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Effects of fisheries on the Cantabrian Sea shelf ecosystem☆

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Abstract

The Cantabrian Sea shelf ecosystem is described using a mass-balance model of trophic interactions, in order to understand the effects of the different fisheries that operate in this area. The study was based on a database of bottom trawl surveys, ICES stock assessment working groups, stomach analyses, fisheries research and was supplemented by published information. The model had 28 trophic groups corresponding to pelagic, demersal and benthic domains, also including detritus and fishery discards. The results indicated that the biomass and production of some groups would be unrealistic if they were independently estimated by single-species assessment approaches. Summaries are given to illustrate the flow distributions between groups. Strong relationships existed between the pelagic, demersal and benthic domains due to key groups, like zooplankton suprabenthic and horse mackerel, that transferred the flow from primary production to the upper trophic levels. Feeding pressure on phytoplankton was low and detritivorous species were an important component of the ecosystem.

Estimations of the trophic level of the fisheries, transfer efficiency between trophic levels and mixed trophic impact analysis, that consider the fishery both as an impacting and as an impacted component, were also included. The results indicated a fisheries impact level in the Cantabrian Sea comparable to that in the most intensively exploited temperate shelf ecosystems of the world. The fishery was operating at a mean trophic level of 3.7. The importance of discards as food in the ecosystem was low, in comparison with detritus, primary producers or other low trophic levels. The negative trophic impact of trawling on the different groups of the system was high and much stronger than the other gears studied. All fishing gears, except the purse seine, had negative impact on fish feeders and elasmobranchs. The mean trophic level of Cantabrian Sea fisheries declined from 1983 to 1993 but has remained steady since then.

Keywords: Cantabrian Sea; Ecosystem dynamics; Ecopath; Mass-balance model; Fishery impact; Food web

1. Introduction

The Cantabrian Sea area forms the subtropical/boreal transition zone of the Eastern Atlantic. As a result, typical temperate-water species from the south occur together with those of northern origin and, consequently, high biodiversity indices exist in comparison with adjacent areas (Olaso, 1990; Sánchez, 1993). In addition, the topographical complexity and wide range of substrates on its continental shelf result in many different types of habitats. This diversity is reflected in the biological richness of the region that includes many species of commercial interest. In addition, it is the winter spawning area for some species, such as hake, megrims, red-sea bream and horse mackerel, and the feeding area for others, e.g. anchovy and tuna. Some migratory species remain outside the ecosystem during different seasons (e.g. mackerel, anchovy and tuna).

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The fisheries, which have been operating for centuries, have become more industrialised over the last 50 years, with the catch reaching about 200,000 t per year. Trawlers fish on the muddy bottoms of the shelf, whereas long-liners operate mainly on the shelf-break bottoms and gill nets are used on rocky grounds near the coast and shelf-break. There are seasonal pelagic fisheries for anchovy (purse seine) and tunas (troll and bait boats) during the fishes' migrations in spring and summer.

Single-species assessment approaches have been used historically for the management of European Atlantic fisheries and they are mainly based on TACs and quota regimes. The latest estimates by ICES stock assessment working groups showed that the southern stocks of hake and anglerfish were below safe biological limits and the southern stocks of megrims and horse mackerel were overfished (ICES, 2000). Landings of hake (the main demersal commercial species) in the last 4 years have been below the agreed TACs and the spawning biomass is at its historical minimum. The main management measures in the Cantabrian Sea adopted by the Spanish Fisheries Administration are focused on reducing fishing effort and increasing the protection of juveniles (through a closed area to fishing). Restricted areas to trawling have been established in zones where hake recruits concentrate all year. The starting point of the current study was to determine the interrelations between species and gears and calibrate in a next step whether the management approaches based on models of ecosystem dynamics could identify the consequences (biological and economic) of the application of this measure.

This work is a first study of the Cantabrian Sea ecosystem using a mass-balance model of trophic interactions. It attempts to determine the possible impact and role of the different fisheries that operate in the area. In addition, it was carried out in order to compare the results with published models from other European areas, such as the North Sea (Christensen, 1995a), and with similar ecosystems, such as the Newfoundland-Labrador shelf (Bundy et al., 2000). Therefore, it was possible to check whether estimates from the single-species assessment approach were mutually compatible and realistic. The present contribution is also of relevance in view of the increasing need for managing the Cantabrian Sea ecosystem, which is currently subjected to strong fishery pressure.

2. Material and methods

2.1. Study area

The Cantabrian Sea is considered as the southern region of the Bay of Biscay and it is generally accepted that its western limit corresponds to a vertical line from Cape Estaca de Bares (7°40′ W) with its eastern limit at the beginning of the French shelf. However, for practical reasons, this study considers the Cantabrian Sea in its wider meaning (ICES Division VIIIc), which includes the Galician shelf to the north of Cape Finisterre (at latitude 43° N) and is the upper limit of the subtropical Lusitanic area (Fig. 1). Division VIIIc has some relatively homogeneous biogeographical characteristics in relation to adjacent areas and fishing statistics and information are available from the evaluation of stocks carried out by the ICES stock assessment working groups, which were indispensable for developing the model. In this study, we refer to the neritic area of the Cantabrian Sea, with a total continental shelf surface of about 16,000 km^2, and the neighbouring oceanic area. The continental shelf is very narrow (10–60 km from the coast). The inner and middle shelf (with a depth of less than 100 m) bottoms are mainly rocky or sandy, whereas the outer shelf has predominantly muddy bottoms. The production of the area is greatly influenced by a seasonal coastal upwelling (spring and summer) and hydrographic mesoscale activity along the northwestern shelf-break. This is a consequence of winter fluxes from the warm poleward current (also known as the "Navidad Current"), which results in a convergent front at the boundary between coastal and oceanic waters (OSPAR, 2000; Sánchez and Gil, 2000). These produce a regular pattern of hydrographic conditions throughout the year characterised by winter mixing and summer stratification, with phytoplankton blooms occurring during the transition periods. This seasonal pattern has a significant effect on the dynamics of the ecosystem.

The Cantabrian Sea area was assumed to be the unit ecosystem for the present study. Nevertheless, this assumption may not be appropriate for some species whose ranges extend beyond this area. Consequently, for migratory species, we considered that only a certain proportion of the population was present in the area.

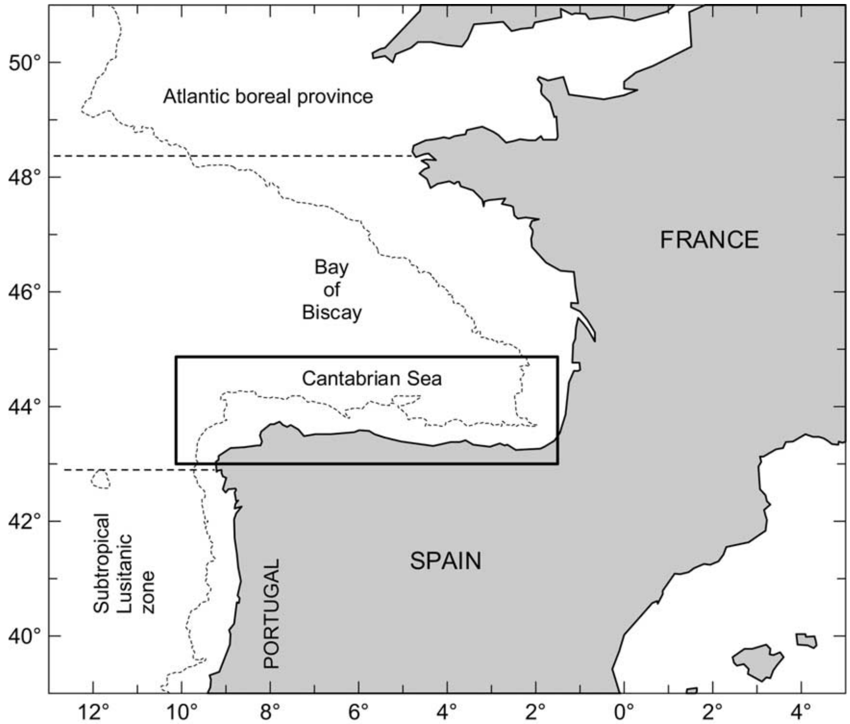

Fig. 1. The Cantabrian Sea area as defined in the ecosystem model.

2.2. The model

The Ecopath model (version 4.0) was applied in order to produce a balanced steady-state description of the Cantabrian Sea shelf ecosystem. The Ecopath model combines estimates of biomass and food consumption of the various components (species or groups of species) in an aquatic ecosystem with an analysis of flows between the ecosystem elements (Polovina, 1984; Christensen and Pauly, 1992, 1993). The energy balance of each trophic group is given by the basic equation:

consumption

= production + respiration + unassimilated food

The production of each trophic group is balanced by its predation by other trophic groups in the system, its exports from the system and mortality. The ecosystem is modelled using a set of simultaneous linear equations (one for each group i in the system), i.e. production by (i) − all predation on (i) − non-predation losses of (i) − export of (i) − biomass accumulation of $(i) = 0$, for all (i).

This can also be expressed as:

$$B_i \frac{P_i}{B_i} - \sum B_j \frac{Q_j}{B_j} \mathrm{DC}_{ji} - \frac{P_i}{B_i}(1 - \mathrm{EE}_i) - \mathrm{EX}_i = 0$$

where, B_i is the biomass of (i); P_i/B_i is the production/biomass ratio (equal to the instantaneous rate of total mortality Z in steady-state systems) of (i); B_j is the biomass of predator j; Q_j/B_j is the consumption/biomass ratio of predator j; DC_{ji} is the fraction of prey (i) by weight in the average diet of predator j; EE_i is the ecotrophic efficiency of (i): expressing the fraction of total production consumed by predators or caught by a fishery, explained by the model (the rest is “other mortality”); and EX_i is export of (i): sum of fisheries catches plus emigration to adjacent ecosystems.

