Reaction of an estuarine food web to disturbance: Lindeman's perspective

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ABSTRACT: Currently, a central demand of coastal and marine food web researchers is the search for holistic and functional ecosystem health indicators. Based on concepts directly derived from R. L. Lindeman's work (Lindeman 1942; Ecology 23:399–418), 6 estuarine food web models were analysed to assess the potential impact of multiple disturbances on the trophic state of food webs. The models described a *Zostera noltii* meadow and a bare sediment site in the Mondego estuary, Portugal, during 3 distinct time periods corresponding to (1) nutrient enrichment, (2) the implementation of mitigation measures, and (3) after a centenary flood. We tested 4 candidate metrics, directly derived from the trophic-dynamic concepts proposed by Lindeman (1942): food chain length, the detritivory/herbivory ratio, trophic efficiency per trophic level and mean trophic efficiency. Based on this case study, none of the metrics are yet ready to be used per se as operational metrics to quantify and interpret the impact of disturbances on the ecosystem's trophic state. Trophic efficiency appeared to be sensitive to external pressures. However, the mean trophic efficiency of the system might not be sufficient to draw conclusions about the trophic efficiency of the ecosystem: trophic efficiency should be observed at the trophic level in order to better understand cascading effects within food webs.

KEY WORDS: Ecosystem function· Food web models · Ecological network analysis · Trophic efficiency · Ecological indicator · Mondego estuary

INTRODUCTION

R. L. Lindeman's (1942) scientific paper entitled 'The Trophic-Dynamic Aspect of Ecology' provided a framework for future research on energy flow and nutrient budgets in ecosystems and set the foundations for the development of systems ecology. Lindeman established a theoretical model for nutrient cycling expressed explicitly in terms of energy flow described by mathematical equations and developed the concept of the trophic pyramid. His adviser, G. E. Hutchinson, acknowledged Lindeman's seminal work in an addendum to Lindeman (1942), writing that 'the final statement of the structure of a biocoenosis consists of a pair of numbers, one an integer determining the level, one a fraction determining the efficiency, [which] may even give some hint of an undiscovered type of mathematical treatment of biological communities' (p. 418). Later, in 1979, Hutchinson added the statement: 'Lindeman's (1942) paper was the first one to indicate how biological communities could be expressed as net-

works or channels through which energy is flowing and being dissipated, just as would be the case with electricity flowing through a network of conductors' (Hutchinson 1979, p. 246).

In the same period, Cook (1977) pointed out that Lindeman's contribution stressed the major role of trophic functions, particularly quantitative relations, in the determination of community patterns through succession, and established the validity of a theoretical orientation in ecology by creating a theoretical model for trophic interactions, quantitatively represented by mathematical relations. This allowed Lindeman to develop a number of predictions with which the validity of the model could be assessed. Finally, the trophic-dynamic approach identified a fundamental dynamic process — energy flow — with which the seasonal trophic relations of organisms could be integrated into the long-term process of community change.

Lindeman's work was also criticised. For instance, Cousins (1985) found Lindeman's description of ecosystems to be an oversimplified description of ecosystems since relationships are rarely linear, and because species often consume at different trophic levels. In response to Cousins' remarks, Ulanowicz (1995) defended the Lindeman scheme as a quantitative description of behaviour at the community level. According to Ulanowicz (1995), it was only necessary to abandon the notion of discrete trophic levels and then most ambiguities concerning trophic status would vanish. That is, a given taxon does not need to be wholly assigned to a single trophic level, and vice versa. This idea built upon the proposition of Odum & Heald (1975) that species could be positioned at some non-integer trophic levels (i.e. the weighted average of the number of links in the various pathways along which it consumes). Ulanowicz proposed the use of what he called the 'Lindeman spine', a linear chain that sums up the information of a complex trophic network by dividing the compartments and their activity into discrete levels, the first level being composed of both primary producers and detritus. This tool maps the complicated networks of the ecosystem's flows into a common topological form that allows distinct ecosystems to be compared.

Complementary to these studies are the concepts developed by Odum (1969, 1985) concerning food web analysis in the context of the development of ecosystems, and in particular in situations of stress, defined as 'unusual external perturbations' (Odum 1985). Today, the key question in ecology remains: How does an ecosystem react to disturbance? Currently, one of the major challenges is to find indicators that can adequately assess the ecological condi-

tion of a natural system, considering it as a functional unit (Rombouts et al. 2013). Interestingly, a candidate metric is 'efficiency', first defined by Lindeman (1942) for each trophic level. Working on Lake Mendota, he produced the first measures of this index described as the percentage of the production of one trophic level converted to production by the next trophic level. Since then, this index has been and is still widely used to assess the trophic state of an ecosystem, and is either known as 'trophic efficiency' or 'transfer efficiency' (e.g. Pauly & Christensen 1995, Jennings et al. 2002, Libralato et al. 2008, Coll et al. 2009, Fiscus 2009, Pranovi & Link 2009, Baird et al. 2012, Heymans et al. 2012). Reflecting on different scenarios of fishing pressure, Gascuel (2005) proposed that trophic efficiency should be considered as a key characteristic of the functioning of ecosystems, associated with its sensitivity to fishing pressure. Pranovi & Link (2009) also showed different trophic efficiency values among fishery-exploited systems, arguing the need for between-site comparisons to make the generalisation that is necessary for successful ecosystem-based management. An emerging specialised literature proposed the use of trophic efficiency as a descriptor of ecosystem health, especially in lakes (Xu & Mage 2001, Hecky 2006) and in ecosystem-based fishery management (Rochet & Trenkel 2003, Libralato et al. 2008, Coll et al. 2009).

Another candidate metric, which was also directly inspired by Lindeman (1942) when he referred to the role of saprophageous organisms and heterotrophic bacteria, and which was formalised by Ulanowicz (1992), is the detritivory/herbivory (D/H) ratio (or herbivory/detritivory ratio). This ratio has already been tested as a candidate for defining functional indicators of the food web, but the observed trend varied according to the situation described. For example, Ulanowicz (1992) observed a lower D/H ratio in disturbed situations, whereas Dame & Christian (2007) observed exactly the opposite trend.

Based on Lindeman's original concepts, the scientific community developed and evaluated new indicators to depict the trophic status of ecosystems and to link them to system stability and resilience (e.g. Ulanowicz & Puccia 1990, Christensen & Pauly 1993, Libralato et al. 2006, 2008, Heymans et al. 2007). With the ultimate goal of providing functional indicators for ecosystem-based management, and following European directives (e.g. Good Ecological Status, Water Framework Directive), specific indicators were proposed. For instance, regarding fishery pressure, different indices were commonly adopted and used in the literature, such as the primary production

required to sustain fisheries (Christensen & Pauly 1993), or the L index, which provides a basis for estimating the maximum number of 'acceptable' catches (Libralato et al. 2008). From a more functional perspective, the 'keystoneness' index was developed by Libralato et al. (2006) in order to assess the structuring role of species (or functional groups) in food webs, and the Mixed Trophic Impact index to address the effect that an increase in the biomass of one impacting group would have on the biomass of another (Ulanowicz & Puccia 1990).

