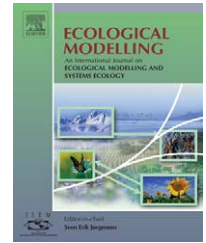


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# Mass balanced models of the food web in three areas along a gradient of eutrophication symptoms in the south arm of the Mondego estuary (Portugal)

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## ABSTRACT

Three Ecopath with Ecosim models were constructed to represent the eutrophication gradient along the south arm of the Mondego estuary (Portugal). Sampling was conducted in three areas representative of different environmental situations along the gradient: (a) a non-eutrophic area (*Zostera noltii* meadows), (b) an intermediate eutrophic area (macrophyte absent, although residual roots can still be found in the sediment, and the occasional formation of abundant macroalgae mats) and (c) a strongly eutrophic area (macrophyte community totally absent for at least a decade and strong, regularly occurring, blooms of *Ulva* spp.). Field, laboratory and literature information were used to construct the models, as well as empirical ecological knowledge gained from years of work on this system. Approximately 76 trophic groups (e.g. Phytoplankton and Zooplankton species), species and genera were included. These species were grouped into 43, 36 and 34 model groups for *Zostera* sp. meadows, intermediate eutrophic area and strongly eutrophic area, respectively. The groups were arranged by trophic similarity and habitat preferences; special distinction is given to macrofauna. Biomass, production, consumption, and diet are among the parameters used to describe each group. The sum of consumptions, exports, respiration, production, flow to detritus, total system throughput and annual rate of net primary production was always higher in the *Zostera* sp. meadows, followed by the strongly eutrophic area and, finally, by the intermediate eutrophic area.

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## 1. Introduction

Ecology can be defined as the scientific study of the relationships between organisms and their environment; and, in general, can be approached from two directions: (1) via reductionism, wherein each relationship is considered by itself and the results are assembled afterwards; and (2) via holism, whereby the system is considered in its entirety and a search is undertaken to reveal properties at the system level (Jørgensen, 2002).

Previous studies have shown that an ecosystem consists of so many interacting components that it becomes impossible ever to understand how it functions by examining the component relationships in isolation (Likens, 1985; Allen, 1988). Often, when individual components of ecosystems are studied via reductionism, the reconstructed ensemble will behave differently than the sum of the parts.

To obviate such problems, since no system can understand itself, the way it can be understood is to develop simplified

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models which have enough of the characteristics of the original system to resemble reality, but at the same time are simple enough to be understood (Brown, 2004). In fact, one might attempt to describe at least part of the reality of ecosystems structure by developing mass-balance models that represent a static description or a ‘snapshot’ of the trophic flows in the ecosystem (Christensen, 1994). Such snapshots can be readily compared and therefore, used to explore the evolution of a system through a series of stages or stable states (Christensen and Pauly, 1993). The study of trophic webs has a number of potential advantages, including the likely prediction of negative effects in cascade caused by anthropogenic impacts in ecosystems, and a greater understanding of ecosystem management (Cohen et al., 1993). Assessment of ecosystem health, conservation of living resources and biodiversity could be advanced if the consequences of trophic web modification were predictable (Arias-González et al., 2004). If a trophic network is defined as a model of energy and material flow between organisms via predation processes, then the adjustment (increase or decrease) of elements from the intricate food web and the changes produced in the community structure by this process should produce a disruption in the trophic structure.

From this viewpoint, the main goal of this paper was to construct mass balanced models of the food web in three areas along an eutrophication gradient in the south arm of the Mondego estuary (Portugal), a small and well described temperate intertidal estuary (Marques et al., 1997, 2003; Pardal et al., 2000, 2004; Cardoso et al., 2004; Ferreira et al., 2004; Neto, 2004), using the “Ecopath with Ecosim” software package. This work was a first study of the Mondego estuary using a mass-balance model of trophic interactions.

## 2. Material and methods

### 2.1. Study area

The Mondego estuary, located on the western coast of Portugal, consists of two arms, northern and southern (Fig. 1), with very different hydrological characteristics. The northern arm is deeper, while the southern arm is silted up, especially in upstream areas, which causes most of the freshwater discharge to flow through the northern arm. This siltation diverts most of the freshwater discharge into the northern arm. Consequently, the water circulation in the southern arm is dependent mainly on tidal flushing and on a relatively small input of freshwater from the Pranto River, the flow of which is controlled artificially by a sluice.

Macroalgal blooms of *Ulva* spp. have regularly been observed in the Mondego over the last 20 years (Flindt et al., 1997; Marques et al., 1997, 2003; Lillebø et al., 1999; Pardal et al., 2000, 2004; Martins et al., 2001; Dolbeth et al., 2003; Cardoso et al., 2004). Nevertheless, such macroalgal blooms may not occur in exceptionally rainy years. This is most probably due to the resulting long periods during which salinity remains below the tolerance limit of macroalgae, coupled with a limitation of phosphorous induced by a heavy nitrogen discharge from the Pranto River (Martins et al., 2001).

Sampling was conducted in three areas in the southern arm of the Mondego estuary that represent different environmental situations along a spatial gradient of eutrophication (Marques et al., 1997, 2003; Lillebø et al., 1999; Pardal et al., 2000, 2004; Dolbeth et al., 2003; Cardoso et al., 2004; Neto, 2004) (Fig. 1): (a) a non-eutrophic area (*Zostera noltii* Hornem

