Ecosystem status and functioning: searching for rules of thumb using an intersite comparison of food-web models of Northeast Atlantic continental shelves

Géraldine Lassalle[1]*, Jérémy Lobry[2], François Le Loc'h[3], Steven Mackinson[4], Francisco Sanchez[5], Maciej Tomasz Tomczak[6], and Nathalie Niquil[7,8]

[1]Littoral Environnement et Sociétés, UMR 7266 CNRS-Université de La Rochelle, 2 rue Olympe de Gouges, 17042 La Rochelle, Cedex, France
[2]Irstea, Research Institute of Science and Technology for Environment and Agriculture, UR EPBX, 50 avenue de Verdun, 33612 Cestas, Cedex, France
[3]IRD, UMR 212 Écosystèmes Marins Exploités, IRD-IFREMER-Université Montpellier 2, Avenue Jean Monnet, BP 171 34203 Sète, Cedex, France
[4]Centre for Fisheries, Environment and Aquaculture Science, Pakefield Road, Lowestoft, Suffolk, NR33 0HT, UK
[5]Instituto Español de Oceanografía, P. Box: 240, 39080 Santander, Spain
[6]Stockholm Resilience Centre, Stockholm University, Kräftriket 10 Stallet, S-106 91 Stockholm, Sweden
[7]CNRS–IRD–UPMC, UMR 7208 BOREA, Biology of Aquatic Organisms and Ecosystems, Muséum National d'Histoire Naturelle, 7 rue Cuvier, 75231 Paris Cedex 05, France
[8]CNRS - FRE 3484 BIOMEA, Biology of marine molluscs and associated ecosystems, Université de Caen Basse-Normandie, Esplanade de la Paix, 14032 Caen, France

*Corresponding Author: tel: +33 5 4650 7646; fax: +33 5 4650 7663; e-mail: geraldine.lassalle@univ-lr.fr; geraldinelassalle2@hotmail.com

This work aimed to provide a better understanding of how the structure and function of marine ecosystems and trophic control mechanisms influence their response to perturbations. Comparative analysis of Ecopath models of four Northeast Atlantic ecosystems was used to search for rules of thumb defining the similarities and differences between them. Ecosystem indicators, related to the ecology of species interactions, were derived from these models and compared. Two main questions were addressed. (i) What are the main energy pathways and mechanisms of control? (ii) Do these ecosystems exhibit the widespread and potentially stabilizing food-web structure such that top predators couple distinct energy pathways? A strong bentho-pelagic coupling operated over the Bay of Biscay Shelf, while energy reached higher trophic levels mostly through pelagic compartments, in northern areas. Zooplankton was demonstrated to be trophically important in all ecosystems, acting as a regulator of the abundance of small pelagic fish. A latitudinal pattern in flow control was highlighted by this analysis, with a significant contribution of top-down effect at higher latitudes. This top-down control of the Baltic Sea, combined with the fact that this ecosystem did not exhibit the potentially stabilizing two-channel structure, suggested a non-stable environment.

Keywords: comparative studies, Ecopath with Ecosim, ecosystem model, graphical analysis, stability, trophic structure.

Introduction

The relative importance of top-down or bottom-up trophic controls in continental shelf ecosystems is known to have important implications in the way ecosystems respond to perturbations caused by fishing activities and changes in the environment (Hunt and McKinnell, 2006; Frank et al., 2007). In simulation studies, dynamics of an upwelling ecosystem were demonstrated to be entirely different in response to fishing depending on how the food-web was controlled (bottom-up, top-down or wasp-waist) (Cury et al., 2000). Not only can trophic control mechanisms determine the resilience to global climate change and human actions, they are also strongly influenced by it the most

dramatic response of an ecosystem being the formation of a regime shift, a change to an alternate ecosystem state typified by fundamentally different structural and functional attributes from the one preceding it (Möllmann *et al.*, 2011).

Continental shelf ecosystems were previously thought by some to be immune to top-down control, because their relatively large spatial scale, high connectivity, high species diversity and food-web complexity were believed to confer on them the ability to buffer or absorb such effects (Frank *et al.*, 2007). Their large spatial scale seemed to "connect" better with the environmentally driven bottom-up process manifest over ocean-basin scales, rather than the supposedly more patchy and localized scale effects that might be expected from top-down control mechanisms (Hunt, 2006; Ayón *et al.*, 2008). Regarding connectivity, continental shelves are open systems, much more open than systems that commonly exhibit top-down control, such as lakes and enclosed seas, and they are dominated by their physical exchange rates (Vander Zanden *et al.*, 2005; Hunt and McKinnell, 2006). This difference is an important one, as currents, migrations, and external effects can become very influential on the structure and functioning of an open system.

The stability of complex ecosystems in their response to large perturbations has also been shown to depend on the maintenance of a structural asymmetry, with energy flowing through distinct channels with differential dynamic properties (alternation of weak and strong pathways); these channels are coupled by mobile, high trophic level predators which consume prey that rely on a detrital-benthic resource base and those that rely on a planktonic-pelagic resource base (Dunne *et al.*, 2005; Martinez *et al.*, 2005; Rooney *et al.*, 2006). More precisely, Rooney *et al.* (2006) showed that across a range of ecosystems, lower-order consumers seemingly derive the bulk of their carbon from one of two resources providing the basis for these resource compartments or energy channels (phytoplankton or detritus in aquatic systems, and fungi or bacteria in terrestrial systems). They also observed that as trophic level increased, so did the tendency to derive carbon from both pelagic and benthic source webs. Examples of this have also been shown in various other types of aquatic ecosystems, including estuaries (Lobry *et al.*, 2008) and lakes (Niquil *et al.*, 2011).

Comparative studies of closely located or similar ecosystems provide the opportunity to investigate the connection between ecosystem structure and functioning, and the role this plays in determining stability and persistence in response to major disturbances, e.g. Coll *et al.* (2006), Tomczak *et al.* (2009). In the present study, existing food-web models representing substantial parts of Large Marine Ecosystems (LME) of the Northeast Atlantic were analysed in searching for "rules of thumb" that define the similarities and differences between them. The four models were developed using the Ecopath with Ecosim (EwE) software (http://www.ecopath.org/models) (Polovina, 1984; Christensen and Pauly, 1992), a popular approach for constructing mass-balance food-web models, and have already been described in detail in previous publications (see Table 1 for references and Supplementary Table S1 for a list of EwE compartments). They cover a continuous latitudinal gradient (20°) of continental shelf from the Baltic Proper to the Portuguese waters (Figure 1). These systems, namely the Central Baltic Sea (Tomczak *et al.*, 2012), the North Sea (Mackinson and Daskalov, 2007), the French Continental Shelf of the Bay of Biscay (Lassalle *et al.*, 2011) and the Cantabrian Sea (Sanchez and Olaso, 2004), are

situated along gradients of environmental settings (temperature and salinity), species diversity and anthropogenic impacts, all subject to intense fishing. This unique spatial configuration allows the comparison of models representing different major ecosystems that all belong, nonetheless, to the same marine realm (temperate northern Atlantic; Spalding *et al.* (2007)). Realms are defined by Spalding and collaborators as "very large regions of coastal, benthic, or pelagic ocean across which biotas are internally coherent at higher taxonomic levels, as a result of a shared and unique evolutionary history". This appurtenance to the same realm could have favoured the share of common characteristics between these four marine systems. In searching for common generic patterns and processes that are unique to particular ecosystems, attention was given specifically to: (i) identification of the major pathways of energy flow (benthic/pelagic, coupling) and of mechanisms of trophic control (bottom-up/top-down) through the determination of potentially important species and of their main ecological features and major direct and indirect food-web interactions; (ii) diagnosis regarding the existence of a structural organization that has been identified as a prerequisite to ecosystem stability, through the estimation of the percentage of carbon derived from two "basal" resources, i.e. phytoplankton and detritus. Rooney *et al.* (2006) also analysed the Cantabrian Sea system. We extended the analysis to a larger set of continental shelves to test the idea of Rooney *et al.* (2006) on this specific type of ecosystem.

Material and methods
Ecopath approach
Food webs of the four ecosystems were modelled using EwE (Christensen and Walters, 2004; Christensen *et al.*, 2008). EwE is a tool for analysing organic matter and energy flows within a steady-state/static (Ecopath) and/or dynamic (Ecosim) mass-balanced model. Originally proposed by Polovina (1984), the Ecopath model has been combined with routines for network analysis. Ecopath model parameterization is based on two "master" equations. One decomposes the production term of each compartment (species or group of species with a similar ecotrophic role):

$$\text{Production} = \text{fishery catch} + \text{predation mortality}$$
$$+ \text{ net migration} + \text{biomass accumulation}$$
$$+ \text{ other mortality.} \quad (1)$$

"Other mortality" includes natural mortality factors such as mortality due to senescence, diseases, etc.

The other equation describes the energy balance of each group:

$$\text{Consumption} = \text{production} + \text{respiration}$$
$$+ \text{ unassimilated food.} \quad (2)$$

More formally, the equations can be written as follows for a group i and its predator j:

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

Table 1. Case studies included in the cross-ecosystem comparison.

