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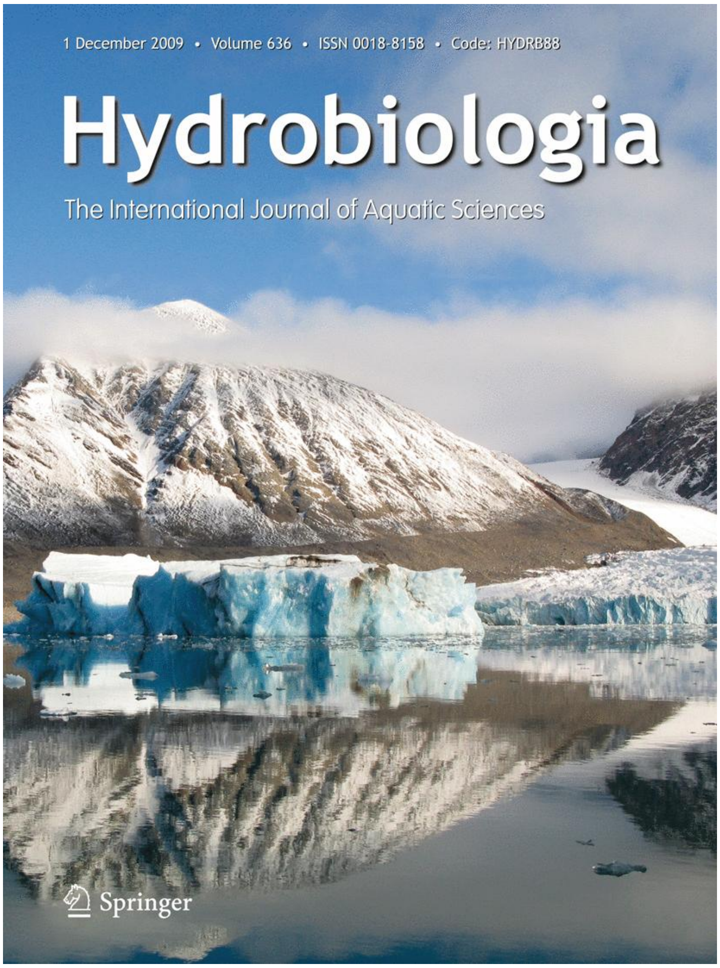

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PRIMARY RESEARCH PAPER

Evaluating ecosystem structure and functioning of the East China Sea Shelf ecosystem, China

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Abstract As China's second-largest large marine ecosystem, the East China Sea Shelf has suffered from overfishing, eutrophication, and physical disturbance over the last several decades. A trophic mass-balance model of this ecosystem was developed in order to characterize the structure and functioning of its food web, to identify its keystone species, and to quantify the ecological impacts of fishing that it sustained during the early 2000s. Using a multivariate statistical analysis, we identified 38 functional groups for the trophic model, including fish and invertebrate groups targeted and not targeted by fisheries. Pelagic sharks and rays were identified as the keystone species in the ecosystem. Strong benthic–pelagic coupling was indicated in this ecosystem. In particular, this study highlighted the interdependent relationships that exist among plankton, benthic invertebrates, and detritus. Recent fishing activities were characterized by high exploitation rates for various commercially targeted and non-targeted species, leading to the removal of much of the ecosystem's fishable production. Overall, our findings give a preliminary explanation of the current problems of eutrophication and fishery depletion and other changes in the East China Sea Shelf, and highlight the need for developing ecosystem-based fisheries management.

Keywords East China Sea Shelf · Food web model · Ecopath with Ecosim · Network analysis · Keystone species · Fishing impact

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Introduction

Large marine ecosystems (LMEs) are defined by their distinct bathymetric and hydrographic features, their productivity, and most of all by their mesoconsumer and predator populations, which contribute approximately 95% of the annual yield of marine fisheries around the world (Sherman, 1993). Nowadays, much public interest has focused on the overall health of the ocean as a system, particularly the coastal region (Hempel & Sherman, 1993). Given our inability to conduct controlled experiments at the scale of LMEs, and in the absence of a comprehensive theory that could predict expected interactions of all the components within LMEs and the evolution of these systems through time, modeling of such systems appears to be a necessary tool to link our understanding of organism-level interactions with the ecosystems dynamics that these interactions produce. Such models can be used to provide the science essential for developing an ecosystem-based management (Toft & Mangel, 1991; Pauly & Christensen, 1995; Ainsworth et al., 2008).

LMEs can be altered in many ways through overexploitation of biological resources, direct habitat modification of coastal and offshore areas, introduction of exotic species, pollution, and climate change. However, fishing activity has been cited as the most pressing human disturbance affecting seas and coastal areas. This fact is underscored by the 50-year decline seen in the mean trophic level of global marine fishery catch (Pauly et al., 1998; Cheung, 2007). Keystone species are critically important in influencing ecosystem dynamics and the abundances of other species and should be the focus of studies because they affect the communities of which they are part in a manner disproportionate to their abundances (Power et al., 1996; Piraino et al., 2002).

In addition to being China's second-largest LME (Sherman, 1990), the East China Sea Shelf (ECSS) is also its most productive and has provided valuable fisheries to coastal communities and regional countries (China, Japan, and Korea) for centuries (Gu et al., 1984; Chen & Shen, 1998; Zheng et al., 2003; Cheng et al., 2006). In the last 50 years, the ECSS has been heavily exploited, and developments in its commercial fisheries have shifted the exploitative focus from top predators in the ecosystem to more abundant species of lower trophic levels (Chao et al., 2005). We observed several signs of "fishing down the food web" (Pauly et al., 1998) occurring in the ECSS through prolonged and intensive fishing pressure over this 50-year period (Zheng et al., 2003; Chao et al., 2005; Cheng et al., 2006). As an overall indicator of fishery impacts on the system, the number of species, species richness, and diversity index declined significantly (Cheng et al., 2006). At the same time, the composition of fishery landings became increasingly dominated by juveniles and relatively small, lower trophic level species with high turnover rates. The mean trophic level of landings decreased from 3.5 in 1965 to 2.8 in 1990 (Chao et al., 2005). Many demersal stocks are fully exploited or overexploited, and some pelagic stocks also show overexploitation trends, although some species are still producing high landings (Gu et al., 1984; Chen & Shen, 1998; Zheng et al., 2003; Cheng et al., 2006). However, despite these clear indications of ecosystem-level consequences arising from current fishing practices, little ecological modeling work has been done for the ECSS, and to date there is still no quantitative assessment of ecosystem structure and functioning for this region.