Because they attract a large human population, and because of their position at the intersection of the marine and terrestrial realms, estuaries are dynamic systems subjected to multiple and diverse pressures. These include pollution, excess nutrient loading, habitat destruction and biodiversity changes (Halpern et al. 2008). Estuaries are also naturally stressed systems, and Elliott & Quintino (2007) emphasised how difficult it is to differentiate natural from human stressors. They are the object of numerous studies on the functioning of ecosystems, and authors often aim to describe how these ecosystems evolve in this multiple-pressure context. Some of these studies have been based on methodologies derived from trophodynamic concepts and have used inter-system comparisons of either different periods or sites (Christian et al. 2005, 2009, Patrício et al. 2006, Leguerrier et al. 2007, Heymans et al. 2012, Niquil et al. 2012, Chrystal & Scharler 2014). In these studies, the set of indices compared is either wide or focused on ascendency-derived indices. The originality of the present paper lies in its focus (for an inter-system comparison) on the indices directly derived from Lindeman's (1942) original paper.

In this paper, we tested whether Lindeman's trophic-dynamic concepts could be used to derive holistic and functional indicators of ecosystem health. For this, we assessed the impact of disturbances affecting estuarine food webs on properties directly derived from Lindeman (1942). We analysed the effects of eutrophication, changes in the hydrodynamic regime during the implementation of mitigation measures and an extreme flood event on several trophic-dynamic attributes: mean trophic level, trophic efficiencies (trophic efficiency per trophic level and mean trophic efficiency from level II to IV),

the D/H ratio and Lindeman's spine length. Due to the large amount of information on the structure and functioning of the intertidal food webs in the Mondego estuary (Portugal) (Patrício & Marques 2006, Patrício et al. 2004, 2009, Baeta et al. 2009a,b, 2011), this system was chosen as a case study.

MATERIALS AND METHODS

Study site

The Mondego estuary is a relatively small (860 ha), warm-temperate, polyhaline intertidal system located on the western Atlantic coast of Portugal. It consists of 2 arms: North arm and South arm (Fig. 1). The southern arm is characterised by intertidal mudflats (almost 75% of the area), which are exposed at low tide. The tidal range varies between 0.35 and 3.3 m depending on the site and the tide coefficient, while the water residence time varies between 1 or 2 d (northern arm) and 3 d (southern arm).

From 1991 to 1997, the communication between the 2 arms of the estuary became totally interrupted in the upstream area, which caused the river discharge to flow essentially through the northern arm. Consequently, water circulation in the southern arm became mainly dependent on tides and on the small freshwater input from a tributary, the Pranto River,
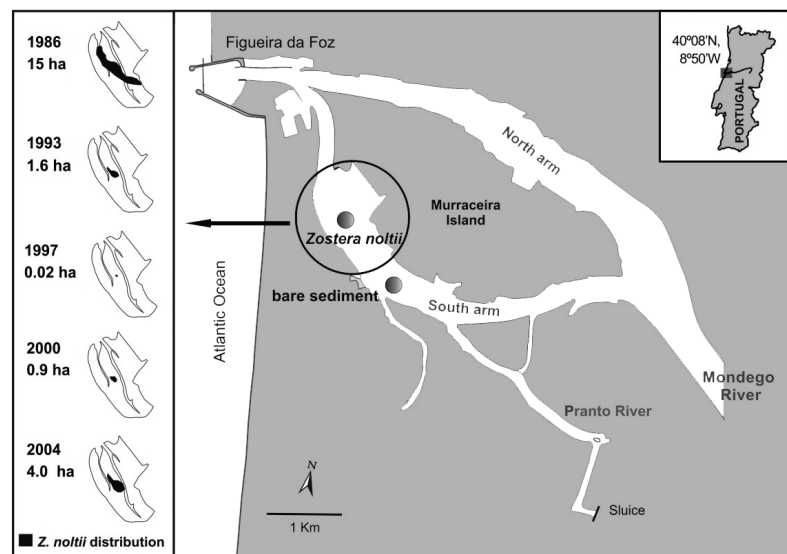

Fig. 1. Locations of the sampling sites in the Mondego estuary: *Zostera* meadows and bare sediment sites (grey circles). Left panel shows the change in area covered by *Zostera noltii* in the southern arm of Mondego estuary between 1986 and 2004. Mapping of benthic vegetation is based on field observations, aerial photographs and Geographical Information System analysis (ArcView GIS v.8.2)

artificially controlled by a sluice (Marques et al. 2009). This led to clear eutrophication symptoms in the southern arm (e.g. green macroalgal blooms) (Leston et al. 2008, Patrício et al. 2009). In 1997, to decrease these eutrophication symptoms and to test ways of improving the system's conditions, the fresh-water discharge from the Pranto River sluice into the southern arm was reduced to a minimum in order to decrease nutrient inputs, and was diverted to the northern arm by another sluice located further upstream. Moreover, the communication between the northern and southern arms was re-established to a very limited extent (periods of only 1.5 to 2 h before and after each high-tide peak through a section of only 1 m^2) to improve water circulation (Marques et al. 2009).

A long-term study of the Mondego estuary ecosystem carried out since the mid-1980s made it possible to determine the system's responses to these modifications to its physical conditions, such as changes in the *Zostera noltii* beds and in the green macroalgae *Ulva* spp. coverage and biomass (e.g. Patrício et al. 2009). Following the interruption of the upstream communication between the 2 arms, ecological conditions in the southern arm rapidly deteriorated. The combined effect of increased water residence time and higher nutrient concentrations was the main driving force behind the seasonal *Ulva* spp. blooms and the consequent severe reduction in the area occupied by *Z. noltii* beds due to competition with the macroalgae (Patrício et al. 2009). The shift in benthic primary producers changed the benthic macrofauna trophic structure (e.g. Marques et al. 1997, 2003, Patrício & Marques 2006). According to Patrício et al. (2009), after experimental mitigation measures were applied in 1998, this trend appeared to reverse to a certain extent, as the area occupied by *Z. noltii* was partially regained, the green *Ulva* spp. blooms decreased markedly and the macrofauna assemblages gave signs of recovering their former condition of the late 1980s.

The winter of 2000/2001 was characterised by unprecedented high precipitation values compared to the average long-term precipitation (2000/2001: 1802 mm; 1940 to 1997: 1031 mm), which caused one of the largest flood events of the century in the Mondego catchment area.