	Cantabrian Sea	French Continental Shelf	North Sea	Central Baltic Sea
LME	Iberian Coastal Shelf	Celtic-Biscay Shelf	North Sea	Baltic Sea
Type	shelf	shelf	shelf	semi-enclosed sea
Period or nominal year	1994	1994–2005	1991	1974
Purpose[a]	(iii)	(ii)	(iii) and (v)	(ii)
Reference	Sanchez and Olaso (2004)	Lassalle et al. (2011)	Mackinson and Daskalov (2007)	Tomczak et al. (2012)
Surface area in km^2	16 000	102 585	570 000	240 669
Number of groups	28	32	68	22
Trophic levels covered	1 to 4.770	1 to 5.179	1 to 4.978	1 to 4.588
Seabirds		2	1	
Marine mammals		5	3	1
Fish	15	9	44[b]	8[b]
Invertebrates	6	8	10	3
Zooplankton	4	3	4	5
Primary producers	1	2	1	2
Bacteria		1	2	1
Discards	1	1	1	
Detritus	1	1	2	2
Fisheries	5	1	12	3
Landings (tons$\cdot$km$^{-2}\cdot$year^{-1})	9.41	1.25[c]	4.90	3
Proportion of small pelagics in landings (%)	61	59	71	81

More details on the models can be found in the references cited and in Supplementary Table S1, where a list of EwE compartments was given for each case-study. [a]The list of general purposes for which ecosystem models were built was proposed by Tomczak *et al.* (2012) (i) to answer ecological questions, (ii) to quantify flows and food-web structure, (iii) to assess fisheries and environmental impacts, (iv) to understand ecological network analysis, and (v) to evaluate fisheries management strategies. [b]Multi-stanza fish groups are groups in which two or more life-stages are represented (e.g. juveniles and adults). [c]Values were converted to tons of fresh weight using the conversion factors given in Lassalle *et al.* (2012).

and

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

where the main input parameters are biomass density (*B*, here in kg C$\cdot$km^{-2} or tons$\cdot$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 C$\cdot$km^{-2} or tons$\cdot$km^{-2}), respiration (*R*; kg C$\cdot$km$^{-2}\cdot$year^{-1} or tons$\cdot$km$^{-2}\cdot$year^{-1}), unassimilated food rate (*U*), and ecotrophic efficiency (*EE*; amount of species production used within the system). The "other mortality" term, *M0*, is internally computed from:

$$M0_i = B_i(1 - EE_i) \times (P/B)_i \qquad (3).$$

Presentation of shelf ecosystems
French Continental Shelf of the Bay of Biscay
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 (Figure 1). 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,

organization and functioning (Varela, 1996). Significant environmental differences, i.e. width and orientation of the continental shelf and degree of continental influence, condition the dynamic of the neritic ecosystem in French and Spanish shelves. The model considered for this zone (Lassalle *et al.*, 2011) was restricted to divisions VIII*a* and *b* of the International Council for the Exploration of the Sea (ICES; www.ices.dk), and to the middle shelf between the 30-m and 150-m isobaths (Table 1).

Cantabrian Sea
The area considered in the model (Sanchez and Olaso, 2004) was delimited by the ICES division VIII*c* and corresponded to the Cantabrian Sea in its wider meaning (Figure 1; Table 1). The Cantabrian Sea is considered to be 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), and its eastern limit to be the beginning of the French Shelf. Here, the Galician Shelf to the north of Cape Finisterre was also included. The study area was restricted to the continental shelf and the close oceanic waters. Fishing statistics and information available from the evaluation of stocks carried out by the ICES stock assessment working groups are provided for each distinct part of the Bay of Biscay.

North Sea
The North Sea is a mid-latitude, relatively shallow continental shelf with an average depth of approximately 90 m, the deepest part in the Norwegian Trench being approximately 400 m deep (Figure 1; Table 1). It is bounded by the coasts of Norway, Denmark, Germany, the Netherlands, Belgium, France and Great Britain. The limits for this zone are defined by the ICES divisions
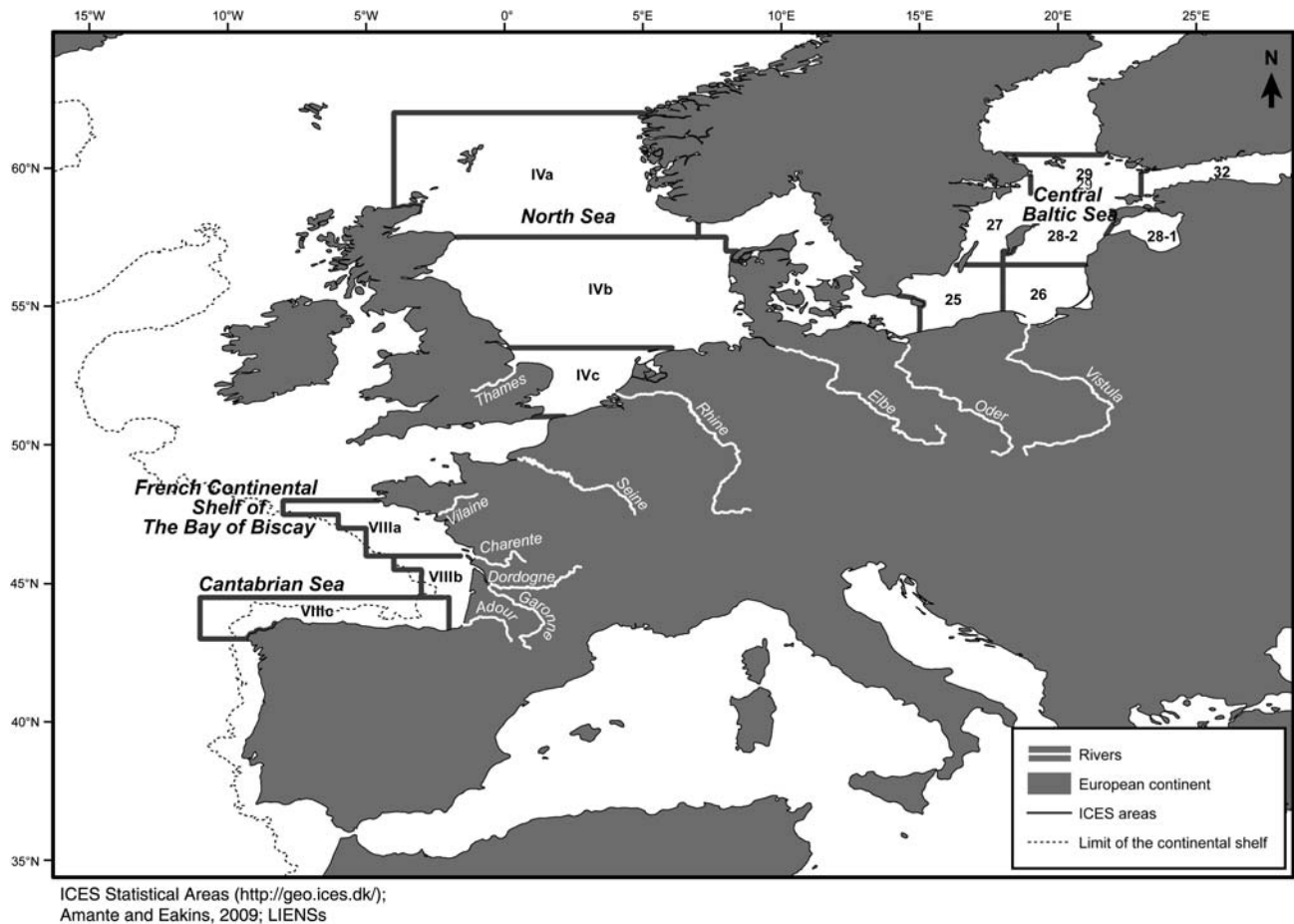
Figure 1. Location of the investigated areas in the Northeast Atlantic and major rivers flowing into it. From south to north: Cantabrian Sea, French Continental Shelf of the Bay of Biscay, North Sea, and Central Baltic Sea. Relevant ICES divisions and subdivisions have been added.

IVa, b and c. The southeast North Sea is subject to the strong influence of fresh water that runs off the continental land mass, significant freshwater inputs coming from the River Thames.

Baltic Sea

The Baltic Sea is a semi-enclosed sea which is characterized by brackish water conditions resulting from riverine and precipitation inputs of fresh water, and on the periodic inflow of saline water from the North Sea through the three Danish straits. The Baltic Sea, which is subjected to multiple human impacts, is managed under ICES division IIId (equivalent to ICES subdivisions 24–32). The area described by the model, the Baltic Proper, mainly comprises the three deep basins of the Central Baltic Sea (ICES subdivisions 25–29, excluding the Gulf of Riga), i.e. the Bornholm Basin (subdivision 25), the Gdansk Deep (subdivision 26), the Gotland Basin (subdivision 28), and the Archipelago Sea (subdivision 29) (Figure 1; Table 1).

Overview of model temporal scales

Comparing different time periods within a system, or between systems, has the potential to change our view of energy flow and, thus, could account for some of the differences or similarities found in comparative studies. The models of the three southernmost

ecosystems, namely the Cantabrian Sea, the French Continental Shelf and the North Sea, correspond to a snapshot of the ecosystem after the major regime shift event of the late 80s (Möllmann et al., 2011). Climate-induced changes in the abiotic environment were considered to be the most important driver. Although most of the biomass data are from the 1990–2005, we cannot ignore the possibility that temporal changes in the ecosystems overlap significant differences between the systems studied. In the Baltic case, Ecopath was setup for 1974 and thus corresponded to a "pre-1980" regime shift situation. However, it represented a perturbed ecosystem as well, following the elimination of marine mammals as top predators by hunting and toxic pollutants and the shift towards a cod-dominated state [see Österblom et al. (2007) for a presentation of drastic changes that occurred in the Baltic Sea]. Consequently, beyond this difference in time period, the four models were considered comparable in the sense that they modelled ecosystems following major perturbation events which differ, nevertheless, in their ratios of abiotic to biotic drivers, and of natural to anthropogenic influences. In all four ecosystems, fishing activities primarily targeted small pelagic fish, with the proportion of forage fish in landings ranging between 61 and 81% (Table 1). Fishing intensities (total catches) appeared more variable. Part of the explanation resided in the model spatial coverage, in which coastal areas were not systematically included.

Model comparison

The natural connectivity among ecosystems pertaining to the same marine realm means that while some features are unique, others are shared. Analysis of the similarities and differences in patterns and processes revealed important drivers in the ecosystems located close to each other, and thus permitted generalizations to be drawn about ecosystem functioning and response to perturbations. This type of knowledge is important in helping establish tools to support implementation of an ecosystem-based management approach (Pranovi and Link, 2009).

Keystoneness index and MTI assessment

First, to elucidate the major pathways of energy flow (benthic/pelagic, coupling) and the main mechanism of ecosystem regulation (bottom-up/top-down), true keystone and key dominant (structuring) species, or groups of species, were identified using two alternatives of keystoneness (KS) index. A true keystone species is defined as one whose effect, by means of top-down processes, is disproportionately large relative to its abundance, and thus is usually rare (Paine, 1969). The original term was coined for a predator with a top-down effect, whose removal fundamentally changed the community composition by releasing predation pressure on highly competitive benthic grazers. Power *et al.* (1996), followed by many others including Libralato *et al.* (2006), extended the definition to species or groups of species with either top-down or bottom-up influence which is out of proportion to their biomass, relative to other groups in the ecosystem. It needs to be distinguished from key dominant species, also called structuring species, defined as ones in which densities or total biomasses are very high, and for which community influence is a direct result of abundance.