Estimations of biomass, production and consumption by different sources for each trophic group were used in the model (see below in the functional groups). To harmonise the information, all the input data were those from 1994. The available data from the ICES stock assessment working groups and ICCAT were used to estimate the biomass and production of species of commercial interest: hake, anglerfish, megrim, blue whiting, horse mackerel, mackerel, anchovy, sardine and tuna. Consumption rates for some fish species were from the FishBase database (Froese and Pauly, 1998). The biomass of some fish groups was estimated from bottom trawl surveys carried out in the area during the same year (ICES, 1997a,b) by applying the swept area method (Sánchez et al., 1995). Total biomass estimation of this species obtained from bottom trawl surveys were underestimated because only an unknown percentage of the population is accessible to the sampling gear. However, a comparison made between the biomass estimated by stock assessments and surveys results of some characteristic species, like hake and megrim, let us predict that the survey only estimates between the 10% (demersal behaviour) to 15% (benthic habits) of the total biomass. We assume the same proportion for the similar species without assessment. In general terms, the groups were parameterised top–down so that the flows at the lower levels were calculated to match the food demands of the upper levels (normally with more available data).

A classification of species according to their prey was carried out as a first step. On this basis, and to construct the mass-balance model, 28 trophic groups were defined, 15 of which were fish, 6 invertebrates, 5 groups of plankton, detritus and fishery discards. In each group, we considered species of similar size, habitat, diets, consumption rates, mortality and production rates. The main commercial species were taken separately, since better information about their different input parameters was available. Table 1 summarises the species composition as a percentage in biomass of each trophic group considered in the model. All the available data for biomass, annual landings and discards were converted into the same unit ($t\,km^{-2}$) expressed as wet weight. An annual average model was described, in which biomass, diets and species composition in different seasons were averaged.

The species assemblages used in the Cantabrian Sea mass-balance model to construct the 28 functional trophic groups are following.

2.3. *Fish groups*

2.3.1. *Tuna*

There are two tuna species, albacore (*Thunnus alalunga*) and bluefin (*T. thynus*), which are present in the area mainly in summer (Cort, 1990, 1995; Ortíz de Zárate and Cort, 1998). The albacore, which is more abundant, belongs to the North Atlantic stock and the fish that arrived in the Cantabrian Sea area are juveniles up to 5 years of age from adjacent waters of the Azores. Based on assessment working groups (Anon, 1997a,b), a total mortality estimate in 1994 was 0.8 per year and 0.6 per year, respectively for these two species. Most of the tuna population that arrived in the Cantabrian Sea remained in oceanic waters (Bay of Biscay); for this reason only 20% of the estimated biomass was considered in the model.

2.3.2. *Hake*

European hake (*Merluccius merluccius*), the most important demersal fishery resource in the area, is separated in two groups: large and small (recruits), with the division at 20 cm length. The largest nursery for the southern stock of this species is found in the Cantabrian Sea and their variability is associated with hydrographic anomalies in the area (Sánchez and Gil, 2000). Information on biomass and production is available from ICES assessment working groups (ICES, 1996a). The large hake biomass considered in the model is 70% of the estimate for the spawning southern stock biomass (ICES Divisions VIIIc and IXa). Consumption rates (QB) for hake are from Velasco and Olaso (2000).

2.3.3. *Anglerfish*

Two species of anglerfish, both in the genus *Lophius*, inhabit the area, *L. piscatorius* and *L. budegassa*. The anglerfish biomass used for Division VIIIc was 50% of the estimate for the spawning southern stock biomass of both species and the total mortality estimates were both 0.38 per year (ICES, 1996a).

2.3.4. *Megrim*

Two megrim species of the genus *Lepidorhombus* inhabit the area, *L. boscii* and *L. whiffiagonis*. The megrim biomass used corresponded to 80% of the biomass estimates for the *L. boscii* southern stock (Division VIIIc and IXa) and the total for *L. whiffiagonis*,

Table 1
Species composition and percentage of biomass by trophic groups in the Cantabrian Sea shelf ecosystem model

GT	Group name	Species	Biomass (%)	GT	Group name	Species	Biomass (%)
1	Tuna	*Thunnus alalunga*	0.80	14	Anchovy	*Engraulis encrasicolus*	1.00
		Thunnus thynnus	0.15	15	Sardine	*Sardina pilchardus*	1.00
2	Large hake	*Merluccius merluccius* >19 cm	1.00	16	Squids	*Illex coindetti*	0.50
						Todarodes sagittatus	0.20
3	Small hake	*Merluccius merluccius* <20 cm	1.00			*Loligo forbesi*	0.10
4	Anglerfish	*Lophius piscatorius*	0.60			*Alloteuthis* sp.	0.10
		Lophius budegassa	0.40			*Todaropsis eblanae*	0.05
5	Megrim	*Lepidorhombus boscii*	0.60			*Loligo vulgaris*	0.05
		Lepidorhombus whiffiagonis	0.40	17	Benthic cephalopods	*Eledone cirrhosa*	0.60
						Octopus vulgaris	0.30
6	Large demersal fish	*Conger conger*	0.29			*Sepia officinalis*	
		Zeus faber	0.28			Sepiolidae	
		Chelidonichthys lucerna	0.28				
		Phycis blennoides >19 cm		18	Benthic invertebrate carnivores	Hermit crabs	0.80
		Helicolenus dactylopterus >19 cm				Gasteropods carnivores	0.15
						Starfish	0.05
7	Dogfish	*Sciliorhynus canicula*	0.80				
		Galeus melastomus	0.15	19	Shrimps	Crustacea natantia	1.00
		Etmopterus spinax	0.02				
		Deania calceus	0.02	20	Polychaetes	Polychaetes	1.00
						Sipunculids	
8	Rays	*Raja clavata*	0.50				
		Raja montagui	0.30	21	Benthic invertebrate deposit feeders	Sea urchins	
		Leucoraja naevus	0.15			Holothuroideans	
						Gasteropoda	
9	Benthic fish	*Chelidonichthys cuculus*	0.20		Benthic invertebrate suspension feeders	*Actinauge richardi*	
		Chelidonichthys gurnardus	0.10			Bivalves	
		Callionymus sp.	0.10			Espogi	
		Phicis blennoides <20 cm	0.10			Ascidiae	
		Arnoglossus sp.	0.20			Crinoidae	
		Mullus surmuletus	0.05				
		Trachinus draco	0.05				
		Gobids (*Lesuerigobius*, ...)		22	Suprabenthic zooplankton	Euphausiids	0.50
		Flatfish (*Arnoglossus*, *Solea*, ...)				Mysids	0.40
10	Blue whiting	*Micromesistius poutassou*	1.00			Isopods	0.01
11	Small demersal fish	*Gadiculus argenteus*	0.50	23	Macrozooplankton (>5 mm)	Jellyfish	
		Macrorhamphosus scolopax	0.20			Tunicata	
		Pagellus acarne	0.05			Fish larvae	
		Argentina sphyraena	0.02				
		Cepola rubescens	0.02	24	Mesozooplankton (1–5 mm)	Copepods	0.90

Table 1 (*Continued*)

GT	Group name	Species	Biomass (%)	GT	Group name	Species	Biomass (%)
		Trisopterus sp.	0.05			Euphausiids and decapods natantia larvae	0.10
		Capros aper	0.10				
		Antonogadus macrophtalmus	0.05	25	Microzooplankton (<1 mm)	Copepods larvae	0.90
		Pagellus bogaraveo	0.02				0.10
12	Horse mackerel	*Trachurus trachurus*	0.90	26	Phytoplankton	Phytoplankton	1.00
		Trachurus mediterraneus	0.10				
				27	Discards	Fisheries discards and offal	1.00
13	Mackerel	*Scomber scombrus*	0.70				
		Scomber japonicus	0.30	28	Detritus	Organic dead material	1.00

since this species is practically non-existent south of Cape Finisterre at 43° N (Sánchez et al., 1998), the limit of the study area. Information on biomass and production was available from ICES (ICES, 1996a).

2.3.5. *Large demersal fish*

This group includes numerous demersal species, among which are the conger eel (*Conger conger*), John Dory (*Zeus faber*), *Trigla lucerna* and adults of *Phycis blennoides* and *Helicolenus dactylopterus* (Table 1). Biomass estimation of these species in the study area had been carried out by bottom trawl surveys (Sánchez et al., 1995).

2.3.6. *Dogfish and rays*

A total of 80% of the dogfish biomass is formed by the lesser-spotted dog fish (*Scyliorhinus canicula*) that inhabits the whole shelf. Other species in this group are small sharks that live on the shelf-break and slope, like *Galeus melastomus* and *Etmopterus spinax*. At least eight species of rays exist in the area (Sánchez et al., 1995) of which the most abundant is *Raja clavata* (50% of the biomass in the model), followed by *R. montagui* and *R. naevus*. Biomass estimation of dogfish and ray species in the study area is obtained from bottom trawl surveys (Sánchez et al., 1995).

2.3.7. *Benthic fish*

This group is formed by bottom species of medium size, such as *Mullus surmuletus*, *Chelidonichthys gurnardus* and the genus *Callionymus* (Table 1). Also included were most of the flatfish present in the area, such as species of the genera *Arnoglossus*, *Psetta*, *Bathysolea*, *Solea*, etc. Biomass estimation of benthic fish species in the study area was also obtained from the earlier bottom trawl surveys (Sánchez et al., 1995).

2.3.8. *Blue whiting*

Micromesistius poutassou is the most abundant demersal species. Information on biomass and production is available from ICES (ICES, 1996b). It was estimated that 10% of the total biomass of the stock is located in ICES Division VIIIc. The biomass of spawners in the Cantabrian Sea is very low. It is a migratory species and most juveniles come from the north (mainly the Bay of Biscay and west of Ireland), in currents that penetrate into the Cantabrian area from spring onwards (Kloppmann et al., 1996). An immigration routine was used in the modelling because the values of estimated blue whiting biomass were insufficient for the demands of their predators and the fishery in the area. According the age-class abundance (ICES, 1996b) 60% of the biomass estimates is included as immigration to the area (recruits from the northern area).

2.3.9. *Small demersal fish*

This group had numerous species in the area. The largest percentage was formed by small schooling fish such as *Gadiculus argenteus*, *Capros aper* and *Macroramphosus scolopax* constitute 80% of the biomass, according to the bottom trawl surveys (Table 1). However, the latter two species usually come from more southerly waters (Galicia and Portugal). Medium-sized fish, which exploit a similar trophic niche to the others, were also present, (e.g. sparids such as *Pagellus acarne* and *P. bogaraveo*).

2.3.10. Horse mackerel

The horse mackerel (*Trachurus trachurus*) has a wide distribution in the East Atlantic. The adults live near the bottom and are usually found in continental shelf waters, whereas the juveniles are more pelagic. The horse mackerel biomass for Division VIIIc (ICES, 1997b) was estimated as 50% of the total biomass for the southern stock (Divisions VIIIc and IXa). The studies carried out do not consider that it is a migratory species in the area (Villamor et al., 1997) and apparently only a 5% of the Cantabrian Sea population coming from the Bay of Biscay (Northern stock). A relatively low total mortality rate (0.32 per year) has been estimated for this species due to its observed longevity (ICES, 1997b).

