Modelling the effects of eutrophication, mitigation measures and an extreme flood event on estuarine benthic food webs

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ABSTRACT

Human-mediated and natural disturbances such as nutrient enrichment, habitat modification, and flood events often result in significant shifts in species composition and abundance that translate into changes in the food web structure. Six mass-balanced models were developed using the "Ecopath with Ecosim" software package to assess changes in benthic food web properties in the Mondego estuarine ecosystem (Portugal). Field, laboratory and literature information were used to construct the models. The main study objective was to assess at 2 sites (a *Zostera* meadow and a bare sediment area) the effects of: (1) a period of anthropogenic enrichment, which led to excessive production of organic matter in the form of algal blooms (1993/1994); (2) the implementation of mitigation measures, following a long period of eutrophication (1999/2000); and (3) a centenary flood (winter 2000/2001). Different numbers of compartments were identified at each site and in each time period. In general, the *Zostera* site, due to its complex community, showed a higher number of compartments and a higher level of system activity (i.e. sum of consumptions, respiration, flow to detritus, production, total system throughput, net primary production and system omnivory index). The differences at the two sites in the three time periods in the breakdown of throughput were mainly due to differences in the biomass of the primary producers (higher primary production at the *Zostera* site). Consumption, respiration and flow to detritus were dominated by the grazers *Hydrobia ulvae* and *Scrobicularia plana* at the *Zostera* and bare sediment sites respectively. At both sites, after recovery measures were implemented there was an increase in *S. plana* and *Hediste diversicolor* biomass, consumption, respiration and flows to detritus, and a decrease in *H. ulvae* biomass and associated flows, which increased again after the flood event. The mass-balanced models showed that the trophic structure of the benthic communities in Mondego estuary was affected differently by each disturbance event. Interestingly, in our study a high system throughput seems to be associated with higher stress levels, which contradicts the idea that higher system activity is always a sign of healthier conditions.

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1. Introduction

Estuaries are among the most productive, diverse, and economically important ecosystems on earth (Hobbie, 2000; Paerl, 2006). With the high population densities and increasing socioeconomic demands typical of coastal areas, estuarine ecosystems are subjected to multiple anthropogenic stressors. These do not usually operate independently, but rather interact to produce combined impacts on biodiversity and ecosystem functioning (Vinebrooke et al., 2004; Dolbeth et al., 2007; Cardoso et al., 2008).

Nutrient enrichment is one of the widespread stressors. Estuaries, which are critical habitats for nutrient recycling and ecosystem productivity, often receive large nutrient inputs derived from human activities and agricultural discharges, which are generally followed by severe eutrophication events (Valiela et al., 1997; Cloern, 2001; Bode et al., 2006; Lotze et al., 2006). Eutrophication severely impacts the diversity of primary producers and consumers, which leads to alterations in the food web structure, ecosystem productivity and functioning. One of the most important aspects of this type of disturbance is the proliferation of fast-growing macroalgae that may replace slow-growing macrophytes and significantly decrease the areal extent of seagrass meadows, which decreases the ecological value of the entire estuary (Short and Wyllie-Echeverria, 1996; Howarth, 1988; Bricker et al., 1999; Valiela, 2006; Patrício et al., 2009).

In addition to the impact of organic loading, estuarine ecosystems are also influenced by natural perturbations, such as extreme

weather events (floods, droughts and heat waves), which can have a strong negative impact on key components of the estuarine system (e.g. Cardoso et al., 2008; Chainho et al., 2007). Apart from the hydrological conditions (e.g. flood and drought periods), variability due to small spatial scale habitat heterogeneity (e.g. plant presence/absence, sediment grain size and organic matter content) may have a large impact on communities, and thus on ecosystem functioning (Pearson and Rosenberg, 1978; Gray, 1997; Raffaelli et al., 1998; Cloern, 2001; Patrício et al., 2009). For instance, seagrass meadows, in comparison to bare sediment, contribute greatly to estuarine functioning by sustaining longer and more complex food webs, which can affect ecosystem productivity and stability in periods of environmental change. Seagrasses increase sedimentation of fine sediment particles and thus enhance the quantity and quality of food for many macrofauna invertebrates, which are the fundamental trophic link between basal resources and predators such as fish and seabirds. Seagrass meadows are also a nursery for economically valuable fish (Pinto et al., 2010) and a refuge from predators (Duarte, 2002). Furthermore, seagrasses, particularly *Zostera noltii*, can contribute to carbon and nutrient sequestration and storage for longer periods than macroalgae. Therefore, the water over the meadow is of higher quality than the water over bare sediment, and thus eutrophication effects are mitigated (Cebrian, 1999).

For all the abovementioned reasons, estuaries are particularly challenging to model. Previous studies (e.g. Patrício and Marques, 2006) have shown that an ecosystem consists of so many interacting components that it is impossible to understand how it functions by examining the component relationships in isolation (Likens, 1985; Allen, 1988). To avoid this problem, simplified models can be developed that contain enough of the characteristics of the original system to resemble reality, but at the same time are simple enough to be understood (Brown, 2004). Mass-balance models represent a "snapshot" of the trophic flows in the ecosystem, and can be used to describe at least part of the reality (Christensen, 1994). Information gained from studying trophic webs can be used to make predictions of the impacts of natural or human-induced events on ecosystems, which can be used for management purposes.

Previous studies of Mondego estuary (Patrício et al., 2004; Patrício and Marques, 2006) described two areas in 1993–1994: one characterized by a *Zostera* bed considered to be in a healthy condition as it had high biodiversity, and a bare sediment site described as highly stressed due to strong eutrophication that had led to the loss of the *Zostera* meadow and the associated species. In the present study, we return to the models established previously for these two sites and add diet information from natural stable isotope ratios to determine how the properties have evolved since the models were originally developed.

Therefore, six mass-balanced models were developed using the "Ecopath with Ecosim" software package (v 5.1) to assess differences in benthic food web properties in the Mondego estuarine ecosystem (Portugal). The main study objective was to assess the effects of:

(1) a period of anthropogenic enrichment of the system which led to overproduction of organic matter in the form of algal blooms (1993/1994);
(2) mitigation measures (e.g. reducing nutrient loading, protecting seagrass beds and enhancing hydrodynamic circulation) that were implemented with the aim of promoting the recovery of the seagrass beds and the entire surrounding environment following a long period of eutrophication (1999/2000);
(3) a centenary flood (winter 2000/2001).

More specifically, the analysis of the properties of the 6 models allowed us to answer the following questions: (1) did the stress events modify the structure of the primary producers? (2) What was the impact of the stress on grazers and other consumers? (3) Did different types of stress (eutrophication *vs* flood) have the same impact on the communities? (4) Did the habitat structure (*Z. noltii* meadows *vs* bare sediment) influence the community response to stress? And (5) did the mitigation measures lead to the "recovery" of the food webs?

2. Materials and methods

2.1. 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 two arms: the northern and southern arms (Fig. 1). The southern arm is characterized by intertidal mudflats (almost 75% of the area) that are exposed at low tide. The tidal range varies between 0.35 and 3.3 m depending on the site and tide coefficient, while the water residence time varies between 1–2 (northern arm) and 3 days (southern arm).

From 1991 to 1997, the communication between the two 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, 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 test ways of improving the system's condition, the freshwater 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 1.5–2 h before and after each high tide peak through a section of only 1 m^2) to improve water circulation (Neto, 2004; Lillebø et al., 2007; 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 in the physical conditions, such as the changes in the *Z. noltii* beds and green macroalgae (*Ulva* spp.) distribution (e.g. Patrício et al., 2009). Following the interruption of the upstream communication between the two arms, the ecological conditions in the southern arm rapidly deteriorated. The combined effect of an increased water residence time and higher nutrient concentrations was a major 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 macroalgae (Marques et al., 2003; Patrício et al., 2009). The shift in benthic primary producers changed the benthic macrofauna trophic structure (e.g. Marques et al., 1997, 2003; Cardoso et al., 2004; Patrício and Marques, 2006; Dolbeth et al., 2007). 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 stopped, and the macrofauna assemblages gave signs of recovering their former condition of the late 80s.