Dynamic simulations of the removal of those groups to measure the impact on system stability could not be performed as Ecosim models were not parameterized for all of the four systems. Consequently, the present analysis was not restricted to the identification in each ecosystem of the functional group with the highest KS index, but was extended to the first four potentially important compartments and to the assessment of important features: (i) their appurtenance to marine domains, (ii) their trophic relationships with each other, (iii) the proportion of their action due to top-down control, (iv) the way they interact with the whole ecosystem as evaluated through the Mixed Trophic Impact (MTI) assessment. The last two features were particularly relevant in determining the main mechanism of ecosystem regulation (bottom-up/top-down). The two analyses, KS index and MTI assessment, are not independent since the first depends on the second to be calculated, and both are unitless.

The MTI assessment identifies the direct and indirect effects that a small increase in the biomass of one (impacting) group would have on the biomass of other (impacted) groups (Ulanowicz and Puccia, 1990). The net impact of i on j, denoted q_{ij}, is given by the difference between positive effects d_{ji} (quantified by the fraction of prey i in the diet of predator j), and negative effects f_{ij} (evaluated as the fraction of total consumption of i used by predator j). Therefore the resulting matrix of the net impacts Q has elements:

$$q_{ij} = d_{ji} - f_{ij} \qquad (4).$$

The mixed trophic impact m_{ij} is then estimated by the product of all the net impacts q_{ij} for all the possible pathways in the trophic

web that link the functional groups i and j. Negative elements indicate a prevalence of negative effects, i.e. the effects of the predator on the prey (top-down effects); analogously, positive elements indicate the prevailing effects of the prey on the predator (bottom-up effects). The bars should not be interpreted in an absolute sense: the impacts are relative, but comparable between groups. An assumption is that the trophic structure remains constant, implying that MTI should not be used in a predictive sense, but rather as a type of sensitivity analysis. Small pelagics are a major natural resource to the European community, and they fluctuate greatly, both on annual and decadal time scales. In all the interactions that we investigated, a special focus was placed on the relationships of important functional groups with their prey and predators.

The KS index proposed by Libralato *et al.* (2006) was designed to estimate without bias the "keystoneness" of living functional groups by combining in a balanced way their overall impact on the system ε_i with their relative importance in terms of biomass p_i [see Figure 1b in Libralato *et al.* (2006)]:

$$
\begin{aligned}
KS_L &= \log\bigl(\varepsilon_i \times (1 - p_i)\bigr) \\
&= \log\left(\sqrt{\sum_{i \neq j}^{n} m_{ij}^2} \times \left(1 - \frac{B_i}{\sum_k B_k}\right)\right) \qquad (5),
\end{aligned}
$$

ε_i is estimated as the sum of all the direct and indirect effects quantified through the MTI analysis, with the exception of the effect of the change in biomass on the group itself. The p_i was calculated as the contribution of the functional group to the total biomass of the food-web, with B_i the biomass of the functional group i. In this version of the KS index, keystone functional groups are defined as relatively low biomass functional groups with high overall effect. From the positive and negative contributions to the overall effect ε_i, it is possible to calculate the bottom-up and top-down effects that contribute to the KS index. The top-down effect of a functional group i corresponds to the sum of the m_{ij}^2, for $m_{ij} < 0$, divided by the overall effect ε_i.

The KS_L index was judged to present problems in the weighting of biomass proportion, by not sufficiently penalizing groups with high abundance, and thus to be not fully able to distinguish between the two categories, true keystone and key dominant (structuring) species or groups of species (Coll and Libralato, 2012). By taking into account the biomass of each functional group in the graphical representation proposed by Libralato *et al.* (2006), this limitation can be partly circumvented and a start in the distinction between these two categories of important species can be made. In the last version of EwE, the KS_L index is reported against overall effect, with the size of circles being proportional to the biomass of functional groups. The overall effect corresponded to the total effect of one functional group on all the others in a given model. For clarity, the first four functional groups with the highest KS_L index have been named "important functional groups" in the manuscript until the Discussion section.

The KS index suggested by Power *et al.* (1996) was also calculated, and results were compared with those obtained from the version proposed by Libralato *et al.* (2006).

$$
KS_P = \varepsilon_i \times \frac{1}{p_i} = \sqrt{\sum_{i \neq j}^{n} m_{ij}^2} \times \frac{1}{B_i / \sum_k B_k} \qquad (6),
$$

This early alternative was recognized as attributing a high KS_P index to low biomass functional groups (as required) but with

low overall effect, which was problematic and led to the development of the version proposed by Libralato *et al.* (2006).

Ecosystem structural organization and stability properties

Secondly, the existence of energy channels coupled by top-predators was investigated in ecosystem organization as it had been demonstrated to be a necessary prerequisite for ecosystem stability (Rooney *et al.*, 2006). Considering the dynamics of natural systems, as one channel increases and the other decreases, a predator moves to regulate the increasing channel, and in doing so, frees the decreasing channel from strong predatory pressure. Therefore, stability arises from top predators linking these asynchronous and asymmetric energy channels. To detect whether this structure was being exhibited in continental shelf food-webs, the percentage of carbon derived from different basal resources (phytoplankton and detritus) was estimated from the food-web representations. The percent of carbon derived from phytoplankton by any given consumer was then plotted against the trophic position of each functional group. This percentage is based on the number of resources consumed by the consumer, the proportion of the consumer diet accounted for by a resource, and the proportion of carbon derived from the basal resource in the resource being consumed. The "Basic estimates" and "Flow from detritus" matrices were used to obtain the trophic level and the percentage of flow derived from detritus for each compartment, respectively.

Influence of model aggregation patterns

The four models had all been developed previously for different purposes and with potentially different assumptions and trophic grouping strategies; some organisms were represented as species and some as diverse groupings of interacting species (Table 1). For example, the two models designed for studying the impact of fisheries were generally characterized by a lower level of aggregation of fish species, by the definition of multi-stanza groups, and by a decomposition of fisheries by fishing fleets or gears. The number of functional groups and aggregation of species into functional groups influence model outputs and analyses, particularly full-system indicators such as Capacity, Overhead and Ascendency (Pinnegar *et al.*, 2005; Johnson *et al.*, 2009). On the contrary, few investigations have been undertaken to clarify the effects of aggregation on indicators related to the ecology of species interactions. All three analyses presented here were based on the same concept: a ranking of ecosystem compartments along a continuum of levels of relative impact, keystoneness and percentage of flow derived from phytoplankton, respectively. When several models of the same ecosystem, but with slightly different aggregations into functional groups were compared, differences in terms of KS index appeared negligible (Simone Libralato, pers. comm.). In addition, among 13 different structural indices, the MTI and the KS index were demonstrated to be the most reliable/robust for assessing the importance ranking of species in an uncertain network model (Fedor and Vasas, 2009). In addition, when plotting the composition by major taxonomic groups of each model (Table 1), the aggregation strategies presented the same general pattern, with a common emphasis put on fish, invertebrates and zooplankton in all four ecosystems and the same number of trophic levels covered. Importantly, models were developed with a majority of data of local origin, not coming from nearby systems, preserving the model independency and comparability. As recommended by Megrey *et al.* (2009), local experts who were familiar with the particular study sites and who participated

in the construction of the different models were involved in the present analysis to provide perspectives regarding a given ecosystem. Beyond the differences in number of functional groups (varying between 22 and 68), the elements cited above gave us assurance that the models were comparable regarding the position/role played by functional groups within ecosystems, and that similarities and differences found in the modelled systems were not much affected by differences in methodology.

Results

Appurtenance to marine domains and trophic linkages between important functional groups

For the two ecosystems modelled in the Bay of Biscay, important functional groups presented a high degree of similarity (Figure 2, Table 2; KS_L index). Importance was given to suprabenthic and demersal organisms that contributed to the trophic coupling between the benthic and pelagic domains. Suprabenthic referred to all bottom-dependent animals, mainly crustaceans, which perform, with varying amplitude, intensity and regularity, seasonal or daily vertical migrations above the sea floor. Demersal mainly referred to fish that are living on or near the bottom and dependent on the proximity of the bottom. Among them, the blue whiting (*Micromesistius poutassou*) frequently exhibits bentho-pelagic behaviour and the suprabenthic zooplankton performs vertical migration in the water column. In the other two ecosystems, the four important functional groups with the highest KS_L indices (listed in Table 2) formed a remarkable pelagic trophic channel with top-predators (TL $\geq$ 3.5), small pelagic fish with high commercial value and zoo- or phytoplanktonic prey. In the Central Baltic Sea, this analysis pointed out well-known trophic relationships involving a predatory fish (cod, *Gadus morhua*), a commercially-valuable small pelagic fish (sprat, *Sprattus sprattus*), and zooplankton; the first being the main predator of the second and both feeding on zooplankton during their whole life cycle, or at specific life stages. In the North Sea, relationships between the important functional groups with the highest KS_L index were not as direct as in the Baltic case study; they did not form a strictly linear key pathway. All the four important functional groups pertained to the pelagic food-web, but sand eels (*Ammodytidae*), which have a bentho-pelagic behaviour, link the two domains by feeding predominantly on both zooplankton and lower trophic-level benthic organisms. Large piscivorous sharks were identified as the most important functional group in the North Sea model, probably because they act as the sole regulator of sharks and rays of lower trophic levels (Figure 3c). This high trophic level group consists mainly of tope (*Galeorhinus galeus*). Sand eels, which presented the highest landings in the model, are also the dominant prey fish. Within zooplankton populations, the carnivorous fraction was found to occupy an important position in the food chain, linking primary producers (phytoplankton) to pelagic and demersal fish.

In all the ecosystems, the first four important functional groups identified with KS_P systematically presented a high trophic level (supplementary Table S1). Any similarities were found between the two classifications (KS_L and KS_P) in the Bay of Biscay ecosystems. The KS_P classification confirmed key top predators identified using the KS_L index in the pelagic trophic channels of the North and Baltic seas, i.e. large piscivorous sharks and cods, respectively.