Construction of mass-balanced models

Six mass-balanced models were constructed using Ecopath software (Christensen & Pauly 1992). The input information came from an extensive field-sampling program, was expanded with stable isotope analysis (SIA) and completed with published references. Fieldwork was conducted in 2 areas located in the southern arm of the Mondego estuary (*Z. noltii* meadows and bare sediment area), during 3 periods: 1993/1994, 1999/2000 and 2001/2002. Detailed descriptions of the study sites, sampling program and protocols, network construction, dietary matrices and SIA can be found in Baeta et al. (2011). The quantitative contribution of the food sources of consumers was estimated using mixing models as well as the quantitative information on sources of nutrition of the estuarine invertebrates inhabiting the 2 study areas. Although information from the literature was used in this study (equations based on local data on individual size for metabolic parameters of all and diets of a few compartments), the majority of the inputs came from data directly collected from the sites during the periods represented by the models (i.e. community structure, biomass of all and diets of several compartments, *P/B* ratios). The food webs were built using data for benthic macrofauna species, representing the benthic food web, and no compartments regarding higher trophic levels — fish and birds — were included in the models, as no information precisely covered the periods of interest (for further details see Patrício et al. 2004).

Trophic analysis

For the 6 food webs built, the trophic analysis was derived from the 'Network Analysis' routine included in the Ecopath with Ecosim software (v.6.3.8648.0).

The 'mean trophic level' was calculated for each consumer compartment as the length of the different consumption pathways, averaged with a weight corresponding to the quantity of carbon that passes along each pathway (Odum & Heald 1975, Ulanowicz 1995). Level I corresponds to the primary producers and the non-living, detrital compartments. The strict herbivores or detritivores consequently occupy a position of II (one plus one). Other consumers are then allocated to several discrete trophic positions, according to the amounts that reach them along feeding pathways of various lengths, and the mean trophic position is calculated as the mean pathway, with a weight corresponding to the flow value in g AFDW m^{-2} yr^{-1}. This indicator was analysed together with the total consumption (sum of all flows from the different preys) of the consumer.

The same distribution of compartments within integer trophic levels was used to build the 'Lindeman

spine' of each food web. This mapping summarises the complicated food web in terms of a single linear chain with discrete trophic levels (Ulanowicz 1995). Once the compartment is decomposed within integer trophic levels, the flows are decomposed accordingly and the contributions of each trophic level to respiration, imports and exports are also evaluated (Baird & Ulanowicz 1989). The building of this linear chain enables the efficiency of the transfer from one aggregated trophic level to the next to be calculated. This index is calculated as the fraction of the total carbon input to a given level that is transmitted to the next, higher level (Baird & Ulanowicz 1989). The 'mean trophic efficiency' of the system is then derived from the geometric mean of the efficiencies of trophic levels II to IV (Baird & Ulanowicz 1989, Heymans et al. 2012). In the Ecopath software, trophic efficiency is calculated from level II up, so the mean trophic efficiency does not consider level I, nor detritus.

The D/H ratio (i.e. the values of the detritivory flow, from detritus to level II, divided by the value of the herbivory flow, from primary producers to level II) was calculated for each of the 6 food webs.

In order to compare these indicators directly derived from Lindeman (1942) with an indicator based on information theory, the 'relative internal ascendency' (internal ascendency/internal development capacity, Ai/Ci) was calculated (Monaco & Ulanowicz 1997).

RESULTS

The mean trophic level for each consumer compartment is presented for the 3 food webs of the *Zostera* bed and for the bare sediment food webs (Fig. 2) over time. The compartments are ranked in decreasing order of mean trophic levels (left axis). The species whose consumption exceeds the maxi-
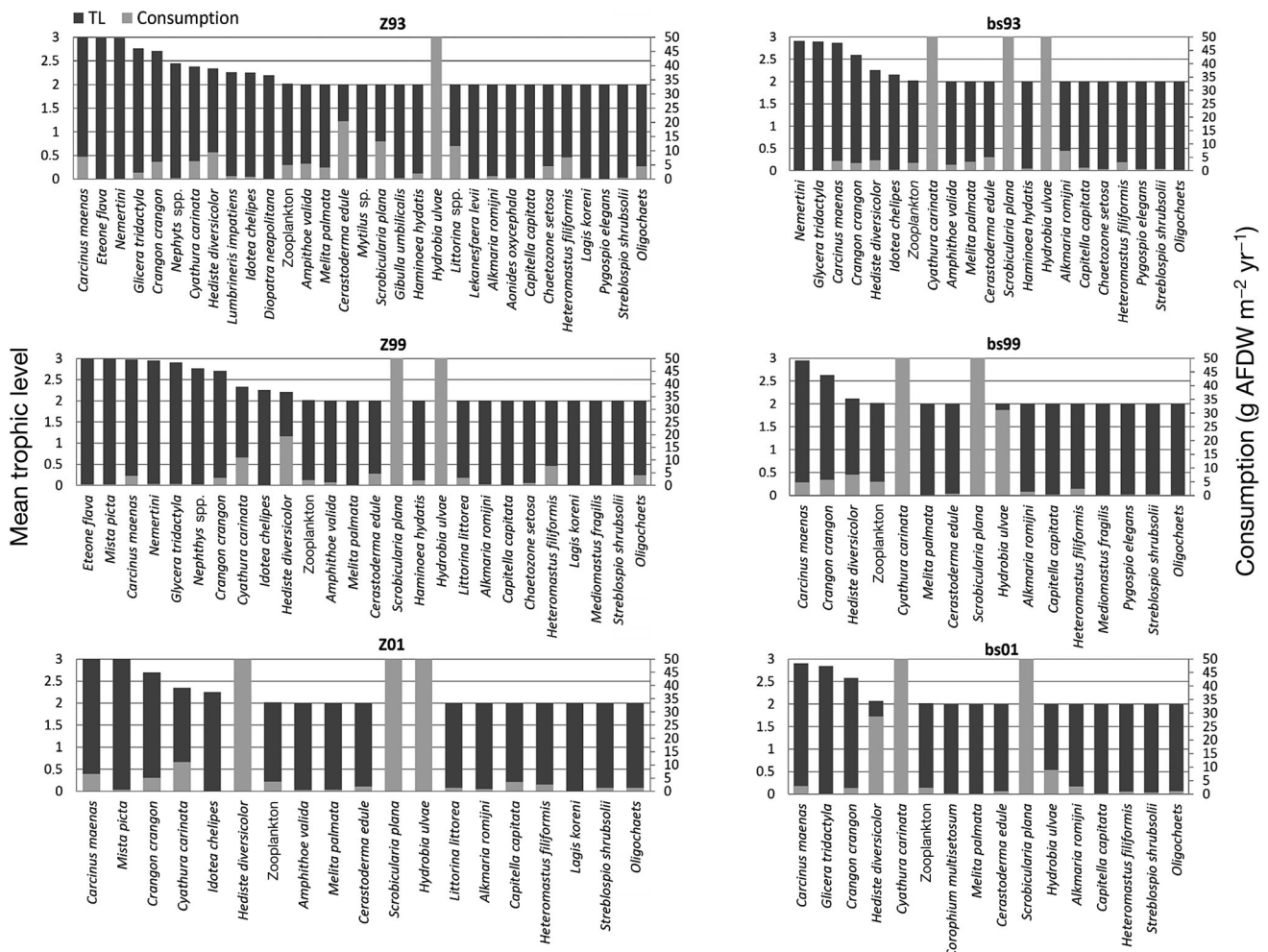

