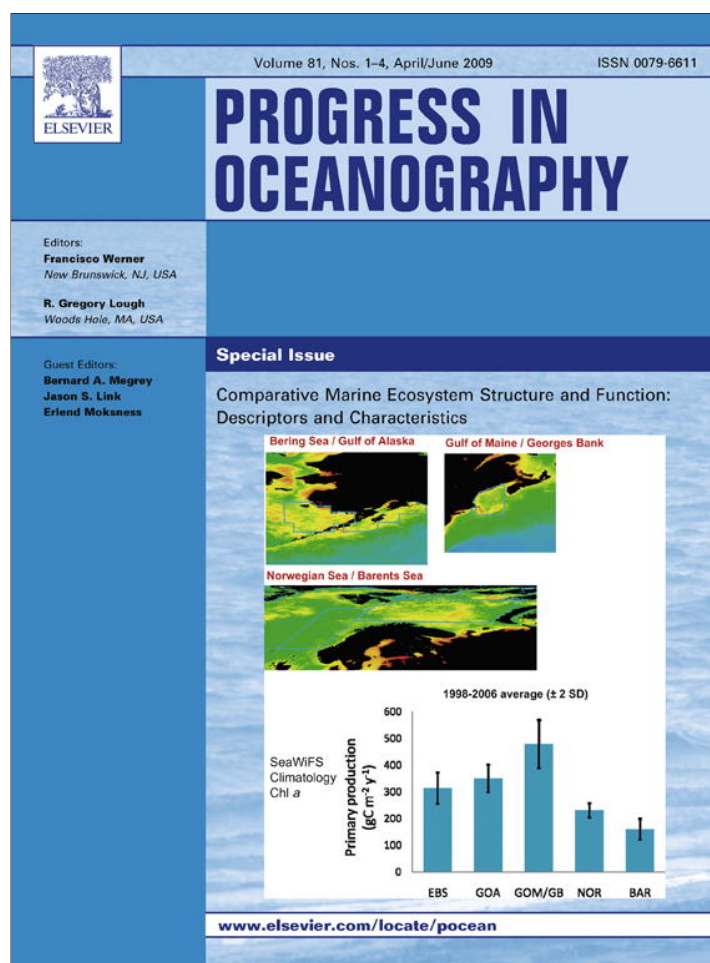


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Ecosystem exploitation and trophodynamic indicators: A comparison between the Northern Adriatic Sea and Southern New England

Fabio Pranovi^{a,*}, Jason S. Link^b

^a Dipartimento di Scienze Ambientali, Università di Venezia, Castello 2737/B, 30170 Venezia, Italy

^b NOAA, National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA 02543, USA

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ABSTRACT

In an ecosystem-based resource management context, it is crucial to assess the relationships between community structure and ecosystem function and how those relationships change with resource extraction. To elucidate how changes in resource use can affect community structure and ecosystem function, we executed a comparative analysis of two different ecosystems subjected to notable fishing pressure. We contrasted the Northern Adriatic Sea (NAS) and Southern New England (SNE) ecosystems by examining outputs from comparable steady-state models. Both ecosystems have relatively high fishing pressure and a high biomass of benthic invertebrates. The basic structure of the food webs shows differences both in the number and definition of the functional groups, as described in the models. Fisheries, on the contrary, show similarities both in terms of catches and discards. Almost all statistics summarizing the structure and flows showed values three times higher in the SNE than in the NAS ecosystem, but despite this difference the two ecosystems exhibited similar, overall properties. Biomass ratios and the Mixed Trophic Impact (MTI) analysis showed that both ecosystems are dominated by the benthic compartment. Removing the biomass effect, however, shows a clear top-down effect, with a high rank achieved by fishing activities. In general terms, the low mean trophic level of catches and the high primary production required (PPR) values result in a high overexploitation level of the ecosystem, as highlighted by the *L* index. We conclude by exploring how comparative studies will continue to be valuable as ecosystem-based management is further implemented.

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1. Introduction

The ecosystem approach to natural resource management has been espoused (WSSD, 2002; FAO, 2003) and, at present, is recommended for adoption as a major policy initiative in Europe, the US, and elsewhere including the EU Water Framework Directive, Common Fisheries Policy and the European Marine Strategy (CBD, 2004; USOC, 2004; FAO, 2003). The aim of the new approach is to ensure that the planning, development and management of the environment will meet social and economic needs without jeopardizing options for future generations to benefit from the full range of goods and services provided by marine ecosystems; i.e. to ensure sustainable development (FAO, 2003; Pickitch et al., 2004). In this context, ecosystem-based management (EBM) aims to conserve the structure and function of ecosystems in order to maintain ecosystem services (CBD, 2004).

One of the main challenges for EBM is the implementation of this more holistic approach, in which the ecosystem represents the management unit (Raffaelli, 2006). Ecosystem considerations

in a marine scientific and management context have been extant for more than a century (e.g. Baird, 1873), but how to make them operational has remained a key challenge. Research needs to be extended to encompass not only the structures of the ecosystem (classically studied components such as populations, species, communities, habitats) but also the processes related to the functioning of the ecological systems (production, consumption, respiration, energy flow and cycling). Ultimately, we need to seek general relationships among patterns and processes at multiple spatial scales (e.g. Zajac, 1999; Hyrenbach et al., 2000).

The relationship between marine ecosystem structure and function has become increasingly prominent in the last decade (Duffy, 2006; Raffaelli, 2006). Yet moving from knowledge of ecosystem structure and function to understanding the relationships between them has been more challenging. Shifting from the assessment of the human-use effects on ecosystem structure towards the assessment of the modifications that these structural changes induce in the processes of perturbed ecosystems requires caution due to the uncertainty, long feedback times and highly nonlinear ecosystem responses to external perturbations (Holling et al., 1995). For example, understanding how changes in biodiversity affect ecosystem function requires integrating diversity within trophic levels

* Corresponding author. Tel.: +39 412347735; fax: +39 41 5281494.

E-mail addresses: fpranovi@unive.it (F. Pranovi), jason.link@noaa.gov (J.S. Link).

(horizontal diversity) and across trophic levels (vertical diversity; including food chain length and omnivory). As another example, the relative importance of top-down or bottom-up trophic controls in continental shelf ecosystems has important implications for how ecosystems respond to perturbations (e.g. Frank et al., 2007). The need to improve our knowledge about the relationships between structure and function is critical for adopting effective EBM strategies and policies.

One way to facilitate a better understanding of the relationship between ecosystem structure and function (and responses to perturbations thereupon) is to engage in comparative ecosystem studies (Hunt and Megrey, 2005; Moloney et al., 2005; Coll et al., 2007). Comparison between similar or comparable ecosystems (i.e. systems with similar latitudinal location and characterized by similar environmental features/constraints) is a useful analytical approach which can allow us to better understand the mechanisms which drive the functioning of ecological systems. In comparable ecosystems, some features will be shared but others will be unique, and analysis of these similar and contrasting patterns and processes can reveal important drivers in each ecosystem. These comparative analyses provide an opportunity for taking a broader ecosystem perspective and permit the ability to draw generalizations important to successful implementation of EBM.

To better elucidate key marine ecosystem properties and to facilitate implementation of EBM, we examined two comparable marine ecosystems; the Northern Adriatic Sea (NAS) and Southern New England (SNE). The reason we chose the NAS and SNE ecosystems are that they both represent relatively shallow, continental shelf ecosystems with a high benthic biomass. Additionally, both have had a notable history of extracting living marine resources, share some physio-chemical features, and have had enough scientific studies to generate adequate databases required for this study. Our objectives in this work were to present summaries of systemic metrics from both ecosystems and to compare those metrics between the two ecosystems.

2. Material and methods

2.1. Ecosystem and model descriptions

The upper portion of the Adriatic Sea (NAS) (Fig. 1) constitutes the widest continental shelf in the Mediterranean Sea and, in the context of the generally oligotrophic conditions of the basin, represents a unique habitat (Pinardi et al., 2006). The NAS is a shallow (<35 m) semi-enclosed basin (14,178 km²), characterized by strong riverine outflows, mainly from the Po River, with high loads of organic matter and nutrients (Revelante and Gilmartin, 1983; Turley, 1999). The NAS is influenced by strong winds in winter causing mixing of the water column and calm summer conditions causing stratification, with occurrence of recurrent eutrophication and the production of mucillagenous aggregates (Malanotte Rizzoli and Bergamasco, 1983; Artegiani et al., 1997a,b). It can be considered as a homogeneous system characterized by the presence of incoherent sediments, mainly mud and relict sand, and by a high level of productivity (Fonda Umani et al., 1992). In relation to climatic and hydrographic features, the basin has been described as the 'Northern Adriatic lacuna', an area more similar to the Atlantic than to the Mediterranean Sea. For instance, the NAS hosts species typical of the cold Atlantic waters (e.g. the brown algae *Fucus virsoides* J. Agardh – a key species in defining a *facies* of the intertidal horizon (Pérès and Picard, 1964; Gamulin-Brida, 1974) – and the sprat, *Sprattus sprattus*). Relatively speaking, the ecosystem structure is dominated by the benthic component, with high standing stocks of biomass sequestered particularly in molluscs (Table 1).