In Figure 2, the size of the circles reflected the functional group biomass. It helped to separate true keystone from key dominant
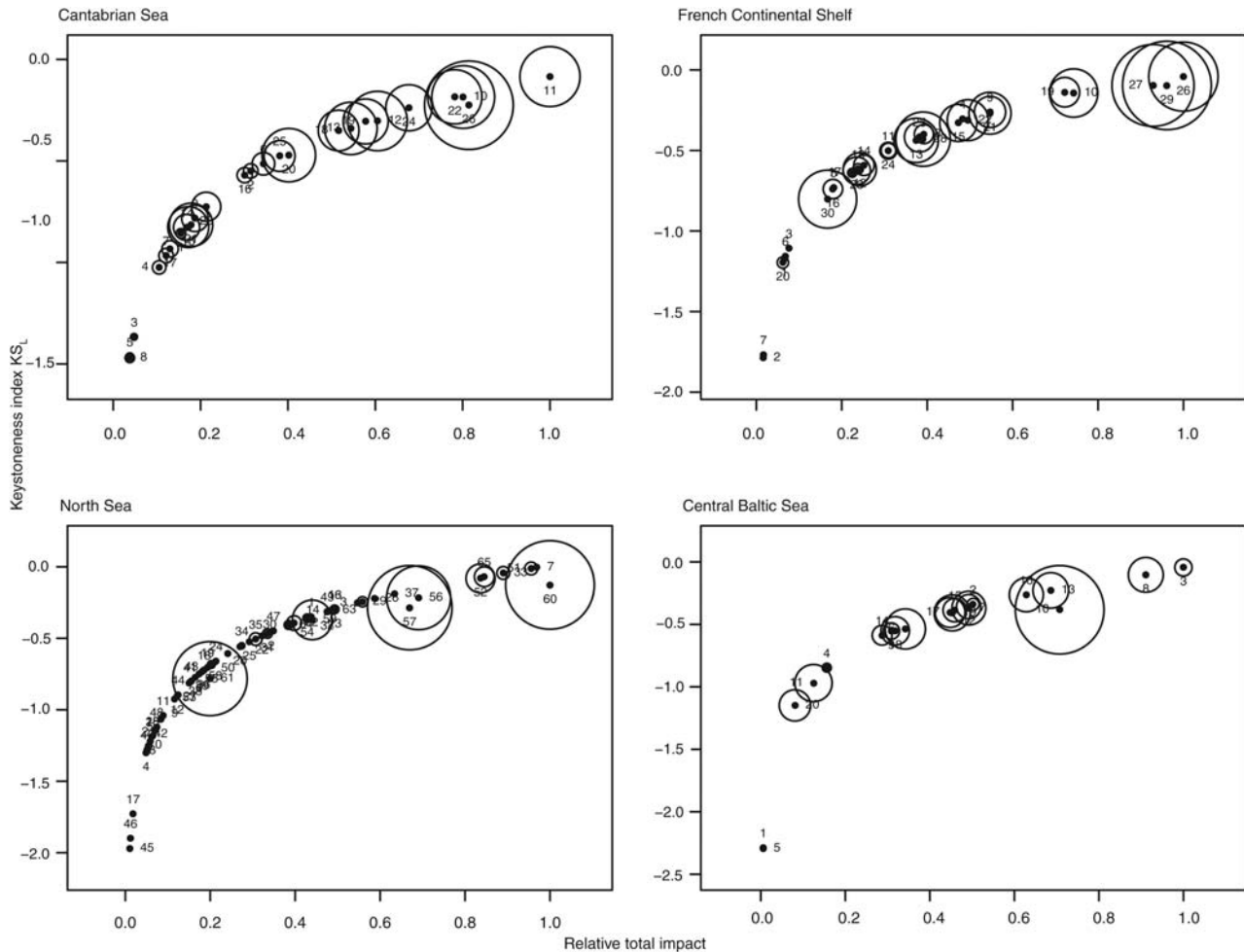
Figure 2. Keystoneness for the functional groups of the four marine trophic webs. For each functional group, the keystoneness index KS_L (*y*-axis) is reported against overall effect (*x*-axis). Overall effects are relative to the maximum effect measured in each trophic web, thus for the *x*-axis the scale is always between 0 and 1. The important 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 Supplementary Table S1. The radii of the circles are proportional to the biomass.

(structuring) compartments within the four functional groups with the highest KS_L index. In all four ecosystems, the KS_L index showed some abundant to very abundant species, such as small pelagic fish, benthic invertebrates and phyto or zooplankton, to be important. The sole functional group that combined a high KS_L (and KS_P) index with a remarkably low biomass was the small pelagic shark group in the North Sea that could as such be considered as a true keystone. Other important functional groups listed in Table 2 are better categorized as key dominant.

Top-down control and the main interactions exerted by important functional groups on the ecosystem

Evaluating the contribution of top-down effects to the overall impact of a set of four important functional groups representative of each shelf shed light on the main mechanism of control within the ecosystem. Based on the mean trophic level of important functional groups and the overall contribution of top-down effects to the response process (Table 2), discrimination between ecosystems was not straightforward, but top-down regulation seemed to

operate in the Central Baltic Sea, while bottom-up control appeared to be dominant in the other three ecosystems. The French Continental Shelf could be positioned at the opposite extreme of the gradient with important functional groups corresponding exclusively to primary producers and lower-order consumers. This was in line with the MTI histograms of important functional groups for the French Continental Shelf case study that depicted a majority of bars pointing upwards, and as such a positive impact of these key resources on other ecosystem components. In addition, top-down control exerted by microzooplankton was concentrated on low trophic level compartments such as bacteria and phytoplankton (Figure 3b).

A focus on small pelagics and zooplankton: importance, positions and roles

When model compartments were classified following the KS_L index, small pelagic fish appeared at the top of the list in the North Sea and Central Baltic Sea (Figure 2, Table 2). Regarding their roles within these ecosystems, in the former, sand eels were

Table 2. The first four functional groups in decreasing order of keystoneness.

	Cantabrian Sea	French Continental Shelf	North Sea	Central Baltic Sea
Rank 1 functional group name	Small demersal fish	Mesozooplankton	Large piscivorous sharks	Cod
Rank 1 trophic level	3.63	2.57	4.92	3.85
KS_L index	−0.085	−0.042	−0.004	−0.044
Td (%)	93.63	6.81	99.98	86.53
Rank 2 functional group name	Suprabenthic zooplankton[a]	Large phytoplankton	Carnivorous zooplankton	Sprat
Rank 2 trophic level	2.74	1	3.23	3.23
KS_L index	−0.184	−0.097	−0.012	−0.103
Td (%)	72	3.37	52.12	93.74
Rank 3 functional group name	Blue whiting	Microzooplankton	Sand eels	*Pseudocalanus* sp.
Rank 3 trophic level	3.79	2.18	3.35	2.3
KS_L index	−0.185	−0.097	−0.043	−0.228
Td (%)	59.41	92.63	22.53	9.59
Rank 4 functional group name	Phytoplankton	Suprabenthivorous demersal fish[b]	Phytoplankton	Other mesozooplankton
Rank 4 trophic level	1	3.49	1	2.2
KS_L index	−0.225	−0.143	−0.069	−0.263
Td (%)	3.35	85.27	2.69	98.17
Mean trophic level ± s.d.	2.8 ± 1.3	2.3 ± 1	3.1 ± 1.6	2.9 ± 0.8
Overall td (%)	57	47	44	72

For each functional group, along with its keystoneness (KS_L), the fraction of the total impact produced by top-down effects (td) is reported. The trophic level of each group is also reported, as estimated by EwE. [a]Euphausiids at 50%. [b]Mostly blue whiting (*Micromesistius poutassou*), with a third of its diet regime composed of suprabenthos.

identified as controlling the abundance of a large range of predators (predatory fish, sea mammals and seabirds) through a bottom-up interaction; negative effects being divided between their prey and fish competitors (Figure 3c). In the latter, sprat was demonstrated to be controlling the abundance of their prey through a top-down interaction (negative impacts in the MTI matrix); positive impacts of sprat on the ecosystem were restricted almost exclusively to the prey of their prey (Figure 3d). These small pelagic species did not occupy a clear intermediate position that would have testified to a wasp-waist mechanism of control. Even if no latitudinal gradient emerged from this analysis, a common identification of zooplankton as a recurrent trophically important functional group was noticed (Table 2). In the Baltic Sea, *Temora* sp., *Acartia* sp. and *Pseudocalanus* sp. were consumed by the same compartments (herring, sprat and cod larvae) but not in the same proportions, *Pseudocalanus* sp. being the major food source for early life stages of cod. In the North Sea, carnivorous zooplankton was eaten by 36 compartments over 68, and the highest predation mortality rates were inflicted by small pelagics, i.e. herring, Norway pout and sand eels. Mesozooplankton over the French Continental Shelf was a major source food, or even the sole source food, for anchovy, sardine and sprat. Given its high absolute biomass, sardine exerted a high predation pressure on this planktonic compartment. In the Cantabrian Sea, suprabenthic zooplankton was eaten by a multitude of small demersal fish, blue whiting and medium-sized pelagic fish (mackerel and horse mackerel). The consumption of mesozooplankton by this compartment corresponded to the major demersal flow. All these important prey-to-predator relationships were converted into bars pointing upwards on the MTI histograms (Figure 3).

Ecosystem structural organization and stability properties

The Cantabrian Sea and the North Sea exhibited the clearest structural organization with lower-order consumers that tended to derive the bulk of their carbon from one of the two resources (phytoplankton or detritus), providing the basis for distinct energy channels. As trophic level increased, so did the tendency to derive carbon from both source webs. Graphically, the percentage of carbon derived from phytoplankton progressively shifted from 0 or 100% for lower trophic levels to 50−60% for higher trophic levels, resulting in a dome-shaped curve (Figure 4). This dome-shaped pattern was fairly consistent in the French Atlantic Shelf, partly because of the decomposition of zooplankton into three size-classes (groups 25, 26 and 27) feeding on both phytoplankton and detritus. This revealed the potential sensitivity of this analysis to trophic grouping. In the Baltic Sea, top trophic levels seemed to obtain carbon from both sources, but the structuring into two discrete trophic chains was not as evident as in other models. The coupling between the grazing and the detrital pathways seemed to be operating at very low trophic levels compared to the other three systems.