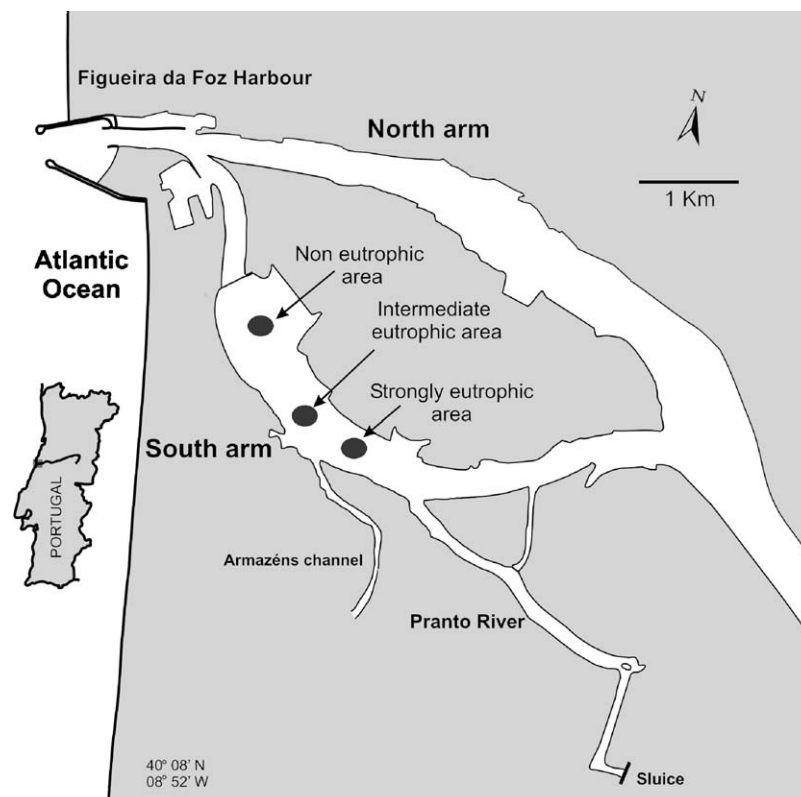


Fig. 1 – Mondego estuary: location of the sampling stations along a spatial gradient of eutrophication.

beds), (b) an intermediate eutrophic area (*Z. noltii* absent, although residual roots can still be found in the sediment, and the occasional formation of abundant macroalgae mats) and (c) a strongly eutrophic area (macrophyte community totally absent for at least a decade and strong, regularly occurring, blooms of *Ulva* spp.).

2.2. Methods

Food webs of the ecosystem in the three areas were constructed using the “Ecopath with Ecosim” software package, which assists the user in casting a balanced carbon budget for each trophic group. The core routine of Ecopath/Ecosim centres on the Ecopath program of Polovina (1984), which was extended to apply to non-steady-state systems (Christensen et al., 2004). It no longer assumes a steady state but instead calculates parameters on the assumption of mass balance over an arbitrary period—usually 1 year. Scores of applications of Ecopath with Ecosim can be found at: <http://www.ecopath.org/>, along with the freely distributed software and documentation. Although the formulations and basic concepts are accessible in these venues, the general approach is summarised here. When applied, Ecopath derives model parameters on the basis of two master equations. The first equation, describes how the production term for each group can be split in components (Eq. (1)). More specifically, it says that the net production of a functional group equals the sum of (1) the total mass (or energy) removed by predators and fisheries, (2) the net biomass accumulation of the group, (3) the net migration of the group’s biomass, and (4) the mass flowing to detritus:

$$B_i \times (P/B)_i \times EE_i - \sum_{j=1}^n B_j \times (Q/B)_j \times DC_{ji} - Y_i - BA_i - E_i = 0 \quad (1)$$

where  $B_i$  and  $B_j$  are biomasses of prey (i) and predators (j), respectively;  $P/B_i$  the production/biomass ratio, equivalent to total mortality (Z) in most circumstances (Allen, 1971);  $EE_i$  the ecotrophic efficiency; the fraction of the total production of a group utilised in the system;  $Y_i$  the fisheries catch per unit area and time (i.e.,  $Y = F \times B$ );  $Q/B_j$  the 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; and  $E_i$  is the net migration of i (emigration less immigration).

In this type of models, the energy input and output of all living groups must be balanced. The basic Ecopath Eq. (1) includes only the production. When balancing a compartment in an ecosystem other flows must be considered. Energy balance is ensured within each group using Eq. (2) (Christensen et al., 2004):

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

The implied thermodynamic constraints of this equation underscore the power of Ecopath models as a focal point for refinement of ecosystem information. The need to reconcile energy production and demand among components of the food web narrows the possible ranges of parameter estimates for particular groups. Inclusion of a biomass accumulation factor and migration factor in the general Ecopath equation

distinguishes Ecopath modelling as an ‘energy continuity’ approach rather than a strictly ‘steady-state’ approach. Conservation of energy (continuity) is assumed for every identified component of the ecosystem, and the whole system. This basic constraint enables representation of changes in populations (i.e., functional groups) when expressed in dynamic form.

2.2.1. Sampling program and laboratory treatment

Chlorophyll a, detritus, macroalgae, macrophytes and macrofauna were sampled fortnightly (February 1993–January 1994), during low tide, at each of the three areas. All biological materials were identified and separated into the lowest possible taxa (for more details concerning the technical procedures see Pardal et al., 2000, 2004). Between March 1996 and January 1997, monthly samples of epiphytes attached to *Z. noltii* were separated from their substrate, dried and weighed. Zooplankton was collected monthly from sub-surface waters at each sampling site from April 1995 to April 1996, using 200 and 335 μm mesh nets (Azeiteiro et al., 1999). Data on fish were taken monthly from January 1991 to December 1992. The captured fish were identified and weighed (wet weight), and the dominant species in the stomach contents were analysed (Jorge et al., 2002). Finally, wading birds were counted from January 1996 to January 1998 at fortnight-tide and monthly low water to provide an accurate census across the three areas (Lopes et al., 2002). Seagulls were counted monthly, from November 1993 to July 1994.

2.2.2. Compartments

Species of similar size, diets or with identical ecological niche were grouped. Different numbers of ecosystem compartments were identified in each situation (Table 1): 43 in the *Zostera* sp. meadows, 36 in the intermediate eutrophic area and 34 in the strongly eutrophic area. Species that were not naturally present in one of the three areas or whose roles in the trophic network were unimportant were not taken into account.