Winter 2000/01 was characterized by unprecedented high precipitation values compared to the average long-term precipitation (2000/01: 1802.1 mm; 1940–1997: 1030.6 mm), which caused one
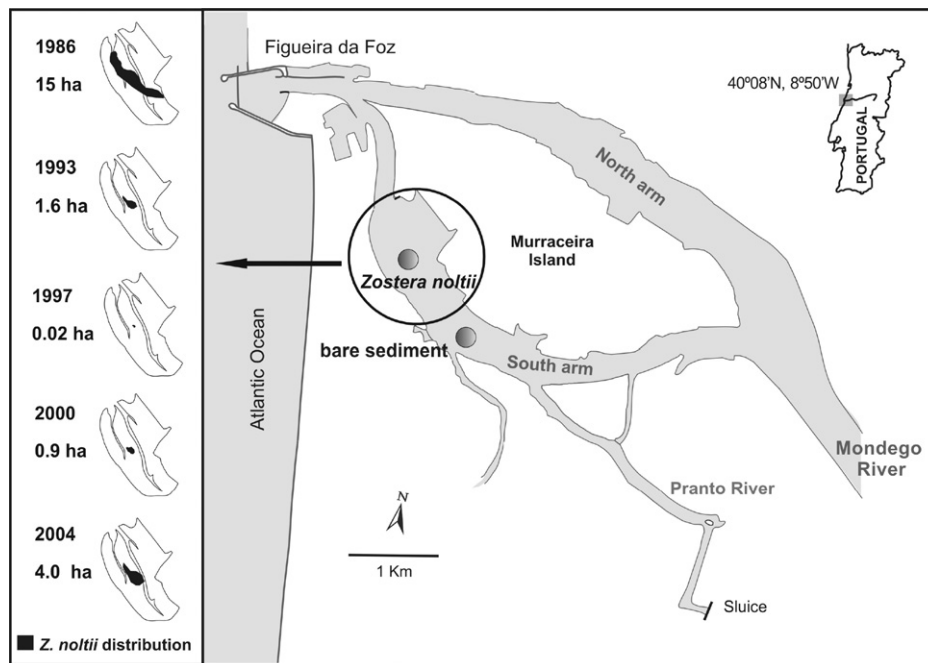
Fig. 1. Map of Mondego estuary showing the sampling sites: *Zostera* and bare sediment sites (grey circles). Change in the area covered by *Zostera noltii* in the southern arm of Mondego estuary. Mapping of benthic vegetation is based on field observations, aerial photographs and a GIS methodology (Arc View GIS version 8.2).

of the largest flood events of the century in the Mondego catchment area.

2.2. Sampling program and laboratory treatment

Intertidal communities, separated apart by approximately 1 km, were sampled fortnightly (February 1993–June 1994), and monthly (July1994–December 1994; January 1999–December 2000; January 2001–December 2002). In all cases, sampling was conducted at two sites in the southern arm (Fig. 1), within the *Z. noltii* meadow, which persisted during the early 1990s, and in an area where the *Z. noltii* had disappeared, now characterized by bare sediment. Each time at each site, six replicate cores were taken along a transect to a depth of 20 cm (13 cm inner diameter) and then pooled together for biological material analyses. The sediment was washed through a 500 mm mesh sieve and the biological material preserved in 4% buffered formalin. Animals and plants were identified to species level and subsequently dried at 70 °C for 72 h to estimate biomass as dry weight (DW), and ash free dry weight (AFDW) after combusting samples for 8 h at 450 °C. For each time period, the weights of all taxa were summed to obtain an annual average standing stock. No data was available for Bacteria, therefore the bacterial biomass was considered has being part of the detritus compartment, as recommended by Christensen and Pauly (1992a,b).

To determine the Chl *a* concentration, water samples were monthly collected at the two habitats, from the water column, during high tide. Sampled water (500–1000 ml) was filtered through GF/C Whatman glass fibre filters (4.7 cm diameter) followed by acetone extraction according to Parsons et al. (1985), and expressed as g Chl *a* m^{-3}. In the absence of a calculated factor for the chlorophyll to carbon conversion, the value of 50 (Eppley et al., 1977) was applied and considered constant.

To obtain an approximate value for the microphytobenthos biomass in the system, in June, July and September 2008, the microphytobenthos biomass was estimated at each sampling location by sampling the top 1 cm of the six 27 cm^{-2} replicates. The samples were carefully mixed, freeze-dried and kept in the dark at −20 °C until further processing. The Chl *a* content of the dried sediment was extracted in 90% acetone over 20 h in the dark; Chl *a* was then measured using a fluorometer, and expressed as g Chl *a* m^{-2}. The C:Chl *a* ratio was considered constant and equal to 40 mg C mg Chl *a*$^{-1}$ (De Jonge, 1980).

Carbon was converted to ash-free dry weight (AFDW) using the relation 1 g C = 0.45 g AFDW (Jørgensen et al., 1991).

2.3. Modelling approach

2.3.1. Compartments

Different numbers of compartments were identified in each situation: 36, 31 and 24 in the *Zostera* site, and 25, 20 and 20 in the bare sediment site, for the three periods, 1993/1994, 1999/2000 and 2001/2002 respectively. Species that were not naturally present in one of the three years or sites or whose roles in the trophic network were unimportant (biomass < 0.001 g AFDW m^{-2}) were not taken into account. The Detritus compartment reflects the standing stock of non-living organic matter in the sediments (including different types of plant tissue, dead microbes, faeces), the suspended organic matter, inputs from the river basin and from the ocean, and flows from living organisms.

2.3.2. Ecopath model equations

Ecopath trophic models are mass-balanced models that account for energy flows (to and from each compartment) in a food web. The parameterization of the Ecopath model is based on two 'master' equations. The first equation divides the production of each compartment included in the system into predation mortality, exports and biomass accumulation:

$$B_i \times \left(\frac{P}{B}\right)_i \times EE_i - \sum_j \left(B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ij}\right) - Y_i - BA_i - E_i = 0$$

(1)

where B_i and B_j are the biomasses of prey (i) and predators (j) respectively; P/B_i the production/biomass ratio; EE_i the ecotrophic efficiency, defined as the fraction of the production of each group that is used in the food web by means of predation and fishing exploitation; Y_i the fisheries catch per unit area and time; Q/B_j the
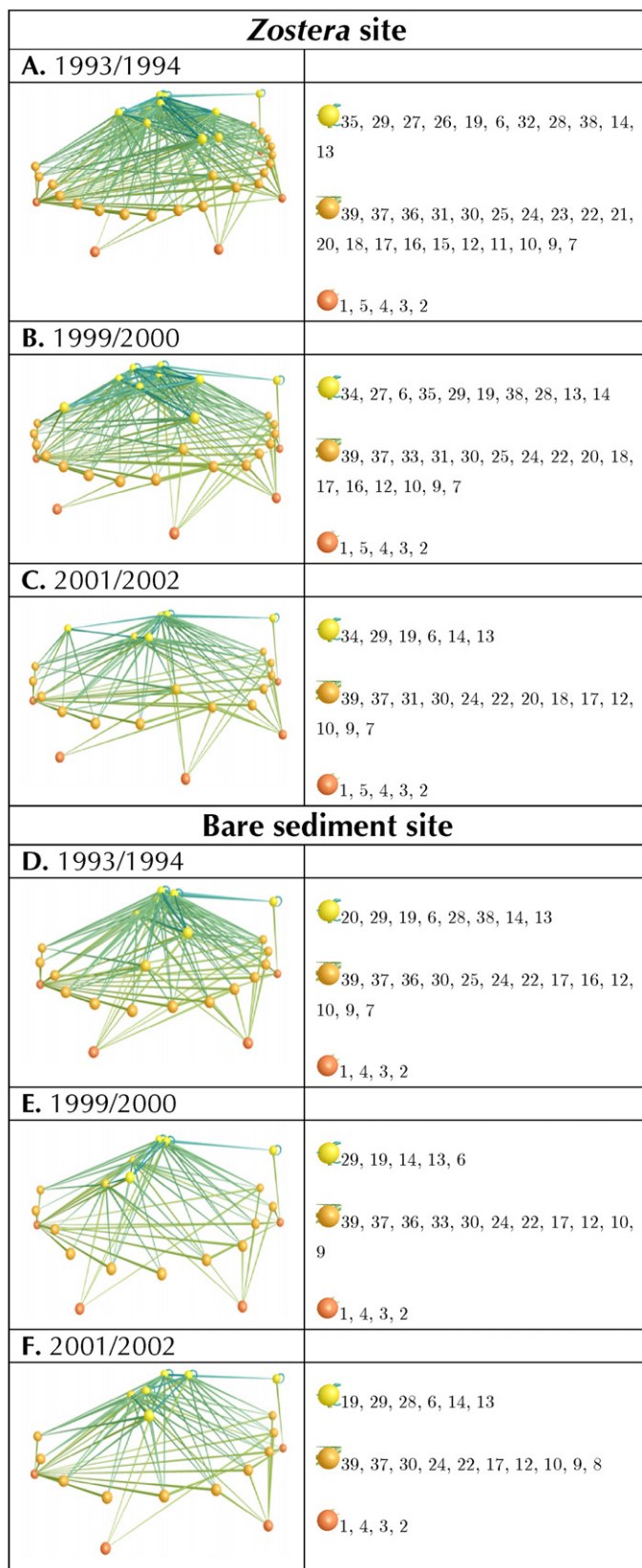
Fig. 2. 3D representation of the six food webs from Mondego estuary. (A–C) *Zostera* site in 1993/1994, 1999/2000 and 2001/2002 respectively. (D–F) Bare sediment site in 1993/1994, 1999/2000 and 2001/2002 respectively. Images produced with FoodWeb3D, written by R.J. Williams and provided by the Pacific Ecoinformatics and Computational Ecology Lab (www.foodwebs.org, Yoon et al., 2004). The different coloured dots represent functional groups from different trophic levels: red = primary producers, orange = primary consumers, and yellow = secondary