Fig. 2. Mean trophic level (TL; no unit, left axis) and consumption (g AFDW m^{-2} yr^{-1}, right axis) for *Zostera* bed and bare sediment food webs. The scale of the right axis was truncated at 50 g AFDW m^{-2} yr^{-1} in order to keep it readable. Values above this threshold are described in 'Results'. Z = *Zostera* bed; bs = bare sediment; 93 = 1993/1994; 99 = 1999/2000; 01 = 2001/2002

mum value of the graph (50 g AFDW m^{-2} yr^{-1}) are the following: (1) *Hydrobia ulvae* (478 g AFDW m^{-2} yr^{-1} in 1993/1994, 319 in 1999/2000, 453 in 2001/2002), *Scrobicularia plana* (84 g AFDW m^{-2} yr^{-1} in 1999/2000, 79 in 2001/2002) and *Hediste diversicolor* (70 g AFDW m^{-2} yr^{-1} in 2001/2002) at the *Zostera* sites (Fig. 2); and (2) *H. ulvae* (161 g AFDW m^{-2} yr^{-1} in 1993/1994), *S. plana* (67 g AFDW m^{-2} yr^{-1} in 1993/1994, 157 in 1999/2000, 123 in 2001/2002) and *Cyathura carinata* (128 g AFDW m^{-2} yr^{-1} in 1993/1994, 72 in 1999/2000, 102 in 2001/2002) (Fig. 2) at the bare sediment sites.

These high consumption values are measured for taxa with a trophic level around 2. For instance, the gastropod *H. ulvae* is a grazer that feeds mainly on benthic diatoms. The same was observed for the suspension feeder *S. plana*, which also consumes phytoplankton and detritus. The trophic level value for these highly active compartments (i.e. with a high consumption) remains low, with maximal values observed for *H. diversicolor* (max. 2.05) and *C. carinata* (max. 2.17). Both are omnivores, feeding on a wide variety of different animals, algae and detritus, but their diet remains dominated by detritus. The main animal prey for *H. diversicolor* is *H. ulvae* (*Zostera* bed in 2001/2002), and for *C. carinata* it is *H. diversicolor* (bare sediment in 2001/2002).

Among less active compartments (i.e. those with the lowest value of total consumption), those belonging to a trophic level above II correspond to the omnivorous and carnivorous annelids *Eteone flava*, *Glicera tridactyla*, *Nephtys* spp., *Mista picta*, *Lumbrinereis*, *Diopatra neapolitana* and Nemertini, and to the decapods *Carcinus maenas* and *Crangon crangon* (Fig. 2). The food sources of these species include animals, algae and detritus (see dietary matrices in Baeta et al. 2011, supplementary material). The compartment that most often is the highest predator at the mean trophic level is *C. maenas*. Its diet, in *Zostera* beds as well as in bare sediment models, is composed of 10 to 15 % detritus (including bacteria) and 4 % primary producers; the remaining 81 to 86 % being a great variety of heterotrophic prey items. Its main prey consists of *H. diversicolor*, *C. crangon* and *S. plana*. Correlated with the highest diversity in the *Zostera* bed models, *C. maenas* is positioned at a higher trophic level (2.98 to 3.05) than in bare sediment models (2.87 to 2.95). In one of the bare sediment food webs (1993/1994), 2 taxa are positioned at a higher level than *C. maenas*: Nemertini and *G. tridactyla*. Their mean trophic levels, however, remain lower than III (2.91 and 2.90, respectively). In one case of the *Zostera* bed model (1999/2000), 2 species are positioned at a higher level

than *C. maenas*: *E. flava* and *M. picta*, both positioned at a mean trophic level of 3.04.

The carbon flow networks of the 6 models were transformed into Lindeman spines (sensu Ulanowicz 1995). The models for the 3 periods of the *Zostera* bed are illustrated in Fig. 3, and those of the bare sediment area in Fig. 4.

In order to make a distinction between detritivory and herbivory, the detritus pool (D) was separated from the primary producers (P). Together, both pools form level I. This allowed the D/H ratio to be calculated, considering a functional emergent property of food web organisation (Table 1). Detritivory was always superior to herbivory, ranging from 1.03 to 2.25. In each food web, the D/H value of the *Z. noltii* meadows food web was higher than that of the bare sediment area, showing that detrital pathways are important for *Zostera* bed functioning. Although the food webs temporally showed differences in the D/H ratio, it is worth noting that in both areas, there was an increase in the D/H value after the century flood.

The D/H ratio was always higher in the *Zostera* meadows, mainly due to the high biomass of *H. ulvae* found in this area. *H. ulvae* feeds not only on microphytobenthos (MPB), but also on detritus (in high proportion). In *Zostera* bed Site Z01, the D/H ratio was slightly higher than in Site Z93, due to the increase in *S. plana* biomass in 1999 and 2001; however, in 1999, the D/H ratio was lower because the biomass of *H. ulvae* was much lower.

In the bare sediment, the D/H ratio was lower in 1993 and higher in 2001. In 1993, the consumption of detritus by *H. ulvae* was significantly lower, since the availability of MPB was significantly higher. The D/H ratio was close to 1, since the consumption of producers by *H. ulvae* was very similar to that of *C. carinata* on detritus (in fact, consumption by *H. ulvae* + *S. plana* of producers = consumption by *C. carinata* + *H. ulvae* of detritus). In 2001, the biomass of *H. ulvae* was very low, and consequently its consumption was also very low. *C. carinata* remained the species with the highest consumption of detritus.

