Progress In Oceanography
Volume 91, Issue 4, December 2011, Pages 561–575
http://dx.doi.org/10.1016/j.pocean.2011.09.002

Lower trophic levels and detrital biomass control the Bay of Biscay continental shelf food web: Implications for ecosystem management

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Abstract:
The Bay of Biscay (North-East Atlantic) has long been subjected to intense direct and indirect human activities that lead to the excessive degradation and sometimes overexploitation of natural resources. Fisheries management is gradually moving away from single-species assessments to more holistic, multi-species approaches that better respond to the reality of ecosystem processes. Quantitative modelling methods such as Ecopath with Ecosim can be useful tools for planning, implementing and evaluating ecosystem-based fisheries management strategies. The aim of this study was therefore to model the energy fluxes within the food web of this highly pressured ecosystem and to extract practical information required in the diagnosis of ecosystem state/health. A well-described model comprising 30 living and two non-living compartments was successfully constructed with data of local origin, for the Bay of Biscay continental shelf. The same level of aggregation was applied to primary producers, mid-trophic-levels and top-predators boxes. The model was even more general as it encompassed the entire continuum of marine habitats, from benthic to pelagic domains. Output values for most ecosystem attributes indicated a relatively mature and stable ecosystem, with a large proportion of its energy flow originating from detritus. Ecological network analysis also provided evidence that bottom-up processes play a significant role in the population dynamics of upper-trophic-levels and in the global structuring of this marine ecosystem. Finally, a novel metric based on ecosystem production depicted an ecosystem not far from being overexploited. This finding being not entirely consistent over indicators, further analyses based on dynamic simulations are required.
Key words : Ecopath; aquatic communities; trophic structure; bottom-up control; multispecies fisheries; ecosystem management; North-East Atlantic, Bay of Biscay, continental shelf.

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1. Introduction

Impacts of fisheries on target species have been abundantly described and reviewed, e.g. modifications of abundance, spawning potential, growth and maturation, age and size structure, sex ratio, genetics (Hall, 1999). However, the effect of fishing is not restricted to commercially exploited species but extends to entire ecosystems. In most cases, by targeting and reducing the abundance of high-value consumers, fisheries profoundly modify trophic networks and the flow of biomass (and energy) across the ecosystem, leading sometimes to trophic cascades (Heithaus et al., 2008) and ultimately to regime shifts (Daskalov et al., 2007). In addition, fishing practices can durably and substantially damage the living and non-living environment of target and associated resources, e.g. poorly-selective fishing activities generate by-catch and discards and sometimes cause local anoxia (Diaz et al., 2008), benthic trawls and dredges cause physical changes to the seabed (Hall-Spencer et al., 2002), and lost fishing gear that preserves its catching abilities leads to temporary “ghost fishing” (Baeta et al., 2009). Consequently, in the last two decades, a consensus has emerged on the need to move from single species- to ecosystem-based fisheries management (EBFM). The goal is “to rebuild and sustain populations, species, biological communities and marine ecosystems at high levels of productivity and biological diversity so as not to jeopardize a wide range of goods and services from marine ecosystems while providing food, revenues and recreation for humans” (Browman et al., 2004).

Although the importance of an ecosystem approach is widely accepted, it remains difficult to put these principles into practice (Tallis et al., 2010). In data-rich situations, multi-species/ecosystem models are valuable tools that bring coherence to a large amount of data from a variety of sources (see Plagànyi (2007) for an exhaustive review). They can be useful to provide initially a holistic understanding of the structure and functioning of a particular aquatic system and then supply concrete elements for managing this exploited ecosystem. For example, they have been used to explore marine protected area (MPA) zoning options or to assist the implementation of EBFM through the identification of critical biological indicators and their corresponding threshold values (Tudela et al., 2005; Coll et al., 2008). Among ecosystem models, Ecopath with Ecosim (EwE) is a well-known and freely-available software package which attempts to represent all trophic groups, in a mass-balanced way (Polovina, 1984; Christensen and Pauly, 1992). The ecosystem is considered as a unit of biological organization, made up of all the organisms in a given area, interacting with the physical environment, so that a flow of energy leads to characteristic trophic structure and material cycles within the system (Odum, 1969). Through the development of new components and modules, EwE has become increasingly powerful in providing information on how a system is likely to respond to potential changes in fisheries management practices and, to a lesser extent, to environmental disturbances (Coll et al., 2007; Shannon et al., 2009). Some of the fundamental strengths of the approach are the achievement of a good trade-off in model structure between simplicity and complexity (i.e. parsimony principle; Fulton et al. (2003)) and the use of a common and rigorous analytical framework that make comparisons between various systems possible (Plagànyi and Butterworth, 2004).

At the western edge of the Eurasian continent, the Bay of Biscay, opening to the Eastern North Atlantic Ocean, supports a large number of anthropogenic activities including tourism and shellfish farming along the coasts and intensive fisheries for human consumption over the shelf and along the slopes (Lorance et al., 2009). Fishing activities in the Bay of Biscay involve several European countries and are characterised by the wide variety of fishing vessels, gears and techniques, the large number of landed species (more than a hundred) and the numerous habitats explored (Léauté, 1998). The major commercially exploited stocks are crustaceans, cephalopods and both pelagic and demersal fish, some of them showing signs of intensive exploitation (ICES, 2005b). For instance, since 2002, European anchovy recruitment has experienced a severe decline that raises growing concerns from the scientific community and EU member states as to what would be the direct and indirect effects of alternative harvest strategies of forage fish on other ecosystem components (ICES, 2010).

In this context of intense multi-species exploitation, a mass-balanced model of the Bay of Biscay continental shelf food web would be of great interest to stakeholders and decision makers to support the implementation of sustainable fisheries policies and the development of ecosystem-based management in the area. Models already exist for different parts of the Bay of Biscay continental shelf with special hydro-morphological characteristics, i.e. the “Grande Vasière” (Le Loc'h, 2004), the Cantabrian Sea (Sanchez and Olaso, 2004). At a broader spatial scale, including the totality of the two ICES sub-divisions VIIIa and b, two models were constructed for the year 1970 and 1998 by Ainsworth et al. (2001). Little help was provided by local researchers for those two previous models and as a consequence, most biomass data in their initial input matrix were lacking or obtained from similar systems (Sylvie Guénette, pers. comm.). Ainsworth et al. (2001) paid particular attention to fish species that were divided, according to a length criterion, into 22 distinct functional groups. These models recently served as a strong basis for a Master’s thesis (Jimeno, 2010), in which the “2007” situation was modelled. Previous models of the Bay of Biscay were lacking of sufficient spatial coverage and amount of local data to be useful. The construction of a new model was made possible by the two successive phases of the French coastal environmental research program (PNEC 1999-2003 and 2004-2007) that both included a specific worksite on the Bay of Biscay and that thus greatly contributed to fill the gaps that existed in the data concerning this area. In the present work, a particular effort was made to combine local information of the same quality, reliability and detail, on both the benthic and pelagic communities, from primary producers to top-predators to better understand the structure, organization and functioning of the Bay of Biscay continental shelf food web. Then, the keystone compartments according to the original definition provided by Power et al. (1996), i.e. components whose effect is large, and disproportionately large relative to their abundance, were determined. Finally, the ecosystem exploitation status was assessed using a set of metrics, some being based on ecosystem production.

2. Material and Methods

2.1 Study area

The Bay of Biscay is a large gulf of the Atlantic Ocean located off the western coast of France and the northern coast of Spain, between 48.5 and 43.5 °N and 8 and 3 °W (Fig. 1). The principal rivers in decreasing order of drainage area are: the Loire, Garonne-Dordogne (Gironde complex), Adour, Vilaine and Charente rivers. The continental shelf reaches widths of about 140 km off the coast of Brittany but narrows to less than 15 km off the Spanish shore. The physical and hydrological features of the Bay of Biscay are of great complexity, e.g. coastal upwelling, coastal run-off and river plumes, seasonal currents, eddies, internal waves and tidal fronts (Planque et al., 2004). These abiotic processes greatly influence the phytoplankton dynamics and as a consequence, the whole food-web composition, structure and functioning (Varela, 1996).

The model was restricted to divisions VIIIa and b of the International Council for the Exploration of the Sea (ICES; www.ices.dk). An ecosystem model has already been built for the Cantabrian Sea, which exhibits particular hydro-morphological characteristics (ICES division VIIIc) (Sanchez and Olaso, 2004). The deep offshore basin (ICES division VIIId) was not sufficiently documented to be included into the modelling process. The study site in the Bay of Biscay was limited to the middle-depth continental shelf, between the 30-m and 150-m isobaths, and its surface area was considered to be 102,585 km^2. There has been long-term, consistent and regular monitoring of the benthic, demersal and pelagic biota in this study area.

2.2 Trophic modelling approach

A mass-balance (neglecting year-to-year change in biomass, compared to flows) model of the Bay of Biscay continental shelf was constructed using Ecopath with Ecosim 6 (Christensen and Pauly, 1992; Christensen et al., 2008). The model combines biomass, production and consumption estimates to quantify flows between the different elements of aquatic exploited ecosystems at a specific point in time. The parameterisation of the Ecopath model is based on satisfying two "master" equations. The first describes the production term for each compartment (species or group of species with similar ecotrophic roles) included in the system:

Production = fishery catch + predation mortality + net migration + biomass accumulation + other mortality.

"Other mortality" includes natural mortality factors such as mortality due to senescence, diseases, etc. The second equation expresses the principle of conservation of matter within a compartment:

Consumption = production + respiration + unassimilated food.

The formal expressions of the above equations can be written as follows for a group *i* and its predator *j*:

$$B_i \times (P/B)_i = Y_i + \sum_j \left(B_j \times (Q/B)_j \times DC_{ij}\right) + Ex_i + Bacc_i + B_i(1 - EE_i) \times (P/B)_i \quad (1)$$

and

$$B_i \times (Q/B)_i = B_i \times (P/B)_i + R_i + U_i \quad (2)$$

where the main input parameters are biomass density (B, here in kg C·km^{-2}), production rate (P/B, year^{-1}), consumption rate (Q/B, year^{-1}), proportion of i in the diet of j (DC_{ij}; DC = diet composition), net migration rate (*Ex*, year^{-1}), biomass accumulation (*Bacc*, year^{-1}), total catch (*Y*; kg $\text{C}\cdot\text{km}^{-2}$), respiration (*R*; kg $\text{C}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$), unassimilated food rate (*U*) and ecotrophic efficiency (*EE*).

Biomass, *Q/B* and *P/B* values of multi-species compartments were determined by the weighted average of the relative abundance of each species. There are as many linear equations as groups in the system, so if one of the parameters is unknown for a group, the model computes it by solving the set of linear equations. In particular, *EE*, which corresponds to the fraction of the production of each group that is used in the food web, is difficult to measure. Hence, it was estimated by the model for most of the groups. The "manual" mass-balanced procedure that includes two major levels of verification was used. First, for those groups with $EE > 1$, the model was modified by adjusting their initial input parameters and the predation intensity exerted by predators on them (slight and gradual increase or decrease in values, within the interval of confidence of the parameter). For this parameter, a value greater than one indicated a demand on the compartment that was too high to be sustainable within the food web. Secondly, the same procedure was applied to the gross food conversion efficiency (*GE*) estimates, also called *P/Q* ratio, which must be in the physiologically realistic range of 0.1-0.3 for most consumers and generally higher for small organisms. *EE* for a detritus group is defined as the ratio between what flows out of that group and what flows into it. Theoretically, under steady-state assumption, this ratio should be equal to one.

The Ecopath model was validated using the pre-balance (PREBAL) diagnostics (Link, 2010) to ensure that any potential and major problems are captured before network outputs are used to address research or management questions. PREBAL provides a set of guidelines presented as a form of "checklist". Diagnostic tests allow evaluation of the cohesiveness of the data despite the natural discrepancies that occur when using myriad data sources measured across varying scales. In brief, each functional group was plotted along the x-axis in order of decreasing trophic level to allow easy visualization of trophic relationships. Byron et al. (2011) summarized the PREBAL analysis into five simple ecological and physiological "rules" that should be met.