2.2.3. Biomass (for data sources see Appendix A)

Chlorophyll a was estimated according to standard procedures (Strickland and Parsons, 1968) and values were transformed into Phytoplankton biomass using a conversion factor taken from Anderson and Williams (1998) and assuming an average depth of 0.5 m over the sampling area. Epiphytes consisted only of the material attached to the aerial part of *Z. noltii*. Plants and macrofauna were dried at 70 °C for 72 h and weighed. The ash free dry weight (AFDW) of biomass was assessed after combusting samples for 8 h at 450 °C (Pardal et al., 2000, 2004). The abundance of each Zooplankton taxon was estimated by multiplying the observed number of that taxon by the average AFDW of an individual belonging to it. The weights of all taxa were summed to arrive at the annual average standing stock.

Sixty-two species of fish were observed and grouped according to their ecological and trophic characteristics. The biomass corresponding to each group was determined by multiplying its wet weight by a conversion factor taken from Jørgensen et al. (1991).

The observed density of each bird species was multiplied by the average AFDW of an individual belonging to that taxon (see Appendix A). Although combining bacteria with detritus

**Table 1 – Input data and calculated estimates (in parenthesis) for the three areas (Z, *Zostera* sp. meadows; I, intermediate eutrophic area; S, strongly eutrophic area) along the eutrophication gradient**

Groups	Biomass			P/B <sup>a</sup>			Q/B <sup>a</sup>			EE <sup>a</sup>		
	Z	I	S	Z	I	S	Z	I	S	Z	I	S
Phytoplankton (A)	0.336	0.324	0.17	185	185	185	–	–	–	0.772	(0.572)	(0.96)
Enteromorpha sp. (A)	1.800	26.975	96.784	3.4	3.4	3.4	–	–	–	0.996	(0.691)	(0.288)
Ulva sp. (A)	0.373	2.504	7.658	3	3	3	–	–	–	0.957	(0.883)	(0.984)
Gracilaria sp. (A)	16.081	2.054	2.322	3	3	3	–	–	–	(0.033)	(0.084)	(0.044)
Fucus sp. (A)		0.084	0.203		3	3		–	–		(0.81)	(0.533)
<i>Zostera noltii</i> (M)	204.84			2.5			–			0.001		
Epiphytes	7.695			180			–			0.149		
Zooplankton	(0.348)	(0.278)	(0.234)	22	18	20	(73.33)	(90)	(100)	0.98	0.95	0.95
<i>Hydrobia ulvae</i> (G)	54.750	4.666	9.745	1.3	4.5	4.5	(6.5)	(22.5)	(22.5)	(0.209)	(0.224)	(0.092)
<i>Gibulla umbilicallis</i> (G)	0.072			1.76			(8.8)			(0.73)		
<i>Littorina</i> spp. (G)	2.489	0.525		3	3		(15)	(15)		(0.082)	(0.468)	
<i>Melita palmata</i> (Am)	(0.109)	(0.181)	0.099	7.2	8.38	8.5	(36)	(41.88)	(42.5)	0.95	0.95	(0.973)
<i>Ampithoe valida</i> (Am)	(0.236)	(0.179)	0.145	5.8	4.8	4.9	(29)	(24)	(24.5)	0.95	0.95	(0.87)
<i>Echinogammarus marinus</i> (My)			0.002			6.3			(31.5)			(0.844)
<i>Corophium multisetosum</i> (Am)		0.002			10			(50)			(0.635)	
<i>Scrobicularia plana</i> (B)	3.260	7.762	11.347	1.8	1.8	1.8	(9)	(9)	(9)	(0.834)	(0.619)	(0.319)
<i>Cerastoderma edule</i> (B)	5.221	0.088	0.216	4.8	4.8	4.8	(24)	(24)	(24)	(0.305)	(0.859)	(0.956)
<i>Modiolus barbatus</i> (B)	0.022			2			(10)			(0.446)		
<i>Cyathura carinata</i> (I)	0.056	0.343	7.268	2.03	3.17	3.17	(10.15)	(15.85)	(15.85)	(0.982)	(0.331)	(0.012)
<i>Idotea chelipes</i> (I)	0.040	0.027	0.02	3.8	3.8	3.8	(19)	(19)	(19)	(0.953)	(0.494)	(0.41)
<i>Sphaeroma hookeri</i> (I)	0.002			3.8			(19)			(0.96)		
<i>Carcinus maenas</i> (D)	1.09	0.58	0.419	6.4	6.4	6.4	(32)	(32)	(32)	(0.384)	(0.431)	(0.511)
<i>Crangon crangon</i> (D)	(0.132)	(0.317)	0.280	6	6	6	(30)	(30)	(30)	0.95	0.95	(0.964)
<i>Alkmaria romijni</i> (P)	0.008	0.022	0.114	2.3	2.3	2.3	(11.5)	(11.5)	(11.5)	(0.443)	(0.69)	(0.804)
<i>Capitella capitata</i> (P)	0.006	0.062	0.038	2.4	1.6	1.6	(12)	(8)	(8)	(0.818)	(0.913)	(0.943)
<i>Heteromastus filiformis</i> (P)	0.610	2.2	0.192	2.4	2.2	2.2	(12)	(11)	(11)	(0.93)	(0.974)	(0.778)
<i>Hediste diversicolor</i> (P)	(0.866)	(0.505)	0.428	5.6	5.4	5.2	(28)	(27)	(26)	0.95	0.98	(0.981)
<i>Diopatra neapolitana</i> (P)	0.019			6.52			(32.6)			(0.914)		
<i>Nephtys hombergii</i> (P)	0.052	0.055		4.6	4.6		(23)	(23)		(0.931)	(0.346)	
<i>Lumbrineris impatiens</i> (P)	0.130			2.4			(12)			(0.734)		
Other macrofauna detritivores (P)	0.600	0.893	0.160	2.9	2.4	2.4	(14.5)	(12)	(129)	(0.983)	(0.784)	(0.919)
Other macrofauna predators (P)	0.355	0.053	0.010	3.43	3.43	3.43	(17.15)	(17.15)	(17.16)	(0.835)	(0.822)	(0.90)
Oligochaets	0.127	0.031	0.005	2.6	2.6	2.6	(13)	(13)	(13)	(0.948)	(0.884)	(0.483)
Microalgae and detritus feeders (F)	1.685	0.894	1.1	0.51	0.49	0.51	10.5	10.5	10.5	(0.719)	(0.687)	(0.821)
Zooplankton consumers (F)	(0.335)	(0.102)	(0.063)	1.3	1	1	7.44	7.44	7.44	0.95	0.95	0.95
Endofauna consumers (F)	0.060	0.06	0.06	0.8	0.77	0.77	3.1	3.1	3.1	(0.79)	(0.617)	(0.870)
Macrofauna predators (F)	0.314	0.14	0.136	0.54	0.9	0.9	9.66	9.66	9.66	(0.347)	(0.771)	(0.789)
<i>Trigla lucerna</i> (F)	0.020			1.4			(7)			0.95		
<i>Pomatoschistus</i> (F)	(0.031)			1.7			(8.5)			0.95		
<i>Larus ridibundus</i> (Gu)	0.006	0.006	0.006	0.02	0.15	0.15	0.24	0.24	0.24	(0.000)	(0.000)	(0.000)
<i>Larus fuscus</i> (Gu)	0.005	0.006	0.006	0.02	0.15	0.15	0.24	0.24	0.24	(0.000)	(0.000)	(0.000)
<i>Charadrius alexandrinus</i> (W)	0.001	0.001	0.001	0.02	0.15	0.15	0.24	0.24	0.24	(0.000)	(0.000)	(0.000)
<i>Charadrius hiaticula</i> (W)	0.001	0.001	0.001	0.02	0.15	0.15	0.24	0.24	0.24	(0.000)	(0.000)	(0.000)
<i>Pluvialis squatarola</i> (W)	0.001	0.002	0.002	0.02	0.15	0.15	0.24	0.24	0.24	(0.000)	(0.000)	(0.000)
<i>Calidris alpina</i> (W)	0.001	0.005	0.005	0.02	0.15	0.15	0.24	0.24	0.24	(0.000)	(0.000)	(0.000)
Detritus	527.31	518.76	309.8	–	–	–	–	–	–	(0.184)	(0.826)	(0.675)