2.3.11. Mackerel

This species also have a wide distribution and, in contrast to horse mackerel, undertake long spawning and feeding migrations. The Cantabrian Sea is a spawning area in winter. Juveniles remain near the coast while adults make feeding migrations to the north in summer (Villamor et al., 1997). Two species, *Scomber scombrus* and *S. japonicus*, were included in this trophic group, although the former is far more abundant. Information on biomass and production was available from ICES (ICES, 1997). The biomass, estimated from egg production surveys, indicated that 15% of the total biomass of the Northeast Atlantic stock was in the area considered by the model. As it can be considered a migratory species, present in the Cantabrian Sea during winter-spring, values for both immigration (12 t km^{-2} per year) and emigration (10 t km^{-2} per year) were considered in the model.

2.3.12. Anchovy

The anchovy (*Engraulis encrasicolus*) population considered in this model was distributed throughout the whole Bay of Biscay. Juveniles remain near the coast, while adults make feeding and spawning migrations in the Bay. It is present in the Cantabrian Sea from March to November. Information on biomass and production was available from ICES (ICES, 1997b). The biomass used in the model was 50% of the whole stock (ICES Division VIII), and was assumed to be present in the area for only half of the year.

2.3.13. Sardine

The sardine (*Sardina pilchardus*) present in the Cantabrian Sea corresponds to the Iberian-Atlantic population; the biomass used in the model was 20% of the southern stock (ICES, 1997b). Although it is a species with similar characteristics to the anchovy, it apparently has much smaller production values because the *Z* estimate from the stock assessment working groups is 0.58 per year.

2.4. Invertebrate groups

Only very limited information was available for all the invertebrate groups. From bottom trawl surveys, the more abundant squid species in the area were *Illex coindetti*, *Todarodes sagittatus*, *Loligo* spp. and *Alloteuthis* spp. The more abundant benthic cephalopods were octopus, *Eledone cirrhosa* and *Octopus vulgaris*, together with other species of the family Sepiolidae.

All the crustacean decapods, the gastropod carnivores and the sea stars were aggregated into the "benthic invertebrate carnivore" trophic group. From bottom trawl surveys, the species that constitute more than 75% of the biomass are *Munida intermedia*, *Pagurus prideauxi*, *Liocarcinus depurator*, *Munida sarsi* and *Nephrops norvegicus*. These surveys showed that more than 90% of the shrimp biomass in the area consists of *Plesionika heterocarpus*, *Pasiphaea sivado*, *Dichelopandalus bonnieri*, *Solenocera membranacea*, *Chlorotocus crassicornis* and *Processa canaliculata*. There is no shrimp fishery because, although they are abundant, they are very small.

Finally, in the "other invertebrates" trophic group, we included benthic deposit feeder species (detritivorous) such as the echinoderms (mainly sea urchins and holothuroideans) and gastropods, and benthic suspension feeders such as bivalve molluscs, cnidarians, ascidians and sponges. Input parameters (PB and QB) from models of similar areas and the alternative input of EE $= 0.95$ were used to estimate the biomass of all invertebrates from the food demands of the upper levels.

2.5. Zooplankton

The zooplankton biomass shows a periodic annual cycle in the neritic area of the Cantabrian Sea. The maximum values occur in late spring and extend into summer, with a high secondary biomass peak in autumn and minimum values in winter. Copepods represent the main taxonomic group in the zooplankton assemblages in terms of abundance (>70%) and persistence (Valdes and Moral, 1998) and they constitute the mesozooplankton trophic group in the model. The mean zooplankton biomass estimates for the Cantabrian Sea area are 53 mg C m^{-2} for microzooplankton (size $<$ 1 mm) and 315 mg C m^{-2} for mesozooplankton (OSPAR, 2000). We used the most common regression to convert carbon units into dry weight and wet weight (Wiebe et al., 1975). The mean daily zooplankton production estimations in the Cantabrian Sea area are 5 mg C m^{-2} per day for microzooplankton and 32 mg C m^{-2} per day for mesozooplankton (OSPAR, 2000).

2.6. Phytoplankton

The annual phytoplankton cycle shows the typical pattern for a temperate sea characterised by a winter mixing period followed by a stratification phase during the summer. For most of the year, diatoms dominate the phytoplankton community in the Cantabrian Sea, particularly during the transition periods of spring and autumn (blooms caused by nutrient inputs from coastal upwelling). Upwelling pulses of central North Atlantic water are a common feature throughout the western Cantabrian Sea, especially in summer, and they have important consequences for phytoplankton growth (OSPAR, 2000). The chlorophyll concentrations in the continental shelf waters varied from 15.64 mg Chl a m^{-2} (winter in the central area) to 57.84 mg Chl a m^{-2} (upwelling in the western area) and the mean biomass for the period 1984–1992 was 1638 mg C m^{-2} (Bode et al., 1996). The average value of annual primary production for the Cantabrian Sea was 428 g C m^{-2} (OSPAR, 2000).

2.7. Diets

The links between groups were their feeding habits; the information needed to create the diet matrix was taken from different sources. Quantitative analysis was undertaken for 10,000 stomach contents from 36 species of fish in the study area. The species selected constituted a significant percentage (90%) of the demersal fish biomass. In order to obtain an appropriate representation of the annual diet of the fish, the seasonal diet change that takes place in many species was also considered. In 1994, 5000 large and small hake stomachs (Velasco and Olaso, 1998), and 1500 dogfish stomachs (Olaso et al., 1998) were analysed. Additionally, in autumn 1994, 6000 stomach contents from anglerfish, megrim, large demersal fish, rays, small demersal fish and benthic fish were analysed (Gutierrez-Zabala et al., 2001). Information was also available on the diets of these fish in spring (Olaso and Velasco, in preparation) and autumn (Olaso and Rodríguez-Marín, 1995; Velasco et al., 1996); similar information was available for horse mackerel and mackerel (Olaso et al., 1999). Abundance indices from bottom trawl surveys carried out in 1994 were used to determine the percentage participation of each species in the multispecies trophic groups. This was necessary in order to generate the feeding matrix of each functional group applying this percentage as a weighted factor on the diets of each species.

An intensive literature search was carried out to determine the diet composition of the other fishes and invertebrates. The following references were used: (Guerra, 1978; Ortíz de Zárate, 1987; Varela et al., 1988; Pereda and Olaso, 1990; Rocha et al., 1994; Freire, 1996; Pages et al., 1996; Rasero et al., 1996; Tudela and Palomera, 1997; Baamstedt and Karlson, 1998; Barquero et al., 1998; Quevedo et al., 1999; Du Sel et al., 2000).

2.8. Placing the fishery into the ecosystem: landings and discards

The statistical data for fisheries landings were provided by the ICES stock assessment working groups and by the IEO Fishery Database team. The data were subsequently summarised and combined by trophic group. To adjust the model for pelagic fisheries (mainly tuna and anchovy), only the proportions of catch from the shelf and close oceanic waters (neritic area) were taken into account. The total landings during 1994 reached a value higher than 140,000 t, which implied an annual extraction rate of 11.6 t km^{-2}.

The tuna landings corresponded to 25% of those for the whole Bay of Biscay, since most catches of the two species considered were obtained in oceanic waters. They are caught by troll and pole-and-line (bait boats). The albacore and bluefin catches during 1994 in the Cantabrian Sea were 11,622 and 1035 t, respectively.

The landings used in the model for the hake, anglerfish, megrim, blue whiting, horse mackerel and mackerel groups were those corresponding to Division VIIIc (ICES, 1996a,b, 1997). Hake is the main target species of the fleet that operates in the area and they are fished by bottom trawl, longlines and gillnets. In 1994, the Cantabrian fleet landed a total of 5473 t of hake. Anglerfish is taken mainly with bottom trawl and gillnets. During 1994, 2260 t of the two species of this functional group were fished. Megrim is caught exclusively by bottom trawl and the landings were 1105 t in 1994. The blue whiting landings were mainly from bottom trawling. Horse mackerel is caught mainly by purse seine and trawl although landings from longlines and gillnets also exist. A total of 24,147 t was caught in the Cantabrian area in the year of study; also 21,146 t of mackerel were caught mainly with longline, trawl, purse seine and gillnet gears.

Since the available anchovy landings did not belong exclusively to the area described in this study, 90% of the landings from area VIII by the Spanish fleet were considered in the model (ICES, 1997), estimated at 14,043 t. The sardine landings used were 60% of those caught by Spanish vessels in Divisions VIIIc and IXa (ICES, 1997), or 15,333 t.

Discards are consumed mainly by sea birds, fish and benthic scavenger species. In this study, information was based on the results of the project “Discards of the Spanish fleets in ICES Divisions” financed by the EU. This discard sampling programme covered the activities of some of the most important Spanish fleets during 1994 in ICES Division VIIIc, such as trawlers, gillnets, long-liners, and purse seiners (Pérez et al., 1996). From the results of this study, an estimation of 20% of the total catches were discarded in the Cantabrian Sea. Blue whiting and horse mackerel were the main species discarded. It has been estimated that 6149 and 5040 t of these two species, respectively, were discarded during 1994. Other heavily discarded trophic groups were dogfish, that survive the process (Rodriguez-Cabello et al., 2001), benthic invertebrate carnivores, small demersal fish and other invertebrates.

From the results of Camphuysen et al. (1995) and Garthe et al. (1996), it was assumed that 20% of the discards were consumed by marine birds. This trophic group was not used in the model, therefore this portion of discard was attributed to exportation. Nevertheless, in order to determine the species that benefit from the discards, some studies have been carried out in the area (Olaso et al., 1998, 2001, 2002). From this studies, *Scyliorhinus canicula*, *Raja naevus*, small demersal fish (*Pagellus* spp.) and benthic fish (*Chelidonichthys* spp. and *Trachinus draco*) are the main fish species that use the carrion as food.

3. Results and discussion

3.1. The unbalanced model

The initial model was not balanced, since there were some ecotrophic efficiencies (EE) greater than 1, which indicated that the demand on them was too high to be sustainable. In the low trophic levels, the microzooplankton biomass and production estimates (OSPAR, 2000) were insufficient to support their predators (mainly mesozooplankton, macrozooplankton and small pelagic fish). The EE of the following fish groups were greater than 1: blue whiting, horse mackerel, anchovy and sardine. All these groups, to a greater or lesser extent, belonged to the pelagic environment. However, the mackerel EE was extremely low.