2.3 Defining the model compartments

Functional groups were defined following three criteria: the similarities between the species in terms of size and food preferences, the amount of ecological data available to determine precise parameters and diet compositions and the main research questions to which the model should respond. On this basis, 32 trophic groups were retained (Table 1), two of which were seabirds, five marine mammals, nine fish, eight invertebrates, three zooplankton, two primary producers, one bacteria, discards from commercial fisheries and detritus corresponding to allochthonous imports into the web and autochthonous internal cycling within the web. Data collections for plankton to top-predators (marine birds and small cetaceans) cover a period long enough for sufficient data to be available, but short enough for massive changes in biomass not to have occurred. They encompassed different seasons and years, starting in 1994 and ending in 2005. The European anchovy *Engraulis encrasicolus* has been affected by a below average recruitment since 2002, which led to the closure of the fishery in the area from June 2006 to December 2009 (ICES, 2010). The model presented in this study corresponded to a typical year between 1994 and 2005, before the collapse of the anchovy fishery. Biomasses, diets and species compositions were averaged across seasons.

2.4 Initial input parameters and diet compositions

2.4.1 *Marine mammals and seabirds*

Birds were counted visually and identified to species level by aerial surveys on a monthly basis from October 2001 to March 2002, in August 2002, in June 2003 and May 2004

(ROMER and ATLANCET surveys). The Bay of Biscay is heavily used as a migration route and as a wintering area for marine birds, so there is a great seasonal variation in their abundance. As this long-distance migratory pattern was included through an annual biomass estimate, imports were not added to their diets. The four most abundant seabird taxa were northern gannets *Sula bassana*, large gulls (i.e. herring gulls *Larus argentatus*, lesser black-backed gulls *Larus fuscus*, great black-backed gulls *Larus maritimus* and yellow-legged gull *Larus michahellis*), kittiwakes *Rissa tridactyla* and auks (i.e. common murres *Uria aalge*, razorbills *Alca torda* and Atlantic puffins *Fratercula arctica*) (Certain and Bretagnolle, 2008) (Table 1). Based on Hunt et al. (2005), the mean body mass for these taxa was set to 3.2, 1.1, 0.4 and 0.9 kg respectively. They were grouped in two categories according to feeding strategies: "surface feeders" for gulls and kittiwakes and "plunge and pursuit divers" for gannets and auks. Wet weights were converted into dry weights and carbon contents based on two conversion factors, i.e. 0.3 and 0.4 respectively. These values were derived from expert's knowledge on the basis of the carbon to wet mass ratio of 0.1 used by Heymans and Baird (2000).

Their diet regime was assumed to be composed mostly of energy-rich pelagic species and large zooplankton crustaceans (Hunt et al., 2005; Certain et al., 2011). Some marine birds are also well-known to feed largely on fisheries discards (Arcos, 2001). This artificial low-quality food source has been shown to be detrimental on a long-term basis for gannets (Grémillet et al., 2008) (Table 2).

Daily ration for wild piscivorous birds (R_c) in g·day^{-1} was calculated according to the following empirical equation (Nilsson and Nilsson, 1976):

$$Log(R_c) = -0.293 + 0.85 \times log(W) \qquad (3)$$

where W is the body mass of birds expressed in g. This value was then multiplied by 365 days and divided by the mean weight of the taxon to provide annual Q/B ratio.

The *P/B* ratio for the two functional groups was based on estimates published in Nelson (1979).

Abundance for the small cetacean community (porpoises and dolphins excluding whales) was derived from the combination of results from (i) the SCANS-II project focusing on small cetaceans in the European Atlantic and the North Sea and carried out in July 2005 by ships and aircraft, (ii) the estimated small delphinid abundance in the Bay of Biscay based on repeated extensive aerial surveys (ROMER and ATLANCET campaigns) in different seasons and years (2001–2004) across the Bay of Biscay continental shelf (Certain et al., 2008), and (iii) the monitoring of marine mammals in the same area based on stranding and spring shipboard observations performed during PELGAS IFREMER cruises (Certain et al. (2011); authors' unpublished data). The five most common species were separated in the model: the common dolphin *Delphinus delphis*, the striped dolphin *Stenella coeruleoalba*, the bottlenose dolphin *Tursiops truncatus*, the long-finned pilot whale *Globicephala melas* and the harbour porpoise *Phocoena phocoena* (Table 1). Following the method developed by Trites and Pauly (1998), mean body weight was calculated for each species according to its maximum body length. A conversion factor of 0.1 for wet weight to carbon content was used (Bradford-Grieve et al., 2003).

Diet compositions were obtained from stomach content analysis of stranded animals found along the North-East Atlantic French coast (Spitz et al., 2006a; Spitz et al., 2006b; Meynier et al., 2008). Some cetacean species forage both on the shelf and on the oceanic domains of the Bay of Biscay. Consequently, the proportion of oceanic prey in their diet was considered as imports (Table 2).

Consumption can be estimated from energy requirements, prey energy densities and prey compositions by percent mass. The daily energy requirement or field metabolic rate (*FMR*) in kJ·day^{-1} is related to mean body mass (W in kg) according to the model developed by Boyd (2002), the coefficient used was the one proposed by the author for marine mammals alone:

$$FMR = 2629 \times W^{0.524} \qquad (4)$$

Daily consumption (R_c) in kg·day^{-1} was calculated by converting energy requirements to food biomass and adjusting by a factor of assimilation efficiency:

$$R_c = FMR/(0.8 \times \sum(P_i \times ED_i)) \qquad (5)$$

where P_i was the proportion by mass of prey species i in the diet and ED_i, the energy density of prey i (kJ·kg^{-1}; Spitz et al. (2010)). Assimilation efficiency was typically estimated at 0.8 (Leaper and Lavigne, 2007). This value was then multiplied by 365 days and divided by the mean weight of the taxon to provide annual *Q/B* ratio.

Values of *P/B* were taken from Christensen et al. (2009); they varied from 0.03 for baleen whales to 0.08 for dolphins and porpoises.

2.4.2 Fish groups

Stocks of the common sole *Solea solea*, the European hake *Merluccius merluccius*, two European anglerfish *Lophius budegassa* and *L. piscatorius* and the megrim *Lepidorhombus whiffiagonis* were assessed from ICES/ACFM advice report (ICES, 2004). The biomass of most other benthic and demersal fish species was estimated from bottom-trawl surveys conducted annually in autumn in the Bay of Biscay (EVHOE IFREMER cruises). Data were averaged over six years, between 1998 and 2003 and then multiplied by four to take into account the mean bottom-trawl capture efficiency below 0.3 (Trenkel and Skaug, 2005). The capture efficiency represents the proportion of individuals in the trawl path being retained by the gear. Wet body weights were converted to dry weights and then to carbon contents using conversion factors of 0.2 and 0.4 respectively (Brey et al., 2010). The biomass of most pelagic fish species was estimated using data from acoustic surveys conducted each spring in the Bay of Biscay (PELGAS IFREMER cruises). Data were averaged over three years, between 2000 and 2003. The distribution range of the horse mackerel *Trachurus trachurus* was not fully encompassed by IFREMER surveys, which resulted in an underestimation of the total biomass. Thus, an ecotrophic efficiency of 0.95 was preferentially entered in the input parameters for this commercially exploited species and the biomass was left to be estimated by the model. Wet body weights were first converted to dry weights with a conversion factor of 0.14 and finally to carbon contents using a conversion factor of 0.45 (Jorgensen et al., 1991) (Table 1).

The *Q/B* ratio was determined using Fishbase (Froese and Pauly (2000); www.fishbase.org). For each species, *Q/B* was estimated from the empirical relationship proposed by Palomares and Pauly (1998):

$$Log(Q/B) = 7.964 - 0.204 \times log(W_\infty) - 1.965 \times T' + 0.083 \times A + 0.532 \times h + 0.398 \times d \quad (6)$$

where W_∞ was the asymptotic weight, *T'* was the mean environmental temperature expressed as 1000/(T (°C) + 273.15), *A* was the aspect ratio of the caudal fin, *h* and *d* were dummy variables indicating herbivores (*h*=1, *d*=0), detritivores (*h*=0, *d*=1) and carnivores (*h*=0, *d*=0). Under steady-state conditions, the *P/B* ratio is equal to instantaneous coefficient of total mortality (*Z*) (Allen, 1971):

$$Z = M + F \quad (7)$$

with *M* being natural and *F* fishing mortality. *M* was calculated using the Fishbase life-history tool from Pauly's (1980) empirical equation:

$$M = K^{0.65} \times L_\infty^{-0.279} \times T^{0.463} \quad (8)$$

where *K* was the curvature parameter of the von Bertalanffy growth function (VBGF), L_∞ the asymptotic length and *T* the mean environmental temperature in °C. If no estimate of *K* was available, *M* was calculated from the preliminary empirical relationship:

$$M = 10^{(0.566-0.718\times log(L_\infty)+0.02\times T)} \quad (9)$$

Parameters of the VBGF were taken from publications, calculated from survey data or, most often, found on Fishbase.

A mean temperature of 11°C for benthic and demersal fish and 14°C for pelagic fish were assumed, considering that former species live on or near the sea bottom. Fishing mortality was set to zero for non-commercial species such as the European sprat *Sprattus Sprattus*. Whenever possible, fishing mortality was taken directly from ICES reports, otherwise, it was estimated from the same sources by dividing catches by biomasses. For the horse mackerel *Trachurus trachurus*, the instantaneous rate of total mortality (Z) was estimated using the Hoenig (1983) empirical equation based on a maximum observed age (t_{max}) of 15 years:

$$Ln(Z) = 1.44 - 0.984 \times \ln(t\_\max) \quad (10)$$

For demersal and benthic fish species, knowledge of their diet came from the literature and Fishbase, as well as stomach contents (Le Loc'h, 2004) and carbon and nitrogen stable isotopic analysis performed on specimens captured on a large sedimentary muddy bank known as the "Grande Vasière" and on the external margin of the continental shelf (Le Loc'h et al., 2008) (Table 2). They were consequently grouped into four categories: "Benthivorous demersal fish" comprised 24 species, including the common sole *Solea solea*; "Suprabenthivorous demersal fish" included eight species such as the blue whiting *Micromesistius poutassou* and small European hakes (< 10 cm) *Merluccius merluccius*; "Piscivorous and benthivorous demersal fish" contained, among 41 other species, the European conger *Conger conger*, the pouting *Trisopterus luscus* and the small-spotted catshark *Scyliorhinus canicula*; "Piscivorous demersal fish" included large specimens of the European hake which have a diet consisting of both demersal and pelagic fish (the full list of species is given in the first supplementary material).

Based exclusively on experts' knowledge, the pelagic species were divided into five groups, each representing a well-known, valuable and strategic species. Three thoroughly-monitored clupeid species, the European anchovy *Engraulis encrasicolus*, the European sprat *Sprattus sprattus* and the European pilchard *Sardina pilchardus*, were taken into account. The first two feed exclusively on mesozooplankton (200 < size < 2000 µm) (Whitehead, 1985). However, an ontogenetic dietary shift to smaller prey represented by microzooplankton (< 200 µm) and large phytoplanktonic cells (> 3 µm) was apparent in approximately one year-old pilchards (individuals < 18 cm) (Bode et al., 2004). Percentages calculated for the whole pilchard population were weighted averages of those for adults with a weigh of 0.76, and those for juveniles with a weigh of 0.24. The fourth group consisted of the Atlantic mackerel *Scomber scombrus*, a zooplankton feeder of which the large individuals prefer macrozooplankton (> 2000 µm). The last group was composed of the horse mackerel *Trachurus trachurus*, a bentho-pelagic species which feeds on both domains (Table 2) (Cabral and Murta, 2002).

2.4.3 Invertebrates

2.4.3.1 Cephalopods

From bottom-trawl surveys conducted annually in autumn in the Bay of Biscay (EVHOE IFREMER cruises), the more abundant pelagic cephalopods in the area appeared to be the broadtail short-finned squid *Illex coindetii*, the European flying squid *Todarodes sagittatus*, and four squid species belonging to the *Loliginidae* family, *Loligo* spp. and *Alloteuthis* spp. The most abundant benthic cephalopods were the horned octopus *Eledone cirrhosa* and the common octopus *Octopus vulgaris*, together with species of the *Sepiidae* family. As there has been little systematic study of catchability and gear selectivity in cephalopods, their biomass was left to be estimated by Ecopath, using an *EE* of 0.95. This value was justified by their commercial exploitation in the ecosystem. For these groups, wet body weights were converted to dry weights then to carbon contents using conversion factors of 0.192 and 0.402 respectively (Brey et al., 2010) (Table 1).

The *P/B* and *Q/B* ratios corresponded to the values proposed by Sanchez and Olaso (2004) for the Cantabrian Sea. The *P/Q* ratio was unusually high for animals of this size, in relation to the special eco-physiological characteristics of cephalopods which allow rapid growth (Jackson and O'Dor, 2001).

In the same way, diet composition was roughly estimated from information gathered for the southern part of the Bay. Part of their diet includes pelagic shrimps, which are considered as macrozooplankton in the present study (Table 2).