Ecological modeling such as the Ecopath with Ecosim (EwE) approach is often employed to describe ecosystem structure and functioning (Li et al., 2004; Christensen et al., 2005). Ecopath has been used to estimate mixed trophic impacts for the purpose of identifying keystone species (Libralato et al., 2006). Identifying keystone species is considered important to LME conservation and management, and specifically to the maintenance of ecosystem integrity and biological diversity in the face of exploitation and other stresses (Paine, 1969; Naeem & Li, 1997; Tilman, 2000).

This work attempted to construct an ecological model of the ECSS using EwE as well as multivariate statistical analysis, with the aim of describing the trophic structures and flows that characterize this LME. We focus on quantitative modeling of this ecosystem in order to define current community trophodynamic linkages and identify the keystone species that are critical to the integrity of the biological community of the ECSS ecosystem.

Materials and methods

The study area

The East China Sea is a typical epicontinental sea and part of the western Pacific Ocean bordered by China, Korea, and Japan. It covers an area of 770,000 km^2 (Zheng et al., 2003), of which 65% is contributed by the ECSS with a mean depth of 72 m (Fig. 1). The ECSS deepens eastward and southward to a maximum depth of 2,300 m in the Okinawa Trough. Large quantities of terrestrially originated nutrients and pollutants flow into the ECSS along with large fresh

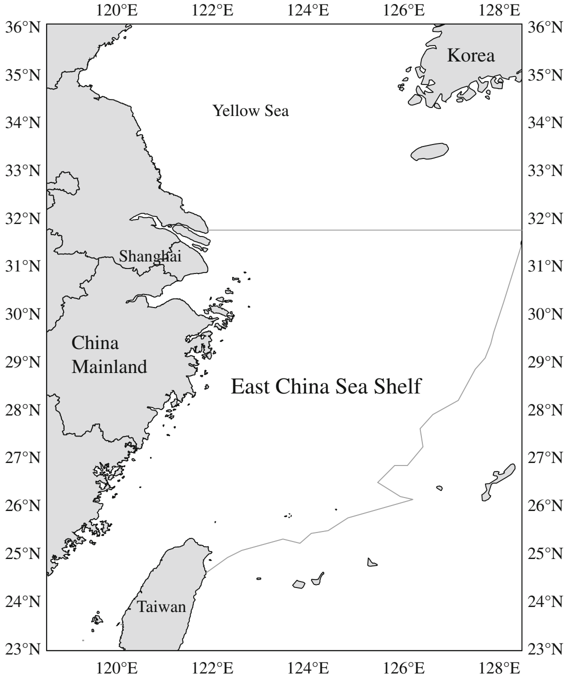


Fig. 1 The continental shelf and upper slope area of the East China Sea Shelf

water inputs, mainly from the Yangtze River. The confluence of the alongshore current, the Yellow Sea cold water mass, and the Kuroshio Current promotes good fishing grounds in the ECSS. Historically, the superior geography of the ECSS supported a highly productive fishery and a rich biodiversity. Numerous studies (e.g., Chen & Shen, 1998) describe the distribution and abundance of marine fauna and flora of the ECSS. This area also includes important populations of endangered marine mammals.

Based on the fishery statistics compiled by the Food and Agriculture Organization of the United Nations (FAO), total reported landings from the sea increased from less than 10 to over 45 million tons between 1950 and the 2000s (Fig. 2). Five main fishery operations work in this region, distinguished by the fishing gear they each employ. These are the trawl fishery (including pair trawl, stern trawl, shrimp trawl, and pelagic hang trawl), the gillnet fishery, the set net fishery, the purse seine fishery, and the hook and line fishery, respectively (FAO, 2004; Cheng et al., 2006). Small pelagic fish, mainly anchovy and chub mackerel, constituted the principal component of pelagic fishery landings in terms of biomass in the 2000s; these are mainly caught by the set net and trawl fisheries. The demersal fishery mainly comprises the traditional fishing targets: hairtail, small yellow croaker, big yellow croaker, and cephalopods. These are caught principally by the trawling fleet, whose landings make the largest single contribution to total catch.

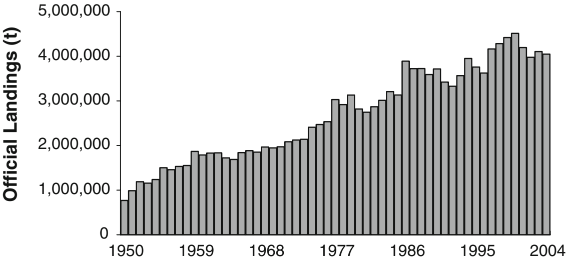


Fig. 2 Total landings in the East China Sea from 1950 to 2004

Modeling approach

The trophic flow model of the ECSS ecosystem was constructed and analyzed using Ecopath with Ecosim 5.1 (Christensen et al., 2005).

Ecopath is a static and mass-balanced ecosystem model that is used to analyze the structure of ecosystems and evaluate the impacts of trophic interactions among organisms at a given time (Christensen et al., 2005). The master equation of Ecopath defines the mass-balance between consumption, production, and net system exports over a given time period for each functional group (i) in an ecosystem:

$$B_i \left(\frac{P}{B}\right)_i EE = \sum_{j=1}^{n} B_j \left(\frac{Q}{B}\right)_j DC_{ji} + Y_i + BA_i + E_i \quad (1)$$

where B_i and B_j are biomasses (the latter pertaining to j, the consumers of i), P/B_i is the ratio of production to biomass, equivalent to total mortality under most circumstances (Allen 1971), EE_i is the ecotrophic efficiency which is the fraction of production that is consumed within, or caught from the system (by definition between 0 and 1), Y_i is the fisheries catch, Q/B_{j} is the food consumption per unit of biomass of j;, and DC_{ji} is the contribution of group i to the diet of group j, and the sum is over all predators (j). BA_i is the accumulation or depletion of group i, and E_i is the net migration (Christensen et al., 2005; Morissette, 2007).