food consumption per unit biomass of j; DC_{ji} the fraction of prey i in the average diet of predator j; BA_i the biomass accumulation rate for i (the default value of zero was used to indicate no biomass accumulation); and E_i is the net migration of i, calculated as immigration (migration into the area covered by the model) minus emigration (migration out of the area) (the default value of zero was used).

Eq. (2) expresses how the consumption within a compartment is divided into production, respiration and unassimilated food:

$$B_i \times \left(\frac{Q}{B}\right)_i = B_i \times \left(\frac{P}{B}\right)_i + R_i + U_i \tag{2}$$

where R_i is the respiration rate, and U_i the unassimilated food rate. The Ecopath software solves the set of Eq. (1) (one for each group i) for one of the following parameters: B, P/B, Q/B or EE. Therefore, at least three of these four parameters are required as input. As EE is both difficult to measure and calculate it was estimated by the model for most of the groups, and the model quality was evaluated by checking if the EE value obtained was realistic (between 0 and 1). The software approach, its methods, capabilities and limitations are explained thoroughly in Christensen and Walters (2004).

2.3.3. The estimation procedure

Once the software had estimated the parameters, the system balanced the input and output of each group. The relationship used is represented by Eq. (2): where *consumption* is the intake of food by a compartment over a given interval of time, and was entered as the ratio of consumption over biomass (Q/B). For the heterotrophic compartments, the P/Q ratios were entered into the program in order to estimate the Q/B ratio indirectly (Hostens and Hamerlynck, 1994).

Production refers to the elaboration of tissue (whether it survives or not) by a compartment over a given period. Thus, the production/biomass ratio (P/B) is the turnover rate of a species' biomass, meaning the amount of time it takes to replace the biomass of the population (McLusky, 1989; Cusson and Bourget, 2005). Long-lived species will have a lower P/B than short-lived species (McLusky, 1989). Previously calculated P/B ratios were used for *Hydrobia ulvae* (gastropoda), *Scrobicularia plana* (bivalvia), *Cyathura carinata* (isopoda), *Hediste diversicolor* (polichaeta), *Ampithoe valida* and *Melita palmata* (amphipoda) for each of the study sites and periods (Dolbeth et al., 2007). Brey's (2001) method, version 4-04 (Brey, 2001, www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.htm) was used to calculate the P/B for the other species (except for zooplankton), for the two study sites and the three periods. The weight-to-energy ratios needed in order to apply the empirical method were also provided by Brey (2001).

Respiration (R_i) is the part of the assimilated fraction that is not used for production and therefore is a nonusable currency. Following Christensen et al. (2000), our models assumed that autotrophs with a $Q/B = 0$ and detritus had zero respiration. Respiration is only used in Ecopath for balancing the flows between groups.

consumers. The light and dark grey links represent feeding links. Species/Compartment: 1-Detritus, 2-Phytoplankton, 3-Microphytobenthos, 4-Green macroalgae, 5-*Zostera noltii*, 6-Zooplankton, 7-*Amphithoe valida*, 8-*Corophium multisetosum*, 9-*Melita palmata*; 10-*Cerastoderma edule*, 11-*Mytilus* sp., 12-*Scrobicularia plana*, 13-*Carcinus maenas*, 14-*Crangon crangon*, 15-*Gibulla umbilicalis*, 16-*Haminoea hydatis*, 17-*Hydrobia ulvae*, 18-*Littorina littorea*, 19-*Cyathura carinata*, 20-*Idotea chelipes*, 21-*Lekanesphaera levii*, 22-*Alkmaria romijni*, 23-*Aonides oxycephala*, 24-*Capitela capitata*, 25-*Chaetozone setosa*, 26-*Diopatra neapolitana*, 27-*Eteone flava*, 28-*Glycera tridactyla*, 29-*Hediste diversicolor*, 30-*Heteromastus filiformis*, 31-*Lagis koreni*, 32-*Lumbrineris impatiens*, 33-*Mediomastus fragilis*, 34-*Mista picta*, 35-*Nephtys* spp., 36-*Pygospio elegans*, 37-*Streblospio shrubsolii*, 38-Nemertini, 39-Oligochaets. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

Finally, the *Unassimilated food* (U_i) is an input fraction of food that is not assimilated (i.e. egested). Following Christensen et al. (2000), our energy models used a U_i default value of 0.20 (i.e. 20% of the consumption for all groups), and the non-assimilated food was allocated to the detritus.

2.3.4. Diet composition

The diet matrices of the benthic species were built using data from a variety of sources (Appendices A and B). Quantitative information on diet composition from the study system was only available for the crab *Carcinus maenas* (Baeta et al., 2006), and qualitative information was available for *H. ulvae*, *S. plana*, *C. carinata*, *A. valida*, *M. palmata*. Baeta et al. (2009a,b) measured isotopic signatures (both δ¹³C and δ¹⁵N) in the tissues of producers and consumers and obtained qualitative information on the trophic structure of the benthic and water column food webs in the Mondego estuary for both the *Zostera* and bare sediment sites. Moreover, possible food sources for the macrobenthos were investigated by using linear mixing models (ISOSOURCE software, http://www.epa.gov/wed/pages/models/.htm) (Phillips and Gregg, 2001, 2003), and the mean dietary proportion of consumers was determined (Baeta et al., submitted for publication). Complementary information on diet composition was gathered using dietary data from the literature (see Rosado-Salórzano and Próo, 1998; Serôdio and Catarino, 2000; Sand-Jensen, 1975; Dolbeth et al., 2003; Pardal, 1998; Grilo et al., 2009; Pérez-Lloréns and Niell, 1993; Brotas and Catarino, 1995; Lillebø et al., 2005; Anderson and Williams, 1998; Almeida et al., 2002; Appendix B) (Azeiteiro et al., 1999; Baird et al., 2004; Bamber, 2004; Beukema, 1991; Bode et al., 2006; Cunha et al., 2000; Dauer et al., 1981; Eklöf et al., 2005; Ferreira et al., 2004; Garcia-Arberas and Rallo, 2002; Gaston and Nasci, 1988; Giere, 1975; Hily et al., 2008; Mancinelli et al., 2005; Mangum et al., 1968; Malaquias et al., 2004; Mazik and Elliott, 2000; McDermott and Roe, 1985; Mistri et al., 2001; Oh et al., 2001; Oug et al., 1998; Pardal et al., 2000; Rakocinski et al., 1997; Solis-Weiss et al., 2004; Thiel and Reise, 1993; Verdelhos et al., 2005; Volkenborn and Reise, 2007).

2.3.5. Catches (Y_i)

A complete network needs estimates of the export rates from the system, including the harvesting of economically important species. In the present work, the harvesting of *S. plana*, *Cerastoderma edule* and *C. maenas* for human consumption and the polychaete *H. diversicolor* and decapod *Crangon crangon* for bait for fisheries was considered small enough to be negligible.