2.4.3.2 Suprabenthic and benthic invertebrates

Suprabenthic/benthic invertebrates were sampled in 2001 in late spring in the “Grande Vasière” (INTRIGAS II survey). Species were grouped into six compartments according to size, feeding ecology and position regarding the seafloor: “suprabenthic invertebrates” (crustacean suspension feeders mainly members of the Euphausiids family), “metazoan meiofauna” (largely dominated by nematodes), “surface suspension and deposit feeders invertebrates” (various species pertaining to polychaetes, bivalves and crustacean decapods), “sub-surface deposit feeders invertebrates” (eight species of polychaetes, sea urchins and sea cucumbers), “necrophagous benthic invertebrates” (four species of isopods), “carnivorous benthic invertebrates” (polychaetes and crustacean decapods such as the Norwegian lobster *Nephrops norvegicus*). The biomass was obtained from Duchemin et al. (2008), Le Loc’h (2004), Le Loc’h et al. (2008) as ash-free dry weight and converted to carbon content using a factor of 0.4 (Steele, 1974) (Table 1).

The *P/B* ratio was estimated from Schwinghamer et al. (1986):

$$P/B = 0.525 \times W\hat{}(-0.304) \qquad (11)$$

with *W*, mean body mass converted to an energy equivalent using conversion factor (1 g C = 11.4 kcal; Platt and Irwin (1973)).

The *P/Q* ratio, also called the gross food conversion efficiency (*GE*), was preferentially entered in the model. Indeed, relevant values are available from the literature and typically range from 0.05 to 0.3 (Christensen and Pauly, 1993).

Dietary profiles were determined from stable isotope analysis (Le Loc'h et al., 2008) (Table 2).

2.4.4 Zooplankton

Microzooplankton includes protozoans < 200 µm, mostly ciliates and heterotrophic flagellates. It was studied in 2004 through four seasonal surveys at three stations located in front of the Gironde River (MICRODYN survey) and three spring surveys in the southern Bay of Biscay in 2003, 2004 and 2005 (PELGAS IFREMER cruises). The cell volume was converted into carbon units using allometric relationships and/or factors (for a complete review of sampling and sample treatments, see Marquis et al. (in press)). Annual *Q/B* ratio was the intermediate value between the estimate of Sanchez and Olaso (2004) for the Cantabrian Sea and the calculation from phytoplankton grazing experiments on Gironde plume waters (Landry and Hassett, 1982). An ecotrophic efficiency of 0.95 was assumed for this compartment.

Mesozooplankton ([200-2000] µm) consists mostly of metazoans with copepods predominating and macrozooplankton (> 2000 µm) consists mainly of metazoans with decapods and jelly plankton (tunicates, cnidarians) predominating. The samples were obtained during BIOMAN surveys covering the South-East of the Bay of Biscay in spring (May and June) for the period 1999-2002 (Irigoien et al., 2009). Achievement of reliable estimates of biomass was based on the statistical relationship between zooplankton sample volume, easily estimated by digital image analysis, and the corresponding organic C and N contents of paired aliquots samples. The semi-automatic method used here allowed estimating individual bio-volume but not the taxonomic composition of zooplankton. So, gelatinous zooplankton which has vastly different biological parameters could not be isolated as a specific Ecopath compartments in the present model. The full procedure was described in Alcaraz et al. (2003). Annual *Q/B* ratios were taken from Sanchez and Olaso (2004) for the Cantabrian Sea. An ecotrophic efficiency of 0.95 was assumed (Table 1 and 2).

2.4.5 Primary producers, bacteria and detritus

These compartments were characterized during 14 IFREMER surveys performed over nine years from 1994 to 2002, in various seasons, covering the spread of the Gironde and Loire plumes as well as a larger proportion of the Bay of Biscay continental shelf (see Labry et al. (2002) for a description of full sampling and sample treatments). Most of the data were comprised between 1998 and 2002 and as a consequence, matched with the period covered by data gathered for other compartments (see the second supplementary material).

Total chlorophyll *a* was determined after size-fractioning filtration between nano- and microplankton (size > 3 µm) and picoplankton (size < 3 µm) and analysed by fluometric acidification procedure (Yentsch and Menzel, 1963). A ratio of carbon to chlorophyll *a* of 50:1 was taken for conversion. Phytoplankton production was determined by the in situ ^{14}C method (Steeman-Nielsen, 1952).

A significant import of allochthonous material probably derives from large rivers flowing into the Bay of Biscay. A value of 454 kg $C \cdot km^{-2} \cdot year^{-1}$ was evaluated from Abril et al. (2002) and the mean discharge value of these systems (www.hydro.eaufrance.fr).

Bacteria were fixed, stained and counted by epifluorescence microscopy (Porter and Feig, 1980). Bacterial production was estimated using the method based on the tritiated thymidine incorporation into DNA (Furhman and Azam, 1982). Values were converted into biomass and bacterial production assuming a cell content of 16 femtogram of carbon. The biomass was multiplied by two to take into account both pelagic and benthic bacteria populations. It is not possible to estimate the *Q/B* ratio for groups that feed exclusively on detritus. *P/Q* ratio for bacteria was derived from the paper by Vézina and Platt (1988) (Table 1 and 2). In Ecopath, detritus is not assumed to respire, although it would if bacteria were considered part of the detritus. This is why it was better to create a separate group for the detritus-feeding bacteria.

2.4.6 Placing the fishery into the system: landings and discards

Total French catches from the Bay of Biscay exceeded 90 000 tons in 1997. Anchovy (*Engraulis encrasicolus*) and pilchard (*Sardina pilchardus*) represented over half the pelagic catch, while hake (*Merluccius merluccius*), sole (*Solea solea*) and anglerfish (*Lophius piscatorius and L. budegassa*) dominated the demersal catch. The major French shellfish fishery is Norway lobster (*Nephrops norvegicus*) and this is located on the “Grande Vasière” in southern Brittany, as well as on the “Vasière” of the Gironde. Prawns and large crustaceans accounted for less of 2500 tons annually from the Bay of Biscay. Catches of cuttlefish (*Sepia officinalis*) and squid (*Loligo vulgaris* and *L. forbesii*) vary from year to year depending on their relative abundance; landings exceeded 6000 tons in 1997 (OSPAR Commission, 2000). Pelagic fish landings were obtained from the relevant working group (WGMHSA; ICES (2005b)). Benthic and demersal fish catches were based on international landings of ICES division VIIIa and b averaged over the 1998-2002 period for surveyed stocks (ICES, 2004) and on French landings statistics for the year 2002 for the main other targeted species. Among suprabenthic and benthic invertebrates, the Norwegian lobster has the greatest economic importance. Catches for this species were also available in the above-mentioned reference.

Cephalopod landings were taken from the relevant ICES working group (WGCEPH; ICES (2005a)) and were averaged over the 1996-2003 period. Since available landings included captures from division VIIIc as well, 86 % of the total value was considered to take into account the relative VIIIab/VIIIabc surfaces.

In pelagic fisheries, discarding occurs in a sporadic way compared to demersal fisheries. Discard estimates are still not available for sardine and anchovy; however, given their high economic value, discard levels are thought to be low. Discard data for cephalopods are still not homogeneously collected by EU member countries. For these compartments, discards were set to zero in the model. Discards for benthic and demersal species were obtained from direct observations on *Nephrops* trawlers operating in the Bay of Biscay, 69 hauls being sampled over the whole 1998 year (Table 1).

2.5 Trophic structure and ecological network analysis

A flow diagram was created to synthesise the main trophic interactions in the ecosystem. Furthermore, to provide a quantitative description of the ecosystem structure, the effective trophic level (*TL*) and the omnivory index (*OI*) were calculated for each functional group, along with the transfer efficiencies (*TE*) between successive aggregated trophic levels along a modified Lindeman spine (Table 1). *OI* is a measure of the variance in trophic level of the prey of a given group. Ecosystem state and functioning were characterized by the total system throughput or activity (*TST*), which quantifies how much matter the system processes, Finn's cycling index (*FCI*), which measures the relative importance of cycling to this total flow, and the total primary production to total respiration ratio (*Pp/R*), which expresses the balance between energy that is fixed and energy that is used for maintenance. The average residence time for energy in the system was estimated as the ratio of total system biomass to the sum of all respiratory flows and all exports (Herendeen, 1989). It has been assumed that the residence time of particles in a system increases to a maximum during succession, as a result of increasing ecological organisation. The connectance index (*CI*) and the system omnivory index (*SOI*) were regarded as two indices reflecting the complexity of the inner linkages within the ecosystem. Taking into account both the size of the ecosystem in terms of flows (*TST*) and organization (information content), ascendency (*A*) has been proposed as an index to characterize the degree of development and maturity of an ecosystem (Ulanowicz, 1986). Capacity (*C*) represents the upper limit of *A*. The relative ascendency measure (*A/C*) is the fraction of the potential level of organization that is actually realized (Ulanowicz, 1986). It is hypothesized that high values of this index are related to low levels of stress in the system and vice-versa. Hence disturbance activities, like fishing, are expected to produce a decrease in *A* (Wulff and Ulanowicz, 1989). The complement to *A* is System Overhead (*O*), which represents the cost to an ecosystem for circulating matter and energy (Monaco and Ulanowicz, 1997). Thus, *O* effectively represents the degrees of freedom a system has at its disposal to react to perturbations (Ulanowicz, 1986).Values were compared with those provided by Sanchez and Olaso (2004) and Jimeno (2010) and for other comparable shelf ecosystems (summary table in Trites et al. (1999)). Finally, the mixed trophic impact (*MTI*) routine indicates the effect that a small increase in the biomass of one (impacting) group will have on the biomass of other (impacted) groups (Ulanowicz and Puccia, 1990). Particular attention was paid to the impacts of fisheries activities on higher trophic-level ecosystem components. Fishing activities were further described using the mean trophic level of the catches (TL_c) and the primary production required to sustain harvest (*PPR*). TL_c reflects the strategy of a fishery in terms of food-web components selected, and is calculated as the weighted average of *TL* of harvested species. The *PPR* required to sustain fisheries has been considered as an ecological footprint that highlights the role of fishing, in channelling marine trophic flows toward human use. To assess the effects of export from the system due to fishing activities, the *L* index has been applied (Libralato et al., 2008). It is based on the assumption that the export of secondary production due to fisheries reduces the energy available for upper ecosystem levels, thus resulting in a loss of secondary production. The index that allows quantifying the effects of fishing at an ecosystem level is calculated as:

$$L = -PPR \times TE^{TL_c - 1}/Pp \times \ln{(TE)} \quad (12)$$

with Pp the primary production of the system. Estimates of *PPR* and Pp were based on the primary producers' food chain and also by including detrital production. It is possible to associate with each index value a probability of the ecosystem being sustainably fished (P_{sust}, Libralato et al. (2008), Coll et al. (2008)). At the same time, the exploitation rates (*F/Z*, fishing mortality to total mortality) by ecological group were also taken into account. Libralato et al. (2006) presented an approach for estimating without bias the "keystoneness"(*KS*) of living functional groups by combining their overall impact on the system (estimated from the *MTI* matrix) and their biomass proportion. Keystones are defined as relatively low biomass species with high overall effect. From the positive and negative contribution to the overall effect, it is possible to calculate the bottom-up and top-down effects that contribute to the keystoneness index. The relative importance of top-down or bottom-up trophic controls in continental shelf ecosystems has important implications for how ecosystems respond to perturbations (e.g. Frank et al. (2007)).

3. Results

The initial model was not balanced, since they were some ecotrophic efficiencies greater than 1. Contrarily, gross food conversion efficiencies were mostly acceptable. Biomass and production estimates of most demersal fish, sardine and anchovy were insufficient to support consumption by mackerel and horse mackerel that constitute the two most abundant fish biomass in the area. More importantly, the biomass of horse mackerel was left to be estimated by the model because of its migratory and bento-pelagic feeding behaviour that renders difficult the estimation of its abundance by scientific surveys. Consequently, proportions of those groups in the diet composition of mackerel and horse mackerel were re-assessed, and when consistent with existing literature, fixed to slightly lower values. In parallel, production terms for piscivorous, piscivorous and benthivorous and benthivorous demersal fish were re-examined to determine higher acceptable values.