Model structure and parameterization

The model represents a state of the ECSS ecosystem inferred mainly from an annualized average of 2000 data. Species were aggregated into functional groups based in most cases on commercial importance, body size, ecology, and the availability of data. However, for demersal fish species, a set of ecologically meaningful criteria was instead defined by which these species (excepting those cases of species already included in other functional groups) could be aggregated into species groups using cluster analysis. Since we were concerned with a model of energy flow, variables related to flows between elements of the ecosystem had to be identified. These variables must necessarily be related to the factors that determine the food consumption of a species. The relevant variables were (1) size, (2) activity level, and (3) type of food. These variables were parameterized using (1) size = asymptotic length L in cm, (2) activity level = aspect ratio A (see Eq. 2), and (3) type of food = degree of herbivory, in %. Aspect ratio was computed as

$$A = h^2/s \quad (2)$$

where h and s are the height and surface area of the caudal fin, respectively. Photoshop was used to estimate the values of these quantities based on photographs from Fishbase (Froese & Pauly, 2000). A higher aspect ratio indicates that a species is a fast and continuous swimmer, while a low aspect ratio refers to a slow and/or "burst" swimmer. The aspect ratio of the caudal fin is thus related to the activity level and energy requirements of a fish. It is therefore an indirect measure of the food consumption of a population of fish (Opitz 1996). According to McGarigal et al. (2000), prior to the execution of a cluster analysis on a given set of elements or variables, it is advisable to carry out a factor analysis to detect dependent variables and exclude them from the aggregation process. These three variables were treated as being of equal importance. Prior variables were transformed such that they evenly covered a range of values. Cluster analysis was performed in R (www.r-project.org) using a prepared matrix of 90 demersal fish species and the three relevant variables. "Quadratic Euclidean distance" was selected as the index of dissimilarity and "Ward" was selected among the agglomerative alternatives.

Input data are listed in Table 1; biomass values were mainly estimated based on trawl and acoustic surveys conducted in the late 1990s and early 2000s, and on information available in stock assessment reports, government reports, and the literature. Production/biomass ratios (*P/B* ratios) and consumption/biomass ratios (*Q/B* ratios) were taken from the literature, from other similar Ecopath models, or else were estimated from an empirical equation based on length and weight data (Pauly, 1980; Palomares & Pauly, 1998; Lin et al., 2005; Cheung, 2007). Diet compositions and assimilation rates were compiled from published information, local surveys (Zheng et al., 2003; Zhang, 2005; Zhang et al., 2005), and the information available in Fishbase (Froese & Pauly, 2000). Official landing statistics were obtained from the FAO national landings statistics of China, Japan, and Korea, and also from the information available in the Sea Around Us Project (SAUP) database (www.seaaroundus.org). Asymptotic length data were obtained from local surveys and Fishbase (Froese & Pauly, 2000; Zheng et al., 2003) (See Appendix 1—Supplementary Material).

Uncertainty and sensitivity analysis

Uncertainties of the input parameters were specified in a "pedigree" index in Ecopath. This index was understood as a coded statement categorizing the origin of a given input and specifying the likely uncertainty associated with it (Christensen et al., 2005). Such a statement was given to each of the parameters by the pedigree routine. Inputs were rated according to how they had been derived: from local data, other locations, "best guesses," empirical relationships, other Ecopath models, or estimates of the current model. Associated with each of these categories was an index of quality that ranged from 0 to 1, with 0 denoting the lowest quality and 1 the highest quality (Cheung, 2007).

The preliminary input data were then introduced into the "Auto-balance" routine of Ecopath, and the coefficient of variation from pedigree analysis was used to obtain a range for each input parameter. Random input variables were repeatedly drawn from normal distributions in order to generate a theoretical frequency distribution for each input and output parameter using Monte Carlo simulations.

Table 1 Input data of the East China Sea Shelf model by functional group

Functional group	B_i	*P/B*	*Q/B*	*EE*	*U/Q*	*P/Q*	Landings
Marine mammals	0.0158	0.112	10.52		0.20		
Seabirds	0.0022	0.06	68.00		0.20		
Marine turtles	0.002	0.10	3.50		0.20	0.3	0.000
Demersal sharks	0.005	1.20	6.00		0.20		0.003
Pelagic sharks		0.68	3.40	0.95	0.20		0.010
Hairtails (A)	0.099	2.90	10.50		0.20		0.101
Hairtails (J)	0.251	3.08	14.90		0.20		0.282
Large croakers	0.170	2.13	8.25		0.20		0.219
Small croakers	0.110	4.30	16.00		0.20		0.037
Flatfishes	0.025	1.75			0.20	0.2	0.036
Lizardfishes	0.328	1.37	5.78		0.20		0.010
Demersal fishes 1	0.155	3.40	12.40		0.20		0.020
Demersal fishes 2	0.312	4.20	16.15		0.20		0.430
Demersal fishes 3		4.75	24.20	0.95	0.20		0.190
Snappers		1.75	8.98	0.95	0.20		0.001
Groupers		1.24	6.27	0.95	0.20		0.044
Bigeyes	0.209	2.74	9.16		0.20		0.025
Large reef-associated fishes		0.38	3.90	0.95	0.20	0.3	0.001
Small reef-associated fishes		1.92	7.97	0.95	0.20	0.3	0.003
Large benthopelagic fishes		1.72		0.95	0.20	0.2	0.430
Small benthopelagic fishes		3.08		0.95	0.20	0.2	0.643
Pomfrets	0.812		6.40		0.20	0.2	0.292
Threadfin bream	0.340	3.08	15.4		0.20	0.28	0.321
Large pelagic fishes	0.422	1.37	6.27		0.20		0.453
Small pelagic fishes	1.772	4.26	17.04		0.20		0.765
Cephalopods	0.780	3.10	8.00		0.20		0.417
Crabs	0.623	3.00	12.00		0.20		0.232
Shrimps		3.60	19.20	0.95	0.20		0.423
Molluscs	9.510	3.00	7.00		0.20		0.308
Benthic crustaceans	1.600	6.56	26.90		0.30		0.042
Echinoderms	3.460	1.20	3.70		0.30		0.001
Polychaetes	3.130	6.70	24.20		0.20		0.000
Other invertebrates	3.160	1.00	9.00		0.20		0.003
Jellyfish	2.150	5.00	25.05		0.20		0.060
Zooplankton	4.572	32.00	192.00		0.40		0.095
Benthic producer	7.830	11.90					0.008
Phytoplankton	16.85	121.00					
Detritus	100						