Discussion
The pivotal role of benthos and the benthic/pelagic interface

Libralato *et al.* (2006) demonstrated the importance of the lower part of the trophic web (phyto- and zooplankton) in shallow coastal ecosystems, where other benthic groups also tend to have a high KS index. Mediterranean Shelf ecosystems that were not
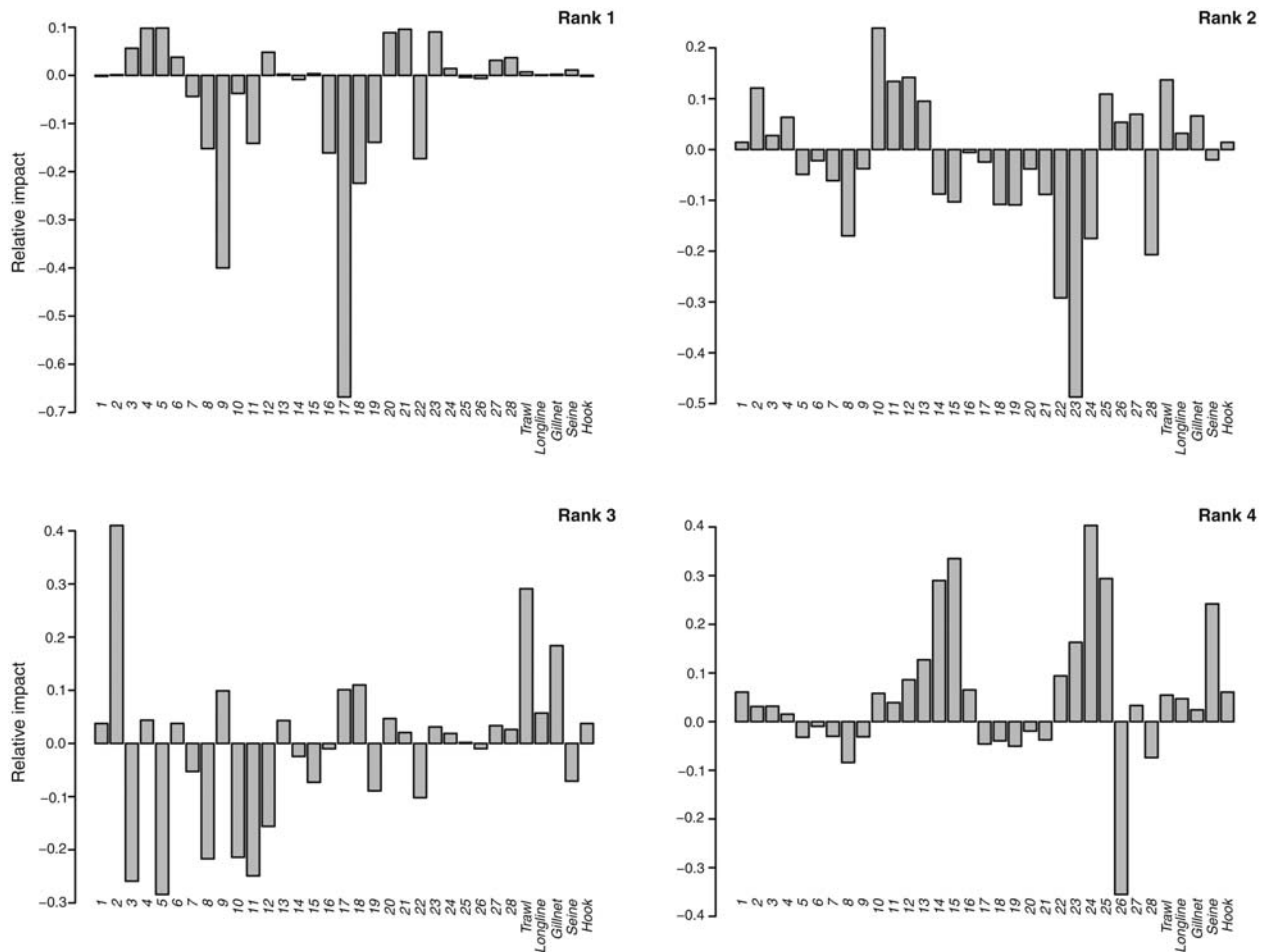
Figure 3. Combined direct and indirect trophic impacts for the first four important functional groups of each case study: (a) the Cantabrian Sea, (b) the French Continental Shelf, (c) the North Sea, and (d) the Baltic Sea, on all the other groups that constituted the model. The *y*-axis corresponds to relative impacts. See Table 2 for the names of important functional groups. Numbers refer to a code for compartments, provided in Supplementary Table S1. The bars pointing upwards indicate positive impacts, while the bars pointing downwards show negative impacts. Given the number of compartments in the North Sea model, potential impacts of important functional groups on the various fishing fleets were not represented.

considered in the previous study, namely the North Aegean, South Catalan and North-Central Adriatic seas (8374, 4500 and 55 000 km², respectively), showed some common features, including a strong benthic–pelagic coupling (Tsagarakis *et al.*, 2010). In the present study, the same key functional aspect, namely the importance of benthos, was identified in the two ecosystems pertaining to the Bay of Biscay, while findings suggested that the large northern shelf ecosystems (the North and Baltic seas) >200 000 km² were dominated by pelagic compartments organized in linear food chains. This dichotomy could be partly explained by the spatial scale at which the food-web is modelled and which is rarely taken into account in comparative studies. Large, long-lived pelagic species, with higher dispersal capacities, such as sharks and cod in the North and Baltic Seas, respectively, most probably better characterize the functioning of large entities, while demersal and benthic organisms, some presenting a sedentary life history, would be more restricted to sub-marine regions reflecting local to regional conditions, such as suprabenthic zooplankton and blue whiting in the Cantabrian Sea and the French Continental

Shelf, respectively (Rogers *et al.*, 2010). Additionally, eutrophication and associated hypoxia, occurring in systems with a low rate of water turnover, and the well-known deleterious impacts on benthic ecosystems, are problems shared across the North Sea and the Baltic Sea. The benthic organisms living in the bottoms depleted of oxygen either die or have to move elsewhere; this leading in extreme cases to defaunated sediments (Callaway *et al.*, 2007). As discussed by Tomczak *et al.* (2012), stochastic interplays between climatic, environmental and anthropogenic forces cause food-web reorganization and redirection of dominant flows within the Central Baltic ecosystem, from benthic-detrital pathways to more pelagic.

Within the Bay of Biscay, the importance of key dominant species with benthic behaviour was even more clearly noted for the Spanish Shelf. Blooms of the Cantabrian Sea generally have a short duration due to exhaustion of nutrients and as such are incapable of generating a stable channelization of energy through the zooplankton (Bode *et al.*, 1996). The result is that a large part of this production is exported to the bottom as phytodetritus,
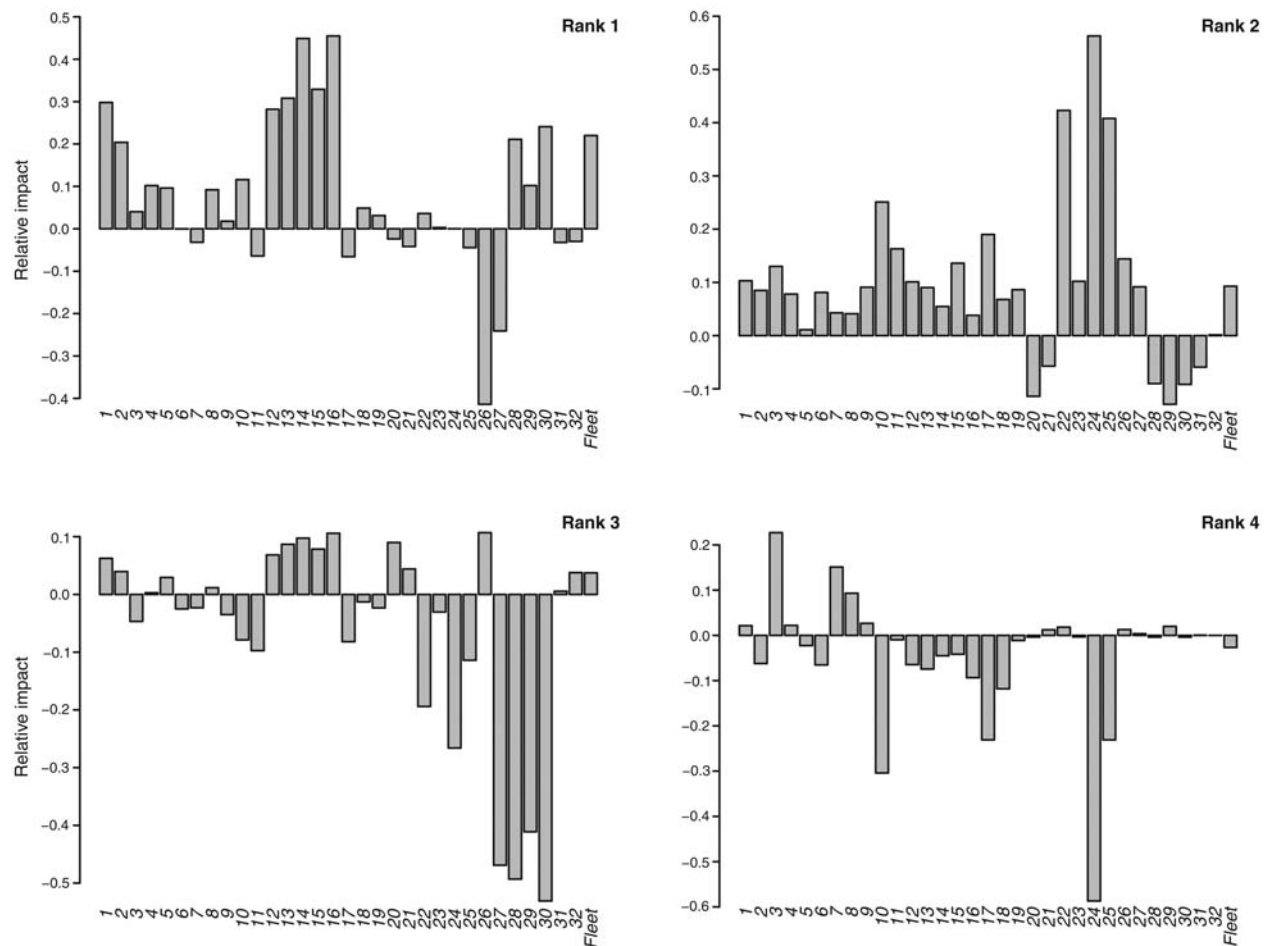
Figure 3. Continued

which forms a substantial basal resource for the benthic energy channel (Greenstreet *et al.*, 2009). In contrast, primary production processes over the French Shelf, associated with the spring river outflows, are more stable, have a wider spatial coverage, and are localized in upper water layers. This is mainly responsible for the high biomass of small pelagic fish that use these waters as a spawning area, guaranteeing the survival of their first life stages (Motos *et al.*, 1996). A second model for the Cantabrian Sea corresponding to the 2004 situation has been developed but publication is still in progress. The first two important functional groups are again strictly benthic organisms (benthos feeder decapods) or groups that link the benthic and pelagic domains through vertical migration (squids) (Francisco Sanchez, pers. comm.). This temporal comparison emphasizes the importance of those organisms that rely on secondary benthic production in the Bay of Biscay.