Examining the detritus pool inputs, it was also possible to differentiate between locally produced detritus and inputs originating outside. Compared to all detritus flows (inputs from outside + locally produced detritus), 59 to 66 % of the detritus was produced locally. The values for the *Zostera* bed food webs (59 to 66 %) were similar to those for the bare sediment models (60 to 63 %). In both systems, this percentage increased from 1993 to 1999 (after the implementation of the mitigation measures), followed by a decrease after the flood event (from 1999 to 2001).
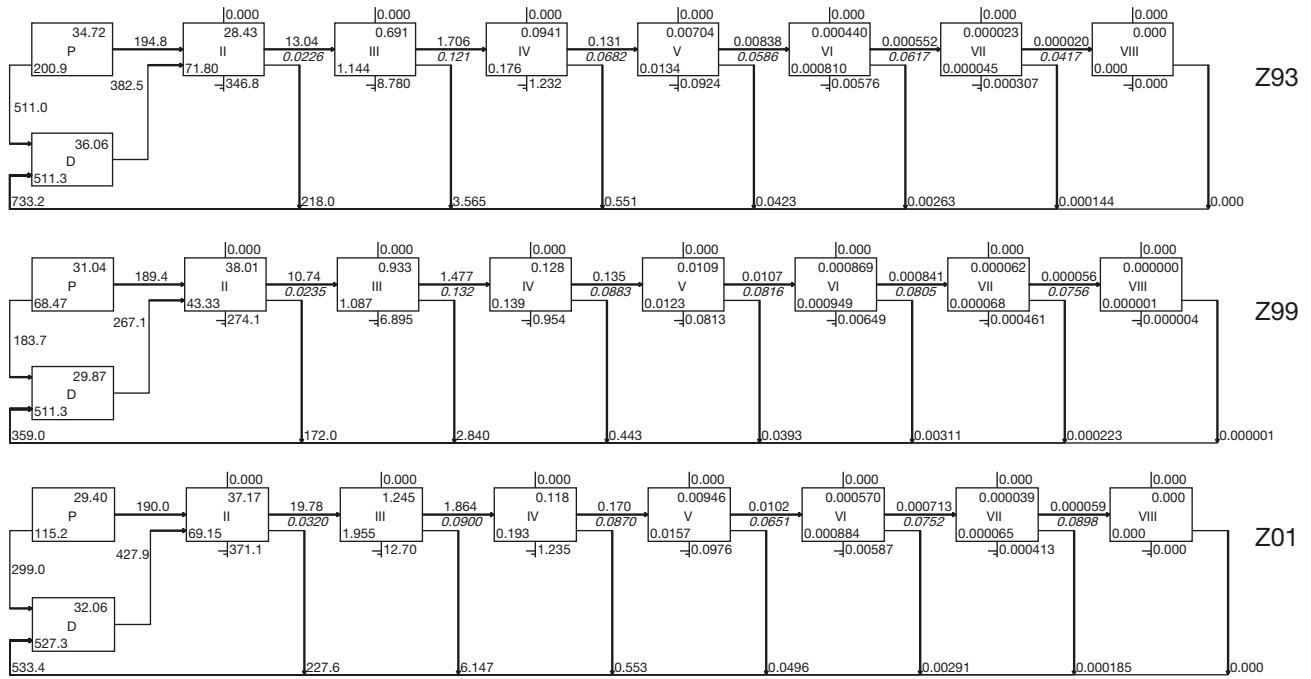
Fig. 3. Lindeman spines for each of the 3 *Zostera* meadow food webs (Z = *Zostera* bed; 93 = 1993/1994; 99 = 1999/2000; 01 = 2001/2002). All flow values are in g AFDW m^{-2} yr^{-1} and all biomass values in g AFDW m^{-2}. P = primary producers; D = detritus pool; TL = trophic level; *TE* = trophic efficiency, TST = total system throughput. Roman numerals indicate trophic levels
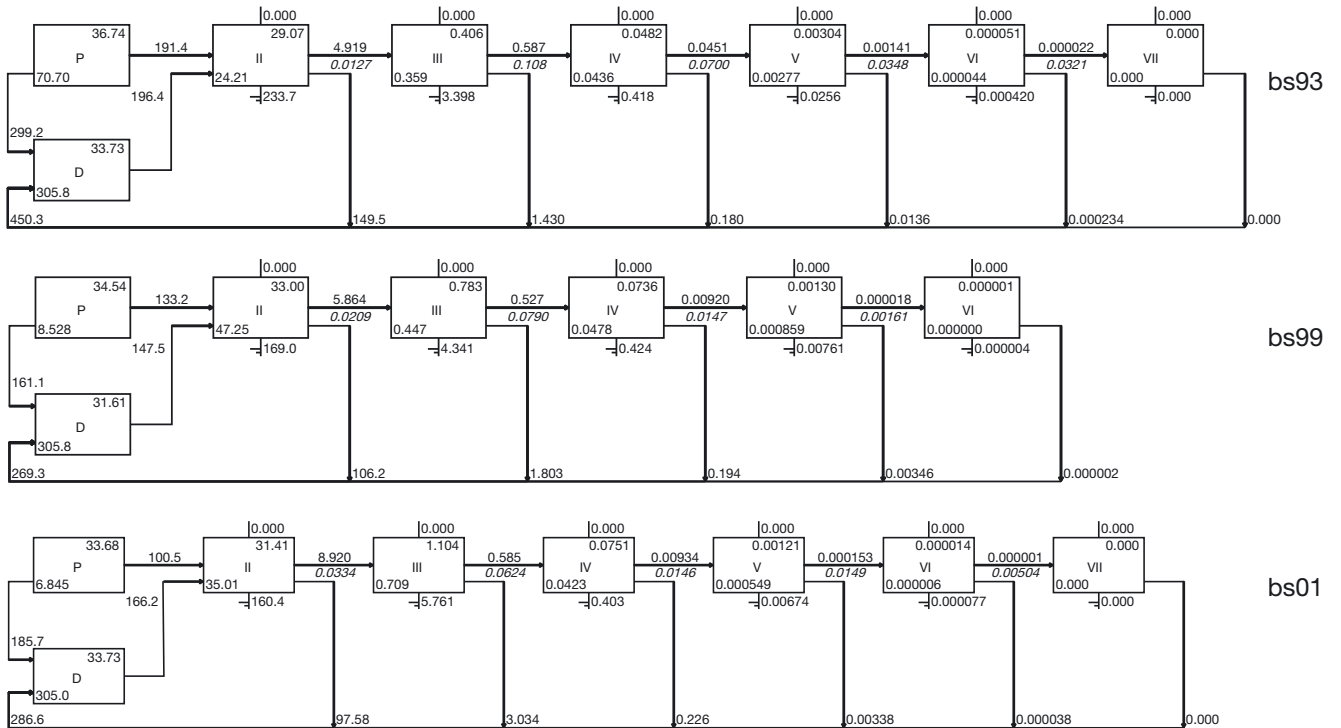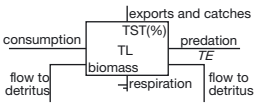

Fig. 4. Lindeman spines for each of the bare sediment area food webs (bs = bare sediment; 93 = 1993/1994; 99 = 1999/2000, 01 = 2001/2002). All flow values are in g AFDW m^{-2} yr^{-1} and all biomass values in g AFDW m^{-2}. P = primary producers; D = detritus pool; TL = trophic level; *TE* = trophic efficiency, TST = total system throughput. Roman numerals indicate trophic levels
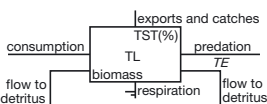
Table 1. Characteristics of the 6 original Ecopath models (Baeta et al. 2011). No. comp = number of compartments; TEm = mean trophic efficiency; D/H = Detritivory/Herbivory; Z = *Zostera* bed site; bs = bare sediment site; 93 = 1993/1994; 99 = 1999/2000; 01 = 2001/2002