B_i initial biomass (t km^{-2}), *P/B* production/biomass ratio, *Q/B* production/consumption ratio, *EE* ecotrophic efficiency, *U/Q* unassimilated food, *P/Q* production/consumption, Landings (t km^{-2})

A series of sensitivity analyses were also conducted to evaluate how robust the results were with respect to uncertainty in the input parameters when the model was balanced. This was performed by systematically increasing and reducing the input parameters of each functional group by 50%, and examining the effects of these changes on all the estimated output parameters for all groups in the system. The output of this sensitivity analysis expressed the resulting change in each estimated parameter as a fraction of its originally estimated value; that is, estimated using Eq. 3 (Christensen et al., 2005):

$$(\text{estimated parameter} - \text{original parameter}) / \text{original parameter} \tag{3}$$

Model analysis and indices

After balancing the model, ecological analysis integrated in EwE was used to examine a number of indicators describing trophic flows. These were variously derived from thermodynamic concepts, information theory, and network analysis (Christensen et al., 2005). Some of these results were related to ecosystem development theory, sensu Odum (Lindeman, 1942; Odum, 1969, 1971; Odum & Heald, 1975; Finn, 1976; Ulanowicz, 1986; Christensen & Pauly, 1993; Christensen, 1995; Ulanowicz, 1995). Indicators of fishing intensity developed recently, such as the primary production required to sustain the fishery (%*PPR*) and the loss in secondary production due to fishing (*L* index), were also investigated (Coll et al., 2008).

The PPR from the primary production and detritus was 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; Coll et al., 2007, 2008):

$$PPR = \frac{1}{9}\sum_{i}\left[Yi \cdot \left(\frac{1}{TE}\right)^{TL_i - 1}\right] \tag{4}$$

where Y_i is the catch of a given group (i), TE is the mean transfer efficiency, TL_i is the trophic level of a group (i) and the factor 1/9 is taken as the average conversion coefficient from wet weight to gC. This index can be expressed per unit of catch relative to primary production and detritus of the ecosystem (%*PPR*) (Coll et al., 2007, 2008).

The loss in production index (*L* index) was proposed by Libralato et al. (2008) to quantify the theoretical depletion in secondary production in an exploited ecosystem due to fishing. This index takes into account both ecosystem properties as well as features of fishing activities (Lindeman, 1942; Pauly and Christensen, 1995; Pauly et al., 1998; Coll et al., 2008):

$$L \cong -\frac{PPR \cdot TE^{TLc-1}}{P_1 \cdot \ln TE} \tag{5}$$

where P_1 is the primary production, and TL_c is the mean trophic level of catch. L index increases with fishing impact and was proposed as a proxy for quantifying ecosystem effects of fishing. It can be used to estimate the probability that the ecosystem is being sustainably fished (P_{sust}, Libralato et al., 2008; Coll et al., 2008).

Mixed trophic impacts and identifying the index of keystoneness

Mixed trophic impact analysis (MTI), derived from economic theory, allowed the quantification of direct and indirect trophic interactions among the functional groups. This analysis quantified the positive or negative impacts that a hypothetical increase in the biomass of one group would have produced upon the other respective groups in the ecosystem. The various fishery operations were also included among these groups. In addition, MTI analysis was also used to calculate the total mixed trophic impact that one functional group would have had on all other groups collectively. This was done by adding up all the various impacts of that group (summed by rows of the prepared MTIs matrix) and weighting them by the inverse of the overall biomass of the impacted groups. This weighted sum gave an indication of the net effect that a unit change in the biomass of the given group would be predicted to have on the overall biomass found in the ecosystem (Ulanowicz & Puccia, 1990; Christensen et al., 2005; Coll et al., 2007). Such an analysis of MTIs matrix can provide an estimate of the net effect upon the whole community that arises from variations in the biomass of any particular group within it (Pranovi et al., 2003).

Supplementing the above analysis, the overall mixed trophic impact of each group i upon the system was also estimated using the following equation, given by Libralato et al. (2006):

$$\varepsilon_i = \sqrt{\sum_{j=1}^{n} m_{ij}^2} \tag{6}$$

where m_{ij} is calculated from the MTI analysis as the product of all net impacts for all possible pathways in the food web linking prey i and predator j. Negative elements of the matrix M can be associated with prevailing top-down effects, and positive ones with bottom-up effects (Libralato et al., 2006). The effect of the original change in the biomass of the impacting group itself is also accounted for in the estimation of ε_i (Coll et al., 2006). Whereas positive and negative elements of M offset one another in the total mixed trophic impact analysis to yield strictly net impacts, in the overall analysis, their magnitudes are summed to give the absolute value of all combined impacts regardless of sign. Accordingly, the overall MTI analysis conveys a measure of the gross impacts of all types that a given group produces within the system.

The keystoneness index is then given by:

$$KS_i = \log\left[\varepsilon_i(1 - p_i)\right] \tag{7}$$

where p_i is the biomass contribution of functional group i to the total biomass of the food web (Power et al., 1996; Libralato et al., 2006). This index is high when functional groups (species or groups of species) have both low biomass proportions within the ecosystem and high overall effects, in line with the definition of a keystone species (Christensen et al., 2005; Coll et al., 2006; Libralato et al., 2006).