Zooplankton: a common foundation for Northeast Atlantic ecosystems

The comparison presented here highlights the fact that ecosystems differing both in terms of real structures (semi-enclosed vs. open basins) and model representations (adoption of different aggregations) share similar features, namely the importance of pelagic and suprabenthic zooplankton in influencing the entire community. In

the first four model compartments ranking high in terms of the KS index, a large majority were identified as key dominant (structuring) functional groups. In these lists, zooplankton appeared trophically important, mainly through their consumption by small pelagics.

Ecological knowledge supports the fact that there are strong interactions between small pelagic fish and zooplankton compartments over temperate continental shelves. Over the Bay of Biscay Shelf, small pelagics were estimated to take between 60 and 65% of the total predation on mesozooplankton and in that respect favour high trophic efficiencies along the planktonic food-web (Marquis *et al.*, 2011). In the Central Baltic Sea, a strong constraint on calanoid copepod dynamics was demonstrated to be exerted by clupeid fish (herring and sprat) predating on this group (Möllmann and Köster, 2002). In a modelling study, Steele and Ruzicka (2011) noted the importance of including lower trophic responses in food-web models which are intended for ecosystem-based managements of fish stocks in shelf upwelling ecosystems. Accounting for variations in the dynamics of planktonic ecosystems has been demonstrated to be an essential step in understanding upper trophic level yields in the context of ecosystem models applied to fishery and marine spatial planning problems (Friedland *et al.*, 2012). Zooplankton usually undergoes consequent spatio-temporal variations and outbreaks, and thus its structuring
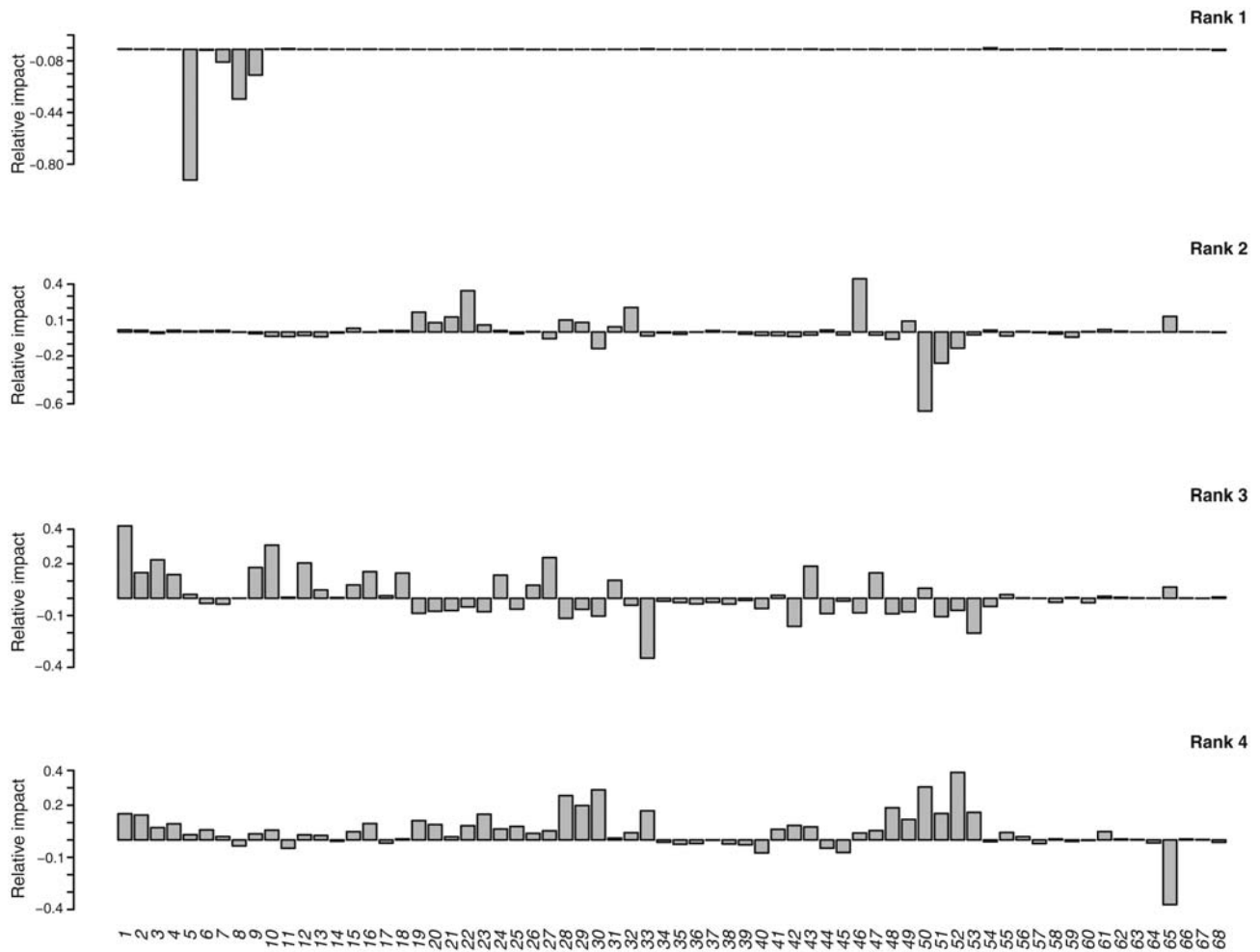
Figure 3. Continued

role might be only played in pulses, or at a regional scale (Casini *et al.*, 2008).

A latitudinal gradient in trophic control of shelf ecosystems

In North Atlantic exploited ecosystems, top-down control was demonstrated to dominate in northern areas, where species diversity and ocean temperatures were low, whereas bottom-up control dominated in warmer, more speciose southern areas (Frank *et al.*, 2007). More realistically, where very cold and species-poor areas might readily succumb to top-down control and recover slowly (if ever), warmer areas with more species might oscillate between top-down and bottom-up control, depending on exploitation rates and, possibly changing temperature regimes. Hence, top-down structuring is considered not to be the norm for shelf ecosystems, but instead to represent a form of biological instability. The authors argue that species diversity, acting through compensation for the overfished predators by non-target species, and temperature, which influences the demographic rates of the component species (recruitment and somatic growth), provide a robust explanation for the resilience to overfishing effects in the southern areas and the manifestation of negative effects in the northern ones, namely the emergence of top-down control.

This latitudinal pattern, demonstrated through the analysis of long time-series was reinforced by the present comparative study based on ecosystem models and ecological network analysis. In the present work, the sole ecosystem controlled by top-down processes, i.e. the Baltic Sea, was located far north and poorly exhibited the structure described by Rooney *et al.* (2006) as a necessary prerequisite to stability for a broad range of ecosystems. The main interactions estimated through dynamic simulations by Tomczak *et al.* (2012) were congruent with our findings and corresponded to top-down effects between the adult sprat and all their prey, as well as cod on the macrozoobenthos and adult herring. In the Baltic proper, climate-related effects and changes in the hydrography and fishery pressure have led to pronounced reorganizations within and across the trophic levels of zooplankton and fish during the late 1980s; such induced changes in the food-web structure and function were demonstrated to affect in the end the trophic control (Österblom *et al.*, 2007). Previous case-specific studies of other high-latitude/boreal systems (e.g. the Northern Gulf of St Lawrence, Newfoundland, the Norwegian and Barents Seas, and the Scotian Shelf) confirmed the key role of large cod combined with a top-down view of marine food-webs (Pedersen *et al.*, 2008).

In a Caribbean marine food-web, Bascompte *et al.* (2005) showed that strong omnivory, strictly defined as a predator that consumes a given prey and also the resource of this prey, often
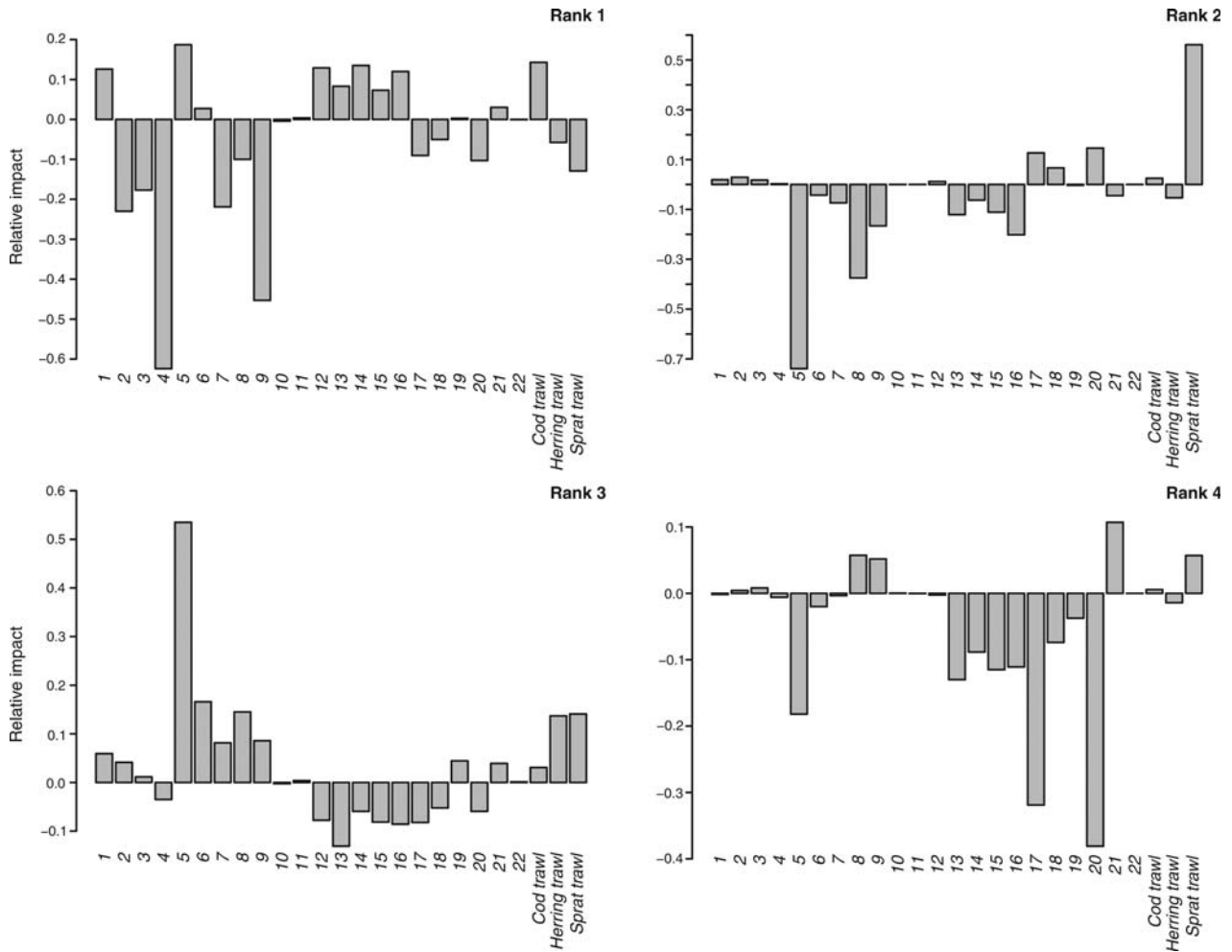
Figure 3. Continued