Among the five ecological and physiological "rules" that should be met, the one concerning the decrease of biomass and vital rates with trophic levels was the more critical in our model. The biomass spectrum has too much biomass in the middle trophic levels, indicating that the model is most likely too focused on fish taxa (Fig. 2a). Twenty-five percent of compartments were fish species or groups. *Q/B* and *R/B* across trophic levels did not show the expected decline contrary to the *P/B* vital rate (Fig. 2b, c and d). This failure was mostly driven by the 7 homeotherms' groups at upper trophic levels which tend to have higher values than the trend line because of a higher consumptive demands per unit body mass than poikilotherms. The normal decomposition pattern was more marked when plotting total or scaled values of *P*, *Q* and *R*. The unique vital rate ratio approaching 1 concerned zooplankton which had a biomass in the same order of that of phytoplankton. This is the sole reasonable exception to this diagnostic given the high productivity and low standing stock biomass of primary producers.

The flow diagram clarified the connections between levels (Fig. 3). Benthic and pelagic food chains appeared to be linked mainly in their upper ranges by demersal fishes, particularly suprabenthivorous species. They optimize foraging benefits by feeding from both systems and they are, in turn, consumed by a large panel of pelagic top-predators. *OI* in this study ranged between 0.037 and 1.914 and it was lowest for the common dolphin, which feeds almost exclusively on high-value pelagic species, and for the large hake, which preys solely on other fish with *TL* values in the same range (Table 1 and 2). In contrast, other marine top-predators appeared far less specialized, with a significant proportion of their diet coming from imports to the system, assigned by Ecopath to a mid-trophic level position (*TL* II+), or from dead discarded organisms, assigned to a basal trophic level (*TL* I).

The ecosystem consisted of five main aggregated trophic levels; biomass values for trophic levels VI to XII were extremely small. Transfer efficiencies between successive discrete trophic levels were regular from lower to higher trophic levels, the mean along this spine being 16.8 %. The primary producers, detritus and discarded organisms in *TL* I took 47.5 % of the throughput of the entire system. *TL* II was mainly bacteria, zooplankton and benthic/suprabenthic invertebrates representing 42.9 % of the total throughput. Thus, most of the activity (90 %) in terms of flow occurred in the lower part of the food web (Fig. 4).

The system was estimated to process 939 10^3 kg C·km^{-2}·year^{-1} (*TST*), with 34.5 % of the total throughput being recycled (*FCI*). The overall residence time was calculated to be 0.046 years equivalent to 17 days. The herbivory to detritivory ratio that quantifies the flow along grazing and detrital food webs is an indication of the importance of detrital components in the system and was equal to 0.76 (Fig. 4). In addition, the *EE* of detritus was estimated to be 0.972, indicating that more or less all the energy entering this compartment is re-used in the system. All these elements suggested a strongly detritus-based trophic organization, with an intensive use of particulate organic matter as a food source. The primary production to respiration ratio (*Pp/R*) was 1.037. Concerning the two proxies for food-chain complexity (Table 3), the global omnivory of 0.212 (*SOI*) is a relatively “intermediate” value when compared with those obtained for other shelf ecosystems in the world and with outputs from previous Bay of Biscay models. The connectance of the trophic compartments of 0.213 (*CI*) was consistent with previous estimates but falls in the lower range. The system showed a relatively low value of *A/C* (22.7 %) and conversely a high value of *O/C*, *A*, *O* and *C* being respectively874,288, 2,981,572 and 3,856,013 flowbits. These values were close to the ones estimated for the French Atlantic shelf, i.e. 31% and 69 %.

The mixed trophic impact routine underlined the fact that marine top-predators had very limited direct or indirect impacts on other trophic groups of the model. Among them, the bottlenose dolphin caused the most pronounced effect (Fig. 5). Fisheries had a direct negative impact on demersal fish stocks, particularly marked for piscivorous species such as large hakes. Fishery wastes, on the other hand, appeared beneficial to surface feeders. Fishing activities could in turn, be positively affected by a small increase in the targeted species, but also by a limited amount of their main food sources, which in the case of forage fish are composed of mesozooplanktonic organisms. In addition, fisheries were characterized by a TL_c of 3.75, a *PPR* of 14.82 % and a *L* index of 0.06 calculated using a *Pp* equal to 445,931 kg $C \cdot km^{-2} \cdot year^{-1}$ and an average transfer efficiency *TE* across trophic levels of 16.8%. This *L* value resulted in a probability of having been subjected to a sustainable fishing regime of 29.86%. Exploitation rates by ecological group ranged between 0.013 for the carnivorous benthic invertebrates and 0.372 for the piscivorous demersal fish, with a median of 0.117.

Another important feature of the *MTI* matrix concerned the joint favourable effect of sardine, pilchard and sprat on apex predators. The influence of detritus as a structuring compartment highlighted in the previous paragraph was reinforced by its positive effect on various groups, with the exception of primary producers, for which indirect negative influences predominated.

Among consumers and producers, the keystone functional groups belonged to the plankton compartments: large phytoplankton, micro- and mesozooplankton (Fig. 6). The bottom-up effect, evaluated through the proportion of positive values contributing to the overall effect was 83, 43 and 70 % respectively.

A sensitivity analysis revealed that the main results concerning the functioning of the ecosystem were not affected by lower *EE* for zooplankton. *EE* were set to lower values for the three zooplankton compartments, i.e. 0.45, 0.35 and 0.35 for macro-, meso- and microzooplankton respectively, and the model was rerun. The herbivory to detritivory ratio calculated using the Lindeman spine was equal to 0.76 with current setting and to 0.56 with lower values of *EE*. Adding to this, the keystone species identified were the three same compartments (mesozooplankton, large phytoplanktonic cells and microzooplankton), with both sets of *EE*.

4. Discussion

Even though our Ecopath model was validated to meet certain standardization requirements on the basis of the PREBAL, gaps exist particularly on model structure that was most likely too focused on fish and that included numerous homeotherms' groups. This particularity of our model was linked to future research questions that would be addressed with the present model on the Bay of Biscay. They necessitate mono-specific boxes for each small pelagics and marine mammals' species frequenting the area. Model structure was recognized in many occasions to greatly influence the effectiveness for a model to capture real ecosystem properties (Fulton et al., 2003).

4.1 Late successional position and implications for stability

According to Odum (1969), the "strategy" of long-term evolutionary development of the biosphere is to increase homeostasis with the physical environment, in the sense of achieving maximum protection from its perturbations through a large, diverse and complex organic structure. The author proposed 24 attributes to characterize ecosystem development from "young" to "late" successional stages (the full list of attributes is given in the third supplementary material; Christensen (1995)). A careful analysis of the present system's characteristics revealed that detritus is central to energy flow within the Bay of Biscay continental shelf food web. This finding was confirmed by the Cantabrian Sea model (Sanchez and Olaso, 2004) that covered a small portion of the Bay presenting distinct hydro-morphological characteristics and the model of Jimeno (2010) that encompassed the same area as our model but that was built with fewer specific local data. In these two previous attempts, detritus accounted for 19.3 % and 39 % of total consumption and constituted one of the main energy flow inputs as well. In the above-mentioned theory of ecosystem development, this (among other elements) is strongly characteristic of the community energetics of mature stages of ecosystem development. These detritus-based systems were demonstrated to be more likely to support energetically feasible food chains and to be more resilient than ecosystems based solely on primary production. The stabilizing effect of detritus on these systems is the result of constant allochthonous imports and/or a longer residence time of energy linked to internal cycling (Moore et al., 2004). Odum (1969) identified an increased degree of cycling as an indicator of more mature communities which tend to internalize flows. The high *FCI* value confirms the strategic position of detritus as a perennial reservoir of energy in the Bay of Biscay. The overall residence time matched with the range already reported for other continental shelves and seas at tropical latitudes (Christensen and Pauly, 1993) and was thus considered as relatively “long” by the present authors. This high value was associated with ecosystem maturity, notably by selecting species with lower growth potential but stronger competitive performances as succession occurs (Odum, 1969).

In addition to the dominance of detritivory in the food-web functioning, the *Pp/R* ratio indicates most likely that the system is in a state of organic carbon balance. According to Odum’s principles of ecological succession, this feature related to ecosystem bioenergetics is also an excellent index of the relative maturity of the system. *CI* and *SOI* are also correlated with system maturity since the internal ecological organization is expected to increase as the system matures. The relatively moderate values for these outputs suggested a “web-like” food chain with an intermediate level of internal flow complexity, through which energy is transferred efficiently (mean *TE* far above the widely accepted value of 10 %). Comparisons with similar or comparable ecosystems (Trites et al., 1999; Jimeno, 2010) suggested that the Bay of Biscay continental shelf is relatively immature (ascendency) and has a high resistance to external perturbations (system overhead). This finding qualified the conclusion derived from other holistic metrics regarding the late maturity stage of the system which seems most probably “still developing”.

However, the apparent dominance of heterotrophic processes in this food web, mostly based on regenerated production, should be viewed with caution in the light of some methodological choices made during model building. The restriction of the study area to the band between the 30-m and 150-m isobaths, corresponding to a zone of relative homogeneity and highly documented, had necessary implications in terms of herbivory to detritivory ratio. First, a large variety of primary producers generally encountered inshore of the 30-m isobath, in the shallowest reaches of the open coast (e.g. seagrasses, macroalgae, and microphytobenthos) were thus partially ignored. Similarly, nutrients and carbon transport between shelves and the open ocean were not taken into account; in the Eastern Biscay, primary production of the shelf has been inferred to depend on oceanic imports (Huthnance et al., 2009).

4.2 Bottom-up forcing as a general mechanism of control

Cury et al. (2003) presented a general overview of the different types of energy flow in marine ecosystems that can be elucidated by plotting time series of predator and prey abundances. They illustrated the bottom-up control with a simplified four-level food web, through which the negative impact of the physical factor on the phytoplankton cascades to the zooplankton, the prey fish and the predators. For the South Bay of Biscay, analysis of quantitative long-term estimates of trophic-level abundances indicates that the coastal phytoplankton-mesozooplankton system was mainly bottom-up regulated (Stenseth et al., 2006).

On the basis of ecosystem models, Libralato et al. (2006) demonstrated the generally high importance of bottom-up effects in keystoneness for shallow coastal ecosystems and semi-enclosed marine environments such as the Chesapeake Bay, Georgia Strait, Prince Williams Sound in the northern hemisphere. Indeed, the lower part of the trophic web (phyto- and zooplankton) appears very important in these ecosystems, even if benthic groups also tend to have a high keystoneness index (*KS*). This finding contrasts with the traditional and widespread notion that keystone species/groups tend to be high-trophic-status species exerting a high impact by means of top-down effects (Paine, 1966). Based on the keystoneness analysis, the middle continental shelf of the Bay of Biscay can be added to the list of ecosystems exhibiting this “non-straightforward” pattern of keystoneness. Previous models of the Bay of Biscay (“Biscaya 1970”, “Biscaya 1998” (Ainsworth et al., 2001) and “Cantabrian Sea 1994” (Sanchez and Olaso, 2004)) were included in the comparative study of Libralato et al. (2006). It was interesting to note that planktonic compartments appeared as well in groups with the highest keystoneness, strengthening the conclusion that low trophic levels had a major structuring role in this food web.

This result, in conjunction with the trophic aggregation in the Lindeman spine, strongly suggests here a “donor driven” ecosystem, and when associated to direct outputs from the *MTI* matrix, highlighted a marked bottom-up control of small pelagic fish by mesozooplanktonic prey. At upper-trophic-levels, although there is some limited evidence for top-down control of forage fish by predator populations, overall many observations suggest bottom-up control of predator populations by forage fish. Bottom-up control by forage fish is particularly noticeable for seabirds whose feeding strategies are usually less flexible because they are physically constrained to the near-surface layer (Cury et al., 2000). When looking at the intersection between top-predators and forage fish communities in the present *MTI* matrix, the same conclusion of a dominant ascending regulation was emphasized.

The relative importance of top-down and bottom-up mechanisms may be scale-dependent. Considering the large spatial scale of the study (> 100,000 km^2), the explanation for this strong bottom-up control may lie in part in the species-energy relationship (Hunt and McKinnell, 2006). Across temperate to polar biomes, at large geographical scales, there is substantial evidence for a broadly positive monotonic relationship between species richness and energy availability. Global scale patterns of animal distribution most probably reflect natural spatial variability in abundance of prey (Gaston, 2000). Within the large-scale (67,000 km^2) fishing areas extending from southern California to western Alaska, a large proportion (87%) of the spatial variation in long-term, averaged, resident fish production was controlled by bottom-up trophic interactions and this linkage extends to regional areas as small as 10,000 km^2 (Ware and Thomson, 2005). The geographical location of the study area was proposed as a potential factor affecting trophic ecosystem regulation. A comparative study including ecosystems of both sides of the Atlantic showed that warmer, southern areas, which are more species rich, exhibited positive predator-prey associations, suggesting that resources limit predator abundance (Frank et al., 2007). The Bay of Biscay was considered as a southern locality in the above-mentioned study.