2.3.6. Balancing the models

For each of the six models (one model per station and sampling period), the software calculated the missing parameters. As expected, initially none of the models were balanced (e.g. negative flows to detritus, EE higher than 1 – which indicates that the demand is too high to be sustainable). According to Christensen et al. (2000) the normal procedure for building Ecopath models is to start with a low quality first model and then adjust the parameters entered within the range of possible values, trying to avoid changing the more reliable data. Therefore, changes were made one at the time, and each time the basic estimates routine was rerun and re-examined. Data were re-edited whenever necessary. In our study, the most reliable data were the macrofauna biomass and production, determined *in situ*, and consequently these values were left unchanged. One exception was the decapod biomass (*C. crangon* and *C. maenas*); for the decapod species the biomass parameter was estimated by the software because the original values were underestimated owing to the sampling strategy used (sampling was carried out using a TASM rather than nets suitable for catching pelagic organisms). For subsequent balancing it was

necessary to re-evaluate the diet composition of some compartments (e.g. *C. maenas*, *C. crangon*, *C. carinata*, *H. diversicolor*, *Littorina littorea*), since the feeding habits of these species are highly labile and mainly depend on the food sources that are available in the ecosystem. Adjustments were made within the range of the minimum and maximum contributions of each source in the consumers' diet, given by the linear mixing models (Baeta et al., submitted for publication), as well as taking into account the trophic group of each species. A diet fraction is impossible if it pushes another diet fraction outside its feasible range. Therefore, we calculated the upper limit of the amount of a given prey item that a predator can consume (i.e. available prey biomass) using the highest possible production rate of the prey and the lowest total consumption of the prey by other predators. The highest fraction for prey *i* in the diet of predator *j* was then given by the highest available biomass of prey *i* divided by the lowest possible consumption rate of predator *j*. The lower limit for the diet fraction was obtained in a similar way (for more details see Baeta et al., submitted for publication).

2.3.7. Summary of ecological statistics and indices

A number of statistics that describe an ecosystem as a whole were calculated for assessing the status of the ecosystem (Christensen et al., 2000) at the two study sites in the three time periods, that is, the sum of all consumptions, exports, respiratory flows, flows to detritus, production (all in g AFDW m⁻² y⁻¹), and total biomass (excluding detritus) (g AFDW m⁻²). Other measures were also estimated:

The *total system throughput*, *TST* (g AFDW m⁻² y⁻¹), is the sum of all flows in a system (consumption + export + flows to detritus + respiration).

The *net primary production* (g AFDW m⁻² y⁻¹) is calculated as the total primary production from all producers.

The *net system production* (g AFDW m⁻² y⁻¹) is the difference between total primary production and total respiration. According to Odum (1969), it will be large in immature systems and close to zero in mature ones. Moreover, systems with large imports may have negative system production.

The *total primary production/total biomass* (y⁻¹) is expected to be a function of the system's maturity. In immature systems, production exceeds respiration for most groups, and therefore the biomass can be expected to accumulate over time, which in turn will lead to a decline in the ratio.

The *total biomass/TST* (y) is expected to increase and reach a maximum in the most mature stages of the system (Odum, 1971).

The *system omnivory index, SOI*, is the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake. It is a measure of how the feeding interactions are distributed among trophic levels, and is useful for characterizing the extent to which a system displays web-like features (Christensen et al., 2000). When the value of the omnivory index is zero, the consumer in question is specialized (i.e. feeds on a single trophic level). A large value indicates that the consumer feeds on many trophic levels (Christensen et al., 2005).

The *keystoneness* and *relative overall effect* were estimated for each compartment in order to indentify keystone species. These two indices derive from mixed trophic impacts analysis (Libralato et al., 2006; Coll et al., 2007). The relative overall effect of a compartment (ε_i) is the square root of the sum of square of all trophic impacts of one compartment on each other. It allows the quantification of direct and indirect effects that one compartment would have on the others. The keystoneness takes into account the biomass of the compartment, a keystone species being one showing a structuring role in the ecosystem whereas having a low biomass. For compartment *i*:

$$KS_i = \log[\varepsilon_i(1 - p_i)] \tag{3}$$

Table 1

Input data and calculated estimates (in parentheses) of all compartments in the food web network for the two areas (Z, *Zostera noltii*; bs, bare sediment area) for the three time periods (1993/1994; 1999/2000; 2001/2002). Biomass given in g AFDW m^{-2} (M, macrophytes; Am, amphipoda; B, bivalvia; D, decapoda; G, gastropoda; I, isopoda; P, polychaeta).