accompanies strong interactions, and reduces the likelihood of fishery-induced trophic cascades. In EwE the calculation of an index which characterizes the diversity of consumer/prey relationships is implemented, i.e. the System Omnivory Index (SOI). Values were substantially lower for the Central Baltic Sea ecosystem and for sub-ecosystems modelled in this area [Puck Bay, Curonian Lagoon, Lithuanian coast, Gulf of Riga coast and Pärnu Bay; Tomczak *et al.* (2009)], meaning that predators do not feed on many trophic levels. Nevertheless, full-system indicators such as SOI are heavily dependent on the model structure, size and complexity (Christensen, 1995) and as such are not fully comparable between ecosystems. Even if multiple mechanisms are at play in driving community dynamics, divergence in species diversity and trophic complexity in the Baltic Proper may partly explain the appearance of top-down control in this zone.

Among the four ecosystems included in this work, the North Sea has very likely been the most studied in terms of major flow control. A majority of studies, including this one, suggest that the North Sea system is mainly driven by bottom-up forces through climate (Frederiksen *et al.*, 2006). A study based on Ecosim simulations demonstrated that the main driving force of the biomass dynamics exploiting fish stocks in the North Sea from 1973–2003 was, nevertheless, fishing effects (Mackinson *et al.*, 2009). The latest study to date concluded there is a possible wasp-waist interaction in the North Sea ecosystem (Fauchald *et al.*, 2011).

Towards the implementation of a new stability analysis in EwE

Beyond the existence of energy channels coupled by top-predators, two dynamic properties confer overall stability to the ecosystem: the ability to respond quickly to changes and the capacity to dampen potentially destabilizing oscillatory fluctuations (Rooney *et al.*, 2006). In this regard, our analysis of ecosystem stability based solely on a graphical representation of energy channels at steady-state should be viewed as the first part of a two-step process. The first part is dedicated to the food-web structural characteristics (compartmentation and coupling) and the second part to the dynamic properties (channel productivity and turnover rates). The present paper provides all the elements required to perform the structural part of the stability analysis proposed by Rooney *et al.* (2006) on every ecosystem model. As such, a practical "bridge" between ecosystem modelling and theoretical ecology has been proposed, which is not often the case in scientific literature.

In the present work, the ecosystem that did not exhibit a structure described as potentially stabilizing was also the one with the lowest level of complexity. This particularly low number of model compartments could prevent, to some extent, the
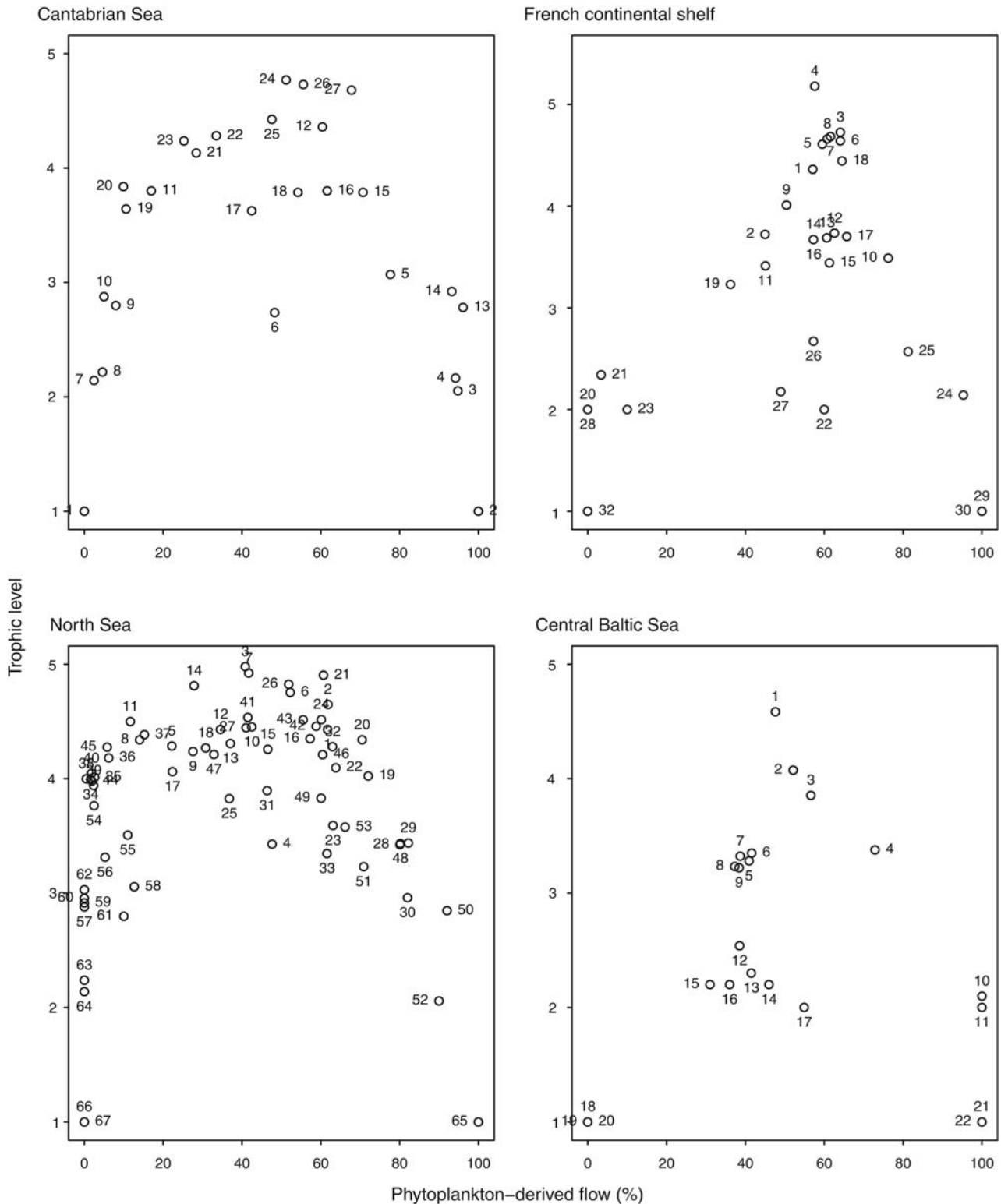
Figure 4. Food-web representations based on estimations of the percentage of flow derived from basal resources. Trophic position/level is shown on the *y*-axis. Numbers refer to a code for compartments provided in Supplementary Table S1.

generation of a dome-shaped curve, which is at the basis of Rooney's analysis of stability. Other potentially important food-web components, such as birds, harbour porpoises (*Phocoena phocoena*), or flounder (*Platichthys flesus*) were missing in the Central Baltic Sea model, because their biomass in the pelagic food-web is low and/or very uncertain. Benthic components were, for the same reasons, insufficiently represented (Tomczak *et al.*, 2012). Another potential drawback of the analysis

concerned detritus and the detrital pathway, which are poorly constrained by lack of data in the majority of marine ecosystem models. As such, the greater uncertainty of detritus estimates entered in Ecopath models, and the potential resulting bias, have been acknowledged as this could have lowered the relative importance of this channel compared to the pelagic one based on plankton.

Conclusions

This study was a comparative analysis of existing food-web models of four LMEs of the Northeast Atlantic, and revealed several underlying similarities and differences in system structure and trophic flows. Zooplankton appeared to play a pivotal role in continental shelves, both as an intermediary in the coupling between benthic and pelagic domains on the Bay of Biscay Shelf, and in the transfer of energy to higher trophic levels through pelagic chains in more northern latitudes. In spite of their geomorphological differences, the Spanish and French parts of the Bay of Biscay Shelf exhibited a coherent set of general characteristics regarding their functioning. In the context of ecosystem-based management, this result could influence living marine resource management as it suggests potential gain in managing these marine systems as a single entity. Bottom-up processes were confirmed as the major control mechanisms operating over temperate continental shelves. Nevertheless, it is likely that there are temporary phases of top-down control, depending to some extent on the exploitation level. In accordance with theory and previous observations, top-down control was demonstrated in the northernmost ecosystem, namely the Baltic Sea, which was also the ecosystem presenting a structure poorly consistent with network stability. This finding could have significant implications for the definition of indicators of Good Environmental Status for these LMEs, as it contrasts with the common view that state or pressure indicators should be systematically selected in the upper part of the food-web.

Supplementary material

Supplementary material is available at the ICESJMS online version of the paper. It corresponds to a list of compartments for the four ecosystem models.

Acknowledgements

Funding

References

Amante, C., and Eakins, B. W. 2009. ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis. NOAA Technical Memorandum NESDIS NGDC-24. 19 pp.

Ayón, P., Swartzman, G., Bertrand, A., Gutiérrez, M., and Bertrand, S. 2008. Zooplankton and forage fish species off Peru: large-scale bottom-up forcing and local-scale depletion. Progress in Oceanography, 79: 208–214.

Bascompte, J., Melián, C. J., and Sala, E. 2005. Interaction strength combinations and the overfishing of a marine food web. Proceedings of the National Academy of Sciences of the United States of America, 102: 5443–5447.

Bode, A., Casas, B., Fernández, E., Marañón, E., Serret, P., and Varela, M. 1996. Phytoplankton biomass and production in shelf waters off NW Spain: spatial and seasonal variability in relation to upwelling. Hydrobiologia, 341: 225–234.

Callaway, R., Engelhard, G. H., Dann, J., Cotter, J., and Rumohr, H. 2007. A century of North Sea epibenthos and trawling: comparison between 1902–1912, 1982–1985 and 2000. Marine Ecology Progress Series, 346: 27–43.