A high possible explanation to this is that all these fish species undergo seasonal migrations and the distribution area for their stocks greatly exceeds that of the Cantabrian Sea, which created problems in the estimation of their biomass as it has been previously described. In order to balance the model, we reconsider the reliability of the biomass estimates or the PB from the assessments, which resulted in a more realistic approach. Bearing in mind that these species constitute the most abundant of biomass prey groups in the area, it was concluded that both the values of total mortality from the stock assessment groups and the biomass percentages present in the area could have been underestimated, and then an slight increase of their values was made.

Table 2
System summary statistics for the Cantabrian Sea ecosytem model for the 1994 scenario

Parameter	Value
Sum of all consumption (t km^{-2} per year)	2458.081
Sum of all exports (t km^{-2} per year)	3097.134
Sum of all respiratory flows (t km^{-2} per year)	990.816
Sum of all flows into detritus (t km^{-2} per year)	3597.345
Total system throughput (t km^{-2} per year)	10143.000
Sum of all production (t km^{-2} per year)	5825.000
Mean trophic level of the catch	3.66
Gross efficiency (catch/net primary production)	0.002397
Calculated total net primary production (t km^{-2} per year)	4852.214
Total primary production/total respiration	4.897
Net system production (t km^{-2} per year)	3861.399
Total primary production/total biomass	27.749
Total biomass/total throughput	0.017
Total biomass (excluding detritus) (t km^{-2})	174.859
Total catches (t km^{-2} per year)	11.633
Connectance index	0.318
System omnivory index	0.268
Ecopath pedigree index	0.669

3.2. The balanced model

The system summary statistics for the Cantabrian Sea ecosystem model are given in Table 2. These indices, drawn from theoretical ecology (Odum, 1969; Holling, 1973; Christensen, 1995b), allow the ecological characteristics of the Cantabrian Sea to be compared with other marine ecosystems. The connectance index was high at 0.32, and was similar to studies of other shelves (Arreguín-Sánchez et al., 1993; Mendoza, 1993). The number of links between groups is important and determines the complexity of internal flows, which is expected to be correlated with the stability and maturity of the ecosystem. In addition, the omnivory index of the system, that explains the variance in the trophic level of the prey groups for a consumer, showed a high level (Table 2). Only large hake and anglerfish (top predators) had low omnivory index values due to their high degree of prey specialisation (piscivorous). The pedigree routine (Pauly et al., 2000), that summarises the quality of the data by categorising the different input sources used to construct the model, gave a pedigree index of 0.67.

A summary of the input parameters for the balanced model, under the assumptions described above, is given in Table 3 together with parameters estimated using Ecopath. The total biomass supported by the ecosystem was estimated at 227.2 t km^{-2}, which corresponded to 49.5, 27.3 and 23.2% of the pelagic, demersal and benthic domains, respectively. This signifies the great importance of the bottom communities and benthic producers in the area.

Tuna (4.71), large hake (4.77) and anglerfish (4.80) showed the highest trophic levels in their respective domains. For the fish species, except for mackerel, the EE indicated that 60–95% of the production was used within the system.

In order to compare the relative role of the pelagic, demersal and benthic sub-systems, Fig. 2 presents the major biomass flows for the Cantabrian Sea ecosystem in 1994. The groups represented by small plankton, invertebrate filter feeders and detritivores were in trophic level II. Part of their production passed to the large plankton, benthic and suprabenthic invertebrates, and clupeiform fish (level III). The planktophagous fish of medium size, together with the rays and benthic fish were at level IV. The highest level, close to level V, corresponded to apex pelagic fish (tuna), squids, and large demersal and benthic fish.

Most of the biomass and production were contained within the pelagic domain. The main flow was determined by the interaction between phytoplankton, mesozooplankton, horse mackerel and tuna. In the benthic and demersal domain, most of the biomass and production was associated with the detritus. Strong relationships existed between the three domains due to key groups that transferred the flow from primary production to the upper trophic levels. Groups that linked the pelagic and demersal domains, through vertical migration, were the suprabenthic zooplankton, horse mackerel and squids. The demersal domain connected at low levels with the mesozooplankton through the suprabenthic zooplankton eaten by a multitude of small demersal fish and blue whiting, and constituted the main demersal flow. Species that linked the benthic and demersal domains were the big demersal fish and dogfish, because their diets included a large quantity of benthic organisms. In Fig. 2, only the main flows in the model that corresponded to each of the three domains are marked.

Table 4 shows the estimates of annual food intake (consumption in t km^{-2}) by trophic group. Phytoplankton and mesozooplankton constitute 41.6 and 14.1% of the total food intake, respectively. Feeding

Table 3
Input values (in italic) and estimates of some parameters in the balanced trophodynamic model of 1994 for each functional group

	Group name	TL	Biomass	PB per year	QB per year	EE	Flow to detritus	Catches	Fishing mortality per year	Natural mortality per year
1	Tuna	4.7	*0.384*	*0.82*	*9.50*	0.85	0.78	0.27	0.70	0.12
2	Large hake	4.7	*0.876*	*0.53*	*3.90*	0.79	0.78	0.37	0.42	0.11
3	Small hake	4.4	*0.185*	*0.80*	*6.50*	0.68	0.29	0.05	0.29	0.51
4	Anglerfish	4.8	*0.746*	*0.38*	*1.90*	0.56	0.41	0.16	0.21	0.17
5	Megrim	4.2	*0.237*	*0.66*	*3.00*	0.84	0.17	0.09	0.38	0.28
6	Large demersal fish	4.3	*2.115*	*0.60*	*2.70*	0.95	1.21	1.18	0.56	0.04
7	Dogfish	4.1	*0.870*	*0.40*	*3.20*	0.93	0.58	0.31	0.35	0.05
8	Rays	3.8	*0.360*	*0.40*	*2.90*	0.88	0.23	0.13	0.35	0.05
9	Benthic fish	3.6	*2.940*	*1.20*	*2.80*	0.89	2.05	0.23	0.08	1.12
10	Blue whiting	3.8	*16.415*	*0.48*	*5.30*	0.98	17.57	1.50	0.09	0.39
11	Small demersal fish	3.6	*15.040*	*1.20*	*6.40*	0.86	21.88	0.20	0.01	1.19
12	Horse mackerel	3.8	*14.771*	*0.32*	*4.30*	0.84	13.48	1.95	0.13	0.19
13	Mackerel	3.8	*11.486*	*0.43*	*4.60*	0.29	14.10	1.57	0.14	0.29
14	Anchovy	2.9	*2.832*	*1.98*	*9.13*	0.83	6.14	1.24	0.44	1.54
15	Sardine	2.8	*6.978*	*0.58*	*8.80*	0.61	13.88	1.58	0.23	0.35
16	Squids	4.4	*0.964*	*3.20*	*7.50*	*0.95*	1.60	0.16	0.16	3.04
17	Benthic cephalopods	3.8	*1.116*	*3.00*	*6.00*	*0.95*	1.51	0.38	0.34	2.66
18	Benthic invertebrate carnivores	2.9	*6.914*	*2.60*	*5.60*	*0.95*	8.64	0.06	0.01	2.59
19	Shrimps	2.8	8.442	4.20	9.67	*0.95*	18.10	0.01	0.00	4.20
20	Polychaetes	2.2	*11.944*	*4.80*	*12.00*	*0.95*	31.53	0.08	0.01	4.79
21	Other invertebrates	2.1	*7.845*	*2.50*	*6.50*	*0.95*	11.18	0.08	0.01	2.49
22	Suprabenthic zooplankton	2.7	*12.261*	*16.00*	*32.00*	*0.95*	88.28	0.00	0.00	16.00
23	Macrozooplankton	3.1	*3.507*	*18.00*	*38.00*	*0.95*	29.81	0.05	0.01	17.99
24	Mesozooplankton	2.2	*8.889*	*39.08*	*80.00*	1.00	143.06	0.00	0.00	39.08
25	Microzooplankton	2.1	*3.981*	*45.28*	*120.00*	*0.95*	104.55	0.00	0.00	45.28
26	Phytoplankton	1.0	*32.760*	*148.11*	–	0.21	3063.83	0.00	0.00	148.11
27	Discards	1.0	*2.294*	–	–	0.98	0.03	0.00	0.00	0.00
28	Detritus	1.0	*50.000*	–	–	0.13	0.00	0.00	0.00	0.00
	Sum		227.152				3595.65	11.63		

TL: trophic level, PB: production/biomass ratio, QB: consumption/biomass ratio and EE: ecotrophic efficiency. Biomass, is in $t\,km^{-2}$, while flow to detritus and catches (landings + discards) are expressed in $t\,km^{-2}$ per year.

pressure on phytoplankton is low in the system (EE = 0.2) which meant that a large percentage of the important primary production of the Cantabrian Sea passed to detritus (3064 $t\,km^{-2}$ per year). This is corroborated by studies in the area that indicate that a high percentage of the primary production is exported to the bottom as particulate organic matter (OSPAR, 2000).