As the NAS is effectively a flat trawlable platform, it is the most exploited Italian basin with more than 15% of the national fishing fleet operating in the area (Bombace, 2002). The most widespread fishing activities target demersal fish and shellfish. The fleet is composed of otter trawls, "rapido" trawls (a sort of beam trawl gear, rigged with 10 cm long iron teeth; for further details see Giovanardi et al., 1998), hydraulic dredges, and mid-water trawls

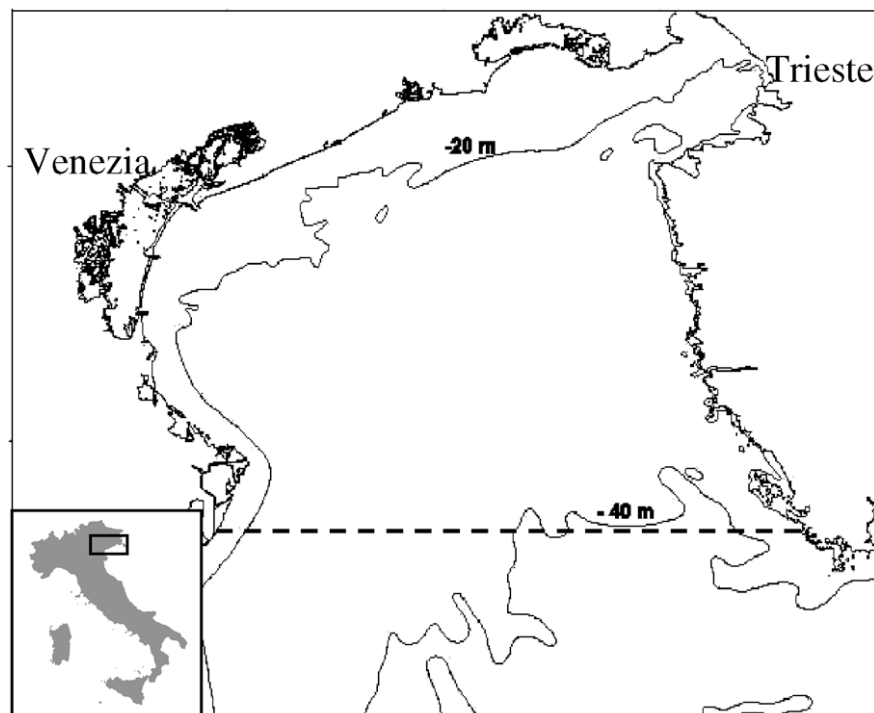


Fig. 1. Northern Adriatic Sea; the southern boundary of the studied area is noted by the dashed line.

Table 1

Inputs of the Northern Adriatic Sea model. TL, trophic level; B, biomass; P/B, Production/biomass ratio; Q/B, consumption/biomass ratio; EE, ecotrophic efficiency; P/Q, production/consumption ratio or gross efficiency. See Appendix A for further details.

Group	TL	B (t km ⁻²)	P/B (yr ⁻¹)	Q/B (yr ⁻¹)	EE	P/Q
Phytoplankton	1	8.4	152.133	–	0.751	–
Bacterioplankton	2.1	2.138	34.348	171.742	0.908	0.2
Microzooplankton	2.03	1.758	219	438	0.215	0.5
Zooplankton	2.35	1.456	18.25	91.25	0.825	0.2
Meiobenthos	2.01	5.311	13.704	68.52	0.681	0.2
Macrobenthos herbivorous	2.05	2.086	1.746	8.732	0.764	0.2
Macrobenthos omnivorous	2.77	3.118	2.313	11.564	0.694	0.2
Macrobenthos detritivorous	2.2	22.834	1.692	8.458	0.919	0.2
Macrobenthos filter feeders	2.44	19.642	1.07	5.351	0.386	0.2
Scallops (Pectinidae)	2.44	0.756	0.7	3.5	0.633	0.2
Clams (Veneridae)	2.44	1.397	1.41	7.05	0.574	0.2
Macrobenthos predator	2.78	7.033	1.5	7.5	0.291	0.2
Planctivorous fish	2.46	19.996	1.295	3.882	0.027	0.334
Cephalopds	3.53	0.35	1.45	4.833	0.285	0.3
Benthic feeders	3.33	0.229	1.895	5.935	0.174	0.319
Flat fish	3.32	0.151	0.98	4.9	0.211	0.2
Necton feeders	3.97	0.012	1.16	4.34	0.852	0.267
Carcasses	1	1	–	–	0.3	–
Organic matter	1	183.884	–	–	0.53	–
Detritus	1	2	–	–	0.687	–

(ICRAM, 2006). The port of Chioggia, located in the Southern part of the Venice lagoon, hosts the most important fishing fleet of the basin, containing 90% of the fishing boats for this region. Therefore, landings from the Chioggia fleet can be considered as largely representative of the studied area (ICRAM, 2006).

The Southern New England (SNE) ecosystem (Fig. 2) is a continental shelf ecosystem of the North-western Atlantic with an average depth of 60 m, being relatively open and influenced by major flow fields. It covers a total area of 64,060 km² and has a substrate predominately of fine-grained sand (Poppe et al., 2003). Water flows in the SNE shelf are primarily northwest to southeast, with sources from Arctic waters along the shelf-slope and from the Gulf

of Maine (via the Great South Channel). The Gulf Stream Current (GSC) is offshore of the SNE and, unlike Georges Bank, warm-water GSC water does not typically become entrained onto the SNE shelf.

The SNE is a highly productive ecosystem, with total primary production on the order of 1.0 g C m⁻² d⁻¹, with annual estimates ranging from 3700 to 4500 g m⁻² yr⁻¹ for total standing biomass (O'Reilly and Zetlin, 1998; Link et al., 2006). As in the NAS, a high fraction of biomass is sequestered in the benthos, with an important role played by bivalve molluscs (Table 2; Link et al., 2006).

The fisheries operating in the SNE are primarily focused on benthic filter feeders (i.e. scallops), flatfish (several pleuronectids), squids and migratory small pelagics (herring, mackerel and butter-

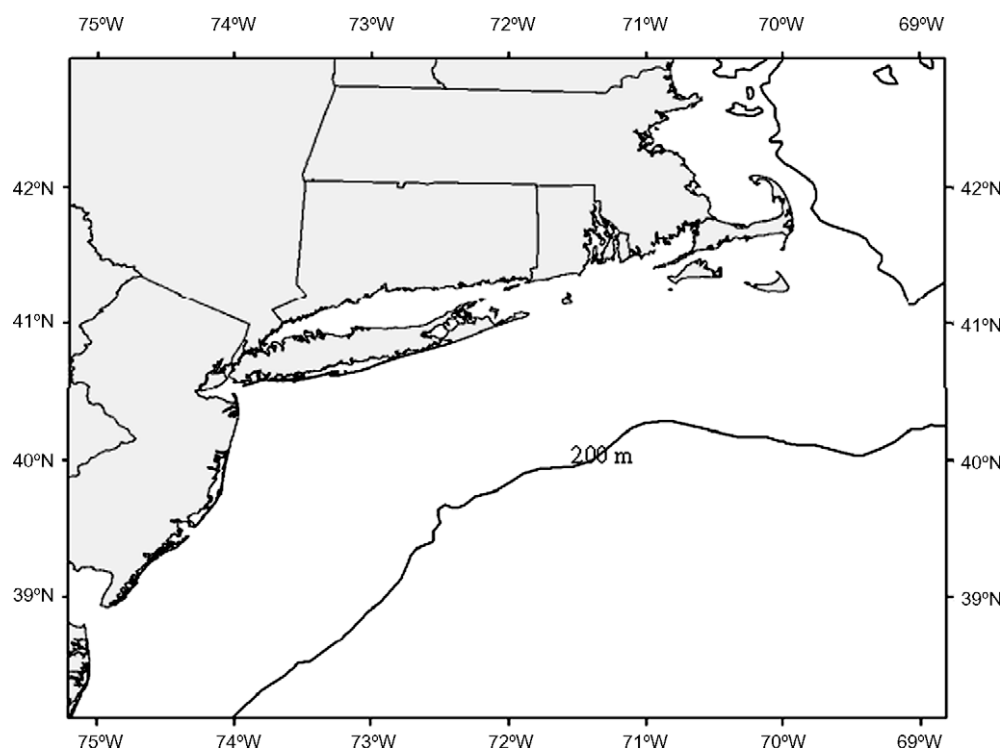


Fig. 2. Southern New England.

Table 2
Inputs of the Southern New England model. TL, trophic level; B, biomass; P/B, Production/biomass ratio; Q/B, consumption/biomass ratio; EE, ecotrophic efficiency; P/Q, production/consumption ratio or gross efficiency. See Link et al. (2006) for further details.