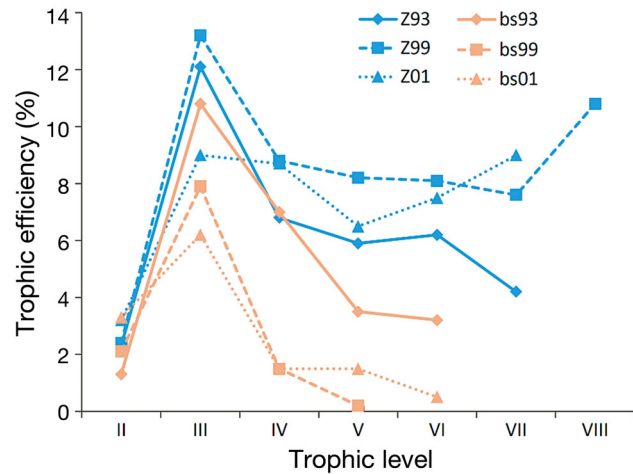| Site	No. comp	TEm (%)	D/H ratio
Z93	36	5.7	1.96
Z99	31	6.5	1.41
Z01	24	6.3	2.25
bs93	25	4.6	1.03
bs99	20	2.9	1.11
bs01	20	3.1	1.65

Fig. 5. Trophic efficiencies per trophic level, for the 6 models (bs = bare sediment; Z = *Zostera* bed; 93 = 1993/1994; 99 = 1999/2000; 01 = 2001/2002). Trophic level efficiency of level III = predation on level III by level IV / consumption of level II by level III
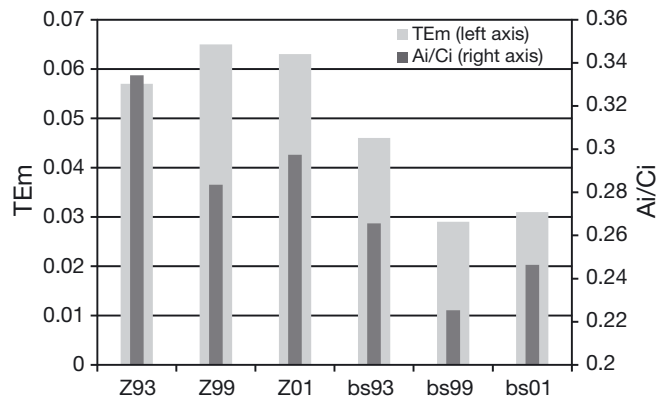

Fig. 6. Mean trophic efficiency, TEm (geometric mean of values for integer levels calculated for trophic levels II to IV) and relative internal ascendency, Ai/Ci, for the 6 models (bs = bare sediment, Z = *Zostera* bed, 93 = 1993/1994, 99 = 1999/2000, 01 = 2001/2002)

The Lindeman spines also illustrate the flows of respiration, detritus production and export, leaving each integer trophic level. In the present case, only respiration and detritus production were taken into account; export was estimated as null in the model (Baeta et al. 2011). Because most of the heterotrophic biomass was located at level II (97 to 99%), respiration flows followed the biomass distribution closely, with higher values at level II.

The *Zostera* meadows food webs have longer chains than the bare sediment food webs. This observation results from the higher number of compartments in the *Zostera* bed food webs, which in turn reflects the higher species richness of this area compared with the bare sediment area. The highest trophic efficiency value was always found at level III (Fig. 5), ranging between 6% (bare sediment in 2001) and 13% (*Zostera* bed in 1999).

In terms of mean trophic efficiency (Fig. 6), the values presented by *Zostera* bed models were higher (5.7 to 6.5%) than those of bare sediment area models (2.9 to 4.6%). The mitigation measures in 1999 corresponded to an increase in mean trophic efficiency in the *Zostera* site compared with the eutrophication period (5.7 to 6.5%), followed by a minute decrease after the flood event. In the food webs of the bare sediment area, the mean trophic efficiency values were higher in the eutrophic period (4.6%) than in the other 2 periods (2.9 to 3.1%). Our observations suggest that the implementation of mitigation measures had a stronger impact on the mean trophic efficiencies than the extreme flood event. Compared to Ai/Ci, which describes the specialisation of the flows, we observed that the trend of variation over time was comparable with the mean trophic efficiency for the bare sediment site, but both were in contradiction to the *Zostera* site. In both sites, Ai/Ci was lower in 1999/2000 and returned to a higher value in 2001/2002.

DISCUSSION

The Mondego estuary monitoring programme began in the mid-1980s. This ecological monitoring programme was developed because it is well known that many ecological processes occur through, or are driven by, factors acting on long temporal and large spatial scales. Many scientists have collected valuable information about the estuary over the last 30 yr, including data on physical conditions, primary producers, zooplankton, benthic macrofauna, fish and birds (e.g. Marques et al. 2003, 2013, Patrício et al. 2004, 2009, Lopes et al. 2005, Dolbeth et al. 2007, Martinho et al. 2007, Cardoso et al. 2010, Falcão et al. 2012, Veríssimo et al. 2012, Neto et al. 2013). The

analysis of these data was the basis for a better understanding of the structure and functioning of this estuarine ecosystem.

In the early and mid-1990s, nutrient enrichment in the system led to macroalgal blooms that decreased the previously dominant macrophyte communities (i.e. *Zostera noltii*). In 1998, mitigation measures were implemented in order to restore the *Z. noltii* beds and the overall quality of the system. A few species responded positively (e.g. higher biomass of *Scrobicularia plana* and *Hediste diversicolor*), others negatively (e.g. lower biomass of *Hydrobia ulvae*), which led to more structured and stable populations, closer to the less disturbed conditions observed in the 1980s (Patrício et al. 2009). According to Baeta et al. (2011), the *Z. noltii* site showed a higher number of trophic compartments and a higher level of system activity (i.e. sum of consumptions, respiration, flows to detritus, production, total system throughput, net primary production and system omnivory index) than the bare sediment site. The differences in total system throughput between the 2 sites, for the 3 periods, were mainly due to differences in the biomass of primary producers (higher primary production at the *Zostera* site). In both habitats, after recovery measures were implemented there was an increase in *S. plana* and *H. diversicolor* biomass, consumption, respiration and flows to detritus, and a decrease in *H. ulvae* biomass and associated flows, which increased again after the centenary flood (Baeta et al. 2011). This study showed that the estuarine food webs were affected differently by each disturbance event, and suggested that a high system throughput seems to be associated with higher stress levels, contradicting the idea that higher system activity is a sign of healthier conditions.

Lindeman's (1942) trophic-dynamic concepts and Ulanowicz's (1995) developments bring about another way to analyse the 6 case studies presented in Baeta et al. (2011).