The impact of copepods (main zooplankton group in biomass) on the phytoplankton bloom is negligible in the Cantabrian Sea; the fate of the accumulated particulate carbon would be mostly determined by sedimentation and water dynamics (Barquero et al., 1998). Wals (1983) determined for a number of temperate and subtropical marine systems that the export of primary production into the detritus was 50% or more. The detritus in the model accounted for 19.3% of total consumption and constituted one of the main energy flow inputs. Consequently, detritivorous species were an important component of the ecosystem and suspension feeders (i.e. suprabenthic zooplankton, shrimps) and deposit feeders (polychaetes and other invertebrates) constituted a high percentage of the biomass between trophic levels 2 and 3 (Table 3; Fig. 2) to the detriment of pelagic plankton. In particular, the high availability of suprabenthic zooplankton in the system, accessible to both medium sized pelagic fish (mackerel and horse mackerel) and to small demersal fish and blue whiting, meant that this whole group of fish, with a trophic level close to 4, had high biomass and consumption values compared to the fish at a lower

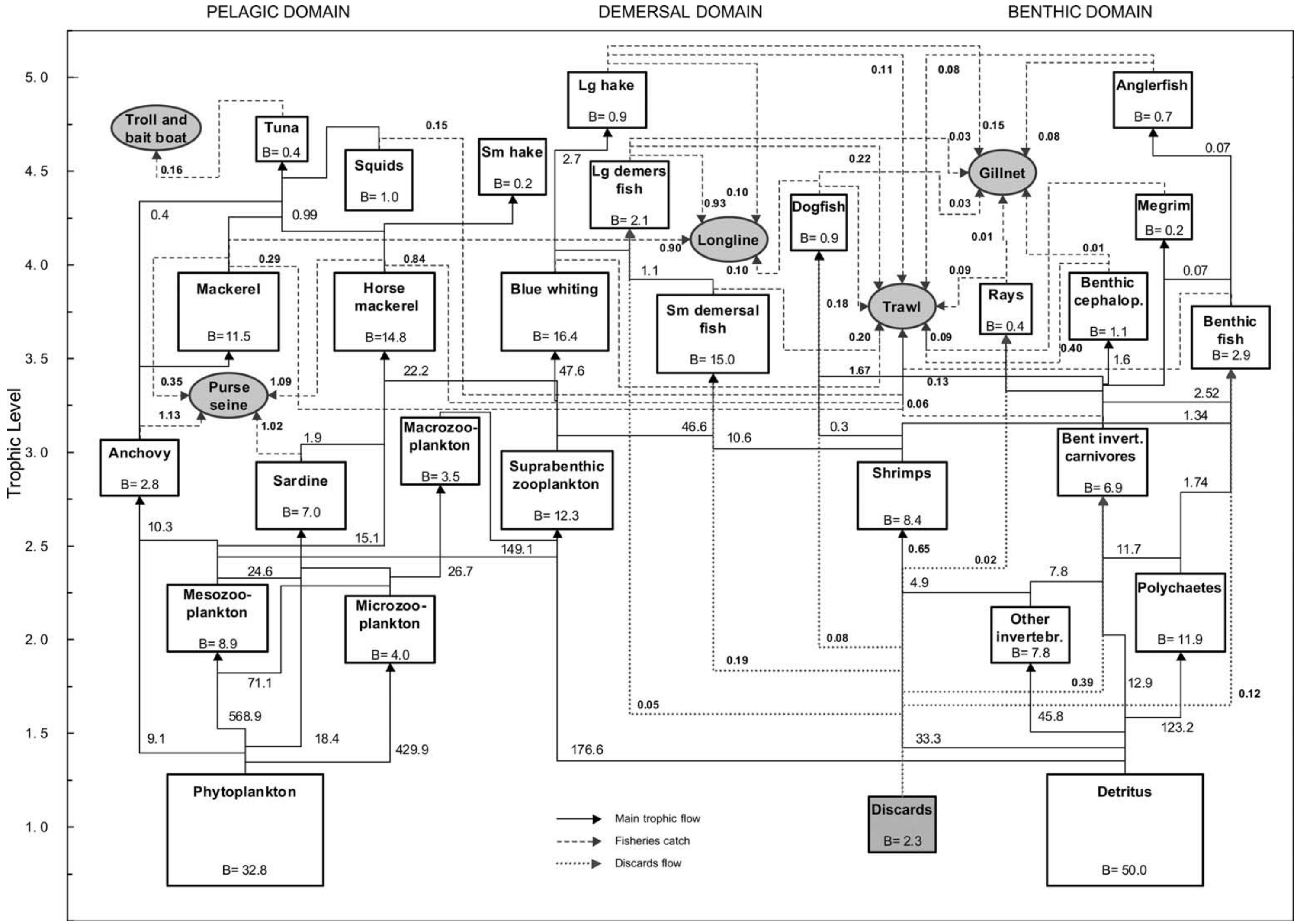

Fig. 2. Main trophic interactions in the Cantabrian Sea, 1994. The boxes (size roughly proportional to the biomass) are arranged on the *y*-axis by trophic level, and to some degree on a pelagic to benthic scale on the *x*-axis. Main flows are expressed in $t\,km^{-2}$ per year and the biomass of each trophic group (*B*) in $t\,km^{-2}$. Minor flows, respiration, catch and all backflows to the detritus are omitted.

Table 4
Estimates of food intake for trophic groups in the Cantabrian Sea ecosystem model

	Prey	Predator													
		Tuna	Large hake	Small hake	Anglerfish	Megrim	Large demersal fish	Dogfish	Rays	Benthic fish	Blue whiting	Small demersal fish	Horse mackerel	Mackerel	Anchovy
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	Tuna	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	Large hake	–	–	–	0.00	–	–	–	–	–	–	–	–	–	–
3	Small hake	–	0.03	0.01	0.00	–	0.01	–	–	–	–	–	–	–	–
4	Anglerfish	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5	Megrim	–	0.00	–	–	0.00	0.02	0.01	–	–	–	–	–	–	–
6	Lg demersal Fish	–	0.01	–	0.01	–	–	–	–	–	–	–	–	–	–
7	Dogfish	–	–	–	–	–	–	0.02	–	–	–	–	–	–	–
8	Rays	–	–	–	–	–	–	–	–	–	–	–	–	–	–
9	Benthic fish	–	0.01	0.10	0.07	0.07	0.86	0.02	0.06	0.33	–	1.35	–	–	–
10	Blue whiting	0.51	2.70	0.14	0.65	0.00	1.20	0.51	–	–	2.87	–	4.13	7.61	–
11	Small demersal fish	–	0.14	0.21	0.23	0.19	1.08	0.26	0.02	0.45	7.30	0.87	8.32	–	–
12	Horse mackerel	1.00	0.24	0.24	0.38	0.08	0.04	0.05	–	–	1.13	–	1.27	–	–
13	Mackerel	0.83	0.05	–	–	–	0.01	–	–	–	–	–	–	–	–
14	Anchovy	0.37	0.09	0.08	–	–	–	–	–	–	1.04	–	4.00	2.91	–
15	Sardine	0.06	0.09	0.05	–	–	0.58	0.03	–	–	1.04	–	1.91	–	–
16	Squids	0.47	0.01	0.07	0.04	0.00	0.01	0.11	0.03	–	0.35	0.96	0.38	–	–
17	Benthic cephalopods	–	0.01	0.00	0.02	0.00	0.01	0.13	0.00	0.10	–	2.22	–	–	–
18	Benthic invertebrate carnivores	–	0.02	0.01	0.00	0.14	1.27	0.77	0.38	2.52	–	8.10	–	–	–
19	Shrimps	0.01	0.02	0.16	0.01	0.18	0.30	0.29	0.40	1.34	8.17	10.61	2.99	–	–
20	Polychaetes	–	–	–	–	0.01	0.12	0.16	0.05	1.74	–	3.95	–	–	–
21	Other invertebrates	–	–	–	–	0.00	0.14	0.05	0.05	0.29	–	1.16	1.59	–	–
22	Suprabenthic zooplankton	–	0.01	0.14	–	0.04	0.02	0.16	0.03	0.94	47.60	46.59	22.23	16.80	1.29
23	Macrozooplankton	0.40	–	–	–	–	–	0.14	–	–	2.61	0.96	–	9.77	–
24	Mesozooplankton	–	–	–	–	–	–	–	–	–	14.88	15.43	15.12	14.85	10.34
25	Microzooplankton	–	–	–	–	–	–	–	–	–	–	–	1.59	0.90	9.05
26	Phytoplankton	–	–	–	–	–	–	–	–	–	–	–	–	–	5.17
27	Discards	–	–	–	–	–	0.05	0.08	0.02	0.12	–	0.19	–	–	–
28	Detritus	–	–	–	–	–	–	–	–	0.41	–	3.86	–	–	–
	Sum	3.65	3.42	1.20	1.42	0.71	5.71	2.78	1.04	8.23	87.00	96.25	63.52	52.83	25.86

Table 4 (*Continued*)

	Prey	Predator										
		Sardine	Squids	Benthic cephalopods	Benthic invertebrate carnivores	Shrimps	Polichaetes	Other invertebrates	Suprabenthic zooplankton	Macrozooplankton	Mesozooplankton	Microzooplankton
		15	16	17	18	19	20	21	22	23	24	25
1	Tuna	–	–	–	–	–	–	–	–	–	–	–
2	Large hake	–	–	–	–	–	–	–	–	–	–	–
3	Small hake	–	–	–	–	–	–	–	–	–	–	–
4	Anglerfish	–	–	–	–	–	–	–	–	–	–	–
5	Megrim	–	–	–	–	–	–	–	–	–	–	–
6	Lg demersal Fish	–	–	–	–	–	–	–	–	–	–	–
7	Dogfish	–	–	–	–	–	–	–	–	–	–	–
8	Rays	–	–	–	–	–	–	–	–	–	–	–
9	Benthic fish	–	–	0.03	–	–	–	–	–	–	–	–
10	Blue whiting	–	0.59	–	–	–	–	–	–	–	–	–
11	Small demersal fish	–	1.38	0.28	–	–	–	–	–	–	–	–
12	Horse mackerel	–	0.58	–	–	–	–	–	–	–	–	–
13	Mackerel	–	0.94	–	–	–	–	–	–	–	–	–
14	Anchovy	–	0.92	–	–	–	–	–	–	–	–	–
15	Sardine	–	0.61	–	–	–	–	–	–	–	–	–
16	Squids	–	0.35	–	–	–	–	–	–	–	–	–
17	Benthic cephalopods	–	0.24	0.08	–	–	–	–	–	–	–	–
18	Benthic invertebrate carnivores	–	0.23	1.61	1.97	–	–	–	–	–	–	–
19	Shrimps	–	0.48	2.67	1.97	4.08	–	–	–	–	–	–
20	Polychaetes	–	–	0.61	11.72	28.85	7.17	–	–	–	–	–
21	Other invertebrates	–	–	0.01	7.83	4.89	–	2.54	–	–	–	–
22	Suprabenthic zooplankton	–	0.67	1.41	1.97	9.86	12.90	2.54	7.85	13.33	–	–
23	Macrozooplankton	–	0.13	–	–	–	–	–	39.24	6.66	–	–
24	Mesozooplankton	24.56	0.11	–	–	–	–	–	149.10	66.63	35.56	–
25	Microzooplankton	18.42	–	–	–	–	–	–	19.62	26.65	71.11	23.89
26	Phytoplankton	18.42	–	–	–	–	–	–	–	–	568.90	429.94
27	Discards	–	–	–	0.39	0.65	–	0.15	–	–	–	–
28	Detritus	–	–	–	12.88	33.30	123.26	45.75	176.56	19.99	35.56	23.89
	Sum	61.41	7.23	6.70	38.72	81.63	143.33	50.99	392.36	133.25	711.12	477.71

All units are in $t\,km^{-2}$ per year.