Group	TL	B (t km ⁻²)	P/B (yr ⁻¹)	Q/B (yr ⁻¹)	EE	P/Q
Phytoplankton – primary producers	1	26.528	182.859	–	0.522	–
Bacteria	2	7.532	91.25	380.208	0.9	0.24
Microzooplankton	2.39	5.083	72	242.424	0.9	0.297
Small copepods	2.23	11.825	45.432	127.75	0.9	0.356
Large copepods	2.66	5.653	61.986	109.5	0.9	0.566
Gelatinous zooplankton	3.35	1.196	40	146	0.9	0.274
Micronekton	2.81	4.233	14.25	139.286	0.776	0.102
Mesopelagics	3.38	0.228	0.95	1.825	0.828	0.521
Macrobenthos – polychaetes	2.39	35.436	2.5	17.5	0.897	0.143
Macrobenthos – crustaceans	2.59	6.392	3	21	0.897	0.143
Macrobenthos – molluscs	2.25	17.805	2	14	0.899	0.143
Macrobenthos – other	2.44	18.933	2.04	17.64	0.895	0.116
Megabenthos – filterers	2.2	3.702	5	19	0.731	0.263
Megabenthos – other	3	3.373	2	16.941	0.899	0.118
Shrimp et al.	2.69	0.27	2	5	0.878	0.4
Larval-juv fish – all	3.28	0.422	21	45	0.592	0.467
Small pelagics – commercial	3.71	14.851	0.363	2	0.788	0.182
Small pelagics – other	3.51	1.946	0.95	2	0.902	0.475
Small pelagics – squid	3.92	3.07	0.95	2.75	0.749	0.346
Small pelagics – anadromous	3.61	0.659	0.459	2	0.925	0.229
Medium pelagics – piscivores and other	4.63	0.35	0.585	1.428	0.907	0.41
Demersals – benthivores	3.83	2.337	0.45	0.9	0.79	0.5
Demersals – omnivores	3.57	3.635	0.45	0.8	0.884	0.563
Demersals – piscivores	4.33	2.334	0.468	1.035	0.91	0.452
Sharks – coastal	4.58	0.0215	0.102	0.876	0.842	0.116
Sharks – pelagics	4.74	0.0388	0.105	0.408	0.855	0.258
HMS	4.57	0.00548	0.584	7.289	0.832	0.08
Pinnipeds	4.65	0.0178	0.106	8.778	0.581	0.012
Baleen whales	3.74	0.14	0.041	4.49	0.068	0.009
Odontocetes	4.71	0.0752	0.041	15.641	0.793	0.003
Sea birds	4.17	0.0107	0.275	9.952	0.746	0.028
Discard	1	0.974	–	–	0.218	–
Detritus-POC	1	40	–	–	0.836	–

fish) (Link et al., 2006). Several gears are utilized, but predominately scallop dredges are used, followed by mid-water trawls and bottom-tending otter trawls.

A mass-balance model was applied to both ecosystems using Ecopath with Ecosim (EwE 5.1; Christensen and Pauly, 1992; Walters et al., 1997), which allows for quantifying and balancing energy flows among the different components of an ecosystem.

The NAS model, representing the ecosystem in 1997–2000, is comprised of 20 nodes, ranging from phytoplankton and bacteria to piscivorous fish (Table 1). The input data were obtained by consulting both the published and unpublished literature; references and further details are reported in Appendix A.

The SNE model, representing the ecosystem in 1996–2000, is comprised of 33 nodes, ranging from phytoplankton and bacteria to whales and highly migratory species (Table 2). The energy budget balancing protocols, input data sources and vital rate parameter estimating methodologies are documented more thoroughly elsewhere (Link et al., 2006). Although the source model used both Ecopath and Ecosim, the results used here for our comparisons are based on the balanced Ecopath model.

2.2. System comparisons

Due to geographical and oceanographic features, choices during model construction, taxonomic emphasis and data availability, the two models were obviously different in structure, with a different degree of aggregation throughout the food web (Tables 1 and 2). In order to reduce these differences and to make the two systems more comparable, the functional groups have been aggregated according to the scheme noted in Table 3. First, we distinguished between invertebrate and vertebrate organisms; then we identified the main ecological functional groups; and finally we divided

the groups targeted by fishing activities according to benthic invertebrates, demersal and pelagic fish (Table 3).

2.3. Metrics

To compare the structure and function of the two ecosystems a set of ecological indices based on biomass ratios, trophic flow analysis, thermodynamic concepts, information theory and associated indicators were examined (Christensen et al., 2004; Christensen and Walters, 2004; Cury et al., 2005; Link, 2005). These were calculated based upon the aggregate, comparable food webs for both ecosystems (Table 3).

We calculated and present a series of production (P), biomass (B) and ratios thereof for several compartments of both models. These metrics not only provide a sense of the differences in structure between the two ecosystems, but also serve as proxies for the ecosystem functioning (Link, 2005). We also calculate a series of ratios of fisheries catches to biological rates (production, respiration, consumption; derived by values reported in Tables 1 and 2). We present a plot of cumulative biomass against trophic level, and percentage cumulative production against total cumulative biomass to elucidate major, systemic patterns in biomass flows.

There are a plethora of network metrics output from the EwE software (Christensen et al., 2004; Christensen and Walters, 2004), which we present. We particularly highlight the System Omnivory Index (a measurement of how the feeding interactions are distributed among trophic levels), Finn's Cycling Index (a measure of the degree of energy re-utilization within a food web, representing the fraction of total flows of the system that is cycled), and the Lindeman pyramid (which measures the amount of biomass sequestered at each trophic level). To provide an indication of energy flow efficiency within each food web, the average trans-

Table 3

Trophic groups described in the two models and aggregation codes (Agg.) used for the analysis. Taxa are noted as invertebrate or vertebrate; B, benthos; P, plankton; N, nekton; M, mammals; D, detritus; F, fishery; B1, commercial benthic species; N1, pelagic commercial species; N2, demersal commercial species.

Taxa	Agg.	NAS	Taxa	Agg.	SNE
Invert.	P	Phytoplankton	Invert.	P	Phytoplankton – primary producers
Invert.	P	Bacterioplankton	Invert.	P	Bacteria
Invert.	P	Microzooplankton	Invert.	P	Microzooplankton
Invert.	P	Zooplankton	Invert.	P	Small copepods
Invert.	B	Meiobenthos	Invert.	P	Large Copepods
Invert.	B	Macrobenthos filter feeders	Invert.	P	Gelatinous Zooplankton
Invert.	B	Scallops (Pectinidae)	Vert.	P	Micronekton
Invert.	B	Clams (Veneridae)	Invert.	P	Mesopelagics
Invert.	B	Macrobenthos detritivorous	Invert.	B	Macrobenthos – polychaetes
Invert.	B	Macrobenthos omnivorous	Invert.	B	Macrobenthos – crustaceans
Invert.	B	Macrobenthos herbivorous	Invert.	B	Macrobenthos – molluscs
Invert.	B	Macrobenthos predators	Invert.	B	Macrobenthos – other
Vert.	N	Planctivorous fish	Invert.	B	Megabenthos – filterers
Vert.	N	Benthic feeders	Invert.	B	Megabenthos – other
Vert.	N	Flat fish	Invert.	B	Shrimp et al.
Vert.	N	Cephalopoda	Vert.	P	Larval-juv fish – all
Vert.	N	Nekton feeders	Vert.	N	Small Pelagics – commercial
	D	Carcasses	Vert.	N	Small Pelagics – other
	D	Organic matter	Vert.	N	Small Pelagics – squid
	D	Detritus	Vert.	N	Small Pelagics – anadromous
	F	Mid-water trawl	Vert.	N	Medium Pelagics – piscivores and other
	F	Hydraulic dredge	Vert.	N	Demersals – benthivores
	F	Rapido flat fish	Vert.	N	Demersals – omnivores
	F	Rapido pectinidae	Vert.	N	Demersals – piscivores
	F	Otter trawl	Vert.	N	Sharks – coastal
			Vert.	N	Sharks – pelagics
			Vert.	N	HMS
			Vert.	M	Pinnipeds
			Vert.	M	Baleen whales
			Vert.	M	Odontocetes
			Vert.	M	Sea Birds
				D	Discard
				D	Detritus-POC
				F	Landings

fer efficiency across trophic levels for both ecosystems was analysed.

Moreover, we examined the informational network indices provided as output by the EwE software such as Ascendency (A). Taking into the account both the size of the ecosystem in terms of flows (total system throughput; TST) and organization (information content) has been proposed as an index to characterize the degree of development and maturity of an ecosystem (Ulanowicz, 1986). Capacity (C) represents the upper limit of A. The Relative Ascendency measure (A/C) is the fraction of the potential level of organization that is actually realized (Ulanowicz, 1986). It is hypothesized that high values of this index are related to low levels of stress in the system and vice-versa. Hence disturbance activities, like eutrophication and fishing, are expected to produce a decrease in A (Wulff and Ulanowicz, 1989). The complement to A is System Overhead (O), which represents the cost to an ecosystem for circulating matter and energy (Monaco and Ulanowicz, 1997). Thus, System Overhead effectively represents the degrees of freedom a system has at its disposal to react to perturbations (Ulanowicz, 1986). For the ranking of the different compartments in term of their contribution to overall system structure and function, Ulanowicz (1997) proposed estimating the relative Ascendency of each group. That is, Ascendency as a percentage of System Overhead is effectively a measure of resilience.

In order to assess the ecological role played by the different compartments within the two ecosystems, we use the Mixed Trophic Impact (MTI). This index, quantifying the direct and indirect interactions between functional groups, allows one to estimate the global impact of each group on the other ones (Ulanowicz and Puccia, 1990). The MTI analysis was carried out by using two different approaches, according to Libralato et al. (2004). In the

first approach, the MTI (m_{ij}), weighted by the inverse of the biomass of impacted group (B_j),

$$aGI_i = \sum_j m_{ij} \frac{1}{B_j} \quad (1)$$

represents the absolute effect (absolute global impact – aGI) of the variation of a unit of the impacting group and assesses the importance in terms of the functioning of a unit of biomass of each.

In the second approach the MTI, weighted by the impacting/impacted biomass ratio (B_i/B_j),

$$rGI_i = \sum_j m_{ij} \frac{B_i}{B_j} \quad (2)$$

quantifies the effect on the ecosystem of a percent variation of the impacting group biomass and assesses the relative effect of a variation of the biomass of each compartment in relation to the present value (relative global impact – rGI).

Closely related to the MTI is the keystone index (Libralato et al., 2006), which identifies those groups that, even if characterized by a low biomass, play an important role in structuring the ecosystem (Power et al., 1996). It is based on a plot of the overall effect (ε_i) vs. the keystone (KS_i).

The overall effect (ε_i) is estimated from the MTI index (m_{ij}) as:

$$\varepsilon_i = \sqrt{\sum_{j=1}^n m_{ij}^2} \quad (3)$$

The keystone (KS_i) of a functional group is calculated as:

$$KS_i = \log |\varepsilon_i (1 - p_i)| \quad (4)$$

where p_i is the proportion of total system biomass made up by functional group i .