	Compartment Name	1993/1994								1999/2000								2001/2002							
		Biomass Z	Biomass bs	P/B[a] Z	P/B[a] bs	Q/B[a] Z	Q/B[a] bs	EE[a] Z	EE[a] bs	Biomass Z	Biomass bs	P/B[a] Z	P/B[a] bs	Q/B[a] Z	Q/B[a] bs	EE[a] Z	EE[a] bs	Biomass Z	Biomass bs	P/B[a] Z	P/B[a] bs	Q/B[a] Z	Q/B[a] bs	EE[a] Z	EE[a] bs
1	Phytoplankton	0.336	0.330	135.00	135.00			(0.55)	(0.79)	0.326	0.350	135.00	135.00			(0.54)	(0.97)	0.316	0.330	135.00	135.00			(0.57)	(0.94)
2	Microphytobenthos	4.200	6.000	40.00	40.00			(0.96)	(0.62)	4.200	6.000	40.00	40.00			(0.97)	(0.36)	4.200	6.000	40.00	40.00			(0.98)	(0.24)
3	Green macroalgae	2.201	64.371	3.20	3.20			(0.97)	(0.03)	1.679	2.178	3.20	3.20			(0.41)	(0.08)	2.462	0.515	3.20	3.20			(0.20)	(0.16)
5	*Zostera noltii* (M)	194.141		2.50				(0.01)		62.266		2.50				(0.00)		108.222		2.50				(0.00)	
6	Zooplankton	(0.069)	(0.030)	22.00	18.00	(88.00)	(90.00)	0.95	0.95	(0.025)	(0.056)	22.00	18.00	(88.00)	(90.00)	0.95	0.95	(0.042)	(0.027)	22.00	18.00	(88.00)	(90.00)	0.95	0.95
7	*Ampithoe valida* (Am)	(0.169)	0.080	6.40	7.05	(32.00)	(35.25)	0.95	0.75	0.039		6.47		(32.35)		0.98		0.018		5.38		(26.88)		(0.95)	
8	*Corophium multisetosum* (Am)																	0.006		6.87		(34.37)		(0.39)	
9	*Melita palmata* (Am)	0.116	0.059	7.10	11.33	(35.50)	(56.65)	(0.98)	(0.62)	0.007	(0.015)	7.79	3.42	(38.97)	(17.10)	(0.62)	0.95	0.021	0.007	5.95	2.11	(29.76)	(10.55)	(0.74)	(0.20)
10	*Cerastoderma edule* (B)	4.484	0.131	0.91	7.91	(4.60)	(39.53)	(0.17)	(0.05)	0.879	0.047	1.07	2.74	(5.36)	(13.70)	(0.07)	(0.14)	0.409	0.092	0.91	2.35	(4.57)	(11.77)	(0.62)	(0.16)
11	*Mytilus* sp.	0.015		4.10		(20.50)		(0.63)																	
12	*Scrobicularia plana* (B)	2.668	8.337	1.00	1.60	(5.00)	(8.00)	(0.40)	(0.06)	16.762	35.000	1.00	0.90	(5.00)	(4.50)	(0.14)	(0.07)	15.756	23.174	1.00	1.06	(5.00)	(5.30)	(0.33)	(0.09)
13	*Carcinus maenas* (D)	0.780	0.252	2.01	2.94	(10.10)	(14.72)	(0.56)	(0.86)	0.342	0.327	2.23	2.93	(11.13)	(14.65)	(0.86)	(0.63)	0.680	(0.138)	1.92	4.29	(9.62)	(21.43)	(0.94)	(0.51)
14	*Crangon crangon* (D)	(0.308)	(0.092)	3.97	6.25	(19.90)	(31.25)	0.95	0.95	(0.149)	(0.152)	3.97	7.57	(19.87)	(37.81)	0.95	0.95	(0.209)	(0.074)	4.87	6.25	(24.36)	(31.25)	0.95	0.95
15	*Gibulla umbilicallis* (G)	0.045		1.81		(9.00)		(0.45)																	
16	*Haminoea hydatis* (G)	0.187	0.066	2.12	2.51	(10.60)	(12.54)	(0.06)	(0.03)	0.101		3.84		(19.21)		(0.03)									
17	*Hydrobia ulvae* (G)	59.809	6.751	2.00	4.78	(8.00)	(23.90)	(0.02)	(0.01)	21.300	1.692	3.00	3.67	(15.00)	(18.35)	(0.03)	(0.03)	45.273	0.537	2.00	3.30	(10.00)	(16.65)	(0.08)	(0.20)
18	*Littorina* spp. (G)	2.117		1.10		(5.50)		(0.12)		0.578		1.03		(5.16)		(0.09)		0.204		1.27		(6.37)		(0.07)	
19	*Cyathura carinata* (I)	0.407	8.077	3.10	3.16	(15.50)	(15.80)	(0.39)	(0.01)	1.095	9.397	2.00	1.53	(10.00)	(7.65)	(0.12)	(0.03)	1.116	8.656	2.00	2.36	(10.00)	(11.80)	(0.12)	(0.02)
20	*Idotea chelipes* (I)	0.036	0.013	4.76	4.23	(23.79)	(21.15)	(0.93)	(0.63)	0.005		5.10		(25.48)		(0.94)		0.010		2.98		(14.89)		(0.77)	
21	*Lekanesphaera levii* (I)	0.002		5.87		(29.37)		(0.55)																	
22	*Alkmaria romijni* (P)	0.022	0.113	9.45	13.15	(47.23)	(65.73)	(0.81)	(0.39)	0.009	0.031	10.65	8.79	(53.25)	(43.94)	(0.31)	(0.63)	0.028	0.057	5.93	9.99	(29.67)	(49.95)	(0.52)	(0.46)
23	*Aonides oxycephala* (P)	0.013		4.90		(24.50)		(0.95)																	
24	*Capitella capitata* (P)	0.009	0.023	7.66	9.72	(38.28)	(48.61)	(0.78)	(0.44)	0.006	0.008	6.47	7.37	(32.35)	(36.83)	(0.37)	(0.39)	0.271	0.006	2.62	9.52	(13.11)	(47.60)	(0.70)	(0.59)
25	*Chaetozone setosa* (P)	0.118	0.008	7.73	13.82	(38.65)	(69.11)	(0.83)	(0.11)	0.032		6.46		(32.28)		(0.40)									
26	*Diopatra neapolitana* (P)	0.012		2.75		(13.76)		(0.59)																	
27	*Eteone flava* (P)	0.002		6.48		(32.40)		(0.66)		0.035		2.39		(11.94)		(0.61)									
28	*Glicera tridactyla* (P)	0.214	0.004	2.18	5.12	(10.89)	(25.62)	(0.99)	(0.62)	0.061		2.02		(10.09)		(0.94)			0.005		5.04		(25.18)		(0.78)
29	*Hediste diversicolor* (P)	(0.795)	0.423	2.40	1.85	(12.00)	(9.25)	0.98	(0.99)	2.417	0.891	1.60	1.72	(8.00)	(8.60)	(0.97)	(0.92)	6.952	2.906	2.00	1.98	(10.00)	(9.90)	(0.37)	(0.96)
30	*Heteromastus filiformis* (P)	0.455	0.142	3.39	4.56	(16.97)	(22.81)	(0.94)	(0.79)	0.473	0.108	3.24	4.44	(16.19)	(22.20)	(0.96)	(0.84)	0.141	0.038	3.60	5.34	(18.01)	(26.72)	(0.90)	(0.74)
31	*Lagis koreni* (P)	0.017		3.40		(17.00)		(0.76)		0.008		3.77		(18.84)		(0.35)		0.005		4.73		(23.67)		(0.49)	
32	*Lumbrineris impatiens* (P)	0.081		2.72		(13.61)		(0.89)																	
33	*Mediomastus fragilis* (P)									0.004	0.005	5.75	6.60	(28.75)	(33.02)	(0.87)	(0.23)								
34	*Mista picta* (P)									0.023		4.21		(21.07)		(0.45)		0.049		2.46		(12.28)		(0.69)	
35	*Nephtys hombergii* (P)	0.034		2.55		(12.76)		(0.85)		0.040		2.27		(11.35)		(0.86)									
36	*Pygospio elegans* (P)	0.002	0.010	8.37	10.12	(41.85)	(50.60)	(0.53)	(0.12)		0.011		6.51		(32.53)		(0.21)								
37	*Streblospio shrubsoli* (P)	0.011	0.009	9.28	13.95	(46.39)	(69.76)	(0.96)	(0.09)	0.003	0.006	9.75	10.04	(48.73)	(50.21)	(0.89)	(0.13)	0.059	0.014	4.42	8.39	(22.08)	(41.94)	(0.59)	(0.44)
38	Nemertini	0.004	0.002	5.06	9.65	(25.31)	(48.24)	(0.89)	(0.45)	0.028		4.11		(20.59)		(0.91)									
39	Oligochaets	0.132	0.004	6.74	12.75	(33.70)	(63.75)	(0.92)	(0.52)	0.148	0.004	5.49	10.01	(27.45)	(50.03)	(0.82)	(0.19)	0.071	0.022	3.66	10.10	(18.28)	(50.27)	(0.80)	(0.61)
40	Detritus	511.28	305.80					(0.49)	(0.43)	511.28	305.8					(0.69)	(0.55)	527.31	305					(0.77)	(0.57)

[a] *P*, production; *Q*, consumption; EE, ecotrophic efficiency.

Table 2
Summary of ecological statistics/indices for the two areas (*Zostera* site and bare sediment site) for the three time periods (1993/1994; 1999/2000; 2001/2002).