Advantages and limitations of the chosen numerical approach

This study was based on high quality models as revealed by the large amount of local information used. Because the 6 models shared comparable structures (differences among considered trophic compartments were directly linked with differences in biodiversity), the comparison could be based on indicators from network analysis shown to be sensitive to the structure of the food web model (Johnson

et al. 2009). However, to maintain the high reliability in the estimated flows, we made the choice not to consider birds and fish. Even if these compartments had been described previously (e.g. Lopes et al. 2005, Martinho et al. 2007), the information was not sufficient to exactly determine their role during each studied period and at each study site. This has to be taken into account in our comparison. In particular, it reduces the possibility of adding other metrics to our comparison, or comparing index values with those derived from models of other estuarine ecosystems that usually consider a wider area and include birds and fish (Christian et al. 2005, Leguerrier et al. 2007, Heymans et al. 2012).

Lindeman spine topology

The length of the Lindeman spines varied between habitats (i.e. inter-habitat changes) and among years within habitats (i.e. inter-annual differences). The *Zostera* bed chains were longer than those of the bare sediment site. At first, it may seem possible to generalise that the trophic chain length is proportional to the number of compartments present in the food web, i.e. that more compartments will result in a longer chain. However, this trend is only verified in some case studies. For example, the food web of the *Zostera* bed site in 2001 has 24 compartments, but its chain is 1 step longer (number of trophic levels: 8) than that of the bare sediment site in 1993 with 25 compartments (number of trophic levels: 7). Other variables besides number of compartments probably contribute to determining the length of the energy chains. Ulanowicz (1992), based on data taken from a tidal marsh tributary creek of the Crystal River (Florida, USA) and from a similar creek that was subject to an average 6°C rise in ambient temperature because of exposure to the effluent from an adjacent power-generating station, proposed that the length of the Lindeman spine is related to the level of stress, i.e. that shorter chains would reflect a higher degree of stress. According to Ulanowicz's (1992) proposal, the bare sediment food webs, with shorter chains, would reflect a higher level of stress in this habitat than in the *Zostera* bed site. If fact, *Z. noltii* has adapted to the challenging conditions affecting intertidal habitats, including environmental heterogeneity and disturbance (Hemminga & Duarte 2000). This macrophyte can act as a buffer to disruption, essentially as a function of shelter offered by foliage, and because this species' root networks stabilise the sediment in which they grow.

Over time, no clear trend in chain length variation was noticeable within each habitat. In the *Zostera* bed area, the 3 food webs had the same chain length, regardless of period and disturbance type. In the bare sediment area, the chain length decreased during and after implementation of the mitigation measures, which somehow contradicts Ulanowicz (1992). Further investigation is needed to clearly understand the connection between chain length and level of disturbance.

Detritivory/herbivory ratio

In general, the food webs of the *Zostera* meadows tended to have higher D/H ratio values than the bare sediment site food webs (except for Site bs01). Within each period, the same result was noticed. Our findings are not unexpected, since macrophyte habitats are characterised by high availability of detritus, either resulting from the direct decay of plants or because their roots constitute traps for detrital particles. In both cases, huge amounts of detritus (and bacteria) are accessible for consumption by benthic organisms.

According to Ulanowicz (1992), systems with higher levels of stress usually show lower D/H values. Based on this observation, we could conclude that the *Zostera* meadows area is at a lower stress level than the bare sediment area. However, the results were less clear when we analysed the differences among periods within each habitat. In both areas, there was an increase in the D/H value after the century flood, mainly driven by changes in the abundance and biomass of *H. ulvae* (feeding on microphytobenthos and detritus), *S. plana*, *Cyathura carinata* and *H. diversicolor*. In this case, after the extreme flood event in 2001 (a high-level disturbance), detritivory increased, largely exceeding herbivory, in whichever habitat was considered. Our findings are in line with those of Dame & Christian (2007), who studied 4 salt-marsh ponds during periods of low stress, high stress and post-disturbance, respectively, and observed an increase in detritivory during the high stress conditions. These findings are in contrast to Ulanowicz's (1992) proposition. Therefore, further tests are necessary before being able to use the D/H ratio as an operational metric to quantify and interpret the impact of disturbances on the trophic state and functioning of an ecosystem.

Moreover, as D/H is mainly related to the diet of species with high consumption (in this case study, species with consumption values above 50 g AFDW

$m^{-2} yr^{-1}$), changes in community composition, species biomass and diet composition are particularly relevant. The diet matrices used to build the 6 food webs of the Mondego estuary were built (for several species) using isotopic ratios assessed from local samples, and analysed with a stable isotope mixing model (ISOSOURCE software; Phillips & Gregg 2003). This analysis confirmed that the dominant species have dietary plasticity over both time and space. For instance, the diet of *H. ulvae* shifted from a main consumption of microphytobenthos in the bare sediment food web in 1993 (75% microphytobenthos, 25% detritus) to a diet dominated by detritus in the *Zostera* bed area (68, 55 and 68% in 1993, 1999 and 2001, respectively). These findings emphasise the importance of building food webs using information about local diets, and it is interesting, for the robustness of the numerical approach, to use mixing model results for constraining food-web models (Baeta et al. 2011, Pacella et al. 2013).

Trophic efficiency

This broad term, which designates a measure that can be estimated from Lindeman spines, has different uses in the scientific literature. Thus, the lack of a unique and clear definition might raise serious difficulties when comparing trophic efficiencies among different studies. Caution is therefore essential. The mean trophic efficiency of an ecosystem is generally considered to be the geometric average of the trophic efficiencies of all trophic levels (Baird & Ulanowicz 1989). For instance, trophic level I considers only primary producers (Miehls et al. 2009), or becomes level I+D when concatenating primary producers and detritus (e.g. Baird et al. 2012). The primary production included in the Ecopath routine is considered as net primary production (the gross primary production minus the respiration of the primary producer considered). Thus, the total value is considered to be available for herbivory, and the value of the respiration by primary producers is not estimated. For this reason, it is not possible to calculate the trophic efficiency at level I when using Ecopath without having information about gross primary production or respiration at level I, and the mean trophic efficiency has been considered for all levels from II to the top (Coll et al. 2009), or from II to IV (Heymans et al. 2012). Unfortunately, this prevents any comparison between the trophic efficiency values of our 6 models and the trophic efficiency values of models that considered trophic level I or I+D (Baird et al. 2004, 2007, Duan et

al. 2009, Miehls et al. 2009). This is disappointing since this first level seems to be highly sensitive to pressures such as eutrophication (Christian et al. 2009) or invasion by non-indigenous species (Baird et al. 2012). For the future, it would be important to include in Ecopath the possibility of estimating the respiration of primary producers. This would allow the trophic efficiency at level I+D to be estimated, and would ensure a better comparability of trophic efficiencies at the system level.