A, macroalgae; M, macrophyte; G, Gastropoda; Am, Amphipoda; B, Bivalvia; I, Isopoda; D, Decapoda; P, Polychaeta; F, fish; Gu, gull; W, wader.

<sup>a</sup> P, production; B, biomass; Q, consumption; EE, ecotrophic efficiency.

can be problematic using the Ecopath software package, bacterial biomass was assigned to the detritus compartment, as recommended by Christensen and Pauly (1992). Finally, the amount of organic matter in the sediment was assessed to be the weight lost after combustion of dry samples for 8 h at 450 °C.

#### 2.2.4. Production, consumption and diet composition

Production refers to the increase of living tissue within a compartment over a given period. Whenever possible,

production/biomass ratios (P/B), previously calculated for local populations (e.g. Marques et al., 1994; Lillebø et al., 1999; Pardal et al., 2000; Ferreira et al., 2004), were used. When this was not feasible, values taken from the literature (Appendix A) were utilised. Special care was exercised to identify values coming from similar Portuguese estuarine systems.

Consumption is the intake of food by a group over a given interval of time. It was entered into Ecopath as the ratio of consumption to biomass (Q/B). Q/B values for birds and fish

were taken from the literature (Appendix A). For the other heterotrophic compartments, the P/Q ratios were entered into the program to estimate indirectly the Q/B ratio (Hostens and Hamerlynck, 1994).

In a trophic model, such as those constructed using the Ecopath, it is predation that links the different groups into a system. Consumption for one group becomes mortality for another, making information on predation paramount to understand the dynamics of ecosystems. Unfortunately, quantitative information on diet composition is sparse. Diet information for almost all the compartments here identified had to be obtained from the literature (e.g. Hughes, 1969; Costa, 1982; Pihl, 1985; Zajac, 1986; Sprung, 1994; Ansell et al., 1999; Azeiteiro et al., 1999; Cunha et al., 2000; Pardal et al., 2000, see Appendix A). Initially, all prey items of each compartment of macrofauna and fishes were listed, along with their corresponding percentages of occurrence. Each observed dietary item was then assigned to an ecologically similar species or group of species as identified in (2) above. Finally, the percentage of occurrence in the diet was assumed to be proportional to the fraction that its biomass comprised of the total biomass of the group. The diets of wading birds and gulls were obtained directly from an analysis of their droppings (Moreira, 1995; Cabral et al., 1999).

### 2.2.5. Captures

A complete network requires estimates of the rates of export from the system, including the harvests of economically important species. In the present work, the harvests of the bivalve *Scrobicularia plana* and the polychaete *Hediste diversicolor* (the only two species of economic importance on the Mondego estuary) were considered small enough to be negligible.

### 2.2.6. Balancing the models

For each of the three models the software has calculated the missing parameters. At first none of the models were balanced (e.g. negative flows to detritus, ecotrophic efficiencies higher than 1 – which indicated that the demand on them was too high to be sustainable – and some P/Q = GE values physiologically unrealistic). Given the distinct data and parameters source, this situation was predictable in advance. An exhaustive set of guidelines for how a model should be balanced

cannot be given. However, according to the methodology proposed by Christensen et al. (2004), the following procedures were followed.

The quality of the data used for each group in the models was variable. For some, there were empirical estimates available from samples taken from within the models areas and time frame (e.g. all macrofauna, macrophytes, macroalgae). For others it was necessary to use empirical data from other areas and/or time frames (e.g. fishes, gulls) or less specific information (e.g. Zooplankton, Phytoplankton). The most reliable data were macrofauna biomass and production, contrary to the majority of studies (e.g. Bundy et al., 2000; Heymans and Baird, 2000). Data proceeding from the south arm of the Mondego estuary (primary producers, macrofauna, waders and detritus biomass, as well as P/B ratios calculated from previous studies at the same location) were left unchanged. Therefore, greater confidence was placed on them. One exception was the decapods (*Crangon crangon* and *Carcinus maenas*) biomass. This parameter had to be estimated due to the fact that the original values were underestimated owing to the sampling strategy used. This was also true for the majority of the fish groups' biomass. Regarding the Zooplankton, due to its complex tidal and seasonal dynamics, it was difficult to estimate a realistic annual average biomass. Thus, the software has calculated the missing parameter for the three models. For subsequent balancing it was necessary to re-evaluate some compartments' diet compositions (e.g. *C. maenas*, *C. crangon*, *H. diversicolor*, *Lumbrineris impatiens* and some fish groups) since feeding habits of some organisms are highly labile and mainly depend on food sources that are available in the ecosystem. This parameter was poorly known, yet it had a large influence on the model estimates.