Statistic/indices	*Zostera* site			Bare sediment site		
	1993/1994	1999/2000	2001/2002	1993/1994	1999/2000	2001/2002
Sum of all consumptions (g AFDW m^{-2} y^{-1})	592.255	470.232	642.164	395.542	289.694	277.682
Sum of all exports (g AFDW m^{-2} y^{-1})	350.632	91.879	105.462	253.583	121.821	120.367
Sum of all respiratory flows (g AFDW m^{-2} y^{-1})	356.904	282.031	385.115	237.927	173.816	166.609
Sum of all flows into detritus (g AFDW m^{-2} y^{-1})	733.167	358.96	533.388	450.049	269.277	286.576
Sum of all production (g AFDW m^{-2} y^{-1})	823	468	618	571	350	342
Total system throughput (g AFDW m^{-2} y^{-1})	2036	1203	1666	1337	855	851
Net primary production (g AFDW m^{-2} y^{-1})	705.756	373.048	489.093	490.537	294.22	286.198
Total primary production/total respiration	1.977	1.323	1.270	2.062	1.693	1.718
Net system production (g AFDW m^{-2} y^{-1})	348.852	91.016	103.979	252.611	120.403	119.589
Total primary production/total biomass (y^{-1})	2.576	3.300	2.622	5.146	5.228	6.718
Total biomass/total system throughput (y)	0.135	0.094	0.112	0.071	0.066	0.050
Total biomass (excluding detritus) (g AFDW m^{-2})	274.01	113.042	186.514	95.327	56.279	42.604
Connectance index	0.196	0.200	0.191	0.226	0.180	0.219
System omnivory index	0.097	0.101	0.097	0.056	0.080	0.066
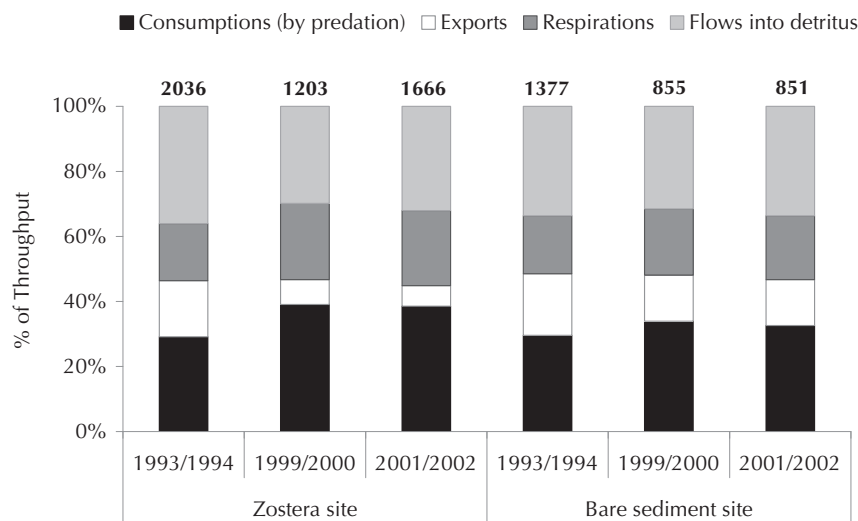
Fig. 3. Partitioning of throughput (total absolute values at the top of each bar) among consumption by predators, exports, flow to detritus and respiration at the *Zostera* site and bare sediment site in the three time periods (1993/1994; 1999/2000 and 2001/2002).
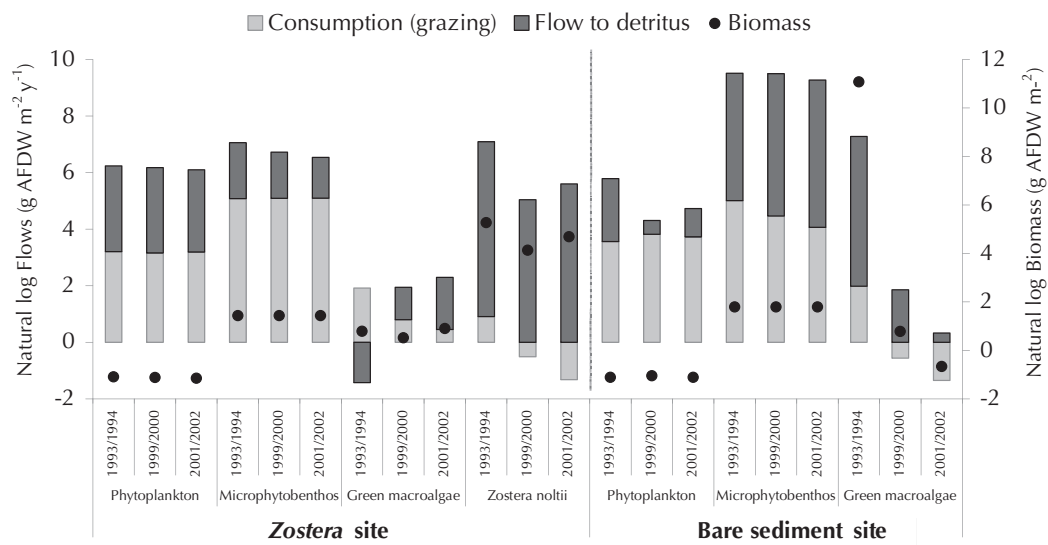
Fig. 4. Flows (consumption, flow to detritus, exports and respiration) from each primary producer at the *Zostera* site and bare sediment site in the three time periods (1993/1994, 1999/2000 and 2001/2002).
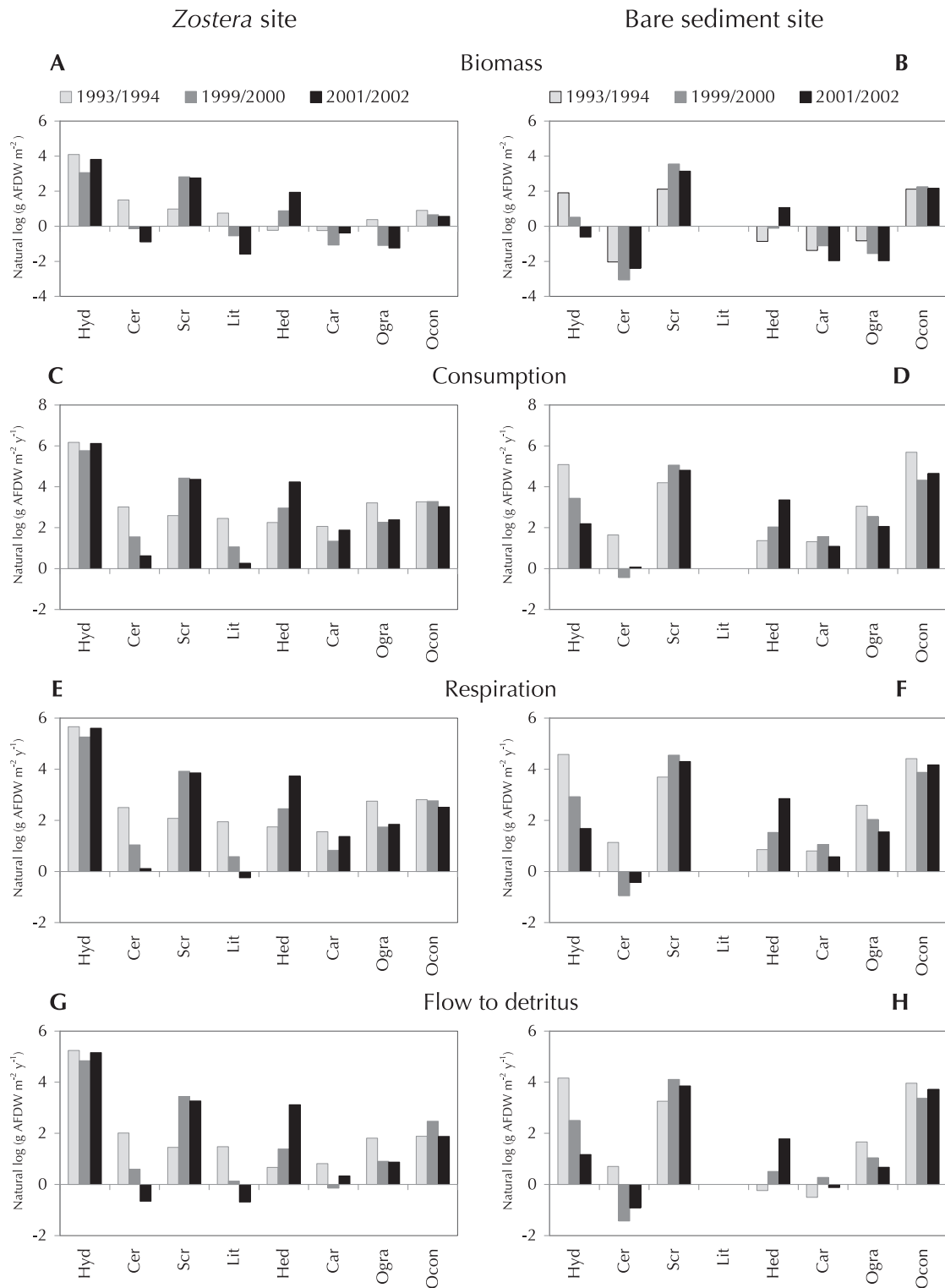
Fig. 5. Biomass (A and B), Consumption (C and D), Respiration (E and F) and Flow to detritus (G and H) for *Hydrobia ulvae* (Hyd), *Cerastoderma edule* (Cer), *Scrobicularia plana* (Scr), *Littorina* spp. (Lit), *Hediste diversicolor* (Hed), *Carcinus maenas (Car)*, other grazers (Ogra) and other consumers (Ocon) at the *Zostera* site and bare sediment site respectively in the three time periods (1993/1994, 1999/2000 and 2001/2002).
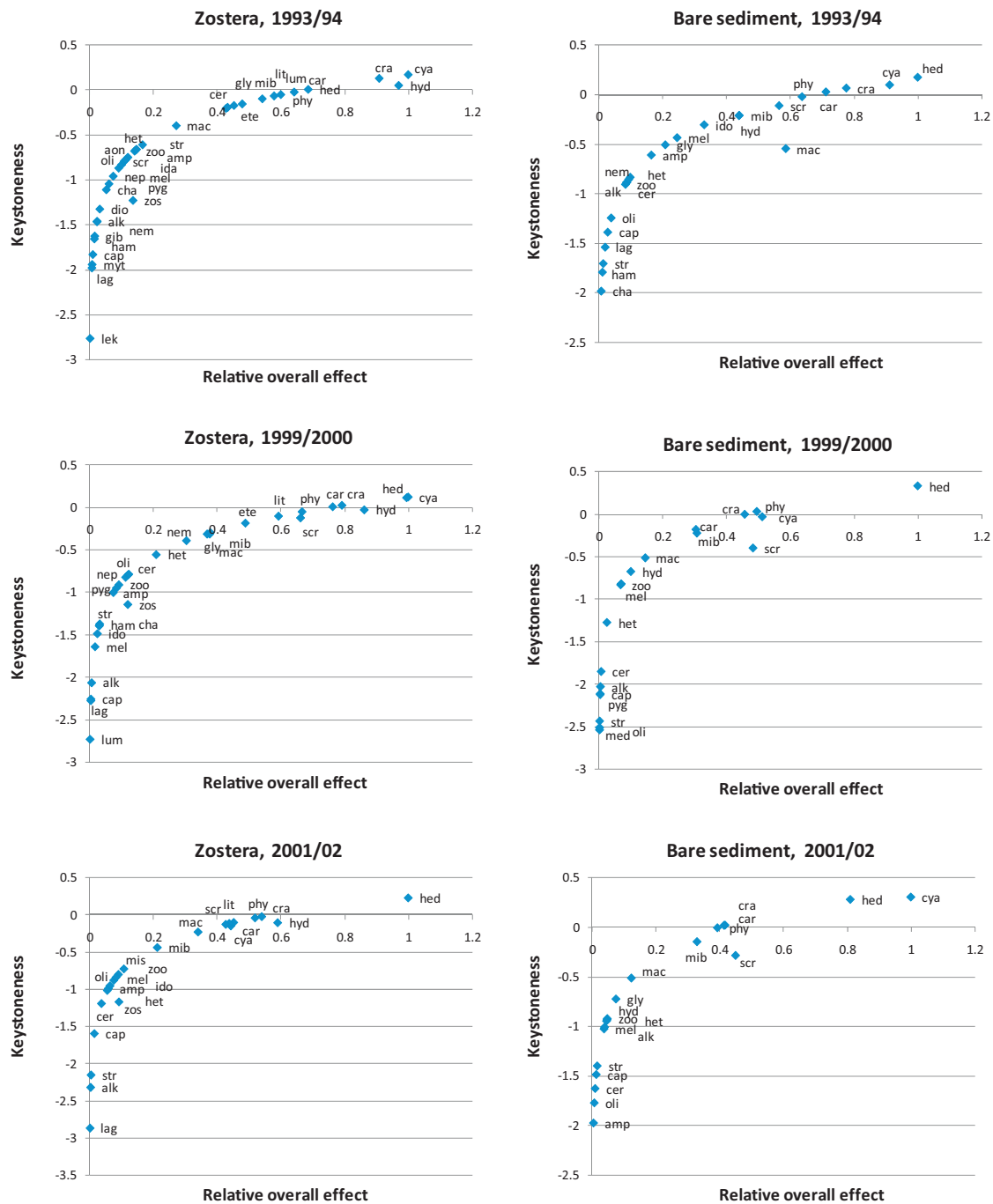
Fig. 6. Keystoneness (KS_i) and relative overall effect (ε_i) of each compartment from the 6 food web models. Keystone compartments are those with high values for both of them. phy = Phytoplankton, mib = Microphytobenthos, mac = Green macroalgae, zos = *Zostera noltii*, zoo = Zooplankton, amp = *Ampithoe valida*, mel = *Melita palmata*, cer = *Cerastoderma edule*, myt = *Mytilus* sp., scr = *Scrobicularia plana*, car = *Carcinus maenas*, cra = *Crangon crangon*, gib = *Gibbula umbilicalis*, ham = *Haminoea hydatis*, hyd = *Hydrobia ulvae*, lit = *Littorina* spp., cya = *Cyathura carinata*, ida = *Idotea chelipes*, lek = *Lekanesfaera levii*, alk = *Alkmaria romijni*, aon = *Aonides oxycephala*, cap = *Capitella capitata*, cha = *Chaetozone setosa*, dio = *Diopatra neapolitana*, ete = *Eteone flava*, gly = *Glycera tridactyla*, hed = *Hediste diversicolor*, het = *Heteromastus filiformis*, lag = *Lagis koreni*, lum = *Lumbrineris impatiens*, nep = *Nephtys* spp., pyg = *Pygospio elegans*, str = *Streblospio shrubsoli*, nem = Nemertini, oli = Oligochaets.