In general, the 'trophic efficiencies per trophic level' (see Fig. 6) at the *Zostera* bed site were higher than those of the bare sediment area. For both habitats and for the 3 periods, the trophic efficiency at level II was low and its value varied within a minor interval (1.3 to 3.3%). Interestingly, the highest trophic efficiency values were found at level III. The trophic efficiency per trophic level found for the 6 food webs of the Mondego estuary was different from the results found for the Sylt-Rømø Bight ecosystem in the northern Wadden Sea (Baird et al. 2004, 2007, 2012) and for the Neuse River estuary in North Carolina, USA (Christian et al. 2009). These 2 ecosystems were characterised by maximum values at level I (primary producers + detritus) and a monotonous decrease in trophic efficiency values with increasing trophic levels. Furthermore, Duan et al. (2009) studied the Pearl River estuary, China, a coastal ecosystem that has been overfished and has received a high level of combined pollution since the 1980s. The authors built 2 food webs, one for 1981 and one for 1998, when the estuary was heavily exploited. In 1981, the highest trophic efficiency value was found at level III (11.8%), like in the Mondego estuary (i.e. with a similar pattern), but that was not the case for the model of the year 1998, where the lowest trophic efficiency was found at level III (5.6%) and the other trophic levels showed values above 11%. This drop in the trophic efficiency of level III was linked to the strong increase in jellyfish biomass that was poorly consumed. These studies show, therefore, that the pattern of variation in trophic efficiency per trophic level varies between ecosystems and disturbance levels.

It is also worth noting that each habitat reacted differently to the type of disturbance acting upon the system. In the *Zostera* area, the mean trophic efficiency was higher after the implementation of the mitigation measures, while in the bare sediment area the trophic efficiency decreased. This might be related to the changes in primary production that occurred in the area. In fact, in 1993, the bare sediment area had an unusual input of energy as a consequence of the macroalgal blooms; since the mitiga-

tion measures, such an input has not been observed. No major changes in mean trophic efficiency were seen after the centenary flood. Analysing the scientific literature on the topic, stress is usually associated with low system efficiency. For example, between 1974 and 1989, the Venetian Lagoon experienced a high level of eutrophication (Libralato et al. 2004). During this period, the mean trophic efficiency of the lagoon was extremely low (i.e. 0.5%; Libralato et al. 2004). Christian et al. (2009) described a decrease in the mean trophic efficiency of the Neuse River estuary after a severe episode of hypoxia. Baird et al. (2012) reported a decrease in mean trophic efficiency in the Sylt-Rømø Bight ecosystem. However, this connection between higher stress levels and a decrease in mean trophic efficiency cannot be generalised. There are cases where stress lowers the values of the trophic efficiencies of some trophic levels, but this is compensated by an increase in the trophic efficiency of another level, resulting in an overall value that is higher in disturbed situations (see for instance Duan et al. 2009, Chrystal & Scharler 2014). In ecosystems affected by fisheries, similar trends were observed by Coll et al. (2009), who made the following hypothesis: 'the food web became more efficient with time, and may be due to less biomass and production in the ecosystem' (p. 2098). The literature also pointed out an increase in the mean trophic efficiency in accordance with the meta-analysis (based on 53 models) provided by Heymans et al. (2012). According to Heymans et al. (2012), mean trophic efficiency increases with fishing pressure (no fishing, low and high fishing pressure scenarios distinguished), and more precisely, the relationship between mean trophic efficiency and the L index seems very close to linearity (Libralato et al. 2008). Heymans et al. (2012) also noticed that mean trophic efficiency depends on the size, longitude, type and depth of the ecosystem. However, all these authors agree with Rochet & Trenkel (2003), who present trophic efficiency as a good indicator for informing on ecosystem function changes and quantifying potential structural changes. Our findings, analysing other disturbances (i.e. eutrophication, hydrodynamic alterations and an extreme climatic event — a centenary flood), suggest that the mean trophic efficiency of the system might not be sufficient to draw conclusions about the trophic efficiency of the ecosystem. Rather, it is essential to take into account 2 levels of integration: the overall efficiency and the efficiency of each trophic level. In order to obtain functional indicators of ecosystem conditions, it is worth comparing the properties of many of the coastal and marine food webs already

published. However, extra care should be taken to cope with differences in the type of ecosystem/ habitat, acting pressures, levels of integration (e.g. mean trophic efficiency and efficiencies per trophic level), and also the lack of standardised methodologies between studies (e.g. number of compartments considered and aggregation level). It is essential to be aware that the lack of straightforward comparability might be a severe constraint to extracting patterns and proposing generalisations.

Finally, comparison of the mean trophic efficiency with the Ai/Ci shows that the relationship between the specialisation of internal flows and trophic efficiency (Monaco & Ulanowicz 1997) is not direct. Although the trend of variation was the same over time for the bare sediment site, the opposite trend was observed for the *Zostera* site. According to theories linking ascendency to maturity (Ulanowicz 1997, Ulanowicz et al. 2009), the most stressful situations for the 2 habitats would be during the mitigation period. This may be associated with the recent changes in nutrient loading, followed by a short period of adaptation for the ecosystem.

CONCLUSIONS

Our results indicated that none of the tested measures (i.e. Lindeman spine length, D/H ratio, mean trophic efficiency and trophic efficiency per trophic level) are yet ready to be used per se as operational metrics to quantify and interpret the impact of disturbances on the trophic state of an ecosystem. It seems neither easy nor linear to establish a clear link between structural characteristics, such as biodiversity, and trophic attributes of ecosystems. However, although the comparability of the models was noteworthy, the fact that only benthos was taken into account precludes comparison with whole ecosystem models. Such research needs to be pursued and would require the development and application of a conceptual framework (with common and useful sets of indicators, i.e. a multi-indices approach), integrating a holistic approach based on as many observations as possible (Cury et al. 2005, Shin et al. 2010, Fu et al. 2012). According to Christian et al. (2009), a framework combining ecological network analysis and functional aspects would result in an improved approach to ecosystem-based management, even if there is no clear consensus on its implementation (Peterson et al. 2000, Dame & Christian 2006). However, despite the vast literature on new trophic attributes derived from ecological network analysis (e.g.

Coll et al. 2009, Pranovi & Link 2009, Heymans et al. 2012), this issue needs further investigations and processes, as recent works (such as Fu et al. 2012) have pointed out the need for improvements to be carried out; for instance, taking into account the sites' specificity and associated local anthropogenic pressures. In this framework, indicators derived from network analysis are promising for defining ecosystem health indicators. They allow the whole ecosystem structure to be considered and to function in a context of maturation and stress (Christensen 1995, Ulanowicz 1997, Bondavalli et al. 2006). They can also be related to resilience (Christensen 1995, Heymans et al. 2007, Lobry et al. 2008) and they allow the detection of non-linear major changes (i.e. abrupt shifts) at the ecosystem level (Savenkoff et al. 2007, Tomczak et al. 2013).

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