4.3 Preliminary implications for ecosystem-based fisheries management

First, comparison of two models of the Eastern Bering Sea ecosystem, separated by a forty year interval, revealed that fisheries tend to greatly reduce ecosystem maturity (Trites et al., 1999). The paper of Christensen (1995) included several ecosystems for which the maturity state could be compared before and after a disturbance, notably fishing, and the findings were in all cases in agreement with disturbances leading to a reduction in maturity (Christensen and

Walters, 2004). The relatively late successional stage highlighted by the ecosystem's attributes did not indicate that such a phenomenon was already taking effect in the Bay of Biscay. Secondly, trophodynamic indicators are particularly useful in synthesizing information made available by means of ecosystem models, for use in ecosystem approach to fisheries and in identifying and tracking ecosystem effects of fishing (Cury et al., 2005). The fairly high percentage of primary production required for harvests in this ecosystem (14.82 %) justifies growing concerns for sustainability and biodiversity. But when compared with previous *PPR* estimates of 24.2 % for tropical and 35.3 % for non-tropical shelves (Pauly and Christensen, 1995) and the fisheries of the Cantabrian Sea using 36.6 % of the total primary production (Sanchez and Olaso, 2004), the present value probably suggests a rate of exploitation that is more respectful of the carrying capacity of the ecosystem and more appropriate to the objective of sustainable fisheries than previously thought. Given the ecosystem-based reference framework relying on $\%PPR/TL_c$ pairs, the Bay of Biscay continental shelf for the period "1994-2005" was classified as an ecosystem that is still "sustainably fished" with a probability around 70 % (Tudela et al., 2005). However, when using the more complex *L* index, the probability of the ecosystem to be sustainably fished decreased to a considerable lower value (30 %), depicting a much more pessimistic situation regarding the level of system exploitation. This index was different from previous one as it integrates both ecosystem properties and features of fishing activities. This inclusion accounts for differences in ecosystem functioning, thus allowing for meaningful results to be derived for different ecosystem types (Pranovi and Link, 2009). Adding to this, when considering stock specific exploitation rates, values for small pelagics and hake, when compared to those obtained for the same species in the Cantabrian Sea (Sanchez and Olaso, 2004) and to those of closely related species in southern coastal upwelling ecosystems (Coll et al., 2006), pointed towards a moderate exploitation of the resources over the Atlantic French continental shelf.

None of them exceeded 0.5, the limit reference point at which stocks should be considered as overexploited (Rochet and Trenkel, 2003).

Conclusions

In the context of other models developed for this area, this was the first attempt to characterize the Bay of Biscay continental shelf functioning with an Ecopath model. The three fundamental characteristics of this system that emerged from the present Ecological Network Analysis were that it was most likely detritus-based, relatively mature and bottom-up controlled, with phytoplanktonic and zooplanktonic keystone species. These conclusions had reinforced partial observations made from previous models of the area about the importance of low trophic levels as drivers of the trophic ecosystem functioning. The model developed here and the findings of the present study provide strong methodological support and relevant scientific basis respectively for addressing additional research questions through Ecosim simulations. Dynamic simulations would help in clarifying the exploitation status of the whole ecosystem and in identifying fishing scenarios that allow the maintenance of forage fish stocks, the conservation of top-predators and the persistence of a stable ecosystem. As a second step, Ecosim would be particularly useful in defining food-web indicator(s) in the light of the Marine Strategy Framework Directive. Based on the ecological properties derived from the model developed here, mesozooplankton abundance, diversity and/or biomass could, along with other factors and especially benthic compartments, be reliable indicators of Bay of Biscay continental shelf changes.

Acknowledgements

This research has been supported by the French program PNEC,”Chantier Golfe de Gascogne”, by EU FP7 grant FACTS (Forage Fish Interactions), grant agreement no. 244966 and by the European project REPRODUCE (EratNet-Marifish, WP7). We would like to thank Alain Herbland, the “Bay of Biscay” worksite coordinator during the first phase of the PNEC programme. The authors are also grateful to all those who participated in the field campaigns in the Bay of Biscay and who were involved in data treatment and further developments. Many thanks go to Gérald Duchemin (University of Angers) and to Jean-Claude Sorbe (CNRS, University of Bordeaux 1) for their help on the meiofauna and suprabenthos determination, to Delphine Bonnet (University of Montpellier) for her help on zooplankton data availability, to Xabier Irigoien (AZTI-Tecnalia) for the access to the BIOMAN data and to Begoña Santos and Graham Pierce (Spanish Institute of Oceanography and University of Aberdeen) for their interest in the project and helpful remarks on the marine mammal compartments. Finally, we wish to thank Graham Pierce for assistance with editing the manuscript and the three anonymous referees who provided valuable criticism and helpful comments at the late stage of the paper.

Figure Captions

Figure 1: Study area of the Bay of Biscay continental shelf and locations of the main rivers flowing into it. For clarification, ICES divisions VIIIa, b, c and d are also added. Boundaries of the first two are shown with a bold line.

Figure 2: PREBAL diagnostics depicting values obtained following the manual mass-balance procedure of the model. *TL* increase from right to left. To offer a better visualization, all primary producers' groups (29 and 30 in Table 1) and zooplankton groups (25, 26 and 27 in Table 1) are summed. Abbreviations of vital rates are given in section 2.2. "Trophic modelling approach". Groups depicted in black are primary producers and detritus in figure 2a and marine mammals and seabirds in figure 2b, c and d.

Figure 3: Trophic model of the Bay of Biscay continental shelf. Boxes are arranged using trophic-level (*TL*) as y-axis and benthic/pelagic partitioning as x-axis. The size of each box is proportional to the biomass it represents. Numbers refer to a code for compartments provided in Table 1.

Figure 4: Biomasses, flows, transfer efficiencies are aggregated into integer trophic levels (*TL*) in the form of Lindeman spine. *P* stands for primary producers, *D* for detritus and *TE* for trophic efficiencies. In the present work, a modified Lindeman Spine is used to demonstrate the contribution of detritus-based and grazing food chains separately.

Figure 5: Combined direct and indirect trophic impacts. Black circles indicate positive impacts and white circles negative impacts.

Figure 6: Keystoneness (*KS*) for the functional groups of the Bay of Biscay continental shelf food web. For each functional group, the keystoneness index (y-axis) is reported against overall effect (x-axis). Overall effects are relative to the maximum effect measured, thus for x-axis the scale is between zero and one. The keystone functional groups are those where the value of the proposed index is close to or greater than zero. Numbers refer to a code for compartments provided in Table 1.

Table 1: Input (regular) and output (bold) parameters for the ecosystem components used in the Bay of Biscay continental shelf model. *TL*: trophic level, *OI*: omnivory index, *B*: biomass (kg C·km^{-2}), *P/B*: production/biomass ratio (year^{-1}), *Q/B*: consumption/biomass ratio (year^{-1}), *EE*: ecotrophic efficiency, *P/Q*: gross food conversion efficiency, *U/Q*: unassimilated consumption, landings (*Y*) and discards expressed in kg C·km^{-2}·year^{-1}, Gear types used to catch each compartment: BT bottom trawler, GN gillnet, LL long-liner, PS purse seiner and PT pelagic trawler.

	TL	*OI*	*B*	*P/B*	*Q/B*	*EE*	*P/Q*	*U/Q*	*Y*	Gear type	Discards
1. Plunge and pursuit divers seabirds	**4.36**	**0.499**	0.27	0.09	57.66	**0**	**0.002**	0.2			
2. Surface feeders seabirds	**3.72**	**1.328**	0.07	0.09	69.96	**0**	**0.001**	0.2			
3. Striped dolphins *Stenella coeruleoalba*	**4.73**	**0.844**	0.59	0.08	20.80	**0**	**0.004**	0.2			
4. Bottlenose dolphins *Tursiops truncatus*	**5.09**	**0.250**	2.18	0.08	21.67	**0**	**0.004**	0.2			
5. Common dolphins *Delphinus delphis*	**4.61**	**0.057**	1.44	0.08	26.11	**0**	**0.003**	0.2			
6. Long-finned pilot whale *Globicephala melas*	**4.65**	**1.914**	0.83	0.05	10.34	**0**	**0.005**	0.2			
7. Harbour porpoise *Phocoena phocoena*	**4.69**	**0.069**	0.06	0.08	40.69	**0**	**0.002**	0.2			
8. Piscivorous demersal fish	**4.67**	**0.037**	48.45	0.55	2.03	**0.996**	**0.271**	0.2	9.90	BT/LL/GN	
9. Piscivorous and benthivorous demersal fish	**4.05**	**0.568**	130	0.66	3.42	**0.994**	**0.192**	0.2	3.51	BT/GN	13.82
10. Suprabenthivorous demersal fish	**3.49**	**0.114**	311.20	0.55	5.30	**0.995**	**0.104**	0.2	0.15	BT	26.79
11. Benthivorous demersal fish	**3.41**	**0.394**	28.97	0.87	5.51	**0.979**	**0.158**	0.2	4.41	BT/GN	0.20
12. Mackerel *Scomber scombrus*	**3.75**	**0.124**	450	0.50	4.40	**0.879**	**0.114**	0.2	24.57	BT/PS	0.49
13. Horse mackerel *Trachurus trachurus*	**3.69**	**0.086**	**614.79**	0.36	4.00	0.950	**0.091**	0.2	20.27	BT/PS	1.01
14. Anchovy *Engraulis encrasicolus*	**3.67**		55.75	1.82	8.68	**0.996**	**0.210**	0.2	12.28	PT/PS	
15. Sardine *Sardina pilchardus*	**3.44**	**0.277**	184.20	0.68	8.97	**0.935**	**0.076**	0.2	9.28	PT/PS	
16. Sprat *Sprattus sprattus*	**3.67**		49.78	1.34	11.59	**0.993**	**0.116**	0.2			
17. Benthic cephalopods	**3.71**	**0.321**	**11.84**	2.75	7.00	0.950	**0.393**	0.2	3.80	BT	
18. Pelagic cephalopods	**4.45**	**0.362**	**22.45**	3.20	7.50	0.950	**0.427**	0.2	2.27	BT	
19. Carnivorous benthic invertebrates	**3.23**	**0.210**	141	2.24	**11.20**	**0.993**	0.200	0.2	2.91	BT	1.09
20. Necrophagous benthic invertebrates	**2**		16.97	1.53	**15.30**	**0.954**	0.100	0.2			
21. Sub-surface deposit feeders invertebrates	**2.34**	**0.224**	234.80	1.60	**8.00**	**0.966**	0.200	0.3			
22. Surface suspension and deposit feeders inv.	**2**		223.90	2.80	**14**	**0.984**	0.200	0.2			
23. Benthic meiofauna	**2**		100	10	**50**	**0.970**	0.200	0.4			
24. Suprabenthic invertebrates	**2.14**	**0.189**	38	20	**100**	**0.975**	0.200	0.2			
25. Macrozooplankton (≥ 2 mm)	**2.57**	**0.512**	120	**10.47**	38	0.950	**0.276**	0.4			
26. Mesozooplankton (0.2-2 mm)	**2.67**	**0.381**	638	**16.44**	80	0.950	**0.206**	0.4			
27. Microzooplankton (≤ 0.2 mm)	**2.18**	**0.154**	894	**45.05**	316	0.950	**0.143**	0.4			
28. Bacteria	**2**		394	115	**328.57**	**0.811**	0.350	0.5			
29. Large phytoplankton (≥ 3 μm)	**1**		1046	119		**0.851**					

30. Small phytoplankton (< 3 μm)	**1**		448	151		**0.752**
31. Discards	**1**		46.67			**0.788**
32. Pelagic detritus	**1**	**0.217**	2800[a]			**0.972**

[a] Pelagic detritus biomass was entered preferentially in the model as its estimation was more precise compared to the one of benthic detritus.

Detritus imports to the system were estimated to be 454 kg C·km^{-2}·year^{-1}.