Finally, to assess the effects of export from the system due to fishing activities, the L index, (proposed by Libralato et al., 2008) has been applied. It is based on the assumption that the export of secondary production due to fisheries reduces the energy available for upper ecosystem levels thus resulting in a loss of secondary production. The index, taking into the account ecosystem properties (primary production and transfer efficiency), and fisheries features (trophic level of catches and primary production required), allows quantifying the effects of fishing at an ecosystem level. It is calculated as:

$$L = - \frac{PPR \cdot TE^{TLC-1}}{P_1 \cdot \ln TE} \quad (5)$$

where PPR is the primary production required to sustain the catches and is obtained by back-calculating the flows (expressed in primary production and detritus equivalents) for all pathways from the caught species down to the primary producers and detritus (Pauly and Christensen, 1995); TE is the transfer efficiency of the system; TLC is the mean trophic level of the catches; and P_1 is the primary production of the system. According to Libralato et al. (2008), it is possible to associate with each index value a probability of the ecosystem being sustainably fished and, by fixing the reference level for this probability, the index provides a basis for estimating, from an ecosystem point of view, the maximum allowable catches (ecosystem-based maximum sustainable catches – EMSC; for further details, please see Libralato et al., 2008).

3. Results

Both ecosystems were dominated by invertebrates in terms of biomass and production (Table 4). Ranking the major compartments in relation to their contribution to the total system biomass showed that for both ecosystems the highest rank is attained by the benthos (64% and 48% for NAS and SNE, respectively). Differences were seen in the secondary ranking, nekton for NAS and plankton for SNE (Table 4). These observations were reflected in the Benthos:Plankton and Nekton:Plankton ratios, which were both higher for NAS than SNE. The Benthos:Nekton ratio were quite similar in the two systems (Table 4).

In terms of production, the ranking by compartments showed a similar pattern between NAS and SNE, with production dominated by plankton followed by benthos and then nekton (Table 4). The various ratios among food web compartments also exhibited the same ranking for both ecosystems. Overall, the values for production are similar between the two systems, with the largest differ-

ence being in the nekton compartment (1.3% and 0.2%, for NAS and SNE, respectively).

When cumulative biomass was plotted against trophic level, a similar pattern emerged for both ecosystems with a major accumulation of biomass between trophic levels 2 and 3 resulting in a sigmoidal curve (Fig. 3). This likely reflects the high benthic biomass that occurs in these systems. After trophic level 3, cumulative biomass is relatively flat, although there is a small abrupt change between TL 3–4 for SNE, due to the higher vertical diversity (in terms of species/groups) of that ecosystem. The difference in the first part of the curve is due to the higher primary producer biomass recorded in the SNE system.

Cumulative biomass vs. cumulative production showed a “hockey stick” configuration, suggesting a steep rise in biomass and production followed by a slow levelling out at the highest values of biomass and production (Fig. 4). The main difference being that the SNE curve exhibited a much more gradual rise than in the NAS. This more gradual rise suggests either a less productive system per unit biomass or perhaps higher vertical diversity.

Network flows and information indices are reported in Table 5. As expected, almost all values referred to the structure and dimension of the flows were 3–4 times higher in the SNE than in the NAS ecosystem (Table 5). In relative terms, however, the two systems are very similar, with Total Consumption dominating total system throughput (43% and 47%, for NAS and SNE, respectively) and the same Total primary production/total respiration ratio (1.23) for both ecosystems (with the reference value about 1.00). Addition-

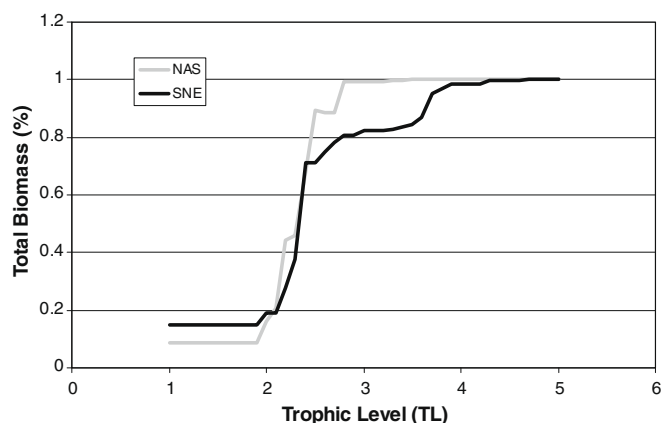


Fig. 3. Cumulative biomass plotted against trophic level for the two ecosystems.

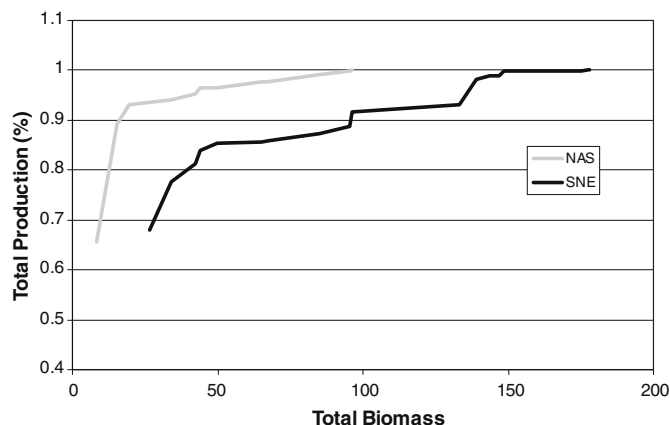


Fig. 4. Cumulative production plotted against cumulative biomass for the two ecosystems.

Table 4

Relative contribution (%) of major compartments to total biomass and total production, and ratios between compartments. B, benthos; P, plankton; N, nekton; M, mammals.

	Biomass		Production	
	NAS	SNE	NAS	SNE
Vertebrates	0.21	0.19	0.01	0.01
Invertebrates	0.78	0.81	0.99	0.99
Invert./Vert.	3.63	4.22	71.06	84.25
P	0.14	0.35	0.91	0.97
B	0.64	0.48	0.08	0.03
N	0.21	0.16	0.01	0.002
M	–	0.001	–	1.91 E–06
B/P	4.52	1.37	0.09	0.03
B/N	2.99	2.94	5.79	14.38
B/M	–	352.52	–	15220.31
N/P	1.51	0.47	0.02	0.002

Table 5
Summary statistics after mass balancing and network flow indices.

Parameter		NAS	SNE
Sum of all consumption	t km ⁻² yr ⁻¹	2128.89	8528.93
Sum of all exports	t km ⁻² yr ⁻¹	242.84	812.82
Sum of all respiratory flows	t km ⁻² yr ⁻¹	1035.69	4038.61
Sum of all flows into detritus	t km ⁻² yr ⁻¹	1518.34	4782.62
Total system throughput	t km ⁻² yr ⁻¹	4926	18163
Sum of all production	t km ⁻² yr ⁻¹	1947	7132
Gross efficiency (catch/net p.p.)		0.0019	0.0008
Calculated total net primary production	t km ⁻² yr ⁻¹	1277.92	4850.90
Total primary production/total respiration		1.234	1.201
Net system production	t km ⁻² yr ⁻¹	242.22	812.29
Total primary production/total biomass		13.30	27.24
Total biomass/total throughput		0.02	0.01
Total biomass (excluding detritus)	t km ⁻²	96.09	178.10
Connectance Index		0.374	0.334
System Omnivory Index		0.201	0.303
Throughput cycled (excluding detritus)	t km ⁻² yr ⁻¹	23.69	498.72
Predatory cycling index	% of throughput w/o detritus	1.04	5.80
Throughput cycled (including detritus)	t km ⁻² yr ⁻¹	395.03	2577.27
Finn's cycling index	% of total throughput	8.02	14.19
Finn's mean path length		3.852	3.744
Finn's straight-through path length	Without detritus	2.167	1.984
Finn's straight-through path length	With detritus	3.543	3.212
Ascendancy/capacity (A/C)	(%)	32.5	18.9
Overhead/capacity (O/C)	(%)	67.5	87.1

ally, the structure of the food web was quite similar for the two systems, as highlighted by the Connectance Index (Table 5). In terms of complexity, both systems showed low values of the System Omnivory Index relative to other published models (e.g. Monaco and Ulanowicz, 1997). This suggests that these two food webs exhibited a relatively linear topology.

The SNE ecosystem showed a higher cycling capacity than NAS, as suggested by the Finn's Cycling Index (FCI). However, in both ecosystems, the high FCI values indicate that these food webs have a large amount of cycling through detritus, revealing a major dependency on detritus-related processes (Table 5). This is especially true for the NAS ecosystem.

Table 6 summarizes the flows organized by integer trophic levels in the Lindeman pyramid. In both ecosystems, the TL 1 and 2 accounted for more than 90% of the flows, with the values recorded in NAS slightly higher than those of SNE. The pattern reverses for the following TLs (3–4), with SNE values higher at those upper trophic levels.

The average transfer efficiency (TE) values were lower for NAS than SNE (8.4 and 15.5, respectively). These values confirm that, on average, food webs more strongly associated with detritus tend to be less efficient than those more directly reliant upon primary producers. The pattern obtained by plotting the TE for each trophic level (TL) elucidates the decline in efficiency as TL increases, with a minor increase at TLs 7 and 8 (Fig. 5).

Upon examining the information indices, both systems showed relatively low values of Ascendancy/Capacity (A/C) and conversely high values of Overhead/Capacity (O/C); that is a high maturity and

Table 6
Lindeman pyramid of flows in each ecosystem; values are expressed as percentage of total system throughput (TST). Integers represent trophic levels.