## 3. Results and discussion

Diagrams showing the trophic flows were constructed, while a summary of all the final input data and the calculated parameters is found in Table 1.

### 3.1. Summary statistics

Table 2 summarises the ecological statistics and indices for the three estuarine networks.

**Table 2 – Summary of ecological statistics/indices for the three estuarine networks**

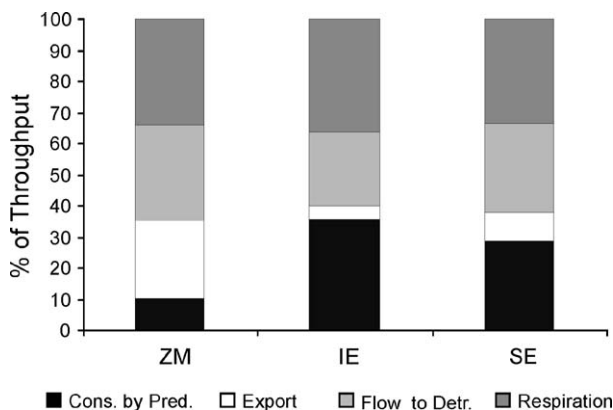
Statistic/indices	Area		
	Zostera sp. meadows	Intermediate eutrophic	Strongly eutrophic
Sum of all consumption (g AFDW m <sup>-2</sup> yr <sup>-1</sup> )	694.91	292.14	521.33
Sum of all exports (g AFDW m <sup>-2</sup> yr <sup>-1</sup> )	1707.51	34.01	169.61
Sum of all respiration (g AFDW m <sup>-2</sup> yr <sup>-1</sup> )	2322.55	297.32	612.67
Sum of all flows into detritus (g AFDW m <sup>-2</sup> yr <sup>-1</sup> )	2092.06	195.09	522.40
Sum of all production (g AFDW m <sup>-2</sup> yr <sup>-1</sup> )	2151	223	494
Total system throughput (g AFDW m <sup>-2</sup> yr <sup>-1</sup> )	6817	819	1826
Net primary production (g AFDW m <sup>-2</sup> yr <sup>-1</sup> )	2014.83	165.58	391.065
Total primary production/total respiration	0.868	0.557	0.638
Total biomass/total system throughput	0.045	0.061	0.076
Total biomass (no detritus) (g AFDW m <sup>-2</sup> )	304.18	49.91	139.24
Omnivory index	0.105	0.110	0.202

The sum of consumptions, exports, respiration, production, and flow to detritus was always higher in the *Zostera* sp. meadows, followed by the strongly eutrophic area and, finally, by the intermediate eutrophic area. This is also the conclusion reached examining the trends for the total throughput (the sum of all flows: consumption, exports, respiratory flows, and flows to detritus) at each trophic level: 6817 g AFDW m<sup>-2</sup> yr<sup>-1</sup> in *Z. noltii* meadows, 1826 g AFDW m<sup>-2</sup> yr<sup>-1</sup> in the strongly eutrophic area and 819 g AFDW m<sup>-2</sup> yr<sup>-1</sup> in the intermediate eutrophic area (Table 2). All these results are, partially, explainable because the non-eutrophic area model has more groups than the other models. This higher number of compartments has an impact on the calculations and increases the TST and subsequently all the flows such as consumption, production, etc. Both eutrophic areas presented a similar partitioning of the total throughput, between 29 and 36% of the total was due to consumption, approximately 4–9% was exported, about 24–28% flowed into detritus, and around 34–36% was respired (Fig. 2).

The major difference verified in the non-eutrophic area concerned a proportionally higher value (25%) due to exports. What is the explanation for these differences in the breakdown of throughput, with so much more exports and flow to detritus in the *Zostera* sp. meadows? It is well known that macrophytes support two types of food webs; first, an herbivorous web in which herbivorous feed directly on the standing plant or on the attached epiphytes, and second, a detritivorous web, where some species feed on plant detritus. According to Enríques et al. (1993), macrophytes are major producers of organic matter but little of this production enters the grazing food chain because there is a time lag between the production and its utilisation.

Therefore, only few animals feed directly on these plants (their production is usually used after decomposition) and a big proportion of the production decays to detritus or is washed away from the production area, being used in other systems. This fact is consistent with the results of the current study.

The annual rate of net primary production presented a similar behaviour, clearly related with the primary producers dynamic in each of the studied areas. A long-term study



**Fig. 2 – Partitioning of throughput among consumption by predators, exports, flow to detritus and respiration in the three estuarine areas. ZM, *Zostera* sp. meadows; IE, intermediate eutrophic area; SE, strongly eutrophic area.**