Results

Cluster analysis of demersal fish species

The factor analysis showed that the variables were largely independent based on the method of Pearson's correlation and that, when clustered into three classes, they explained 40.0, 31.9, and 27.7% of the total variability, respectively. The results from the cluster analysis—hierarchically aggregating 90 demersal fish species stepwise into clusters and, ultimately, into the entire species group upon which the analysis was performed—are depicted in Fig. 3. This dendrogram includes the names of the fish species combined into the respective clusters defining the three classes.

Class 1 is composed of large demersal fish species with mixed trophic habits, their main prey being small, demersal, reef-associated fish, and benthic crustaceans. This class was termed "demersal fishes 1."

Class 2 is composed of median-sized demersal fish species with trophic habits relying on benthic invertebrates and detritus as their main food sources. This class was termed "demersal fishes 2."

Class 3 is composed of small demersal fish species with trophic habits that focus on benthic crustaceans, zooplankton, and detritus. This class was termed "demersal fishes 3."

Input parameters and sensitivity analysis

Modified input parameters and the resulting output parameters of the model are shown in Table 2, and the diet matrix of the final run of the model is shown in Table 3. Ecotrophic efficiencies were high for most functional groups, while respiration/assimilation ratios (*R/A* ratios), production/respiration ratios (*P/R* ratios), and net food conversion efficiencies were within the expected ranges (Christensen et al., 2005). The minimum biomass of demersal fish groups that was required to balance the model was larger than that estimated from surveys, even though the initial, preliminary biomasses were estimated using the swept area method. The same was also true of shrimp because of the low catchability of shrimp by the survey trawl nets.

The assigned pedigree index of the ECSS model was 0.504, which ranked among the highest values when compared with those of 50 other previously constructed models, for which pedigree values ranged between 0.164 and 0.676 (Coll et al., 2006, 2007; Morissette, 2007). The sensitivity analysis showed that, when an input parameter belonging to a functional group changed by 50%, the output parameters of that group could vary by more than 110%. This was expected, as the input parameters are tightly linked with each other. As an example, Fig. 4 represents the results of the sensitivity analysis carried out by modifying input parameters related to the ecotrophic efficiencies of the large benthopelagic fishes (functional group 20). The consequent effects upon the biomass of this same group and upon the biomass and ecotrophic efficiencies of other groups are plotted.

Trophic levels and flows

Ecological groups were organized from TL 1 to TL 4.55, the highest values corresponding to pelagic sharks and marine mammals. The remaining groups, principally fish species, were classified between 4.00

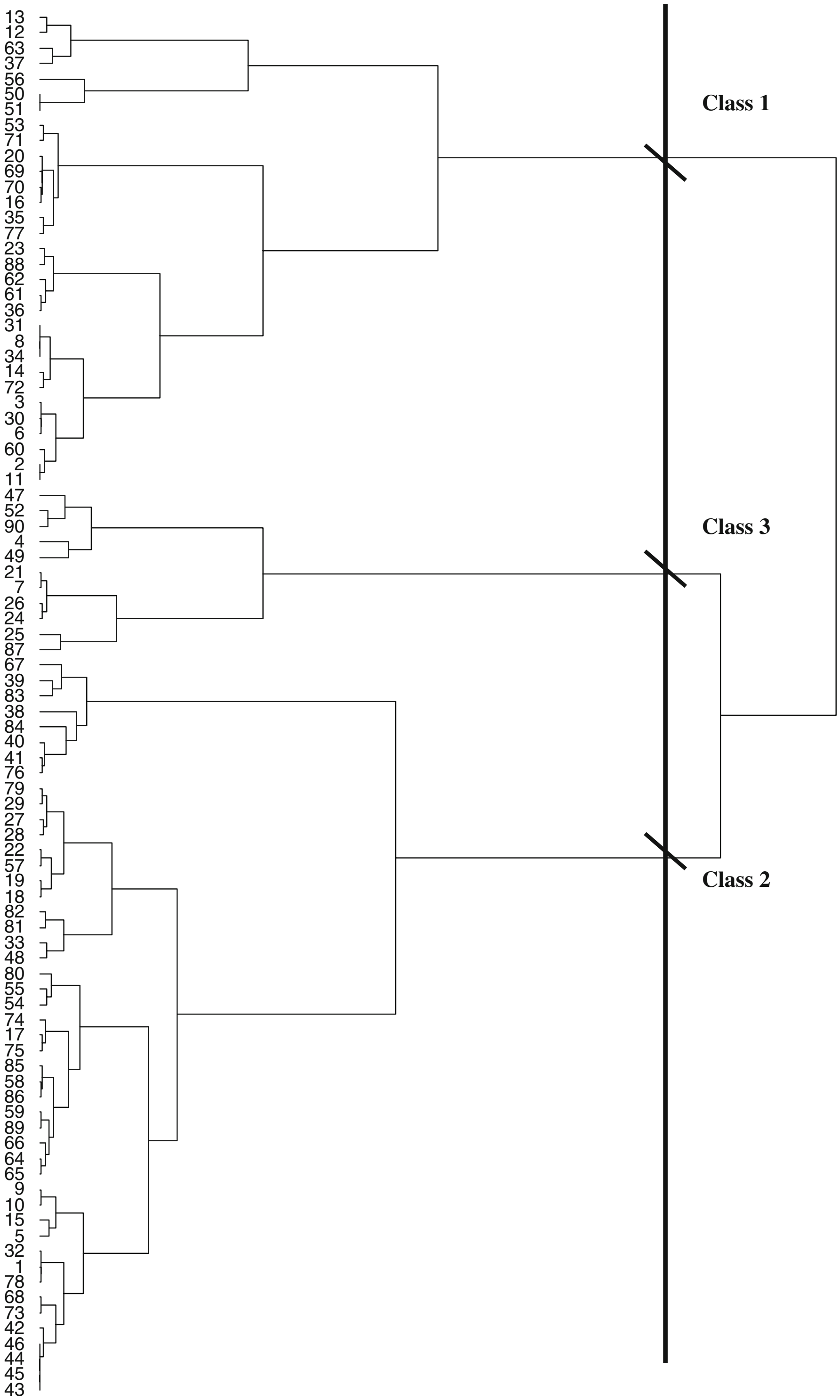


Fig. 3 Cluster analysis representing the similarity among 90 demersal fish species compared using Pearson correlation analysis. Species are listed in Appendix 2—Supplementary Material

and 3.00 (with the exception of three groups: demersal fishes, small reef-associated fishes, and small pelagic fishes, whose trophic levels were slightly less than 3 due to the herbivory and detritivory in their diets). The trophic level of seabirds was estimated to be 3.56, which was in accordance with the range of values