TL	NAS	SNE
6	0.001	0.014
5	0.018	0.129
4	0.4	1.0
3	4	7
2	38	37
1	57	55

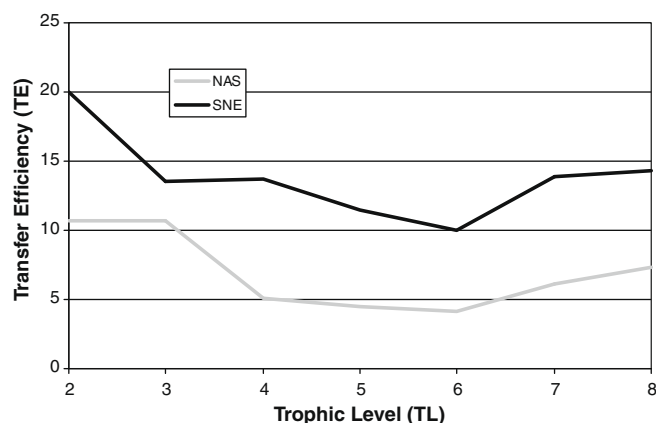


Fig. 5. Transfer efficiency plotted against trophic level for the two ecosystems.

a high potential resistance to external perturbation (Table 5). The contribution of each group to Ascendancy showed the importance of detritus in the NAS and detritus and plankton in SNE (Table 7). Benthos and nekton exhibited the same ranking values in the two systems, even with different contributions to Ascendancy.

The MTI values, evaluated as relative global impact (rGI), confirm the importance of invertebrates for both ecosystems (Fig. 6).

Table 7
Relative contribution to Ascendancy by the major compartments in the two ecosystems. Vert., vertebrates; invert., invertebrates; B, benthos; P, plankton; N, nekton; M, mammals; D, detritus.

	NAS	SNE
Vert.%	0.03	0.05
Invert.%	0.51	0.59
P%	0.36	0.55
B%	0.15	0.08
N%	0.03	0.005
M%	–	0.0002
D%	0.46	0.37

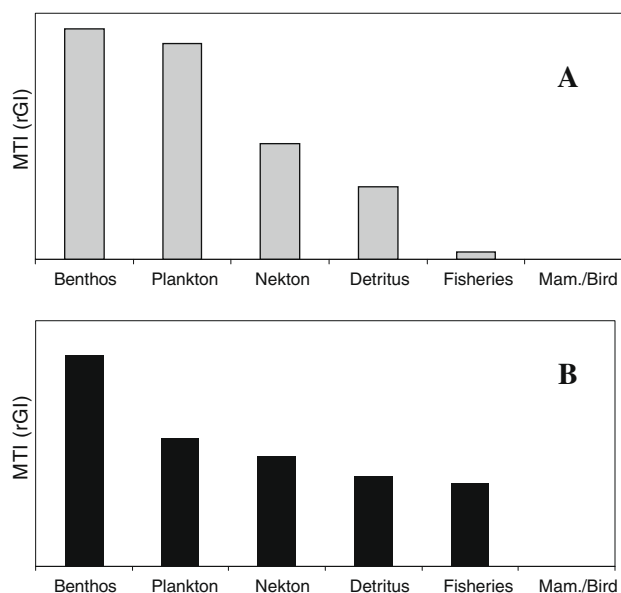


Fig. 6. Mixed Trophic Impact, overall (MTI rGI) analysis; (A) NAS, (B) SNE.

The ranking for the compartments reflects the biomass patterns, highlighting the importance of the benthos. Regarding the exploited groups, the same pattern is observed in NAS and SNE, with the pelagic fish playing the most important role (Table 8 and Fig. 4). The analysis of the MTI, evaluated as absolute global impact (aGI) showed the importance of vertebrates in determining the functioning of both systems, with particular emphasis to the top-down effects due to the nekton group (Table 8 and Fig. 7). The ranking for the compartments also underpins the important ecological role played by both fishing activities and plankton, respectively, for NAS and SNE (Table 8 and Fig. 7). Finally, the presence of top-down effects is implied by the higher values for the fishery groups (Table 8 and Fig. 7).

The keystone index analysis was performed without any aggregation and the original nodes can be recognized. The top groups were phytoplankton and two macrobenthic groups (detri-

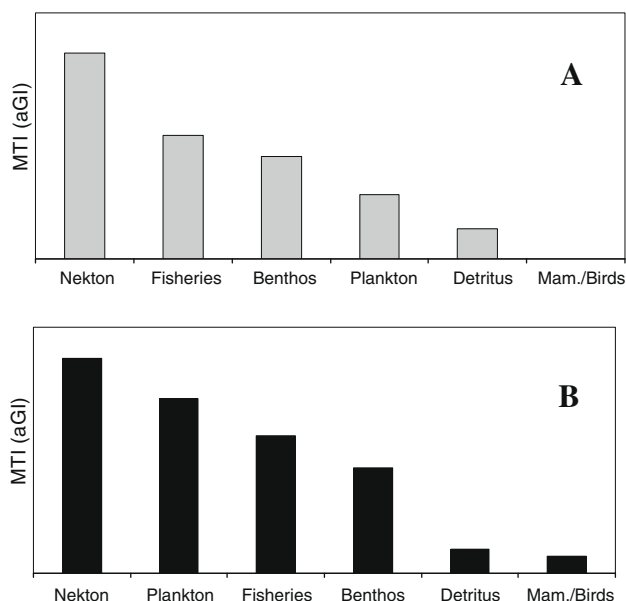


Fig. 7. Mixed Trophic Impact, biomass effect (MTI aGI) analysis; (A) NAS, (B) SNE.

Table 8

Mixed Trophic Impact (biomass ratio) analysis. B, benthos; P, plankton; N, nekton; M, mammals; D, detritus; F, fishery; B1, commercial benthic species; N1, pelagic commercial species; N2, demersal commercial species.

	MTI (overall effect) rGI		MTI (unit of biomass effect) aGI	
	NAS	SNE	NAS	SNE
Vert.	306.72	1459.16	58.46	476.71
Invert.	430.32	4035.86	47.43	461.92
P	102.78	1559.21	18.26	320.18
B	327.54	2588.33	29.17	192.98
N	306.71	1345.67	58.46	393.38
M	–	1.81	–	32.08
D	163.99	1102.67	8.44	44.44
F	11.07	1014.63	35.18	252.40
B1	3.98	220.48	5.18	64.97
N1	303.10	1233.63	21.05	226.25
N2	3.62	108.65	37.41	48.19

tus feeders and omnivores) for the NAS ecosystem, whereas for the SNE the top groups were large copepods, gelatinous zooplankton and phytoplankton (Fig. 8). This again confirms the relative importance of planktonic groups in SNE when compared to NAS.

Relative to the exploitation of natural resources by fishing activities (Table 9), the higher productivity of the SNE ecosystem is re-

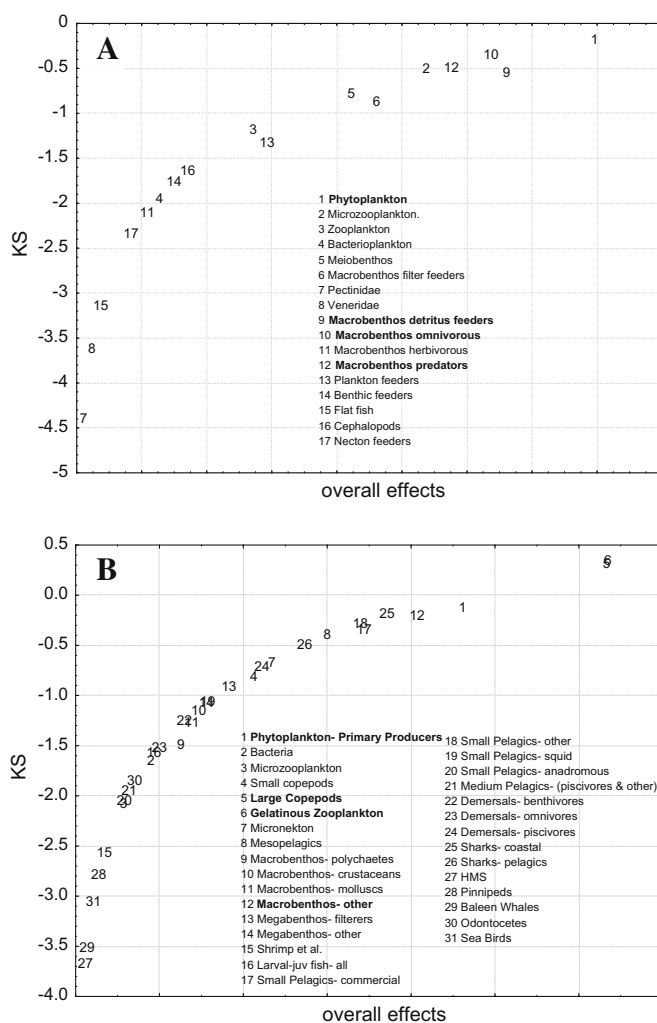


Fig. 8. Keystone index (KS_i) and overall effect (e_i) of each functional group; (A) NAS, (B) SNE. Keystone groups are those with higher e_i and higher KS_i .

Table 9
Comparison between the two ecosystems in terms of species targeted and discarded by fishing activities.