Table 5
Estimates of prey overlap between trophic groups in the Cantabrian Sea for the 1994 scenario

	Group name	Tuna	Large hake	Small hake	Anglerfish	Megrim	Large demersal fish	Dogfish	Rays	Benthic fish	Blue whiting	Small demersal fish	Horse mackerel	Mackerel	Anchovy
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	Tuna	1.00	–	–	–	–	–	–	–	–	–	–	–	–	–
2	Large hake	0.33	1.00	–	–	–	–	–	–	–	–	–	–	–	–
3	Small hake	0.54	0.31	1.00	–	–	–	–	–	–	–	–	–	–	–
4	Anglerfish	0.57	**0.82**	0.64	1.00	–	–	–	–	–	–	–	–	–	–
5	Megrim	0.16	0.06	0.72	0.32	1.00	–	–	–	–	–	–	–	–	–
6	Lg demersal fish	0.19	0.45	0.57	0.57	0.68	1.00	–	–	–	–	–	–	–	–
7	Dogfish	0.25	0.39	0.48	0.47	0.65	**0.82**	1.00	–	–	–	–	–	–	–
8	Rays	0.02	0.01	0.31	0.03	0.73	0.50	0.69	1.00	–	–	–	–	–	–
9	Benthic fish	0.00	0.01	0.31	0.05	0.66	0.56	0.77	**0.81**	1.00	–	–	–	–	–
10	Blue whiting	0.05	0.07	0.42	0.10	0.29	0.12	0.23	0.17	0.31	1.00	–	–	–	–
11	Small demersal fish	0.01	0.01	0.36	0.01	0.31	0.14	0.32	0.32	0.47	**0.96**	1.00	–	–	–
12	Horse mackerel	0.11	0.15	0.51	0.22	0.34	0.25	0.28	0.13	0.28	**0.90**	**0.87**	1.00	–	–
13	Mackerel	0.22	0.27	0.31	0.24	0.08	0.16	0.28	0.04	0.17	0.80	0.77	**0.86**	1.00	–
14	Anchovy	0.00	0.00	0.03	0.00	0.01	0.00	0.01	0.01	0.02	0.29	0.29	0.46	0.48	1.00
15	Sardine	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.21	0.37	0.41	**0.98**
16	Squids	0.58	0.23	0.78	0.44	0.58	0.54	0.48	0.22	0.29	0.36	0.31	0.52	0.32	0.05
17	Benthic cephalopods	0.01	0.01	0.43	0.03	0.73	0.39	0.63	**0.90**	**0.81**	0.50	0.61	0.41	0.26	0.04
18	Benthic invertebrate carnivores	0.00	0.00	0.07	0.00	0.13	0.12	0.22	0.24	0.54	0.11	0.23	0.11	0.07	0.01
19	Shrimps	0.00	0.00	0.09	0.00	0.09	0.05	0.15	0.14	0.48	0.22	0.32	0.18	0.14	0.02
20	Polychaetes	0.00	0.00	0.02	0.00	0.01	0.00	0.02	0.01	0.14	0.09	0.16	0.07	0.06	0.01
21	Other invertebrates	0.00	0.00	0.01	0.00	0.01	0.00	0.01	0.01	0.11	0.05	0.11	0.04	0.03	0.00
22	Suprabenthic zooplankton	0.04	0.00	0.01	0.00	0.00	0.00	0.02	0.00	0.09	0.22	0.28	0.35	0.44	0.50
23	Macrozooplankton	0.02	0.00	0.05	0.00	0.02	0.00	0.03	0.01	0.07	0.42	0.44	0.60	0.66	**0.85**
24	Mesozooplankton	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.02	0.03	0.04	0.44
25	Microzooplankton	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.35

Table 5 (*Continued*)

	Group name	Sardine	Squids	Benthic cephalopods	Benthic invertebrate carnivores	Shrimps	Polychaetes	Other invertebrates	Suprabenthic zooplankton	Macrozooplankton	Mesozooplankton	Microzooplankton
		15	16	17	18	19	20	21	22	23	24	25
1	Tuna	–	–	–	–	–	–	–	–	–	–	–
2	Large hake	–	–	–	–	–	–	–	–	–	–	–
3	Small hake	–	–	–	–	–	–	–	–	–	–	–
4	Anglerfish	–	–	–	–	–	–	–	–	–	–	–
5	Megrim	–	–	–	–	–	–	–	–	–	–	–
6	Lg demersal fish	–	–	–	–	–	–	–	–	–	–	–
7	Dogfish	–	–	–	–	–	–	–	–	–	–	–
8	Rays	–	–	–	–	–	–	–	–	–	–	–
9	Benthic fish	–	–	–	–	–	–	–	–	–	–	–
10	Blue whiting	–	–	–	–	–	–	–	–	–	–	–
11	Small demersal fish	–	–	–	–	–	–	–	–	–	–	–
12	Horse mackerel	–	–	–	–	–	–	–	–	–	–	–
13	Mackerel	–	–	–	–	–	–	–	–	–	–	–
14	Anchovy	–	–	–	–	–	–	–	–	–	–	–
15	Sardine	1.00	–	–	–	–	–	–	–	–	–	–
16	Squids	0.03	1.00	–	–	–	–	–	–	–	–	–
17	Benthic cephalopods	0.00	0.33	1.00	–	–	–	–	–	–	–	–
18	Benthic invertebrate carnivorus	0.00	0.05	0.27	1.00	–	–	–	–	–	–	–
19	Shrimps	0.00	0.07	0.27	**0.94**	1.00	–	–	–	–	–	–
20	Polychaetes	0.00	0.02	0.05	0.61	0.71	1.00	–	–	–	–	–
21	Other invertebrates	0.00	0.01	0.02	0.59	0.67	**1.00**	1.00	–	–	–	–
22	Suprabenthic zooplankton	0.48	0.04	0.01	0.49	0.55	0.70	0.69	1.00	–	–	–
23	Macrozooplankton	0.78	0.08	0.07	0.19	0.23	0.26	0.25	0.80	1.00	–	–
24	Mesozooplankton	0.58	0.00	0.00	0.04	0.04	0.06	0.06	0.09	0.11	1.00–	
25	Microzooplankton	0.49	0.00	0.00	0.03	0.04	0.06	0.06	0.04	0.03	**0.99**	1.00

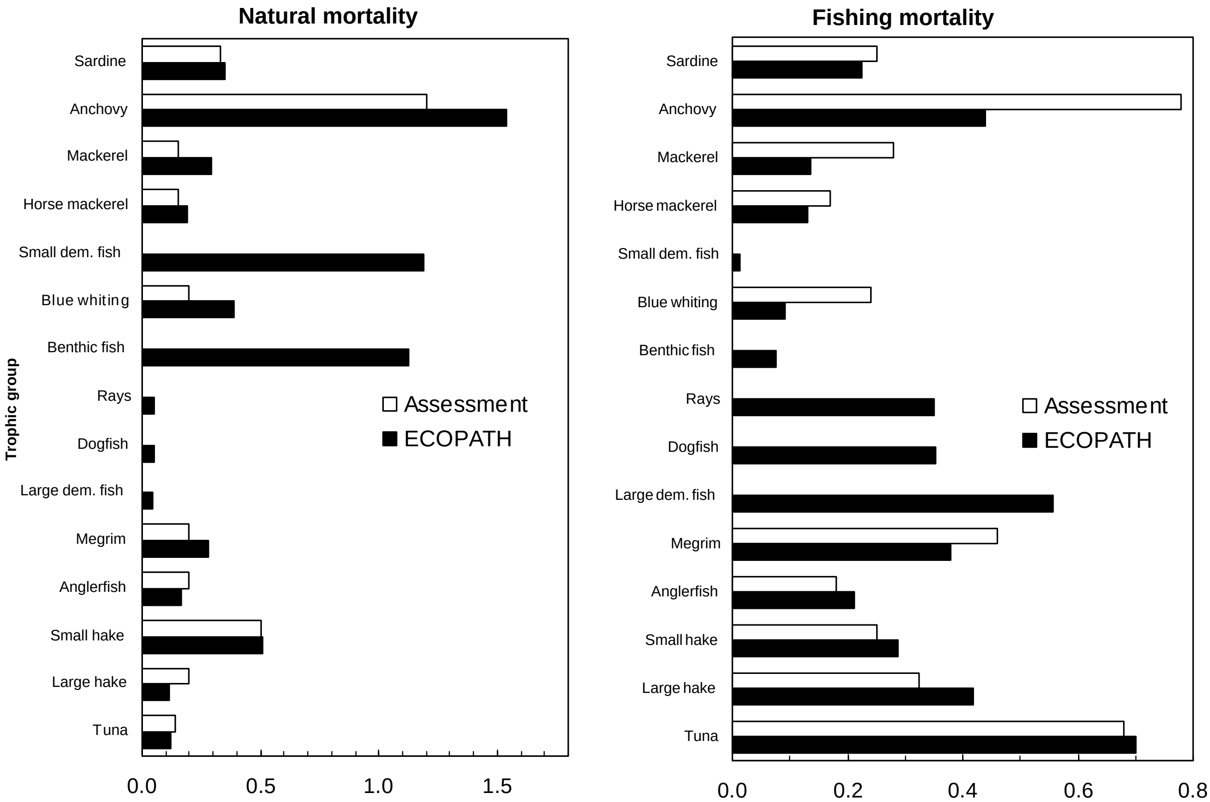

Fig. 3. Annual mortality rates of fish based on the Ecopath model (black bar) and VPA analyses from ACFM reports of southern stocks and from ICCAT reports (white bar).

trophic level (anchovy and sardine) that only have access to the pelagic plankton (Table 4).

3.3. Mortalities

The mortality rates from VPA (ICES, 1996a,b) and estimates by the Ecopath model are presented in Fig. 3 for comparison. Ecopath provides the natural mortality M broken down into three components: mortality by predation (M_1), migration and other mortalities (M_0). The model provided mortality estimates for the non-assessed groups. It also detected some discrepancies in the natural mortality (M) provided by the model with the values used in the single-species analytical assessment methods (ICES, 2000). The M values for some groups (mainly pelagic fish species) were slightly higher in the Ecopath model than in the VPA, where they are generally assumed to have values between 0.2 and 0.8 (depending on species). For example, the M values for blue whiting, mackerel, anchovy and sardines (the main food intake for tuna, hake, anglerfish, and large demersal fish in the area) were higher in the model. In some cases, mortality by predation (M_1) provided by Ecopath was higher than the total value of M used in the stock assessment groups, while fishing mortalities for blue whiting and small pelagic fish, such as mackerel, anchovy and sardines, were lower in the model. The inclusion of the discards of these species in the model (which is not considered by the stock assessment groups) does not explain this discrepancy since Ecopath (version 4) includes them as an increase of the fishing mortality in combination with the landings.