where p_i is the contribution of the compartment i to the total biomass of the food web.

3. Results and discussion

3.1. Summary statistics: comparing three time periods at two intertidal sites

The basic input data and model estimations of the dietary composition matrices at each site and in each period are given in Table 1 and Appendix A, respectively. The ecological system statistics and indices for the *Zostera* and bare sediment sites for the three periods are given in Table 2.

Different numbers of compartments were identified in each situation: 36, 31 and 24 at the *Zostera* site, and 25, 20 and 20 at the bare sediment site, for the three periods, 1993/1994, 1999/2000 and 2001/2002 respectively. There was no aggregation of compartments; species that were not naturally present in one of the three areas or whose roles in the trophic network were unimportant (biomass $< 0.001\,\mathrm{g\,AFDW\,m^{-2}}$) were not taken into account at a specific time and space.

No aggregation of macrofauna species was also used in other studies (e.g. Baird et al., 2004, 2007), as each species has its own specificity, and the same threshold value for negligible species. This is confirmed by the observation that there are some variations in isotopic contents among the species (Baeta et al., 2009a,b). The same choice is not always done, as some authors gather species into functional groups which has been shown to modify the properties described by indices (e.g. Abarca-Arenas and Ulanowicz, 2002; Angelini and Agostinho, 2005). In this study, due to the very precise data obtained no aggregations of species were made.

The total consumption, exports, respiration, flow to detritus and production were higher in the *Zostera* site for the three time periods compared to the bare sediment site, except for the total exports, which was lower at the *Zostera* site in 1999/2000 and 2001/2002. The *Zostera* site in the period 99/00 showed the lowest values for the total exports. For the bare sediment system, the lowest values for the sum of each type of flow were found in the 1999/2000 and 2001/2002 periods, which had very similar values. Similarly, the total system throughput was always higher at the *Zostera* site (Table 2), which shows that there is a higher level of system activity in this community. Fig. 2 illustrates the six food webs (one for each site and time period).

The overall structure of flows is partially influenced by the number of compartments. Respiration, flow to detritus and exports are not sensitive to the number of compartments, but consumption and the TST are. Accordingly, the *Zostera* site, due to its complex community, had a larger number of compartments than the bare sediment site, and showed a higher level of system activity (e.g. TST). Probably for the same reason, both areas showed their highest TST values during the period of nutrient enrichment (1993/1994).

To measure how the feeding interactions are distributed between trophic levels, Ecopath calculates the Omnivory Index (OI) for each compartment (Christensen et al., 2005). According to Heymans (2003), this index is dependent on the number of compartments in the model: more compartments have more connections, and there is less omnivory when compartments are combined and diets consolidated. In this study, despite the disturbance events (nutrient enrichment or flood) and the different numbers of compartments, the *Zostera* site showed a similar SOI for all the time periods and always had higher values than the bare sediment site. Interestingly, the index decreased, although only slightly, during the disturbance periods (1993/1994 and 2001/2002).

In comparison with the previous preliminary attempt to model the food web characteristics of the two sites during the period of nutrient enrichment (1993/1994) (Patrício and Marques, 2006), we found several differences with regard to community structure and flows in the present study (e.g. present study: lower TST, total production, total respiration, total exports, flow to detritus, SOI). In our models the species were not aggregated, the P/B ratios were calculated for the two sites for each period, and new information and measurements of the diets of benthic species (Baeta et al., 2006, 2009a,b, submitted for publication) were used for model balancing, which probably modified the previous models' results. This allowed the quantitative contribution of the consumers' food sources to be estimated more accurately using mixing models and index values as well as the quantification information on nutrition sources of the estuarine invertebrates inhabiting the two study areas.

3.2. Effects of different ecological conditions on primary producers

The *Zostera* area in 1999/2000 and 2001/2002 showed similar partitioning of the total throughput: between around 39% of the total flow was due to consumption, approximately 6–8% was exported, about 30–32% flowed to detritus, and around 23% was respired (Fig. 3). At the *Zostera* site, the major difference concerned a higher value (18%) for exports during the nutrient enrichment period (1993/1994).