Table 2 Modified input parameters and output parameters from the ECSS model

Functional group	*TL*	B_f	*EE*	*P/Q*	*F*	*M*2	*M*0	*F/Z*	*OI*	*R/A*	*P/R*	*NE*
Marine mammals	4.00	0.02	0.00	0.01	0.00	0.00	0.11	–	0.16	0.99	0.01	0.01
Seabirds	3.56	0.0022	0.01	0.00	0.00	0.00	0.30	–	0.53	0.99	0.01	0.01
Marine turtles	3.71	0.002	0.79	0.30	0.05	0.03	0.02	–	0.28	0.96	0.39	0.38
Demersal sharks and rays	3.50	0.01	0.90	0.10	0.54	0.00	0.06	0.90	0.24	0.88	0.14	0.13
Pelagic sharks and rays	4.02	0.02	0.95	0.20	0.60	0.05	0.03	0.88	0.08	0.75	0.33	0.25
Hairtails (A)	3.95	0.10	0.41	0.28	1.02	0.17	1.71	0.35	0.16	0.66	0.53	0.35
Hairtails (J)	3.90	0.25	0.51	0.21	1.12	0.44	1.52	0.36	0.25	0.74	0.35	0.26
Large croakers	3.57	0.17	0.92	0.26	1.29	0.68	0.16	0.60	0.28	0.68	0.48	0.32
Small croakers	3.35	0.14	0.90	0.27	0.25	3.61	0.44	0.06	0.15	0.66	0.51	0.34
Flatfishes	3.11	0.02	0.97	0.20	1.64	0.05	0.06	0.93	0.53	0.75	0.33	0.25
Lizardfishes	3.84	0.09	0.97	0.25	0.11	2.28	0.07	0.05	0.12	0.69	0.46	0.31
Demersal fishes 1	3.47	0.13	0.95	0.27	0.16	3.07	0.18	0.05	0.20	0.66	0.52	0.34
Demersal fishes 2	3.11	0.31	0.94	0.26	1.38	2.56	0.26	0.33	0.37	0.68	0.48	0.33
Demersal fishes 3	2.92	0.56	0.95	0.20	0.34	4.17	0.24	0.07	0.27	0.76	0.33	0.25
Snappers	3.71	0.01	0.95	0.20	0.09	1.57	0.09	0.05	0.13	0.76	0.32	0.24
Groupers	3.73	0.06	0.95	0.20	0.73	0.45	0.06	0.59	0.17	0.75	0.33	0.25
Bigeyes	3.44	0.13	0.73	0.21	0.19	1.22	0.53	0.10	0.23	0.74	0.36	0.27
Large reef-associated fishes	3.55	0.09	0.95	0.30	0.01	1.30	0.07	0.01	0.28	0.89	0.42	0.38
Small reef-associated fishes	2.74	0.43	0.95	0.30	0.01	1.82	0.10	0.00	0.30	0.89	0.42	0.38
Large benthopelagic fishes	3.15	0.56	0.95	0.20	0.77	0.86	0.09	0.45	0.50	0.75	0.33	0.25
Small benthopelagic fishes	2.78	0.88	0.95	0.20	0.73	2.20	0.15	0.24	0.34	0.75	0.33	0.25
Pomfrets	3.50	0.51	0.78	0.20	0.57	0.43	0.28	0.45	0.22	0.75	0.33	0.25
Threadfin bream	3.28	0.34	0.83	0.28	0.94	1.60	0.54	0.31	0.12	0.96	0.36	0.35
Large pelagic fishes	3.37	0.42	0.87	0.22	1.07	0.12	0.18	0.78	0.20	0.73	0.38	0.27
Small pelagic fishes	2.78	1.77	0.83	0.25	0.43	3.09	0.74	0.10	0.17	0.69	0.46	0.31
Cephalopods	3.29	0.78	0.87	0.27	0.53	2.15	0.42	0.17	0.15	0.66	0.52	0.34
Crabs	2.42	0.62	0.71	0.25	0.37	1.76	0.87	0.12	0.31	0.69	0.46	0.31
Shrimps	2.31	0.66	0.95	0.19	0.64	2.78	0.18	0.18	0.22	0.77	0.31	0.23
Molluscs	2.18	9.51	0.40	0.27	0.03	1.16	1.81	0.01	0.16	0.66	0.52	0.34
Benthic crustaceans	2.20	1.60	0.77	0.24	0.03	5.04	1.49	0.00	0.18	0.65	0.54	0.35
Echinoderms	2.33	3.46	0.43	0.32	0.00	0.52	0.68	0.00	0.36	0.54	0.86	0.46
Polychaetes	2.00	3.13	0.87	0.28	0.00	5.86	0.84	0.00	0.00	0.65	0.53	0.35
Other invertebrates	2.60	4.16	0.79	0.11	0.00	0.79	0.21	0.00	0.24	0.86	0.16	0.14
Jellyfish	2.94	0.38	0.95	0.20	0.16	4.59	0.25	0.03	0.09	0.75	0.33	0.25
Zooplankton	2.00	4.57	0.61	0.17	0.02	19.53	12.45	0.00	0.00	0.72	0.39	0.28
Benthic producer	1.00	7.83	0.40	–	0.00	4.71	7.19	0.00	0.00	–	–	–
Phytoplankton	1.00	16.85	0.31	–	0.00	38.44	85.56	0.00	0.00	–	–	–
Detritus	1.00	100	0.23	–	–	–	–		–	–	–	–