		NAS	SNE
Target species (t km ⁻² yr ⁻¹)	Zooplankton	–	–
	Macrobenthos	1.177	1.851
	Pelagic fish	0.444	0.873
	Benthic fish	0.140	0.317
	Sharks	–	0.008
	Marine mammals	–	0.001
	Sea birds	–	–
	Total catch	1.761	3.050
Discarded species (t km ⁻² yr ⁻¹)	Zooplankton	–	0.009
	Macrobenthos	0.586	0.582
	Pelagic fish	0.017	0.255
	Benthic fish	0.007	0.122
	Sharks	–	0.004
	Marine mammals	–	3.0 E–08
	Sea birds	–	6.3 E–05
	Total catch	0.610	0.972

flected in the higher biomass of total catches (4.02 t km⁻² yr⁻¹ and 2.37 t km⁻² yr⁻¹, respectively) for SNE compared to NAS. Differences were also seen in the mean trophic level of the catch (2.57 for NAS and 2.90 for SNE). However, the two ecosystems showed similarities, particularly in the macrobenthic compartment, with both ecosystems having comparable values for targeted and discarded quantities of macrobenthos (Table 9). The fishing activities result in an exploitation of 46% of the production of macrobenthic commercial groups in the NAS and only 3% in the SNE (Table 10). The values were more comparable between the two systems for the exploited groups in the Nekton compartment (Table 10).

Despite differences in terms of production, flow structures and transfer efficiency, both systems showed almost the same value of the L index (0.108 and 0.116, respectively, for NAS and SNE; Table 11). By using the classification parameters proposed by Libralato et al. (2008), these values result in a very high probability (>80%) of having been subjected to an unsustainable fishing regime (Table 11). Extended further, a key interpretation of these results would be that in order to increase the probability of sustainably fishing

Table 10
Ratios between total catch and production or consumption for the major targeted groups. B1, commercial benthic species; N1, pelagic commercial species; N2, demersal commercial species.

	Total catch/P		Total catch/Q	
	NAS	SNE	NAS	SNE
B1	0.46	0.03	0.09	0.01
N1	0.02	0.06	0.01	0.01
N2	0.11	0.14	0.03	0.07

Table 11
Estimated probabilities of the ecosystem being sustainably fished (p_{sust}) and ecosystem-based maximum sustainable catches (EMSC) for different values of p_{sust} (75% and 95%). TE, transfer efficiency; PP, primary production; TLC, trophic level of catch; PPR, primary production required.

	TE (%)	PP (g C m ⁻² yr ⁻¹)	TLC	Catch and discards (t km ⁻² yr ⁻¹)	PPR (%)	L index	p_{sust} (%)
NAS	8.4	142	2.57	2.372	13.0	0.1081	18.9
SNE	15.5	539	2.90	4.026	7.6	0.1165	18.9

Table 12
Ecosystem-based maximum sustainable catches (EMSC) for different values of p_{sust} (50%, 75% and 95%).

	EMSC ₅₀ (t km ⁻² yr ⁻¹)	Change ₅₀ (%)	EMSC ₇₅ (t km ⁻² yr ⁻¹)	Change ₇₅ (%)	EMSC ₉₅ (t km ⁻² yr ⁻¹)	Change ₉₅ (%)
NAS	1.095	–57	0.450	–82	0.193	–92
SNE	1.725	–41	0.709	–76	0.304	–90

these food webs to 75%, a reduction of about 80% of present total catches would be required for both ecosystems (Table 12).

4. Discussion

4.1. Contrasts between NAS and SNE

In general terms, results from the structure and trophic flow analysis of the two ecosystems studied here demonstrated congruence with previous studies carried out in both ecosystems. The South New England (SNE) ecosystem is confirmed as one of the most productive marine areas on the planet (Bax, 1991; Cohen et al., 1982; Grosslein et al., 1980; Sissenwine et al., 1984); whereas, the Northern Adriatic Sea (NAS) system is confirmed as one of the most productive areas within the Mediterranean basin (Bosc et al., 2004; Turley, 1999). The semi-enclosed (NAS) vs. open system (SNE) comparison results in a large absolute difference between the structure and flows of the two ecosystems, with the NAS model 3–4 times less than the SNE model results.

Notwithstanding the differences in the ecosystems and models thereof, some similar features were noted. Both ecosystems are dominated by benthic biomass and plankton production. In terms of structure (e.g. biomass composition), the importance of the benthic compartment was also confirmed by the ‘accumulation’ of biomass recorded between TL 2 and 3, which results in a sort of inverted trophic pyramid. This pattern would be in accordance with the hypothesis suggested by Fath and Killian (2007) about the typical marine ecosystem trophic structure which is different from the classic (and terrestrial-based) Eltonian pyramid.

The transfer efficiency for the SNE food web is higher than the upper end of average values (8–15%) reported by other authors (e.g. Christensen and Pauly, 1993; Wolff, 1994; Wolff et al., 1996), but comparable with those reported for other North-western Atlantic ecosystems (Link et al., 2006). On the contrary, NAS TE values are very close to those reported by Coll et al. (2007) for the North Central Adriatic basin and are in the lower part of the range. This highlights a significant difference in the efficiency between the two ecosystems. The higher efficiency of SNE is also confirmed by several of the other cycling indices. This difference could be related to the higher complexity of the SNE ecosystem. Further, in the SNE ecosystem there is a more even biomass distribution among different compartments, whereas the NAS is dominated by benthos. With almost 65% of the total biomass in the benthos, the biomass ratios are skewed towards the benthos in the NAS compared to SNE. All these properties can directly affect the resistance/resilience of the systems. According to theoretical and real system analysis, both energy cycling and transfer efficiency relate in a nonlinear but notable way to other system properties such as stability (de Ruiter et al., 1995; McCann et al., 1998; Neutel et al., 2007). This would suggest the importance of taking into

the account the vertical biodiversity (multi-trophic analysis) of an ecosystem (Raffaelli, 2006).

Results indicate that for both ecosystems there is the presence of an important coupling between the pelagic and demersal compartments – mainly due to the link among detritus, benthic and pelagic invertebrates. This is likely explained by the shallow waters and the oceanographic features of both these areas which create specific ecological conditions related to water exchanges and recirculation of nutrients. Moreover, the link between detritus and benthic organisms could be partially enhanced by fishing activity, which generates important amounts of discards (0.610 and 0.972 t km⁻² for NAS and SNE, respectively) and increases biomass and energy flows towards detritus. These detrital enhancement activities also directly influence trophic webs, shortening path length, by-passing predation cycles and increasing microbial loops (Azam et al., 1983; Jones, 1992; Dayton et al., 1995; Kaiser and de Groot, 2000).

In terms of fishing activities, the NAS and SNE show interesting similarities. The gross efficiency of the fishery from both ecosystems was high when compared to the average of 0.0002 reported from global data (Christensen et al., 2004). The mean trophic level of the catch (TLC) recorded for both was lower than values obtained for other systems, such as the North and Central Adriatic basin (TL = 3.07, Coll et al., 2007) and the Mediterranean Sea (TL = 3.0, Pauly et al., 1998), reflecting the composition of catches and particularly the important contribution of benthic invertebrates (67% and 39%, respectively, for NAS and SNE) and small pelagic fish (25% and 29%, respectively, for NAS and SNE). The incidence of discarding of total catch was about 25% (26% for NAS and 24% for SNE), with this value probably indicative of low sustainability of the fishing activity (Kelleher, 2005).

4.2. Utility of novel metrics

Ascendency and capacity represent two holistic measures derived from the analysis of networks of trophic exchanges. Again Ascendency is defined as an index that characterizes the degree of system development and maturity, incorporating both growth and development (Ulanowicz, 1986). Capacity is associated with the scope of the system for further development and represents the mathematical upper bound on Ascendency (Ulanowicz and Norden, 1990), with System Overhead being the difference between the two. Results suggest (Ortiz and Wolff, 2002) that both ecosystems are immature (low Ascendency) and have a high resistance to external perturbations (i.e. high System Overhead). The differences in terms of System Overhead between NAS and SNE (a lower value for NAS) would suggest a higher risk for the NAS ecosystem in relation to external pressures.

The preceding cybernetic considerations are confirmed by the cycling indices, such as Finn's Cycling Index. Odum (1969) notes that the FCI is expected to increase with maturation of the ecosystem. It has been observed, however, that disturbed systems often exhibit greater degrees of recycling. The explanation would be that such an increase in cycling in disturbed systems is a homeostatic response that maintains in circulation resources which previously were stored as biomass in higher trophic level organisms before the perturbation (Ulanowicz and Wulff, 1991; Patricio et al., 2006). The ranking of different compartments according to their contribution to total Ascendency highlights an important difference between the two systems. In the context of the importance of the lower trophic level production, the results suggest that NAS is more dependent on detritus whereas SNE is more dependent upon primary production. Environmental management deals with dynamic systems which change through time. In this context, concepts of stability and maturity (sensu Odum, 1969) seem to play a crucial role for the possible success of management policies.

Ecosystem stability is an important emergent property determining the sustainability of all ecological functions, goods and services conveyed to society. Ecosystem stability can be assessed through two traits. The resistance of the ecosystem to external forcing and disturbance and the resilience of the ecosystem, referring to its capacity to return to the original state after this has been altered by significant disturbance (Holling, 1996). Thus, ecosystem stability is an essential feature to consider in the framework of renewable resources management, since ecosystems that have low resilience will be particularly vulnerable to external forcing factors. When change occurs resilience allows (via the various ecosystem components) for renewal and reorganization (Gunderson and Holling, 2002; Berkes et al., 2002). Vulnerability is the opposite of resilience: when an ecological system loses resilience it becomes vulnerable to change that previously could be absorbed (Kasperson and Kasperson, 2001). Anthropogenic pressures (such as fishing activities or eutrophication) that change the ecosystem structure can also affect ecosystem functioning, thereby making the system more vulnerable to other disturbances (both natural and human-induced), while at the same time reducing resilience, and so on. Conversely, once the system has been shifted to another stable state, it is possible that the new state, even if less desirable, is more stable in terms of resistance than the previous one (Scheffer et al., 2001).