The differences in the breakdown of throughput, with higher exports and flows to detritus in the period 1993/1994, were mainly due to differences in the macrophyte biomass. It is well known that macrophytes support two types of food webs: a herbivorous web, in which herbivores feed directly on the plant, and a detritivorous web, in which some species feed on the plant detritus. According to Enriques et al. (1993), macrophytes are major producers of organic matter; however, little of this production enters the grazing food chain because there is a time lag between production and utilisation since few animals feed on these plants directly. This production is usually used after decomposition and a large proportion of the production decays to detritus or is washed away from the production area and used in other systems. This is consistent with the results of the current study (Fig. 4).

Similar results were obtained over time in the bare sediment models, with a similar partitioning of the total throughput. Between 30 and 34% of the total throughput was due to consumption, about 32–34% flowed to detritus, and approximately 18–20% was respired (Fig. 3). The major difference found for the three periods was a higher exports value in 1993/1994 compared to the other two periods (19% *vs* 14% respectively). Although the microphytobenthos data used in the six models were obtained from only sampling collections during June, July and September of 2008 (corresponding to the growing season), it is likely that this compartment play a crucial role in this system production (Fig. 4). In 1993/1994, although the macroalgae biomass was extremely high ($64.4\,\mathrm{g\,AFDW\,m^{-2}}$) (Fig. 4), the consumption of this primary producer was very low. Consequently, at the bare sediment site, during the period of nutrient enrichment, a large percentage of the primary production (that led to excessive production of organic matter in the form of green algal blooms) passed to the detritus compartment (Fig. 4).

The annual rate of net primary production showed higher values in 1993/1994 for both sites (Table 2), which clearly reflects the primary production dynamic in each time period (Fig. 4). The *Zostera* site had higher production than the bare sediment site, which is consistent with the hypothesis that less impacted systems exhibit higher rates of net primary production (Odum, 1969).

Studies on the effects of different ecological conditions, for example hurricanes and flood events, on primary producers do not show, however, a clear direction. On one hand, hurricanes effects are low on primary producers; Anton et al. (2009) report: "Overall,

natural temporal changes recorded before the storm were larger than any post-hurricane changes. These findings indicate that this seagrass meadow was naturally highly dynamic and very resistant to Hurricane Katrina". On another hand, seagrass meadows seems to shrink a lot due to flood events; Campbell and McKenzie (2004) report: "Mapping surveys showed that approximately 90% of intertidal seagrasses in the northern Great Sandy Strait disappeared after the February 1999 flooding of the Mary River. Full recovery of all seagrass meadows took 3 years".

3.3. Effects of disturbances on grazers and other consumers

The grazers accounted for most of the consumer biomass (Fig. 5). In particular at the *Zostera* site, independently of the time period, *H. ulvae*, *C. edule*, *S. plana*, *L. litorea*, *H. diversicolor* and *C. maenas* represented 99% of the total grazer biomass and approximately 95% of the total consumer biomass (Fig. 5A). At the bare sediment site, *S. plana*, *H. diversicolor*, *H. ulvae* and *C. maenas* corresponded to 64–79% of the total consumer biomass (Fig. 5B). It is also worth noting that in this habitat the other consumers play a relevant role in the system consumption flows, unlike what was observed in the *Zostera* meadow community, in which the flows were totally dominated by grazers. It is well known that engineer species, and especially *Z. noltii*, lead to high diversity (Duarte, 2002) and also favour epibenthic compared to endobenthic species (Bouma et al., 2009), by leading to a more complex habitat above ground. In the present study, both endo and epibenthic species are favoured by the *Zostera*, possibly because the roots of the macrophyte are not too dense.

In summary, *H. ulvae* is the species dominating the biomass in the macrophyte meadows and *S. plana* plays the dominant role in the bare sediment habitat. Not surprisingly, the consumption, respiration and flow to detritus are dominated by these two species, each in its preferred habitat (Fig. 5C–H). For all *Zostera* meadow models, *H. ulvae* appears as being one of the 3 most important species. It shows, at the same time, one of the highest relative overall effects, which means that its influence is high, directly or indirectly, on all other species, and a high keystoneness. This means that even when considering only a unit of its biomass, the effect remains very high. So the key role of *H. ulvae* is not only connected to its biomass, but also to the trophic situation inside the food web. Two other species are found as key compartment in the *Zostera* food webs: *C. carinata* and *H. diversicolor.* The keystoneness in the bare sediment habitat is also high for these two compartments. *H. ulvae* is not anymore among the key species, nevertheless *S. plana* is always present among the 6 most important species.

What was the effect of the different types of disturbances (i.e. nutrient enrichment, mitigation measures and centenary flood) on consumers?

At both sites, *H. ulvae* showed the highest biomass, consumption, respiration and flow to detritus during the period of organic enrichment. After preliminary mitigation measures were implemented, the structure and activity indices decreased, and then rose again after another disturbance event, i.e. the centenary flood during the winter of 2001. In Fig. 6, the position of *H. ulvae* shows that it remains among the key species in the 3 models at the *Zostera* meadow. Its relative overall effect reduces from 1993/1994 to 1999/2000 and also to 2001/2002, however the keystoneness remains high, showing that even a reduced biomass remains with a high effect on other compartments.

Patrício et al. (2009) used the Mondego estuary to test the performance and robustness of a set of ecological indicators to highlight the changes in the ecological state of intertidal areas over a period of 17 years (1985–2002). They tested differences over periods characterized by different anthropogenic disturbances. Indices were compared with biological and abiotic descriptors

(macroalgae, macrophytes, benthic macrofauna, nutrient concentrations, sediment grain size and total organic carbon). Their results showed that during the period of works and closure of the channel between the 2 arms of the estuary (1993/1994), the abundance of some opportunistic polychaete species of Tubificidae and *H. ulvae* (*Alkmaria romijni*, *Heteromastus filiformis*, *Capitela capitata* and *Chaetozone setose*) was much higher than in the period before the disturbance (1986) and the period following mitigation measures (1998–2002). Our model results are in line with the abovementioned study, and among these opportunistic polychaete species, *H. filiformis* shows the highest value of keystoneness and relative overall effect.

Moreover, at both sites after mitigation measures were implemented there was an increase in *S. plana* and *H. diversicolor* biomass, consumption, respiration and flow to detritus. At the *Zostera* site, these species were apparently not affected by the flood event; however, at the bare sediment site, *S. plana* decreased in biomass and flows after the winter 2001 extreme weather event. Fig. 6 shows that the main keystones species of the bare mudflat are by far the *H. diversicolor* and *C. carinata*.

Finally, during the nutrient enrichment period, at the bare sediment site it was clearly visible that the other consumers played a substantial role in the system flows. Their contribution decreased after the mitigation measures then regained importance after a new disturbance event (i.e. the flood). Numerous species have high keystoneness values in 1993/1994, however only *H. diversicolor* becomes dominant in 1999/2000 and it remains more or less the same after the flood event.

3.4. Can food web analysis have management implications?

In the early and mid 1990s, nutrient enrichment of the system led to macroalgal blooms which depressed the previously dominant macrophyte communities (Marques et al., 2003; Patrício et al., 2009). 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 *S. plana* and *H. diversicolor*; lower biomass of *H. ulvae*), which led to more structured and stable populations, closer to the less disturbed conditions observed in the 80s (Patrício et al., 2009). The results of the mass-balanced models show that the trophic structure of the benthic communities of Mondego estuary was affected differently by distinct disturbance events. Interestingly, in this study, a high system throughput seems to be associated with higher stress levels, which contradicts the idea that higher system activity is always a sign of healthier conditions (the period of mitigation measures presented lower TST). This observation should serve as a warning and require special precautions in terms of ecological quality assessment and management. Moreover, knowing that the direct and indirect responses to changes in hydrology, nutrient enrichment, and extreme weather events can be different in different habitats (Cloern, 2001), realistic management actions need to be based on a new paradigm that takes the entire system into account. Our results show that some important properties are only revealed at the system level (Jørgensen, 2002). Therefore, a succeeding manuscript is already in preparation to take full advantage of the results, since further research is needed to link the overall system indices (e.g. biomass/total system throughput, net system production and system omnivory index) with recognized theories of maturity and system development (e.g. Odum, 1971).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2010.12.010.

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