3.4. Niche overlaps

To determine to what extent any two groups seek the same prey, the prey overlap was considered by using the Pianka index (Pianka, 1973), as shown in Table 5. High values of niche overlapping appeared among fish from the low trophic level both in the pelagic (sardine and anchovy—98%) and in the demersal domain (blue whiting and small demersal fish—96%). The two top predators from the demersal and benthic domain, large hake and anglerfish, also had a high dietary overlap (82%) mainly because both showed a high consumption of blue whiting, that constitute the main fish biomass close to the bottom.

The results indicated a low level of niche overlap between large hake and small hake (31%). This was due to their different diets—large hake mainly based their diet on blue whiting whereas small hake preyed on horse mackerel, small demersal fish and shrimps. Blue whiting inhabit deeper waters than do small hake (Sánchez, 1993), and therefore the coexistence of hakes with large size differences is rare on the bottom and explains the low level of cannibalism observed in the hake of the Cantabrian Sea (Olaso, 1990; Velasco and Olaso, 1998).

In the benthic domain, the marked presence of invertebrate carnivores and shrimps in the lower trophic levels, produced a strong overlapping of diets between the benthic cephalopods, rays and benthic fish.

3.5. The fishery in the ecosystem

Fig. 4 shows the primary production required to sustain consumption and catches by trophic groups. Estimates of primary production required by fisheries (PPR) are based on the trophic level of the species caught, the energy transfer efficiency between trophic levels, and the primary productivity of the shelf area. The present study shows that the fisheries utilised 36.6% of the total primary production. This high PPR value corroborates the hypothesis that the fisheries of the Cantabrian Sea use a large proportion of the productive capacity of the shelf ecosystem. The results indicate a level of fisheries impact in the Cantabrian Sea comparable to the most intensively exploited temperate shelf ecosystems of the world. Similar systems exhibit values of PPR from 24.2 to 35.3% (Pauly and Christensen, 1995); 29% of the primary production is required to sustain the catches in the North Sea ecosystem (Christensen, 1995a). The major PPR fractions in the Cantabrian Sea were to sustain the catches of tuna (9.35%), large hake (3.6%) and horse mackerel (4.5%). Catches were dominated by medium trophic level species such as blue whiting, horse mackerel, mackerel, anchovy and sardines (Table 3).

Overall, the fishery was operating at a trophic level of 3.7; i.e. the average catch was more than two trophic levels above the primary producers. Using the mass-balance model, the trophic levels of the different fisheries were estimated; each gear was considered as a predator in the biomass flow scheme (Fig. 2). In the pelagic domain, planktivorous fish of small and medium size were captured by the purse seine. This gear had the lowest trophic level fishery (3.25). Bait and troll (surface hook) boats caught tuna exclusively and had the highest trophic level fishery (4.71). In the demersal domain, large piscivorous fish, such as hake and other large demersal fish, were captured by bottom longlines of trophic level 4.08. In the benthic domain, the bottom trawl caught a great variety of organisms and had a medium trophic level, 3.83. Gillnets exploited certain predators from the demersal as well as the benthic domain, and operate at a high trophic level, 4.45.

The biomass of fishery discards (2.29 t km^{-2} per year) was close to the biomass level of living groups benthic cephalopods or benthic fish. Fig. 2 shows the main flows for discards in the Cantabrian Sea ecosystem. The main benefited of discards are those from the demersal and benthic domain (Table 4), especially small demersal fish, benthic invertebrate carnivores, shrimps, benthic fish and dogfish (Olaso et al., 2002). These are groups with medium trophic levels (between 2.8 and 4.1), since species belonging to higher trophic levels require moving living prey and the species from lower levels are basically filter feeders or detritivores. The importance of discards as food in the ecosystem is low with respect to detritus, primary producers or other low trophic levels, and constitute 0.07% of the total food intake (Table 4). Nevertheless, discard consumption has considerable importance if we compare it with some fish prey groups of medium TL (e.g. it is equal to mackerel consumption in the ecosystem), and as food for the scavenger species that inhabit in the area.

3.6. Fisheries mixed trophic impact

Fig. 5 shows the mixed trophic impact of different gears on other groups using the Leontief economic

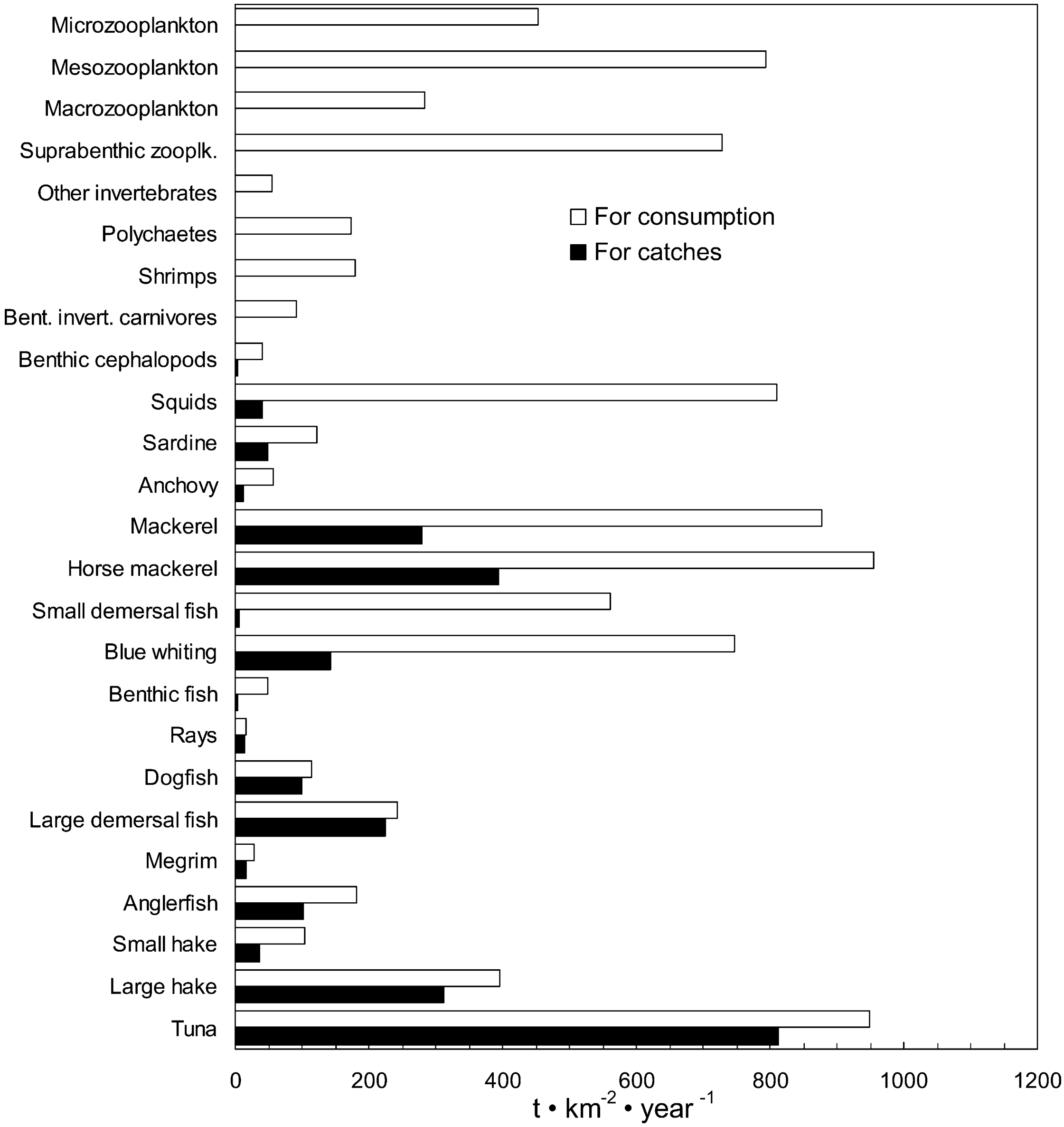

Fig. 4. Estimates of primary production required to sustain consumption by the functional groups (white bar) and catches (black bar) in the Cantabrian Sea ecosystem, 1994.

matrix routine implemented in Ecopath, following the subsequent development described by Ulanowicz and Puccia (1990). This analysis quantifies the direct and indirect interactions in a balanced system. The mixed trophic impact routine gives an idea of how important the different fisheries are in the trophic dynamics of the system.