in the Mondego estuary has indicated that years of low precipitation have been associated with reductions in turnover rates and with increases in water column stability, salinity and light penetration (Martins et al., 2001). These changes in habitat conditions favoured the initiation of macroalgal blooms, which then served to depress the previously dominant macrophyte communities (Marques et al., 1997, 2003; Martins et al., 2001; Dolbeth et al., 2003; Cardoso et al., 2004). In the intermediate and strongly eutrophic areas, primary production is largely the result of such macroalgal blooms (Marques et al., 1997). As a consequence, production in these two systems appears as a strong pulse during the course of the blooms, but remains at very low levels for the rest of the year (Dolbeth et al., 2003). The short duration of the abundant primary production in these areas averages over the year to a significantly lower annual rate of net primary production. Odum (1969) had suggested that less-impacted systems (e.g. *Zostera* sp. beds) should exhibit higher rates of net system production—a fact that is consistent with the results of the current study. In fact, Patrício et al. (2004), by means of network analysis showed that when the whole-system properties of the three areas were compared, the measures associated with the area hypothesised as intermediate in terms of eutrophication symptoms did not present intermediate conditions at all. Rather, the intermediate eutrophic area exhibited the lowest ascendancy, average mutual information, total system throughput and development capacity values and the highest figures for redundancy, cycling index, so to say it appears to be the most disturbed of the three areas. Moreover, it was suggested that the most likely explanation appears to be in the highly labile nature of the intermediate system. Indeed, observations using other ecological indicators (e.g. Shannon-Wiener, Margalef) have showed that the communities built around both edges of the eutrophication gradient (*Zostera* beds and *Ulva* sp. dominated areas) represent more stabilised communities. For more details regarding the eutrophication effects please see Patrício et al. (2004).

The system omnivory index (SOI) is the average group omnivory index weighted by the logarithm of the total food consumption. A group's omnivory index is calculated as the variance of the trophic levels of a consumer's preys (Christensen and Pauly, 1992). The SOI is a measure of how the feeding interactions are distributed between trophic levels (Vasconcellos et al., 1997). If a predator has only a prey on one trophic level its omnivory index will equal zero, while a large omnivory index indicates that the trophic positions of a predator's preys are variable. Heymans (2003), comparing different models of the Newfoundland community, observed that the reduction of a 50 compartments model to a 30 compartments model reduced the SOI in these systems. According to the author, this index is dependent on the number of compartments in the model: more compartments would have more connections and there would be less omnivory when compartments are combined and diets consolidated. However, in this study, the *Zostera* sp. meadows despite having 43 compartments exhibited the lower value for this index. In fact, this community is the one with more groups, and still had the lowest SOI, which indicates that it is probably not an effect of different group size.

### 3.2. Transfer efficiency

According to Lindeman (1942), ecosystem components can be grouped into discrete trophic levels, and transfer efficiencies estimated. Ecopath, using the trophic aggregation routine calculates the transfer efficiencies as the fraction of total flows at each trophic level (throughput) that are either exported or transferred to another trophic level through consumption. Since Lindeman (1942), it has often been assumed that trophic transfer efficiencies vary around 10%, so that one-tenth of the energy that enters a trophic level is transferred to the next trophic level. Hence, transfer efficiencies are usually greater at the beginning of the food web compared with higher trophic levels, because of intrinsic characteristics of organisms at different levels in the food web (Christensen and Pauly, 1993). Nevertheless, the transfer efficiencies for the three studied areas (Table 3) suggest a pattern of low herbivore transfer efficiencies (most of the production does not originate from the Phytoplankton, but from the macroalgae and macrophytes whose embodied energy is available for consumers only after decaying into detritus), higher efficiencies on trophic level 3 and lower efficiencies at the higher levels. This fact has already been reported in the literature (e.g. Christensen and Pauly, 1993; Baird and Ulanowicz, 1989). Based on the system and the trophic level specific transfer efficiencies, Christensen and Pauly (1993) estimated the average transfer efficiency for different systems (as geometric mean, weighted after flow). The average efficiencies in the three areas in the south arm of the Mondego estuary (Table 3) are within the range of those described in the literature for temperate systems (3–7%).

### 3.3. Limitations and strengths of the approach

The uncertainty over the input parameters for some of the groups at the lower trophic levels (e.g. Zooplankton, Phytoplankton) has already been discussed above. However, there were also several areas of uncertainty for groups at higher trophic levels (e.g. gulls, fishes, waders). Weakness in diet data has been noted in many compartments of the three models. The present models provided estimates of the contribution by various predators or groups of predators, but it must be clear that the diet information for all these predators is inadequate for obtaining accurate estimates of their consumption of minor preys. For example, the information on predation by many fish groups came largely from personal observations obtained at different sampling stations during a distinct time frame. These uncertainties are transmitted down the food

web, since all productions and losses must be balanced for each group. A high consumption at the top of the food web requires high production at all lower levels. The model is particularly sensitive to some of the groups (e.g. *H. diversicolor*, *C. crangon*, *C. maenas*, Zooplankton, and Phytoplankton). The results described above indicate a system for which the available information contains significant uncertainty. As a consequence, there are several possible versions of the models.

Some other limitations of the model were observed, mainly associated with the steady-state assumption: high seasonal variations occurred, especially in the strongly eutrophic area following the macroalgae bloom event, and these produced major changes in the trophic structure and production. This is not reflected in the present models which report average conditions, but it could have been done by constructing seasonal models for each of the three situations. Moreover, uncertainty and time delays in processes associated with ecosystem dynamics were not considered, which will constrain their direct use for management purposes. Nevertheless, lack of historical data and difficulty in measuring some ecosystem components and processes will likely always plague efforts to understand trophic structure and interactions. This is not a problem with Ecopath, but rather with aquatic ecology in general (Ludwig et al., 1993).

Lastly, even with all the limitations that this approach seems to have, why are flux estimates vital to ecosystem science? Many hypotheses and concepts about ecosystem function and food web dynamics focus on the nature of flows of energy in these systems. For example, previous authors have proposed a number of ecosystem attributes, and hypothesised about their relationship to productivity, successional state, and the level of human disturbance in an ecosystem (Odum, 1969; Ulanowicz and Kay, 1991). Some of these attributes, such as gross production, community respiration quotients, energy cycling or feedback loops require estimates of fluxes between functional groups in their calculation. Patten (1995) showed that five indices used to describe ecosystems, Ascendency, Emergy, Eco-Exergy, Indirect Effects, and Maximum Power, are related through the structure of networks and flows of energy within the networks. Thus, most of the 'descriptive statistics' for ecosystems include transfers of energy between groups, and estimating fluxes is as fundamental to ecosystem and food web ecology as estimating demographic rates is to population ecology. In addition, to simply describe ecosystems or food webs, ecologists can also use this information to test hypotheses and draw conclusions regarding management decisions. Just as food webs were summarised and analysed

**Table 3 – Trophic transfer efficiencies (%) (proportion of energy transferred from one trophic level to the next) for each trophic group for the three estuarine networks**

Trophic level	Area		
	<i>Zostera</i> sp. meadows	Intermediate eutrophic	Strongly eutrophic
2	6.6	8.9	3.7
3	9.6	9.0	10.0
4	4.2	5.4	5.8
5	1.8	1.6	2.2
6	1.1	1.5	0.8
7	0.2	0.8	0.0

for their structural characteristics (Pimm, 1982; Cohen et al., 1993), ecologists have now begun summarising the patterns of energy and nutrient flows between functional groups in food webs and ecosystems.

