inter-specific trophic interactions despite the uncertainties. Knowledge gaps were identified for important components of the ecosystem. This information is important to direct future studies in the area. The next step for future research should be the application of dynamic models such as Ecosim and Ecospace to better understand the cause and impact of sardine abundance decline (Walters et al. 1997, 1999). Moreover, the dynamic model would allow simulations of different ecological and management scenarios (Heymans et al. 2016) that will support an advance to an ecosystem approach to fisheries management in the Portuguese coastal shelf ecosystem.

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Appendix 1. Formulas used to calculate production/biomass (P/B) ratio for the functional groups included in the model

Fish groups

The P/B ratio for fish groups was calculated using the assumption by Allen (1971) that assumes that in a steady-state ecosystem:

$$P/B = Z = M + F$$

where Z = total mortality, M = natural mortality and F = fishing mortality. Natural mortality (M) was calculated using the empirical equation by Pauly (1980):

$$\log(M) = -0.0066 - 0.279 \times \log(\text{Lin}f) + 0.6543 \times \log(k) + 0.4634 \times \log(T)$$

where $\text{Lin}f$ and k are parameters of the von Bertalanffy growth equation and T is the mean environmental temperature ($^{\circ}\text{C}$). F was calculated as catch/biomass. When no biomass estimates were available, a mean F for the group was assumed based on literature and expert knowledge.

Appendix 2. Formulas used to calculate consumption/biomass (Q/B) ratio for the functional groups included in the model**Seabirds**

Daily ration for seabirds (DR) in $g\ d^{-1}$ was calculated using the empirical equation from Nilsson & Nilsson (1976):

$$\log(DR) = -0.293 + 0.85 \times \log(W)$$

where W is the mean body mass of birds expressed in g. DR was multiplied by 365 d and divided by the mean weight of the species to provide the Q/B ratio.

Fish groups

For fish groups, Q/B was calculated with the empirical equation from Pauly et al. (1990):

$$\log(Q/B) = 6.37 - 1.5045 \times T' - 0.168 \times \log(\text{Winf}) + 0.1399 \times \text{Pf} + 0.2765 \times \text{Hd}$$

where $T' = 1000/T$ is mean water temperature in Kelvin ($K = ^\circ C + 273.15$), Winf is the asymptotic body weight

(g), Pf and Hd express feeding types: $\text{Pf} = 1$ for apex and/or pelagic predators and/or zooplankton feeders and 0 for all others, and $\text{Hd} = 1$ for herbivores and 0 for carnivores (Pauly et al. 1990). Pf and Hd of benthic carnivores are assumed to be zero. Winf was estimated by replacing L by Linf in length–weight relationships compiled from literature (Table S2 in the Supplement).

Henslow's swimming crab

For Henslow's swimming crab, Q/B was calculated using the empirical equation for the daily consumption rate of invertebrates (Cammen 1979):

$$C = 0.381 \times W^{0.742}$$

where C is the daily consumption rate and W the mean body weight.

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