The importance of resistance/resilience in a management context is complicated by the absence of appropriate metrics to quantify it. Indeed, which metrics reflect these ecosystem features, especially in real systems, still remain an unsolved issue. According to Cury et al. (2005), a modeling approach could be used to explore dynamic stability (see also Vasconcellos et al., 1997; Pérez-España and Arreguin-Sánchez, 1999), but the specific relevant metrics remain to be determined. Thus, our proposal is that some of the novel metrics here should at least be considered to enhance ecosystem-based management.

In the context of analysis of ecosystem function, the keystone-ness and MTI index quantify the trophic interactions among the different functional groups. These indices define the relative importance of the ecological role played by each group. Our results describe a similar pattern for both ecosystems, despite some small distinctions, emphasizing the prominence of benthic and planktonic organisms. In terms of 'keystone species/groups' the importance of planktonic invertebrates for the SNE system and benthic groups for the NAS system are highlighted, confirming the differences previously described. The keystone-ness index application confirms the hypothesis that keystone species/groups do not always exert a high impact by means of top-down effects (Libralato et al., 2006), a feature initially suggested to be a defining characteristic of keystone species (Paine, 1969).

Furthermore, the MTI analysis demonstrates that both ecosystems are controlled by the benthic compartment in terms of overall effects (MTI rGI), with a general pattern reflecting the importance of each compartment in terms of biomass. Removing the biomass effect raises the importance of the ecological role played by the nekton, with a clear top-down effect. In this context, the high rank achieved by the fisheries is noteworthy, emphasizing the important ecological role of exploitation. In sum, these observations could have important consequences to ecosystem function in relation to the disturbances associated with exploitation. This would be similar to the hypothesis suggested by Frank et al. (2006, 2007) of a top-down control within mid-latitude marine ecosystems that is strongly modulated by bottom-up productivity. According to Strong (1992), top-down control would not represent the norm for marine ecosystems, but instead represent a form of biological instability, particularly if in response to heavy exploitation by fisheries. The existence of top-down controls in exploited ecosystems does not necessarily lead to trophic cascades, but can

be viewed as an initial step towards alternate states (Frank et al., 2007). All these points underpin the importance of analyzing the state of ecological systems to be managed in relation to the main features of stability via these novel metrics.

The *L* index highlights the presence of an ecosystem overfishing proxy (sensu Murawski, 2000; Link, 2005) in both ecosystems. As suggested by the high values of the fishery efficiency index, the fishing in these ecosystems harvests at low trophic levels. This results in a low mTL of catches and high PPR, features usually linked to unsustainable fishing strategies (Pauly et al., 2002). As demonstrated by Libralato et al. (2008), high PPR values are only compatible with fisheries harvesting the higher part of the food web. The *L* index results obtained for NAS and SNE concur with similar values reported globally for other ecosystems (Libralato et al., 2008). To increase the probability of fishing in a sustainable manner to 50%, it would be necessary to reduce the present level of exploitation by more than 40%. In the implementation of ecosystem-based fishery management, the values reported here can serve as a first approximation of potential systemic reference levels.

We assert that to fully capture patterns and spatial/temporal trends when dealing with dynamic systems, it is necessary to have multiple perspectives. In this context and relative to the discussion about implications of stability for ecosystem management, multiple metrics are more insightful than just a few limited ones.

4.3. Value of comparative studies

The implementation of an EBM approach can benefit from the developing body of knowledge on ecosystem functioning and ecosystem responses to perturbations such as fishing. In this context, there is a need to move towards larger spatial and temporal scales, towards greater trophic complexity and towards connections to biodiversity policy being developed at the ecosystem level (Jorgensen, 1992; Link, 2002). Small-scale experiments will remain useful for identifying mechanisms and testing specific hypotheses, but macro-ecological and ecosystem ecology approaches have a stronger potential for successfully addressing issues of scale, complexity and socio-economic concerns. To reach these goals, models and comparisons between different ecosystems can serve as a useful tool (Raffaelli, 2006).

The comparisons presented here highlight that quite different ecosystems, both in terms of real structure (semi-enclosed vs. open basin) and model representations (different aggregations adopted) show similar features. Being subjected to high levels of fishing pressure resulted in similar responses in these ecosystems, such as: a simplified trophic web topology (relatively linear); ecosystem control shifted towards high trophic levels and benthic compartments; and the keystone roles played by nekton compartment. Thus, it seems feasible to recognize signals of ecosystem effects induced by exploitation activities. It also seems apparent that there are fundamental ecosystem processes occurring in both ecosystems that may lead to a better general understanding of ecosystem responses to over-exploitation (sensu Murawski, 2000; Link, 2005).

It is virtually impossible to conduct experiments on full ecosystems, particularly at the scales associated with large marine ecosystems. Therefore, comparative studies are highly valuable to elucidate those common, fundamental, and unique processes and patterns in these marine ecosystems. In many respects, comparisons of comparable ecosystems serve as “replicate” responses in a pseudo-experimental sense. The work presented here particularly highlights both common and unique features of SNE and NAS ecosystems. Comparative analyses such as this will continue to provide an opportunity for taking a broader ecosystem perspective and permit the ability to draw generalizations important to the successful implementation of EBM.

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Appendix A

The Northern Adriatic Sea (NAS) model is composed of 20 nodes, ranging from phytoplankton and bacteria to piscivorous fish, plus three groups for non-living organic matter and detritus. This formulation represents the ecosystem during 1997–2000. The complete list of nodes is reported in Table A1. Due primarily to the lack of data for the reference years, marine mammals and birds were not represented in the model. Units of the model are expressed in $t\ km^{-2}\ yr^{-1}$ wet weight organic matter for flows and $t\ km^{-2}$ for biomasses.

For the lower trophic levels, we established phytoplankton, bacterioplankton, microzooplankton and zooplankton nodes for the model. These nodes were kept as aggregate groups due to the generally limited information available for such taxa. Biomass estimates as well as vital rate parameters (P/B) were taken from multiple literature sources from studies conducted in the region (Table A2). There were no consumption (Q/B) or respiration estimates, and thus we allowed the model to fit those values for these nodes. Estimates of feeding by and on these nodes were also obtained from literature values (Tables A3 and A4).

Because the NAS is relatively shallow with a well-developed shelf, the benthic component of the food web was particularly emphasized. For the benthic organisms, there were eight nodes

Table A1
Species composition of the NAS model groups.

Group	
Phytoplankton	
Bacterioplankton	
Microzooplankton	
Zooplankton	
Meiobenthos	Crustacea, Nematoda, Polychaeta, Protozoa
Macrobenthos herbivorous	Crustacea, Echinata, Gastropoda, Polychaeta
Macrobenthos omnivorous	Crustacea, Gastropoda, Ophiuroidea, Polychaeta
Macrobenthos detritivorous	Crustacea, Gastropoda, Holoturoidea, Polychaeta, Sipunculida
Macrobenthos filter feeders	Bivalvia, Crustacea, Polychaeta,
Scallops (Pectinidae)	<i>Pecten jacobaeus</i> , <i>Aequipecten opercularis</i>
Clams (Veneridae)	<i>Chamelea gallina</i> , <i>Callista chione</i>
Macrobenthos predator	Asteroidea, Decapoda, Gastropoda, Polychaeta, Stomatopoda
Planktivorous fish	<i>Engraulis encrasicolus</i> , <i>Sardina pilchardus</i> , <i>Scomber scombrus</i> , <i>Sprattus sprattus</i>
Cephalopods	<i>Alloteuthis media</i> , <i>Eledone moscata</i> , <i>Loligo vulgaris</i> , <i>Octopus vulgaris</i> , <i>Sepia elegans</i> , <i>S. officinalis</i>
Benthic feeders	<i>Gobius niger</i> , <i>Lepidotrigla cavillone</i> , <i>Mullus barbatus</i> , <i>M. surmuletus</i> , <i>Pagellus erythrinus</i> , <i>Sparus aurata</i> , <i>Trachurus trachurus</i> , <i>T. mediterraneus</i> , <i>Trigla lyra</i> , <i>T. lucerna</i> , <i>Trigloporus lastoviza</i> , <i>Trisopterus minutus capelanus</i> , <i>Umbrina cirrosa</i>
Flatfish	<i>Arnoglossus laterna</i> , <i>Buglossidium luteum</i> , <i>Citharus linguatula</i> , <i>Microchirus variegatus</i> , <i>Platichthys flesus</i> , <i>Psetta maxima</i> , <i>Scophthalmus rhombus</i> , <i>Solea vulgaris</i>
Nekton feeders	<i>Dicentrarchus labrax</i> , <i>Lophius budegassa</i> , <i>L. piscatorius</i> , <i>Merluccius merluccius</i> , <i>Mustelus mustelus</i> , <i>M. asterias</i> , <i>Squalus acanthias</i>
Carcasses	
Organic matter	
Detritus	

Table A2
Input data and references by functional group for the Northern Adriatic Sea model.