3.6.1. Trawl

The negative impact of trawling on the different groups of the system is high and much stronger than for the other gears, mainly on large fish-feeders (hake, anglerfish, megrim) and crustacean feeders (dogfish, rays and benthic cephalopods). The trawl fishery has a negative effect on all fishing gears that focused on the

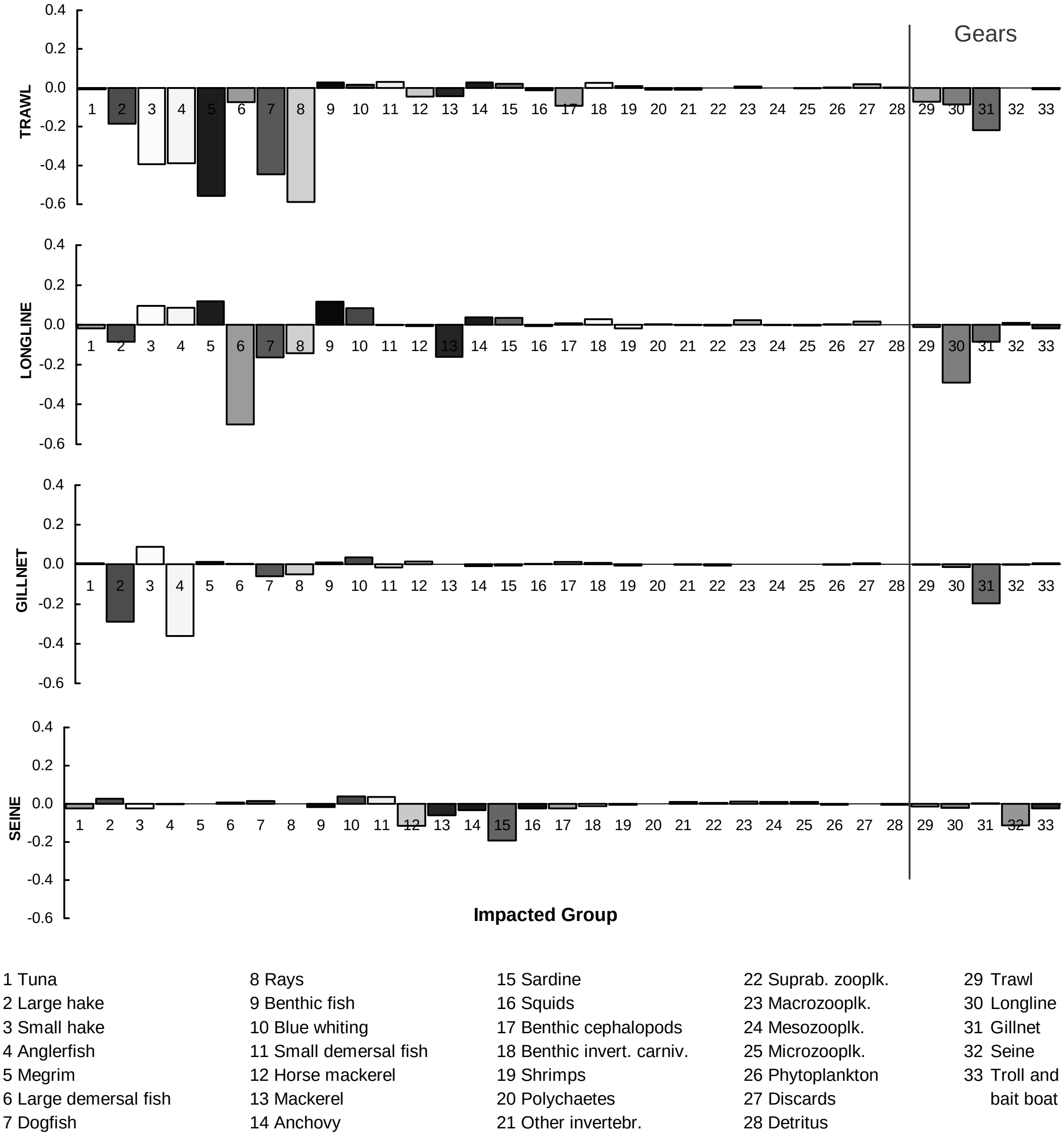

Fig. 5. Fisheries mixed trophic impact using the Leontief matrix. Values of the computed impact are relative on a scale from −1 to 1, where 0 indicates no impact; but they are comparable between groups. The bars quantify the direct and indirect trophic impact that the groups indicated on the left (fisheries) have on the groups listed at the bottom.

benthic domain, particularly the gillnet fishery because they compete for the same species.

3.6.2. Longline

Bottom longlining impactes negatively on large hake, large demersal fish and elasmobranchs through its fishing mortality. There are positive impacts on benthic fish (including anglerfish and megrims), which were species not accessible to the gear and which competed for the same food resources as the large hake and demersal fish and elasmobranchs. The gear also has a positive impact on demersal fish of medium size such as small hake and blue whiting because it acts on their natural predators. Longlining has a negative effect on selective bottom fishing gears (longline and gillnet), which reflects the high competition within this fishery (due to the low number of target species).

3.6.3. Gillnet

Gillnetting impacts negatively on large piscivores (hake and anglerfish) and elasmobranchs (dogfish and rays), which are practically the only targets. The rest of the ecosystem is not affected at all. This very selective gear has a negative effect on its own fishery and inhibits the other gears, which emphasises the impact of longline fishing intensity on the selection of target species.

3.6.4. Purse seine

Purse seining has a negative impact on small and medium planktivorous fish that are important as forage fish for diverse trophic groups. Thus, this fishery has a negative effect on the other fisheries.

All the fishing gears except the purse seine have a negative impact on large hake and elasmobranchs. The impact of fisheries on all the invertebrate groups was low and benthic cephalopods are negatively affected only by the trawl. A shrimp fishery does not exist in the area and the proportion of Norway lobster (the main invertebrate commercial species) in the 'benthic invertebrate carnivore' group was very small. Each gear has a negative impact on the other gears, which explains the strong spatial competition in the different bottom fisheries on the narrow shelf of the Cantabrian Sea, and the inherent social conflicts present in the area.

3.7. Historical fishery trophic level

By combining the TL results of the model and landings for the main commercial species from 1983 to 1999, we could follow variations in the mean trophic level of the fishery. These are presented as a time series in Fig. 6. In this analysis, only the fleets fishing for demersal and benthic species were used (i.e. trawl, longline and gillnet). Catches of the pelagic fleets come mainly from oceanic waters and are of species with a wide distribution. Here, we were concerned only within the Cantabrian Sea ecosystem.

From 1983 to 1993, the mean trophic level of the demersal and benthic fisheries declined (Fig. 6). This is reflected in a gradual transition of landings from long-lived, high trophic level piscivorous bottom fish (hake, anglerfish, megrim) towards lower trophic level planktivorous fish (blue whiting, horse mackerel). Globally, the trophic levels of fisheries

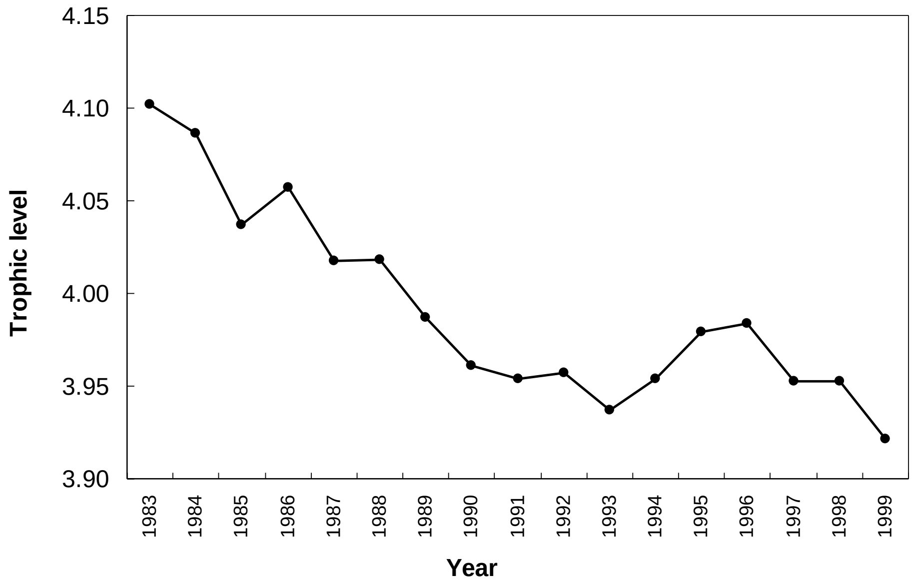

Fig. 6. Changes in the mean trophic level of the demersal fisheries on the Cantabrian Sea shelf from 1983 to 1999.

landings appear to have declined in recent decades at a rate of about 0.1 per decade (Pauly et al., 1998). The Cantabrian Sea shows a decadal rate from 1983 to 1993 of about 0.15. From 1994 until the present, the mean trophic level of these fisheries has remained at very low values. This makes us suspect that the Cantabrian Sea fisheries have reached their lowest historical trophic level limit.

4. Conclusions

The Cantabrian Sea mass-balance model provides a summary of current knowledge of the biomass, consumption, production, food web and trophic structure in an ecosystem strongly exploited by the ICES Division VIIIc fishery. The Ecopath model can be a valuable tool for understanding ecosystem functioning, and for design of ecosystem-scale adaptive management experiments. Using Ecosim and Ecospace routines, in a future step, it could be possible to simulate the consequences of certain management measures, such as effort reduction or closed areas, on the ecosystem. Nevertheless, further research is required in order to improve input data and to support or refute the results presented in this preliminary model. In particular, the limited availability of parameter estimates on an annual basis for the invertebrate groups of the Cantabrian Sea reflects a need for such studies.

The ecosystem of the Cantabrian Sea receives seasonal migrations of species from other waters; for tuna, blue whiting, mackerel, anchovy and sardine it was necessary to make important assumptions. Consequently, the conclusions for these trophic groups and the PPR estimations have to be considered carefully. The greater stability of the demersal and benthic communities, together with the good information available for their associated higher trophic levels groups, means that the results offered by this model have greater reliability for these two particular domains.

Seasonally driven production agents such as upwelling and mesoscale activity have a large influence on the dynamics of the ecosystem, producing seasonal changes in trophic structure. Two different periods are recognised, spring-summer (upwelling, high primary production, anchovy and tuna immigration, etc.) and autumn-winter (water layers mixing, main recruitment processes for benthic and demersal fish). Analysis of the differences in structure and dynamics of these two seasons would provide important improvements in modelling the Cantabrian Sea ecosystem.

The conclusions from the present analysis of this system are:

- Strong relationships exist between the pelagic, demersal and benthic domains due to key groups that transfer production from primary production to the upper trophic levels.
- Feeding pressure on phytoplankton is low; a large percentage of primary production of the Cantabrian Sea passes to detritus. Consequently, detritivorous species are an important component of the ecosystem.
- The level of fisheries impact in the Cantabrian Sea is comparable to the most intensively exploited temperate shelf ecosystems in the world. The high PPR value corroborates the fact that most commercially important shelf stocks in the area are either fully exploited or overexploited, and landings are expected to decrease with the current fishing pressure.
- The importance of discards as food in the ecosystem is low with respect to detritus, primary producers or other low trophic levels. Nevertheless, discard consumption has considerable importance when compared with consumption of some fish prey groups of medium TL.
- The negative trophic impact of trawling on the different groups of the system is high and much stronger than for other gears. Longlining produces the most positive impact in the ecosystem.
- All fishing gears, except the purse seine, impact negatively on piscivores fish and elasmobranchs.
- From 1983 to 1993, the mean trophic level of Cantabrian Sea fisheries declined to 3.7. Since 1993 there has been no further decrease and the fisheries may have reached their lowest historical trophic level limit.
- The depressed abundance and productivity of top predators impedes the recovery of the trophic levels in the catch.

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