Casini, M., Lövgren, J., Hjelm, J., Cardinale, M., Molinero, J. C., and Kornilovs, G. 2008. Multi-level trophic cascades in a heavily exploited open marine ecosystem. Proceedings of the Royal Society B: Biological Sciences, 275: 1793–1801.

Christensen, V. 1995. Ecosystem maturity - towards quantification. Ecological Modelling, 77: 3–32.

Christensen, V., and Pauly, D. 1992. ECOPATH II - a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling, 61: 169–185.

Christensen, V., and Walters, C. J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling, 172: 109–139.

Christensen, V., Walters, C. J., Pauly, D., and Forrest, R. 2008. Ecopath with Ecosim version 6. User guide - November 2008. Lenfest Ocean Futures Project 2008. Fisheries Centre, The University of British Columbia, Vancouver. 235 pp.

Coll, M., and Libralato, S. 2012. Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea. Fish and Fisheries, 13: 60–88.

Coll, M., Shannon, L. J., Moloney, C. L., Palomera, I., and Tudela, S. 2006. Comparing trophic flows and fishing impacts of a NW Mediterranean ecosystem with coastal upwelling systems by means of standardized models and indicators. Ecological Modelling, 198: 53–70.

Cury, P., Bakun, A., Crawford, R. J. M., Jarre, A., Quinones, R. A., Shannon, L. J., and Verheye, H. M. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES Journal of Marine Science, 57: 603–618.

Dunne, J. A., Brose, U., Williams, R. J., and Martinez, N. D. 2005. Modeling food-web dynamics: complexity-stability implications. In Aquatic Food Webs - an Ecosystem Approach, pp. 117–238. Ed. by A. Belgrano, U. M. Scharler, J. A. Dunne, and R. E. Ulanowicz. Oxford University Press.

Fauchald, P., Skov, H., Skern-Mauritsen, M., Johns, D., and Tveraa, T. 2011. Wasp-Waist interaction in the North Sea ecosystem. PLoS ONE, 6: e22729.

Fedor, A., and Vasas, V. 2009. The robustness of keystone indices in food webs. Journal of Theoretical Biology, 260: 372–378.

Frank, K. T., Petrie, B., and Shackell, N. L. 2007. The ups and downs of trophic control in continental shelf ecosystems. Trends in Ecology and Evolution, 22: 236–242.

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C., and Wanless, S. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. Journal of Animal Ecology, 75: 1259–1268.

Friedland, K. D., Stock, C., Drinkwater, K. F., Link, J. S., Leaf, R. T., Shank, B. V., Rose, J. M., et al. 2012. Pathways between primary production and fisheries yields of Large Marine Ecosystems. PLoS ONE, 7: pe28945.

Greenstreet, S., Fraser, H., Cotter, J., and Pinnegar, J. 2009. Assessment of the "State" of the Demersal Fish Communities in OSPAR Regions II, III, IV and V. Monitoring and Assessment Series, OSPAR Commission, London, UK. 88 pp.

Hunt, G. L. 2006. Evidence for bottom-up control of upper-trophic-level marine populations: is it scale dependent? *In* Whales, Whaling and Ocean Ecosystems, pp. 50–67. Ed. by J. A. Estes, D. P. DeMaster, D. F. Doak, T. M. Williams, and R. L. Brownell. University of California Press, Berkeley, CA.

Hunt, J. G. L., and McKinnell, S. 2006. Interplay between top-down, bottom-up, and wasp-waist control in marine ecosystems. Progress in Oceanography, 68: 115–124.

Johnson, G. A., Niquil, N., Asmus, H., Bacher, C., Asmus, R., and Baird, D. 2009. The effects of aggregation on the performance of the inverse method and indicators of network analysis. Ecological Modelling, 220: 3448–3464.

Lassalle, G., Gascuel, D., Le Loc'h, F., Lobry, J., Pierce, G. J., Ridoux, V., Santos, M. B., et al. 2012. An ecosystem approach for the assessment of fisheries impacts on marine top-predators: the Bay of Biscay case study. ICES Journal of Marine Science, 69: 925–938.

Lassalle, G., Lobry, J., Le Loc'h, F., Bustamante, P., Certain, G., Delmas, D., Dupuy, C., et al. 2011. Lower trophic levels and detrital biomass control the Bay of Biscay continental shelf food web: implications for ecosystem management. Progress in Oceanography, 91: 61–75.

Libralato, S., Christensen, V., and Pauly, D. 2006. A method for identifying keystone species in food web models. Ecological Modelling, 195: 153–171.

Lobry, J., David, V., Pasquaud, S., Lepage, M., Sautour, B., and Rochard, E. 2008. Diversity and stability of an estuarine trophic network. Marine Ecology Progress Series, 358: 13–25.

Mackinson, S., and Daskalov, G. M. 2007. An ecosystem model of the North Sea to support an ecosystem approach to fisheries management: description and parameterisation. Science Series Technical Report, Cefas Lowestoft, UK, 142. 196 pp.

Mackinson, S., Daskalov, G., Heymans, J. J., Neira, S., Arancibia, H., Zetina-Rejón, M., Jiang, H., et al. 2009. Which forcing factors fit? Using ecosystem models to investigate the relative influence of fishing and changes in primary productivity on the dynamics of marine ecosystems. Ecological Modelling, 220: 2972–2987.

Marquis, E., Niquil, N., Vézina, A. F., Petitgas, P., and Dupuy, C. 2011. Influence of planktonic foodweb structure on a system's capacity to support pelagic production: an inverse analysis approach. ICES Journal of Marine Science, 68: 803–812.

Martinez, N. D., Williams, R. J., and Dunne, J. A. 2005. Diversity, complexity, and persistence in large model ecosystems. *In* Ecological Networks: Linking Structure to Dynamics in Food Webs, pp. 163–185. Ed. by M. Pascual, and J. A. Dunne. Oxford University Press.

Megrey, B. A., Link, J. S., Hunt, G. L., and Moksness, E. 2009. Comparative marine ecosystem analysis: applications, opportunities, and lessons learned. Progress in Oceanography, 81: 2–9.

Möllmann, C., Conversi, A., and Edwards, M. 2011. Comparative analysis of European wide marine ecosystem shifts: a large-scale approach for developing the basis for ecosystem-based management. Biology Letters, 7: 484–486.

Möllmann, C., and Köster, F. W. 2002. Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. Journal of Plankton Research, 24: 959–978.

Motos, L., Uriarte, A., and Valencia, V. 1996. The spawning environment of the Bay of Biscay anchovy (*Engraulis encrasicolus* L.). Scientia Marina, 60: 140–177.

Niquil, N., Kagami, M., Urabe, J., Christaki, U., Viscogliosi, E., and Sime-Ngando, T. 2011. Potential role of fungi in plankton food web functioning and stability: a simulation analysis based on Lake Biwa inverse model. Hydrobiologia, 659: 65–79.

Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R., and Folke, C. 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. Ecosystems, 10: 877–889.

Paine, R. T. 1969. A note on trophic complexity and community stability. American Naturalist, 103: 91–93.

Pedersen, T., Nilsen, M., Nilssen, E. M., Berg, E., and Reigstad, M. 2008. Trophic model of a lightly exploited cod-dominated ecosystem. Ecological Modelling, 214: 95–111.

Pinnegar, J. K., Blanchard, J. L., Mackinson, S., Scott, R. D., and Duplisea, D. E. 2005. Aggregation and removal of weak-links in food-web models: system stability and recovery from disturbance. Ecological Modelling, 184: 229–248.

Planque, B., Lazure, P., and Jégou, A. M. 2004. Detecting hydrological landscapes over the Bay of Biscay continental shelf in spring. Climate Research, 28: 41–52.

Polovina, J. J. 1984. Model of coral reef ecosystem I. The Ecopath model and its application to French Frigate Shoals. Coral Reefs, 3: 1–11.

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., Daily, G., et al. 1996. Challenges in the quest for keystones. BioScience, 46: 609–620.

Pranovi, F., and Link, J. S. 2009. Ecosystem exploitation and trophodynamic indicators: a comparison between the Northern Adriatic Sea and Southern New England. Progress in Oceanography, 81: 149–164.

Rogers, S., Casini, M., Cury, P., Heath, M., Irigoien, X., Kuosa, H., Scheidat, M., et al. 2010. Marine Strategy Framework Directive – Task group 4 report food webs. EUR - Scientific and Technical Research series, Joint Research Centre, Luxembourg: EUR 24343 EN. 55 pp.

Rooney, N., McCann, K., Gellner, G., and Moore, J. C. 2006. Structural asymmetry and the stability of diverse food webs. Nature, 442: 265–269.

Sanchez, F., and Olaso, I. 2004. Effects of fisheries on the Cantabrian Sea shelf ecosystem. Ecological Modelling, 172: 151–174.

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdana, Z. A., Finlayson, M., Halpern, B. S., et al. 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. BioScience, 57: 573–583.

Steele, J. H., and Ruzicka, J. J. 2011. Constructing end-to-end models using Ecopath data. Journal of Marine Systems, 87: 227–238.

Tomczak, M. T., Müller-Karulis, B., Järv, L., Kotta, J., Martin, G., Minde, A., Põllumäe, A., et al. 2009. Analysis of trophic networks and carbon flows in south-eastern Baltic coastal ecosystems. Progress in Oceanography, 81: 111–131.

Tomczak, M. T., Niiranen, S., Hjerne, O., and Blenckner, T. 2012. Ecosystem flow dynamics in the Baltic Proper - using a multitrophic dataset as a basis for foodweb modelling. Ecological Modelling, 230: 123–147.

Tsagarakis, K., Coll, M., Giannoulaki, M., Somarakis, S., Papaconstantinou, C., and Machias, A. 2010. Food-web traits of the North Aegean Sea ecosystem (Eastern Mediterranean) and comparison with other Mediterranean ecosystems. Estuarine, Coastal and Shelf Science, 88: 233–248.

Ulanowicz, R. E., and Puccia, C. J. 1990. Mixed trophic impacts in ecosystems. Coenoses, 5: 7–16.

Vander Zanden, M. J., Essington, T. E., and Vadeboncoeur, Y. 2005. Is pelagic top-down control in lakes augmented by benthic energy pathways? Canadian Journal of Fisheries and Aquatic Sciences, 62: 1422–1431.

Varela, M. 1996. Phytoplankton ecology in the Bay of Biscay. Scientia Marina, 60: 45–53.

Handling editor: Jason Link