Table 2: Predator/prey matrix (column/raw). The fraction of one compartment consumed by another is expressed as the fraction of the total diet, the sum of each column being equal to one.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.
1. Plunge and pursuit divers seabirds														
2. Surface feeders seabirds														
3. Striped dolphins *Stenella coeruleoalba*														
4. Bottlenose dolphins *Tursiops truncatus*														
5. Common dolphins *Delphinus delphis*														
6. Long-finned pilot whale *Globicephala melas*														
7. Harbour porpoise *Phocoena phocoena*														
8. Piscivorous demersal fish			0.014	0.335	0.015	0.002	0.011							
9. Piscivorous and benthivorous demersal fish			0.097	0.169	0.031	0.085	0.240	0.150	0.040		0.010			
10. Suprabenthivorous demersal fish	0.100		0.345	0.081	0.004	0.006	0.216	0.180	0.055	0.005	0.030	0.017	0.010	
11. Benthivorous demersal fish			0.148	0.125	0.032		0.012	0.050	0.010		0.010			
12. Mackerel *Scomber scombrus*	0.090	0.070		0.023	0.056	0.004	0.009	0.100	0.09	0.005		0.033	0.005	
13. Horse mackerel *Trachurus trachurus*	0.140	0.070		0.132	0.050	0.039	0.276	0.220	0.135	0.005	0.020	0.030	0.005	
14. Anchovy *Engraulis encrasicolus*	0.070	0.130	0.002	0.002	0.226		0.003	0.130	0.022	0.005		0.011	0.005	
15. Sardine *Sardina pilchardus*	0.380	0.210		0.031	0.449	0.006	0.213	0.115	0.040	0.005		0.009	0.007	
16. Sprat *Sprattus sprattus*	0.140	0.110		0.009	0.080			0.055	0.018	0.005		0.007	0.005	
17. Benthic cephalopods			0.006		0.032	0.243	0.009		0.010	0.002	0.003			
18. Pelagic cephalopods			0.122	0.093	0.025	0.006	0.008		0.005	0.003	0.007	0.005	0.010	
19. Carnivorous benthic invertebrates									0.275		0.200		0.020	
20. Necrophagous benthic invertebrates									0.020		0.050			
21. Sub-surface deposit feeders invertebrates									0.030		0.120			
22. Surface suspension and deposit feeders invertebrates									0.220		0.540			
23. Benthic meiofauna														
24. Suprabenthic invertebrates									0.010	0.038			0.010	
25. Macrozooplankton (≥ 2 mm)		0.120				0.050				0.175		0.200	0.150	
26. Mesozooplankton (0.2-2 mm)										0.410		0.655	0.723	1
27. Microzooplankton (≤ 0.2 mm)												0.033	0.050	
28. Bacteria														
29. Large phytoplankton (≥ 3 µm)														
30. Small phytoplankton (< 3 µm)														
31. Discards	0.080	0.290							0.020		0.010			
32. Pelagic detritus														
Import			0.266			0.559	0.003							

Table 2: (continued)

	15.	16.	17.	18.	19.	20.	21.	22.	23.	24.	25.	26.	27.	28.
1. Plunge and pursuit divers seabirds														
2. Surface feeders seabirds														
3. Striped dolphins *Stenella coeruleoalba*														
4. Bottlenose dolphins *Tursiops truncatus*														
5. Common dolphins *Delphinus delphis*														
6. Long-finned pilot whale *Globicephala melas*														
7. Harbour porpoise *Phocoena phocoena*														
8. Piscivorous demersal fish														
9. Piscivorous and benthivorous demersal fish			0.060	0.100										
10. Suprabenthivorous demersal fish				0.070	0.005									
11. Benthivorous demersal fish			0.002											
12. Mackerel *Scomber scombrus*				0.190										
13. Horse mackerel *Trachurus trachurus*				0.085										
14. Anchovy *Engraulis encrasicolus*				0.080										
15. Sardine *Sardina pilchardus*				0.057										
16. Sprat *Sprattus sprattus*				0.073										
17. Benthic cephalopods			0.040	0.035	0.004									
18. Pelagic cephalopods				0.050	0.005									
19. Carnivorous benthic invertebrates			0.210	0.050	0.051									
20. Necrophagous benthic invertebrates					0.005									
21. Sub-surface deposit feeders invertebrates			0.079		0.205									
22. Surface suspension and deposit feeders invertebrates			0.079		0.270									
23. Benthic meiofauna					0.210		0.340							
24. Suprabenthic invertebrates			0.180	0.090	0.035									
25. Macrozooplankton (≥ 2 mm)			0.350	0.090	0.060									
26. Mesozooplankton (0.2-2 mm)	0.800	1		0.030	0.110					0.050	0.200	0.050		
27. Microzooplankton (≤ 0.2 mm)	0.090									0.050	0.200	0.500	0.040	
28. Bacteria													0.130	
29. Large phytoplankton (≥ 3 µm)	0.110							0.600	0.100	0.900	0.600	0.300	0.290	
30. Small phytoplankton (< 3 µm)													0.180	
31. Discards					0.010	0.020								
32. Pelagic detritus					0.030	0.980	0.660	0.400	0.900			0.150	0.360	1
Import														

Table 3: Values taken by indices (*SOI* and *CI*) reflecting the complexity of the inner linkages within the ecosystem for the present model and previous attempts to modelize parts of the Bay of Biscay continental shelf.

	Present model	French Atlantic shelf (Jimeno, 2010)	Cantabrian Sea (Sanchez and Olaso, 2004)
SOI	0.212	0.164	0.268
CI	0.213	0.340	0.318

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The species composition of the four demersal fish compartments in the Bay of Biscay continental shelf ecosystem model.

Benthivorous demersal fish
Arnoglossus laterna
Arnoglossus imperialis
Arnoglossus thori
Callionymus lyra
Microchirus variegatus
Solea solea
Chelidonichthys cuculus
Liza ramada
Balistes carolinensis
Enchelyopus cimbrius
Mullus surmuletus
Raja clavata
Raja montagui
Sparus auratus
Microstomus kitt
Callionymus maculatus
Buglossidium luteum
Chelidonichthys obscurus
Dicologlossa cuneata
Lesueurigobius friesii
Leucoraja circularis
Pomatoschistus minutus
Syngnathus acus
Umbrina canariensis

Suprabenthivorous demersal fish
Capros aper
Micromesistius poutassou
Argentina silus
Boops boops
Cepola macrophthalma
Ammodytes tobianus
Aphia minuta
Merluccius merluccius (juveniles)

Piscivorous and benthivorous demersal fish
Scyliorhinus canicula
Conger conger
Gaidropsarus vulgaris
Lepidorhombus boscii
Lepidorhombus whiffiagonis
Lophius budegassa
Lophius piscatorius
Merlangius merlangus
Trisopterus luscus
Trisopterus minutus

Argentina sphyraena
Dicentrarchus labrax
Galeorhinus galeus
Leucoraja naevus
Myliobatis aquila
Zeus faber
Spondyliosoma cantharus
Squalus acanthias
Torpedo marmorata
Trachinus draco
Molva molva
Molva dypterygia
Chelidonichthys gurnardus
Mustelus asterias
Pollachius pollachius
Melanogrammus aeglefinus
Chelidonichthys lucerna
Mustelus mustelus
Galeus melastomus
Dasyatis pastinaca
Dicentrarchus punctatus
Diplodus vulgaris
Echiichthys vipera
Helicolenus dactylopterus dactylopterus
Hyperoplus lanceolatus
Labrus mixtus
Lithognathus mormyrus
Pagellus acarne
Pagellus bogaraveo
Phycis blennoides
Scophthalmus maximus

Piscivorous demersal fish
Merluccius merluccius
Argyrosomus regius
Torpedo nobiliana
Hexanchus griseus

Supplementary_file_2

Table summarizing campaigns and years of the biomass data for each of the 32 compartments. The 14 Ifremer campaigns used to estimate phytoplankton, bacteria and detritus parameters in the Bay of Biscay continental shelf model were also given in full. PNOCAT, BIOMET and PLAGIA were localized in the Gironde plume, GASPROD in the Loire plume and PELGAS over the continental shelf.

	Campaigns	Periods
1. Plunge and pursuit divers seabirds	ROMER/ATLANCET	2001-2004
2. Surface feeders seabirds		
3. Striped dolphins *Stenella coeruleoalba*	ROMER/ATLANCET	2001-2005
4. Bottlenose dolphins *Tursiops truncatus*	SCAN	
5. Common dolphins *Delphinus delphis*	PELGAS	
6. Long-finned pilot whale *Globicephala melas*		
7. Harbour porpoise *Phocoena phocoena*		
8. Piscivorous demersal fish	EVHOE	1998-2003
9. Piscivorous and benthivorous demersal fish		
10. Suprabenthivorous demersal fish		
11. Benthivorous demersal fish		
12. Mackerel *Scomber scombrus*	PELGAS	2000-2003
13. Horse mackerel *Trachurus trachurus*		
14. Anchovy *Engraulis encrasicolus*		
15. Sardine *Sardina pilchardus*		
16. Sprat *Sprattus Sprattus*		
17. Benthic cephalopods		
18. Pelagic cephalopods		
19. Carnivorous benthic invertebrates	INTRIGAS II	2001
20. Necrophagous benthic invertebrates		
21. Sub-surface deposit feeders invertebrates		
22. Surface suspension and deposit feeders inv.		
23. Benthic meiofauna		
24. Suprabenthic invertebrates		
25. Macrozooplankton (≥ 2 mm)	BIOMAN	1999-2002
26. Mesozooplankton (0.2-2 mm)		
27. Microzooplankton (≤ 0.2 mm)	MICRODYN/PELGAS	2003-2005
28. Bacteria	PNOCAT	May 1994
29. Large phytoplankton (≥ 3 µm)	BIOMET 1	May 1995
30. Small phytoplankton (< 3 µm)	BIOMET 2	January 1998
32. Pelagic detritus	BIOMET 3	March 1998
	PEGASE	June 1998
	PLAGIA 1	February 1999
	PLAGIA 2	April 1999
	PLAGIA 3	May 1999
	PLAGIA 4	June 1999
	PLAGIA 5	July 1999
	PLAGIA 6	October 1999
	GASPROD	April 2002
	PELGAS	May 2000
	PELGAS	May 2001
31. Discards	*Nephrops* trawlers	1998

Supplementary_file_3

The 24 attributes proposed by Odum to define the successional status of an ecosystem. Five attributes were retained in the present study as they can be applied to marine ecosystems and be easily evaluated through “Network Analysis” in Ecopath. They were depicted in bold in the table.

Ecosystem attributes	Developmental stages	Mature stages
	Community energetics	
1/ Gross production/community respiration (P/R ratio)	**Greater or less than 1**	**Approaches 1**
2/ Gross production/standing crop biomass (P/B ratio)	High	Low
3/ Biomass supported/unit of energy flow (B/E ratio)	Low	High
4/ Net community production High	Low	
5/ Food chains	**Linear, predominantly grazing**	**Web-like, predominantly detritus**
	Community structure	
6/ Total organic matter	**Small**	**Large**
7/ Inorganic nutrients	Extrabiotic	Intrabiotic
8/ Species diversity-variety component	Low	High
9/ Species diversity-equitability component	Low	High
10/ Biochemical diversity	Low	High
11/ Stratification and spatial heterogeneity	Poorly organized	Well-organized
	Life history	
12/ Niche specialization	Broad	Narrow
13/ Size of organism	Small	Large
14/ Life cycles	Short, simple	Long, complex
	Nutrient cycling	
15/ Mineral cycles	**Open**	**Closed**
16/ Nutrient exchange rate between organisms and environment	Rapid	Slow
17/ Role of detritus in nutrient regeneration	Unimportant	Important
	Selection pressures	
18/ Growth form	**for rapid growth**	**for feedback control**
19/ Production	Quantity	Quality
	Overall homeostasis	
20/ Internal symbiosis	Undeveloped	Developed
21/ Nutrient conservation	Poor	Good
22/ Stability	Poor	Good
23/ Entropy	High	Low
24/ Information	Low	High