#### 4. Conclusions

The Ecopath models presented here allowed summarising of our current knowledge of the biomass, consumption, production, food web and trophic flows in the three areas along the eutrophication gradient in the south arm of the Mondego estuary (Portugal).

These models also highlight data uncertainties allowing a gap analysis regarding our knowledge on the system (diet compositions, site-specific  $P/B$ ,  $Q/B$  ratios, ecological role of a number of abundant species, etc). Unfortunately, uncertainties concern all trophic levels and many constituent groups of the models, including some parameters regarding those groups that are regularly surveyed and assessed. Despite this, Ecopath with Ecosim provided a useful scheme for organising the communities' trophic structures.

As a final word, it is important to note that the process of constructing models such as these is essentially open-ended.

The data available for inputs are constantly being added to and revised. These models should be considered as a first step. Doubtless, the three models could be further enhanced, but these versions embody our closest approximation to the system, using the available data. Others are invited to critique the models structure, the input data, and the assumptions, so that the models can be improved in the future.

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#### Appendix A. Models data sources

Compartments	Parameter	Source
Phytoplankton	Biomass	Pardal (1998)
	C:Chl $a$ ratio	Anderson and Williams (1998)
	$P/B$	Wolff et al. (2000)
<i>Enteromorpha</i> sp.	Biomass	Pardal (1998)
<i>Ulva</i> sp.	$P/B$	Aníbal (1998)
<i>Gracilaria</i> sp.	Biomass	Pardal (1998)
	$P/B$	Duarte and Ferreira (1997)
<i>Fucus</i>	Biomass	Pardal (1998)
	$P/B$	Niell et al. (1996)
<i>Zostera noltii</i>	Biomass	Pardal (1998)
	$P/B$	Sand-Jensen (1975) and Pérez-Lloréns and Niell (1993)
Epiphytes	Biomass	Pardal (1998) and Martins et al. (1999)
	$P/B$	Wolff et al. (2000)
Zooplankton	Biomass and diet	Azeiteiro et al. (1999)
	$P/B$	Rosado-Salórzano and Próo (1998)
<i>Hydrobia ulvae</i>	Biomass	Pardal (1998)
	$P/B$	Lillebø et al. (1999) and Sola (1996)
	$P/Q$	Hostens and Hamerlynck (1994)
	Diet	Hootsmans and Vermaat (1985), López-Figueroa and Niell (1987), Morrisey (1988) and Philippart (1995)
<i>Gibulla umbilicalis</i>	Biomass	Pardal (1998)
	$P/B$	Baird and Milne (1981)
	$P/Q$	Hostens and Hamerlynck (1994)
	Diet	Parker et al. (1993) and Watson (1985)
<i>Littorina</i> sp. <i>L. littorea</i> , <i>L. saxatilis</i>	Total biomass	Pardal (1998)
	$P/B$ of the group	Baird and Milne (1981)
	$P/Q$ of the group	Hostens and Hamerlynck (1994)
	Diet	Orth and Montfrans (1984), Konan et al. (1992), Parker et al. (1993) and Watson (1985)



## Appendix A (Continued)

Compartments	Parameter	Source
<i>Melita palmate</i>	Biomass	Pardal (1998)
<i>Ampithoe valida</i>	P/B	Pardal (1998)
	P/Q	Hostens and Hamerlynck (1994)
	Diet	Sprung (1994), Alonso et al. (1995) and Greze (1968)
<i>Echinogammarus marinus</i>	Biomass	Pardal (1998)
	P/B and diet	Marques and Nogueira (1991)
	P/Q	Hostens and Hamerlynck (1994)
<i>Corophium multisetosum</i>	Biomass	Pardal (1998)
	P/B	Casabianca (1975) and Cunha et al. (2000)
	P/Q	Hostens and Hamerlynck (1994)
	Diet	Cunha et al. (2000) and Smith et al. (1996)
<i>Scrobicularia plana</i>	Biomass	Pardal (1998)
<i>Cerastoderma edule</i>	P/B	Sprung (1994)
<i>Modiolus barbatus</i>	P/Q	Hostens and Hamerlynck (1994)
	Diet	Hughes (1969), Loo (1992) and Prins and Smaal (1989)
<i>Cyathura carinata</i>	Biomass	Pardal (1998)
	P/B and diet	Ferreira et al. (2004) and Pardal (1998)
	P/Q	Hostens and Hamerlynck (1994)
<i>Idotea chelipes</i>	Biomass	Pardal (1998)
	P/B	Sprung (1994)
	P/Q	Hostens and Hamerlynck (1994)
	Diet	Nienhuis and Groenendijk (1986) and Schaffelke et al. (1995)
<i>Sphaeroma hookeri</i>	Biomass	Pardal (1998)
	P/Q	Hostens and Hamerlynck (1994)
	Diet	Pardal (1998)
<i>Amage adspersa</i>	Biomass	Pardal (1998)
	P/B	Sprung (1994)
	P/Q	Hostens and Hamerlynck (1994)
	Diet	Pardal (1998) and Sprung (1994)
<i>Capitella capitata</i>	Biomass	Pardal (1998)
	P/B	Sprung (1994)
	P/Q	Hostens and Hamerlynck (1994)
	Diet	Tenore (1983) and Tenore and Chesney (1985)
<i>Heteromastus filiformis</i>	Biomass	Pardal (1998)
	P/B and diet	Sprung (1994)
	P/Q	Hostens and Hamerlynck (1994)
<i>Hediste diversicolor</i>	Biomassa	Pardal (1998)
	P/B	Abrantes et al. (1999) and Sprung (1994)
	P/Q	Hostens and Hamerlynck (1994)
	Diet	Nielsen et al. (1995) and Riisgård et al. (1996)
<i>Diopatra neapolitana</i>	Biomass	Pardal (1998)
	P/B	Sprung (1994)
	P/Q	Hostens and Hamerlynck (1994)
	Diet	Mangum et al. (1968)
<i>Nephtys hombergii</i>	Biomass	Pardal (1998)
	P/B	Sprung (1994)
	P/Q	Hostens and Hamerlynck (1994)
	Diet	Beukema (1987) and Oyenekan (1986)
<i>Lumbrineris impatiens</i>	Biomass	Pardal (1998)
	P/B	Venier (1997)
	P/Q	Hostens and Hamerlynck (1994)
	Diet	Petch (1986) and Valderhaug (1985)