TL trophic level, B_f final biomass (t km^{-2}), *EE* ecotrophic efficiency, *F* fishing mortality (year^{-1}), *M*2 predation mortality (year^{-1}), *M*0 other natural mortality (year^{-1}), *F/Z* exploitation rate, *OI* omnivory index, *NE* net efficiency, *R/A* respiration/assimilation ratio, *P/R* production/respiration ratio

obtained from studies of seabird feeding ecology, i.e., 3.5–4.0 (Hobson et al., 1994). The trophic level of jellyfish was estimated to be 2.94, which is comparable to the diet information of jellyfish in the published literature (TL ranges between 2.3 and 3.3 with the median of 3.0; Arai, 1997; Pauly et al., 2009). The

Table 3 Diet composition matrix for the functional groups in the East China Sea Shelf model

Prey	Predator											
Functional group	1	2	3	4	5	6	7	8	9	10	11	12
Marine mammals					0.000							
Seabirds					0.000							
Marine turtles					0.000							
Demersal sharks and rays					0.000							
Pelagic sharks and rays				0.010	0.009							
Hairtails (A)	0.006				0.001	0.010						
Hairtails (J)	0.010				0.001	0.010	0.010	0.002				0.010
Large croakers	0.004	0.015	0.000	0.005	0.001		0.008		0.001		0.004	0.001
Small croakers	0.014	0.050	0.004	0.017	0.013	0.070	0.076	0.007				0.010
Flatfishes	0.001		0.001	0.001						0.005		
Lizardfishes	0.005		0.001	0.041		0.035	0.035	0.002			0.019	0.010
Demersal fishes 1	0.001		0.009	0.001				0.008				
Demersal fishes 2	0.006		0.082	0.007		0.142	0.102	0.013	0.021	0.005		0.001
Demersal fishes 3	0.030		0.001	0.186			0.139	0.125	0.033	0.160	0.198	0.194
Snappers	0.020		0.001	0.000				0.002				
Groupers	0.030		0.001	0.005							0.002	0.005
Bigeyes	0.019		0.005	0.005			0.009	0.002	0.020		0.036	0.010
Large reef-associated fishes	0.013					0.001	0.002	0.001			0.001	
Small reef-associated fishes	0.020	0.008		0.007	0.026	0.001	0.003	0.001	0.012	0.020	0.001	0.100
Large benthopelagic fishes	0.049	0.030	0.011	0.007	0.079	0.040	0.061	0.031				0.007
Small benthopelagic fishes	0.120	0.075	0.043	0.020	0.100	0.057	0.092	0.157	0.101	0.020		
Pomfrets	0.063	0.050	0.016		0.066			0.058				
Threadfin bream	0.020		0.005	0.005		0.034	0.047	0.009			0.050	0.010
Large pelagic fishes	0.056	0.015	0.001		0.030			0.001				
Small pelagic fishes	0.359	0.100	0.066		0.432	0.390		0.117	0.051	0.050	0.407	0.007
Cephalopods	0.080	0.115	0.018		0.242	0.100	0.156	0.014			0.092	0.010
Crabs	0.000	0.001	0.011	0.052	0.000	0.010	0.005	0.001	0.001	0.010		0.001
Shrimps		0.148	0.009	0.070		0.050	0.094	0.002	0.131	0.020	0.190	0.002
Molluscs	0.035	0.136	0.011	0.115	0.001			0.019	0.007	0.100		0.137
Benthic crustaceans		0.019	0.011	0.360		0.010	0.032	0.100	0.154	0.100		0.338
Echinoderms	0.035	0.003	0.011				0.010	0.040	0.042	0.050		0.015
Polychaetes		0.009					0.008		0.056	0.040		0.047
Other invertebrates								0.002	0.002	0.140		
Jellyfish		0.100	0.500					0.013	0.050			0.001
Zooplankton	0.004	0.003	0.138	0.086		0.040	0.109	0.253	0.318	0.010		0.084
Benthic producer		0.120	0.044							0.100		
Phytoplankton			0.001									
Detritus		0.003						0.020		0.170		

Prey	Predator											
Functional group	13	14	15	16	17	18	19	20	21	22	23	24
Marine mammals												
Seabirds												

Table 3 continued

Prey	Predator											
Functional group	13	14	15	16	17	18	19	20	21	22	23	24
Marine turtles												
Demersal sharks and rays												
Pelagic sharks and rays												
Hairtails (A)												0.002
Hairtails (J)	0.005											0.005
Large croakers	0.000	0.005			0.001	0.001		0.001				0.000
Small croakers	0.005				0.060	0.009		0.002				0.005
Flatfishes												
Lizardfishes												
Demersal fishes 1	0.056	0.006		0.060								
Demersal fishes 2	0.010	0.006	0.100	0.100	0.020							
Demersal fishes 3	0.029	0.006	0.380	0.200	0.239	0.020	0.003				0.099	
Snappers	0.000			0.000		0.005		0.002				
Groupers				0.001		0.005		0.002				
Bigeyes					0.008			0.003			0.001	
Large reef-associated fishes					0.001	0.020		0.020				
Small reef-associated fishes	0.003		0.100	0.050	0.001	0.050		0.060	0.001	0.001	0.050	0.004
Large benthopelagic fishes			0.050	0.002		0.050		0.005		0.003	0.006	
Small benthopelagic fishes	0.011		0.050	0.060		0.150	0.010	0.105	0.009	0.010	0.009	0.040
Pomfrets						0.050	0.003					
Threadfin bream			0.010		0.012			0.050				
Large pelagic fishes						0.050					0.001	
Small pelagic fishes				0.050	0.020	0.100	0.003	0.050	0.086	0.020	0.050	0.375
Cephalopods	0.004	0.010		0.084	0.005		0.019	0.010	0.006	0.008		0.018
Crabs	0.026	0.001	0.050	0.091	0.100			0.020	0.010	0.024	0.001	
Shrimps	0.028	0.002	0.050	0.084	0.007			0.050		0.010	0.005	
Molluscs	0.125	0.056	0.050	0.046	0.015	0.010		0.100	0.020	0.023	0.384	0.009
Benthic crustaceans	0.227	0.192	0.100	0.172	0.084	0.050		0.050	0.050	0.002	0.156	0.058
Echinoderms	0.002	0.002				0.050				0.002	0.030	
Polychaetes	0.092	0.010	0.010		0.086	0.020	0.038	0.050	0.029	0.020	0.073	0.011
Other invertebrates	0.010	0.045			0.003	0.010	0.019			0.014		0.006
Jellyfish	0.009									0.478		
Zooplankton	0.208	0.466	0.050		0.338	0.350	0.588	0.220	0.470	0.375	0.120	0.454
Benthic producer	0.031	0.033					0.198	0.100	0.145			
Phytoplankton	0.013	0.014					0.119	0.100	0.145	0.010	0.015	0.011
Detritus	0.104	0.146							0.029			0.002