Figure_1

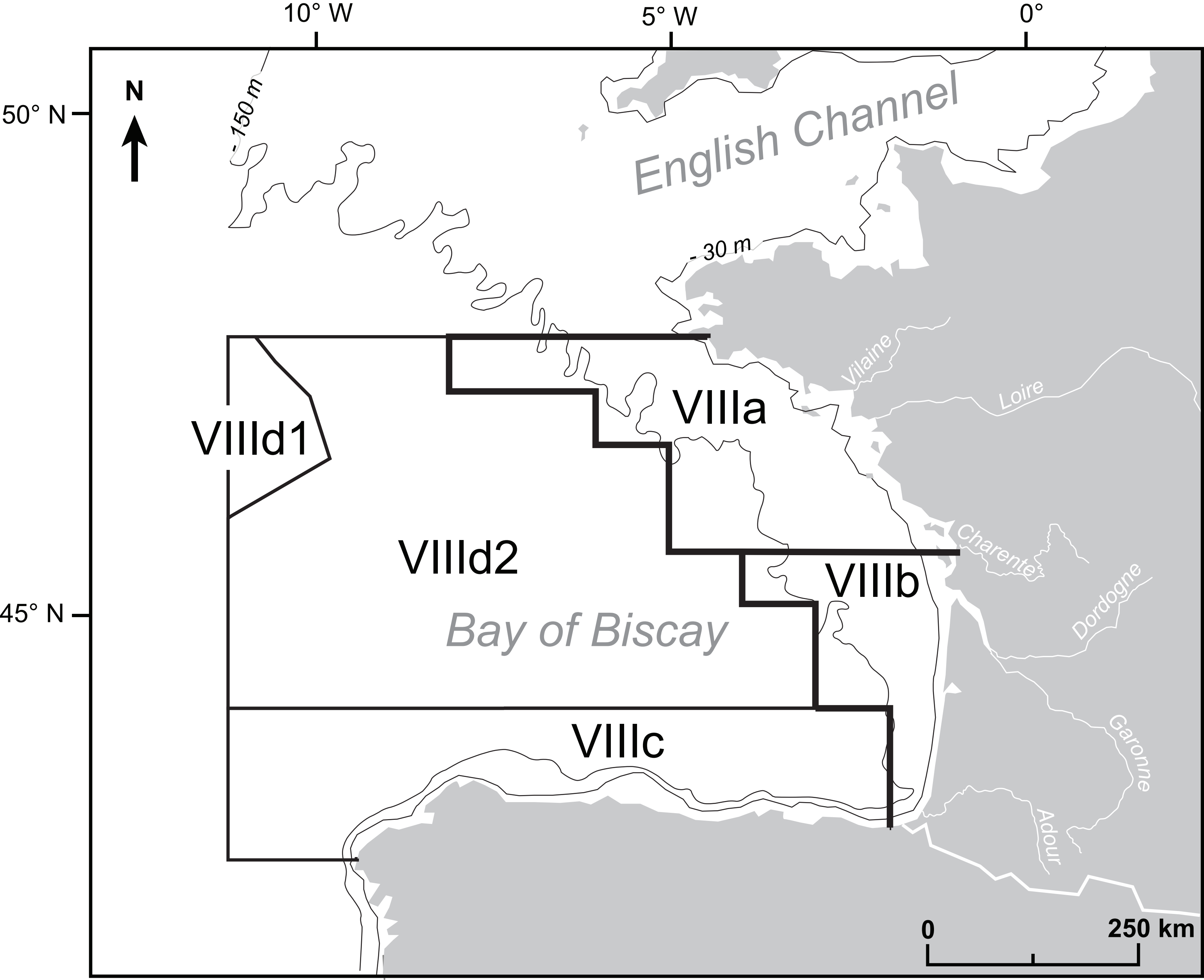

10° W
5° W
0°
50° N
45° N
N
- 150 m
- 30 m
English Channel
Vilaine
Loire
Charente
Dordogne
Garonne
Adour
VIIIa
VIIIb
VIIIc
VIIId1
VIIId2
Bay of Biscay
0
250 km

Figure_2

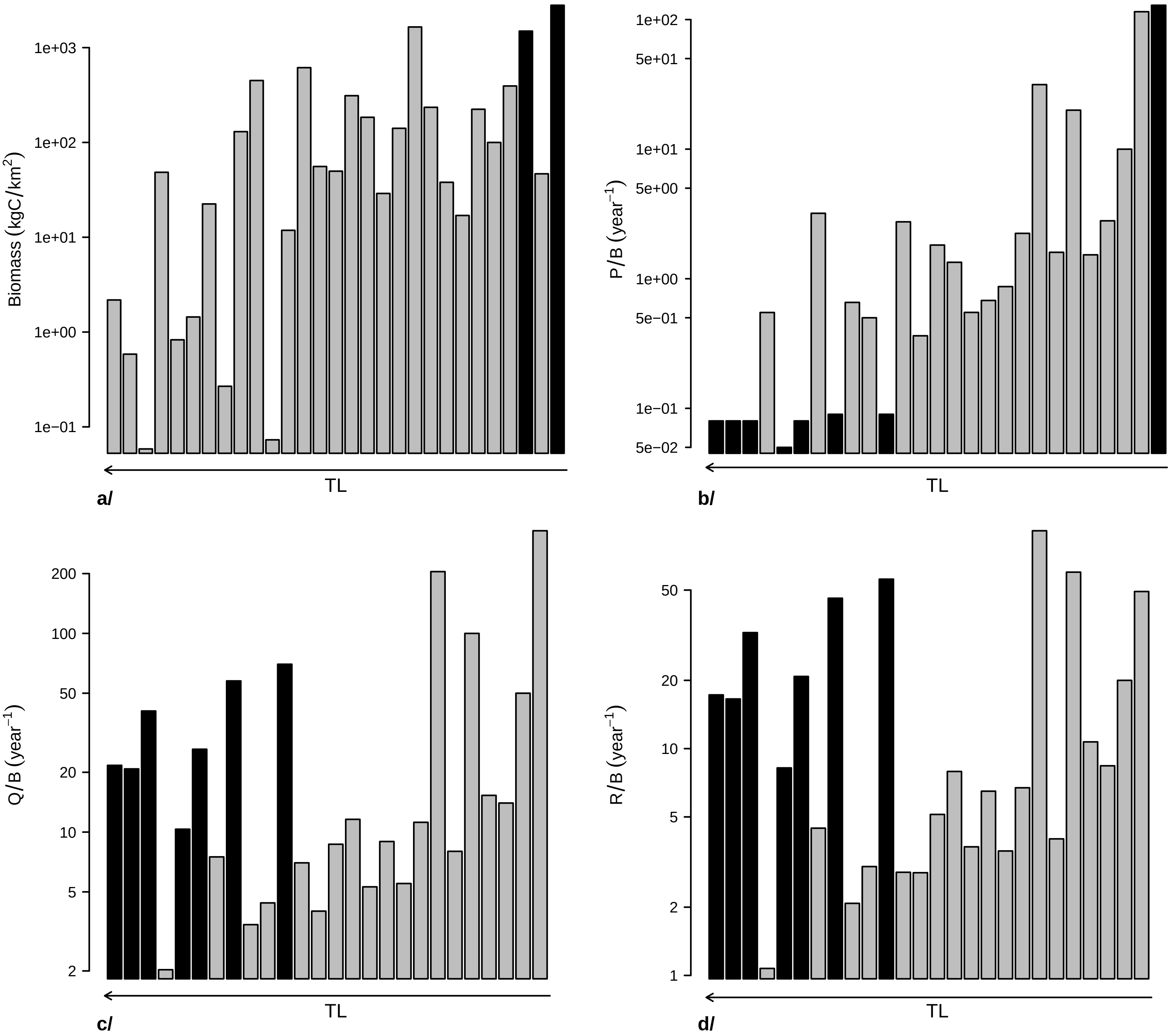
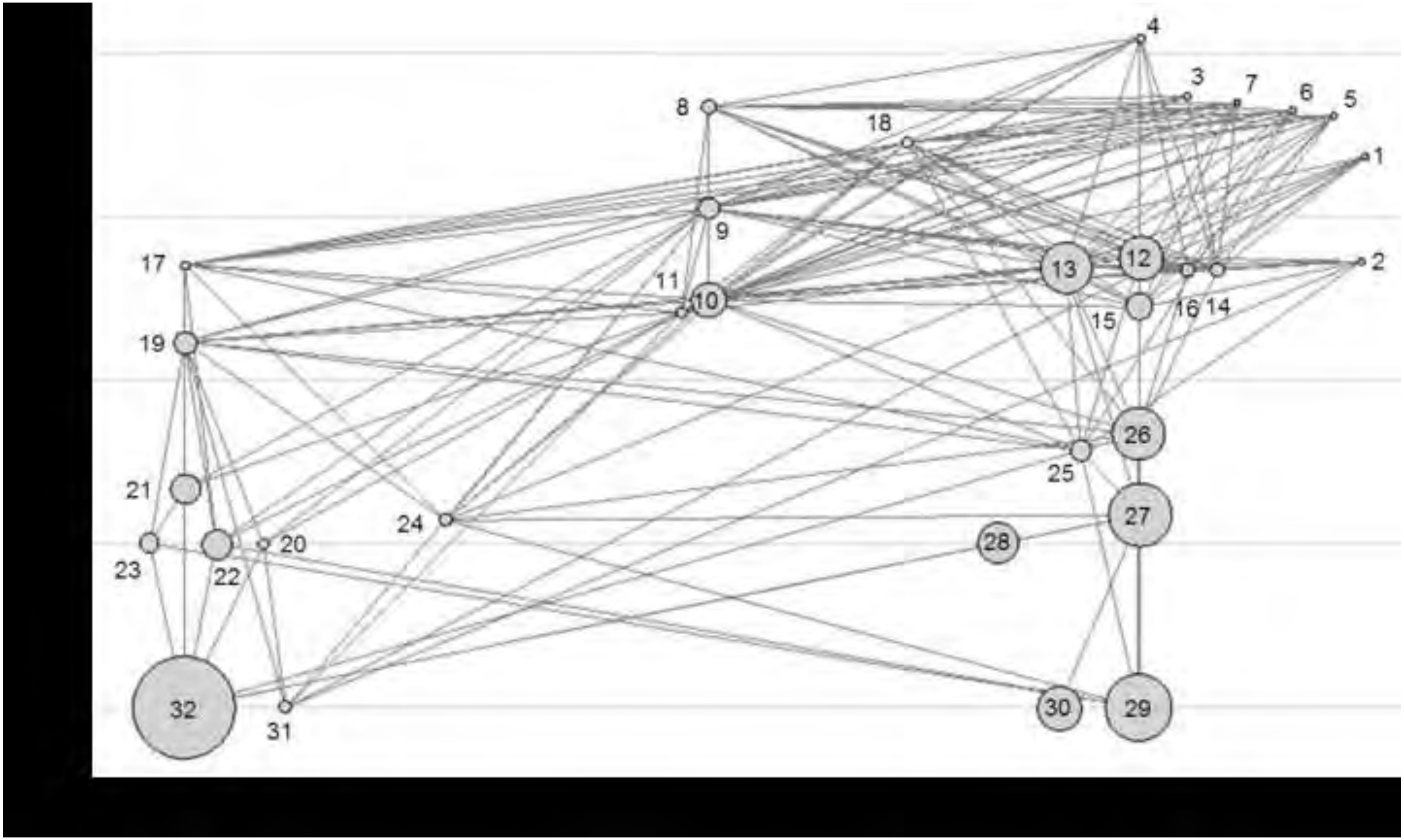

Biomass (kgC/km^2)
1e+03
1e+02
1e+01
1e+00
1e−01
TL
a/
P/B (year^{-1})
1e+02
5e+01
1e+01
5e+00
1e+00
5e−01
1e−01
5e−02
TL
b/
Q/B (year^{-1})
200
100
50
20
10
5
2
TL
c/
R/B (year^{-1})
50
20
10
5
2
1
TL
d/

Figure_3


4
3
7
6
5
8
18
1
9
17
12
13
2
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22
32
31
30
29