Group	B (t km ⁻²)		P/B (yr ⁻¹)		Q/B (yr ⁻¹)	
Phytoplankton	8.4	A, B, C	152.133	B, C		
Bacterioplankton	2.138	A, B, C	34.348	D		
Microzooplankton	1.758	E	219	F		
Zooplankton	1.456	A, B, C	18.25	B, C		
Meiobenthos	5.311	G, H			68.52	L
Macrobenthos herbivorous	2.086	G, H, M	1.746	I, J, K		
Macrobenthos omnivorous	3.118	G, H, M	2.313	I, J, K		
Macrobenthos detritivorous	22.834	G, H, M	1.692	I, J, K		
Macrobenthos filter feeders	19.642	G, H, M	1.07	I, J, K		
Scallops (Pectinidae)	0.756	G, H, M	0.7	N		
Clams (Veneridae)	1.397	O, P	1.41	I, J, K		
Macrobenthos predator	7.033	G, H, M	1.5	I, J, K		
Planktivorous fish	19.996	Q, R	1.295	S, T	3.882	S
Cephalopods	0.35	U	1.45	S, T	4.833	S
Benthic feeders	0.229	U, M	1.895	S, T	5.935	S
Flatfish	0.151	U, M			4.9	S
Nekton feeders	0.012	U	1.16	S, T	4.34	S
Carcasses	1		–		–	
Organic matter	183.884	V	–		–	
Detritus	2		–		–	

A, Fonda Umani (1996); B, Heilmann and Richardson (1996); C, Fonda Umani et al. (2000); D, Danovaro et al. (2000); E, Fonda Umani and Beran (2003); F, Sorokin et al. (1999); G, Raicevich (2000); H, Da Ponte (2001); I, Brey (1990); J, Brey (2001); K, Moodley et al. (1998); L, Carrer and Opitz (1999); M, Pranovi et al. (2001); N, Caddy (1989); O, Paolini et al. (1998); P, Pellizzato et al. (1998); Q, Azzali et al. (2002); R, Cingolani et al. (2002); S, Pauly (1980); T, Froese and Pauly (2003); U, Relini et al. (1999); V, Salvi et al. (1999).

Table A3
Diet composition matrix for the functional groups of the Northern Adriatic Sea model. Predator groups are placed down the vertical axis and prey groups are along the horizontal axis; grey cells indicate values lower than 1%.

Prey/predator	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 Phytoplankton	0.02	0.97	0.67		0.05			0.60	0.60	0.60		0.61				
2 Bacterioplankton	0.04	0.03	0.16					0.05	0.05	0.05						
3 Microzooplankton	0.05		0.16					0.24	0.24	0.24		0.20				
4 Zooplankton						0.07		0.10	0.10	0.10		0.10			0.01	0.10
5 Meiobenthos				0.01	0.05	0.20	0.20				0.02					
6 Macrobenthos herbivorous						0.06					0.01		0.08	0.07	0.10	
7 Macrobenthos omnivorous						0.04					0.05		0.14	0.10	0.08	
8 Macrobenthos detritivorous						0.16					0.45	0.06	0.18	0.44	0.45	0.08
9 Macrobenthos filter feeders						0.10					0.05	0.02	0.02	0.14	0.05	
10 Scallops (Pectinidae)															0.01	
11 Clams (Veneridae)															0.01	
12 Macrobenthos predator											0.02	0.01	0.41	0.14	0.14	0.01
13 Planktivorous fish													0.10	0.01	0.04	0.40
14 Cephalopods													0.03	0.01		0.17
15 Benthic feeders														0.01		0.20
16 Flatfish																0.01
17 Nekton feeders																0.10
18 Carcasses						0.25	0.05				0.39		0.03	0.06	0.03	
19 Organic matter	0.89							0.01	0.01	0.01						
20 Detritus				0.99	0.90	0.12	0.75									

Table A4
References for the diet matrix.

Bacterioplankton	Fonda Umani and Beran (2003)
Microzooplankton	Fonda Umani and Beran (2003)
Zooplankton	Baamstedt and Karlson (1998)
Meiobenthos	Carrer and Opitz (1999)
Macrobenthos herbivorous	Fauchald and Jumars (1979), Carrer and Opitz (1999), Riedl (1992)
Macrobenthos omnivorous	Fauchald and Jumars (1979), Carrer and Opitz (1999), Riedl (1992)
Macrobenthos detritivorous	Fauchald and Jumars (1979), Carrer and Opitz (1999), Riedl (1992)
Macrobenthos filter feeder	Fauchald and Jumars (1979), Riedl (1992), Sorokin and Giovanardi (1995)
Scallops (Pectinidae)	Sorokin and Giovanardi (1995)
Clams (Veneridae)	Sorokin and Giovanardi (1995)
Macrobenthos predator	Fauchald and Jumars (1979), Froggia and Giannini (1989), Riedl (1992), Carrer and Opitz (1999)
Planktivorous fish	Demirhindi (1961), Tudela and Palomera (1997), Ticina et al. (2000)
Cephalopods	Castro and Guerra (1990), Pierce et al. (1994), CephBase (2006)
Benthic feeders	Giovanardi and Rizzoli (1984), Pinnegar and Polunin, (1999), Froese and Pauly (2003)
Flatfish	Giovanardi and Piccinetti (1981), Giovanardi and Piccinetti (1984), Froese and Pauly (2003)
Nekton feeders	Arias (1980), Pinnegar and Polunin (1999), Froese and Pauly (2003)

Table A5Biomass export in terms of commercial catches (1 km^{-2}) by the five main finishing activities identified in the study area; grey cells indicate values lower than 1 kg.

	Group name	Mid-water trawl	Hydraulic dredge	Rapido trawl (flatfish)	Rapido trawl (scallops)	Otter trawl	Total
1	Phytoplankton						
2	Bacterioplankton						
3	Microzooplankton						
4	Zooplankton						
5	Meiobenthos						
6	Macrobenthos herbivorous						
7	Macrobenthos omnivorous					0.015	0.015
8	Macrobenthos detritivorous						
9	Macrobenthos filter feeders						
10	Scallops (Pectinidae)				0.152		0.152
11	Clams (Veneridae)		1.010				1.010
12	Macrobenthos predator						
13	Planktivorous fish	0.444					0.444
14	Cephalopods					0.078	0.078
15	Benthic feeders					0.036	0.036
16	Flatfish			0.023			0.023
17	Nekton feeders					0.003	0.003
18	Carcasses						
19	Organic Matter						
20	Detritus						
	Sum	0.444	1.010	0.023	0.152	0.132	1.761

established which each represent a composite of species in various functional groups (Table A1). In relation to the available data, the meiofauna was grouped into a single node, whereas macrobenthic species were grouped mainly according to five trophic nodes. Moreover, due to their importance as target species for local fishing, two groups of bivalve molluscs (scallops and clams targeted by rapido trawling and hydraulic dredging, respectively) were separately defined in order to better describe the ecological effects of these two fleets. Biomass estimates were taken from experimental studies carried out in the study area during the research activities conducted by the Environmental Science Department of the University of Venice (Table A2; Raicevich, 2000, 2003; Da Ponte, 2001; ICRAM, 2006). Vital rate parameters and estimates of feeding by and on these nodes were obtained by literatures values (Tables A2–A4).

The nekton compartment was characterized by five nodes, defined according to both ecological and fisheries features. The model therefore accounted for pelagic and benthic fish, cephalopods and flatfish (all targeted by specific fishing activities) and nekton feeders to represent the top predators. Biomass estimates were obtained both by field surveys carried out by in the context of the national programs for the stock assessment and on-board surveys (Table A2; Relini et al., 1999). Vital rate parameters and estimates of feeding by and on these nodes were obtained both from studies conducted in the region and from more general literatures sources (Tables A2–A4).

To better reflect reality and to help in the model balancing, elements of the microbial loop, such as the dissolved organic carbon (modelled by using suspended organic matter as proxy) and car-

Table A6Biomass export in terms of discards ($t \text{ km}^{-2}$) by the five main fishing activities identified in the study area; grey cells indicate values lower than 1 kg.

	Group name	Mid-water trawl	Hydraulic dredge	Rapido trawl (flatfish)	Rapido trawl (scallops)	Otter trawl	Total
1	Phytoplankton						
2	Bacterioplankton						
3	Microzooplankton						
4	Zooplankton						
5	Meiobenthos						
6	Macrobenthos herbivorous		0.075	0.008	0.007	0.014	0.104
7	Macrobenthos omnivorous		0.115	0.088	0.011	0.035	0.249
8	Macrobenthos detritivorous		0.003				0.003
9	Macrobenthos filter feeders		0.197	0.004			0.202
10	Scallops (Pectinidae)						
11	Clams (Veneridae)						
12	Macrobenthos predator		0.002	0.020	0.006	0.001	0.030
13	Planktivorous fish					0.017	0.017
14	Cephalopods						
15	Benthic feeders			0.002		0.004	0.005
16	Flat fish			0.001			0.001
17	Nekton feeders						
18	Carcasses						
19	Organic matter						
20	Detritus						
	Sum		0.392	0.124	0.024	0.071	0.611

Estimates of the discarded fraction for each functional group were obtained by on-board surveys (Pranovi et al., 2001; Raicevich, 2003).

cases produced by the discarding activities, were included in the model.

In comparison with the other parameters, the diet matrix was considered the most uncertain aspect of the model and thus was adjusted iteratively by using the Automatic Mass Balance Procedure (Kavanagh et al., 2004). During the balancing process, the diet matrix was slightly modified to avoid inconsistent solutions of the energy budget when the parameters are randomly changed around the nominal value (Christensen et al., 2000; Christensen and Walters, 2000). The small differences between initial values and those obtained after the iterative adjustments affirmed the relatively good initial estimates included in the diet matrix. All the main fishing activities (mid-water trawling, otter trawling, rapido trawling and hydraulic dredging) have been explicitly included in the model. Official landings statistics from 1990 to 2000 were available from the Chioggia fish market and the Fishermen Consortium for the clam exploitation (COGEVO). The mean value was calculated for the 1997–2000 period and used for the model (Table A5). Moreover, catch data were corrected by considering estimates of unreported/illegal catches (Mattei and Pellizzato, 1996; Raicevich, 2000; Giovanardi, unpublished data), by extending to the official catches the ratio observed during on-board surveys (Table A6).

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