## Appendix A (Continued)

Compartments	Parameter	Source
Other macrofauna detritivores <i>Aonides oxycephala</i> , <i>Chaetozone setosa</i> , <i>Lagis koreni</i> , <i>Polydora ligni</i> , <i>Pygospio elegans</i> , <i>Streblospio shrubsolii</i> , <i>Haminea hydatis</i> , Diptera larvae	Total biomass	Pardal (1998)
	P/B of the group	Sprung (1994)
Other macrofauna predators Nemertini, <i>Glycera convoluta</i> , <i>M. picta</i> , <i>A. mucosa</i> , <i>P. laminosa</i>	P/Q of the group	Hostens and Hamerlynck (1994)
	Diet	Dauer et al. (1981), Lambeck and Valentijn (1987) and Zajac (1986)
Oligochaeta <i>Tubificoides benedeni</i> , <i>Oligocheta</i> sp.	Total biomass	Pardal (1998)
	P/B of the group	Sprung (1994)
<i>Carcinus maenas</i> <i>Crangon crangon</i>	P/Q of the group	Hostens and Hamerlynck (1994)
	Diet	Giere (1975)
Microalgae and detritus feeders <i>Mugil cephalus</i> , <i>Chelon labrosus</i> , <i>Liza aurata</i> , <i>Liza ramada</i> , <i>Alosa fallax</i> , <i>A. alosa</i>	Biomass	Pardal (1998)
	P/B	Sprung (1994)
Zooplankton consumers <i>Sardina pilchardus</i> , Syngnathidae, <i>Engraulis encrasicolus</i>	P/Q	Hostens and Hamerlynck (1994)
	Diet	Ansell et al. (1999), Lee and Seed (1992) and Pihl (1985)
Endofauna consumers <i>Solea vulgaris</i> , <i>Solea senegalensis</i> , <i>Platichthys flesus</i>	Total biomass	Jorge (unpublished data)
	P/B, Q/B group	<a href="http://www.fishbase.org">http://www.fishbase.org</a>
Macrofauna predators <i>Dicentrarchus labrax</i> , <i>Anguilla anguilla</i> , <i>Gobius niger</i> , <i>Ciliata mustela</i> , <i>Sparus aurata</i> , <i>Diplodus sargus</i> , <i>Diplodus vulgaris</i> , <i>Mullus surmuletus</i> , <i>Atherina boyeri</i> , <i>A. presbyter</i>	Stomach content	Correia et al. (1997), Oliveira and Soares (1996) and Jørgensen et al. (1991)
	DW/WW, C/DW	Jørgensen et al. (1991)
<i>Trigla lucerna</i>	Total biomass	Jorge (unpublished data)
	P/B, Q/B group	<a href="http://www.fishbase.org">http://www.fishbase.org</a>
<i>Pomatoschistus minutus</i>	Stomach content	Convay et al. (1994) and Jorge (unpublished data)
	DW/WW, C/DW	Jørgensen et al. (1991)
Pomatoschistus minutus	Total biomass	Jorge (unpublished data)
	P/B, Q/B group	<a href="http://www.fishbase.org">http://www.fishbase.org</a>
Pomatoschistus minutus	Stomach content	Correia et al. (1997), Costa (1982), Rebelo (1993) and Rosacchi (1987)
	DW/WW, C/DW	Jørgensen et al. (1991)
Pomatoschistus minutus	Biomass	Jorge (unpublished data)
	P/B, Q/B	<a href="http://www.fishbase.org">http://www.fishbase.org</a>
Pomatoschistus minutus	Stomach content	Correia et al. (1997), Costa (1982) and Morte et al. (1997)
	DW/WW, C/DW	Jørgensen et al. (1991)
Pomatoschistus minutus	Biomass	Jorge (unpublished data)
	P/B, Q/B	<a href="http://www.fishbase.org">http://www.fishbase.org</a>

Appendix A (Continued)

Compartments	Parameter	Source
<i>Larus ridibundus</i> <i>Larus fuscus</i>	Stomach content	Costa (1982) and Jorge (unpublished data)
	DW/WW, C/DW	Jørgensen et al. (1991)
	Biomassa	Lopes (unpublished data)
	P/B, Q/B	<a href="http://www.cbl.umces.edu/atlss">http://www.cbl.umces.edu/atlss</a>
	Diet	Moreira (1995)
<i>Charadrius alexandrinus</i> <i>Charadrius hiaticula</i> <i>Pluvialis squatarola</i>	Av. weight/ind.	Cramp and Simmons (1983)
	DW/WW, C/DW	Jørgensen et al. (1991)
	Biomass	Lopes (unpublished data)
<i>Calidris alpina</i>	P/B, Q/B	<a href="http://www.cbl.umces.edu/atlss">http://www.cbl.umces.edu/atlss</a>
	Diet	Lopes et al. (1998)
Detritus	Av. weight/ind.	Zwarts et al. (1990)
	DW/WW, C/DW	Jørgensen et al. (1991)
	Biomass (O.M in the sediment)	Pardal (1998)

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