Figure_4

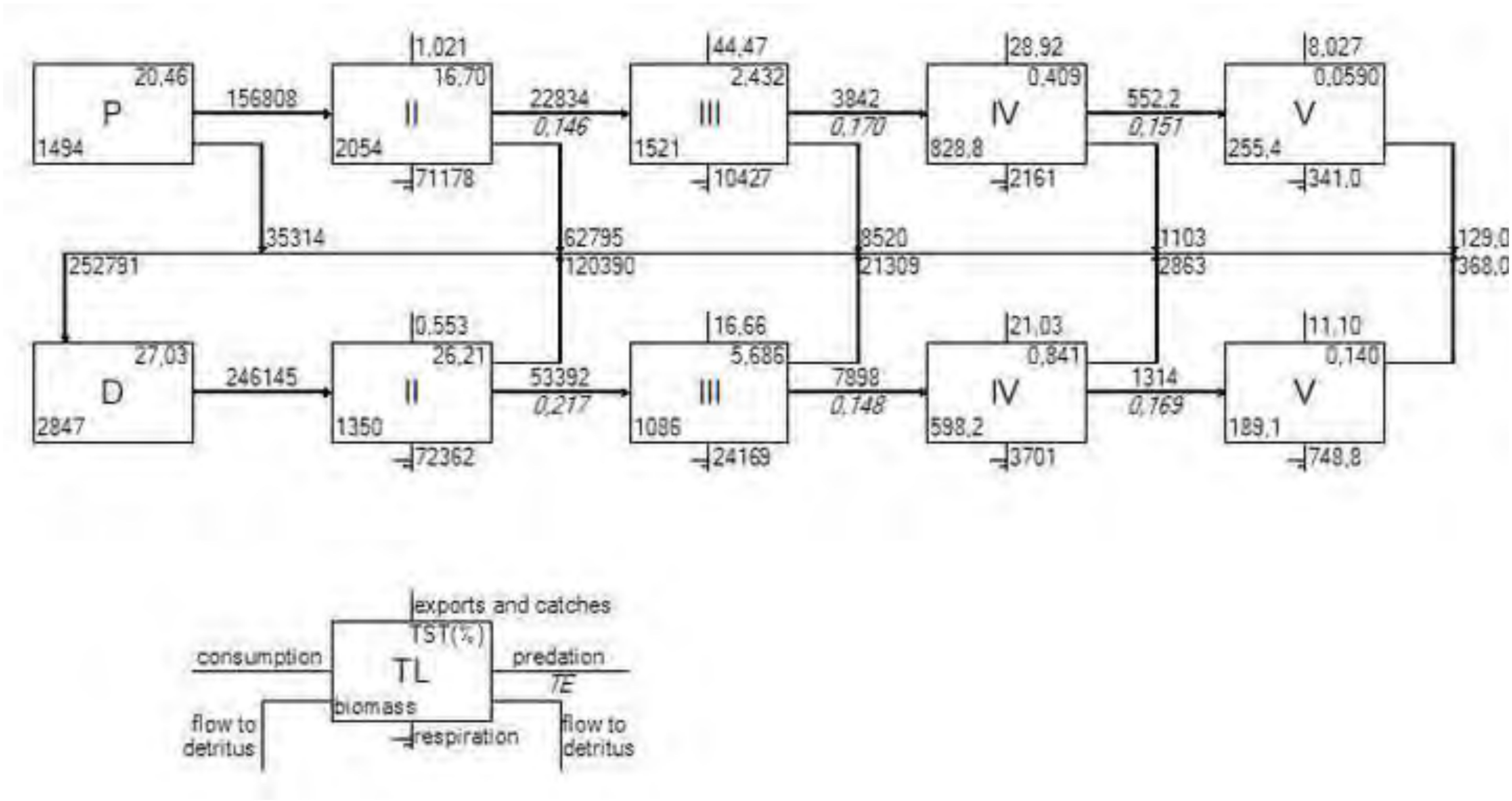

P
20,46
1494
156808
35314
II
1,021
16,70
2054
71178
22834
0,146
62795
III
44,47
2,432
1521
10427
3842
0,170
8520
IV
28,92
0,409
828,8
2161
552,2
0,151
1103
V
8,027
0,0590
255,4
341,0
129,0
252791
120390
21309
2863
368,0
D
27,03
2847
246145
II
0,553
26,21
1350
72362
53392
0,217
III
16,66
5,686
1086
24169
7898
0,148
IV
21,03
0,841
598,2
3701
1314
0,769
V
11,10
0,140
189,1
748,8
exports and catches
TST(%)
TL
biomass
consumption
predation
TE
flow to detritus
respiration
flow to detritus

Figure_5

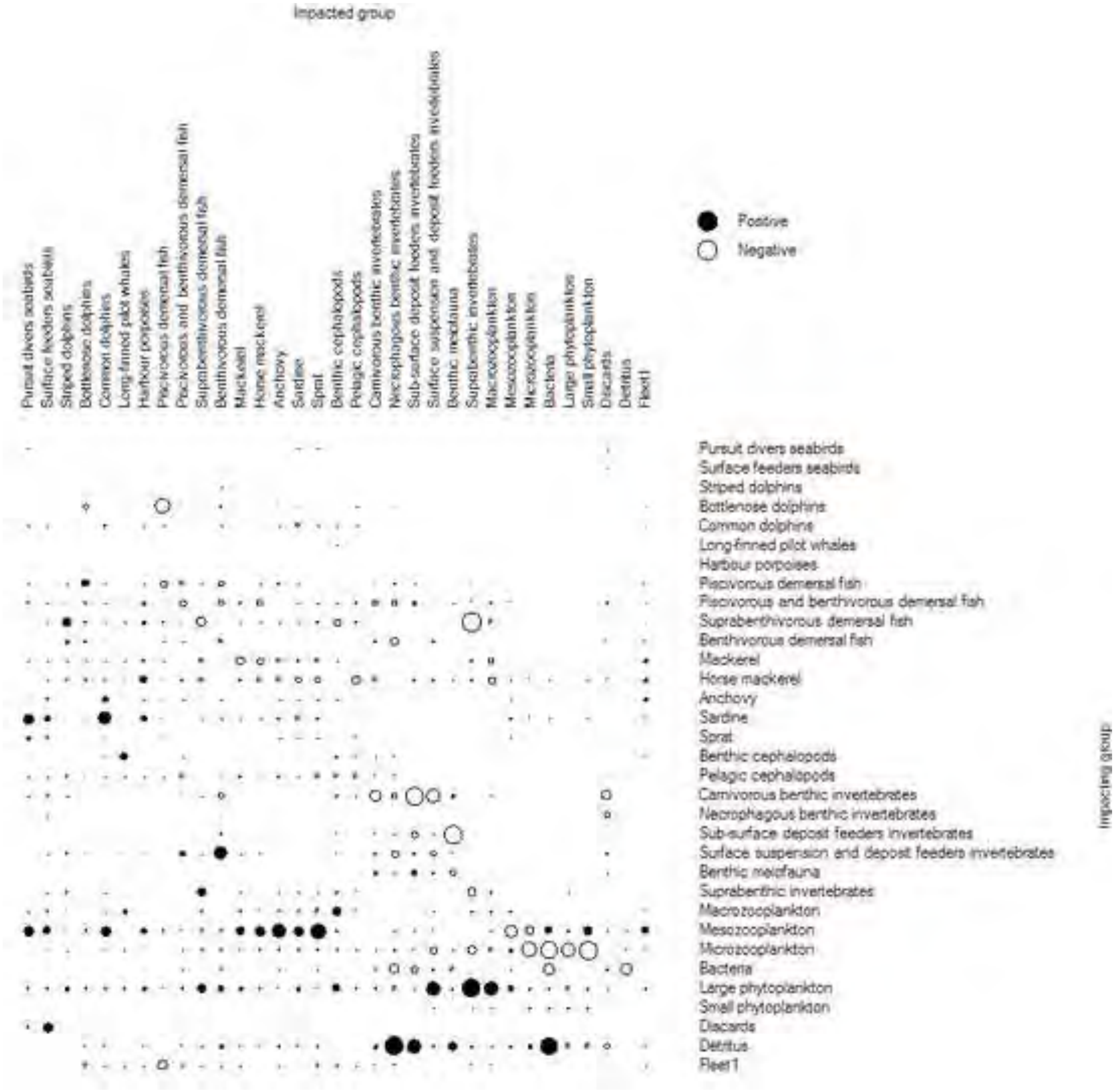
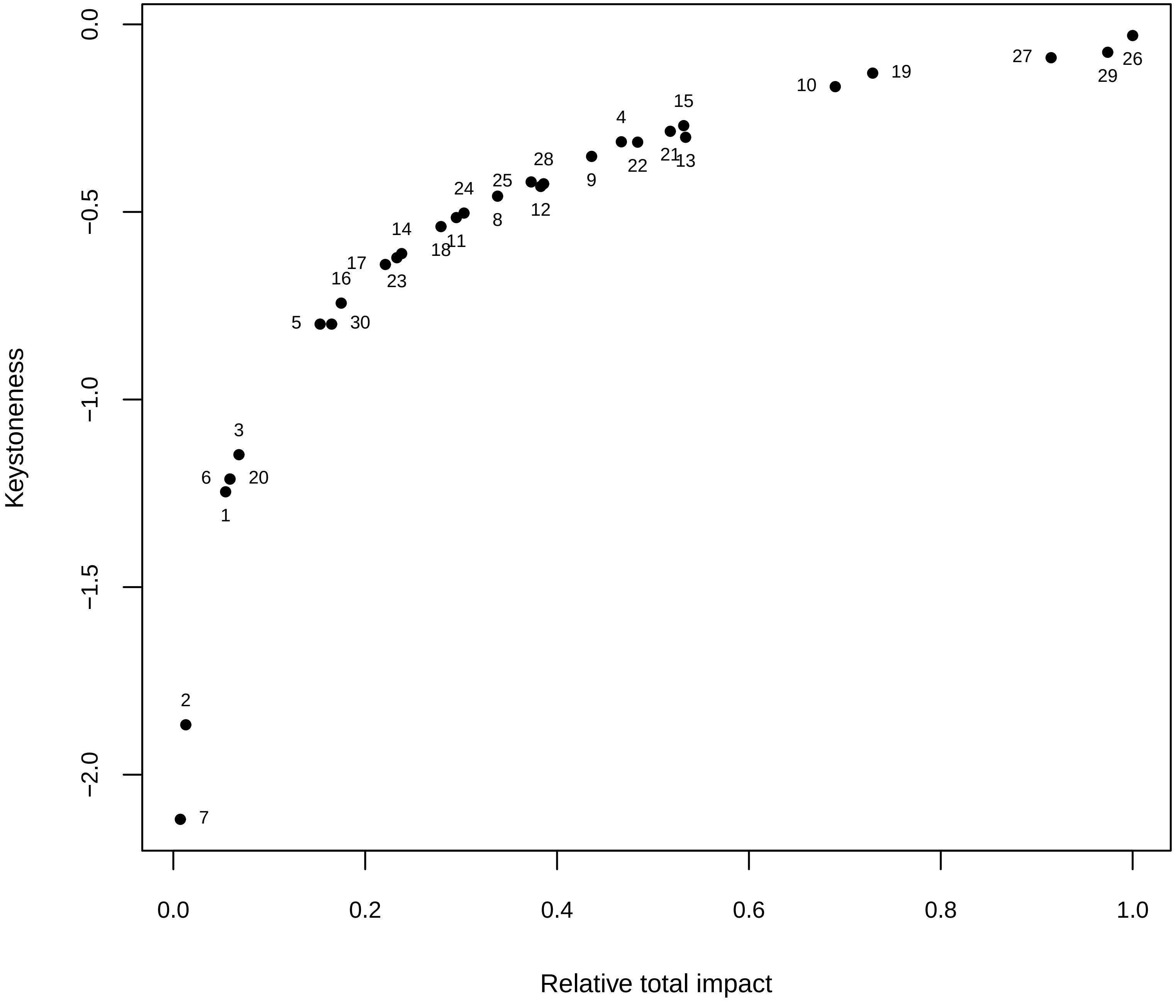

Impacted group
Pursuit divers seabirds
Surface feeders seabirds
Striped dolphins
Bottlenose dolphins
Common dolphins
Long-finned pilot whales
Harbour porpoise
Piscivorous demersal fish
Piscivorous and benthivorous demersal fish
Suprabenthivorous demersal fish
Benthivorous demersal fish
Mackerel
Horse mackerel
Anchovy
Sardine
Sprat
Benthic cephalopods
Pelagic cephalopods
Carnivorous benthic invertebrates
Necrophagous benthic invertebrates
Sub-surface deposit feeders invertebrates
Surface suspension and deposit feeders invertebrates
Benthic meiofauna
Suprabenthic invertebrates
Macrozooplankton
Mesozooplankton
Microzooplankton
Bacteria
Large phytoplankton
Small phytoplankton
Discards
Detritus
Fleet1
Positive
Negative
Pursuit divers seabirds
Surface feeders seabirds
Striped dolphins
Bottlenose dolphins
Common dolphins
Long-finned pilot whales
Harbour porpoises
Piscivorous demersal fish
Piscivorous and benthivorous demersal fish
Suprabenthivorous demersal fish
Benthivorous demersal fish
Mackerel
Horse mackerel
Anchovy
Sardine
Sprat
Benthic cephalopods
Pelagic cephalopods
Carnivorous benthic invertebrates
Necrophagous benthic invertebrates
Sub-surface deposit feeders invertebrates
Surface suspension and deposit feeders invertebrates
Benthic meiofauna
Suprabenthic invertebrates
Macrozooplankton
Mesozooplankton
Microzooplankton
Bacteria
Large phytoplankton
Small phytoplankton
Discards
Detritus
Fleet1
Impacting group

Figure_6



Keystoneness
0.0
−0.5
−1.0
−1.5
−2.0
Relative total impact
0.0
0.2
0.4
0.6
0.8
1.0
1
2
3
4
5
6
7
8
9
10
11
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