Prey	Predator										
Functional group	25	26	27	28	29	30	31	32	33	34	35
Marine mammals											
Seabirds											
Marine turtles											
Demersal sharks and rays											

Table 3 continued

Prey	Predator										
Functional group	25	26	27	28	29	30	31	32	33	34	35
Pelagic sharks and rays											
Hairtails (A)											
Hairtails (J)		0.000									
Large croakers											
Small croakers											
Flatfishes											
Lizardfishes		0.000									
Demersal fishes 1											
Demersal fishes 2											
Demersal fishes 3		0.000									
Snappers		0.000									
Groupers		0.000									
Bigeyes											
Large reef-associated fishes											
Small reef-associated fishes											
Large benthopelagic fishes		0.006									
Small benthopelagic fishes		0.007									
Pomfrets		0.010									
Threadfin bream		0.000									
Large pelagic fishes		0.000								0.001	
Small pelagic fishes		0.157								0.019	
Cephalopods		0.043									
Crabs		0.050									
Shrimps		0.005	0.050								
Molluscs	0.006	0.068	0.140		0.010	0.080	0.056				
Benthic crustaceans		0.125	0.020				0.003				
Echinoderms		0.062	0.010				0.059				
Polychaetes	0.021		0.140	0.121	0.100	0.054	0.022				
Other invertebrates	0.001		0.010		0.010	0.001	0.100				
Jellyfish											
Zooplankton	0.752	0.466		0.193	0.050	0.050	0.003		0.600	0.900	
Benthic producer			0.200	0.125	0.151	0.151	0.554			0.080	
Phytoplankton	0.220			0.027	0.070	0.070	0.003				0.700
Detritus			0.430	0.534	0.609	0.594	0.200	1.000	0.400		0.300

%*PPR*, *L* index and P_{sust} were estimated to be 19.51%, 0.19 and 0, respectively, which could be obtained from the highly exploited ecosystem (Libralato et al., 2008) and were in accordance with the range of values obtained from the studies of Coll et al. (2008).

Total flows by functional group, excluding detritus, showed that 87.2% of the total system throughput (TST) was related to the pelagic domain. Moreover, in terms of biomass, phytoplankton, molluscs, zooplankton, other invertebrates, and benthic producers were the dominant groups, contributing 70.7% of the total biomass excluding detritus. These were followed by small pelagic fishes, small benthopelagic fishes, and cephalopods. The production of phytoplankton, benthic producers, and zooplankton in the ECSS ecosystem reached 2,304.96 t km^{-2} year^{-1}, accounting for 98% of the total system production (2,352 t km^{-2} year^{-1}). 91% of the consumption in

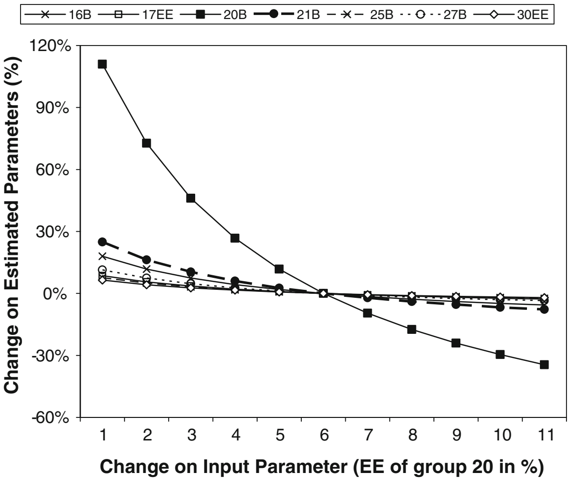


Fig. 4 Example of results from the sensitivity analysis applied to input parameters of the East China Sea Shelf model

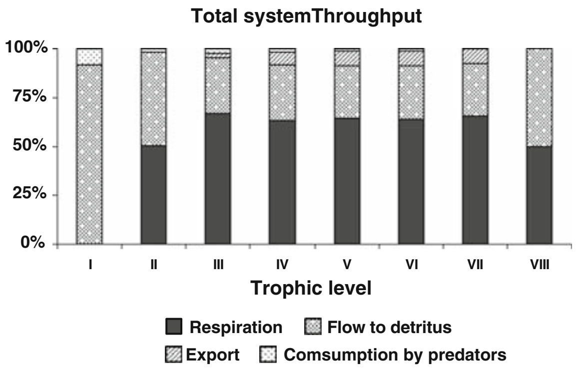


Fig. 5 The fate of total system throughput in percentage per intertrophic level

the ecosystem was carried out by zooplankton, molluscs, polychaetes, benthic crustaceans, various other invertebrates, and small pelagic fishes. Figure 5 depicts the overall fate of TST per discrete trophic level, expressed in terms of the percentage contribution that each type of flow made to this fate. A large proportion of total throughput went to detritus at TL 1, in direct contrast to the small proportion that was consumed by predators.

Summary statistics

Major ecosystem properties are summarized in Table 4. Flows into detritus dominated the TST, accounting for 36.8% of overall ecosystem flow. These were followed by export flows (totaling 28.4%) and consumption flows (totaling 23.7%). Many attributes related to the ecosystem's maturity were also obtained from modeling, following the theories of Odum (1969) and Christensen (1995) regarding the developmental stages that ecosystems undergo. The ratio of total primary production to total respiration (*PP*/*R*) was 3.50, indicating that total primary production was approximately 250% greater than total respiration. The ratio of total primary production

Table 4 Ecological indicators related to community energetics, community structure, cycling of nutrients, and information theory

Statistics and flows	
Sum of all consumption	1283.13 t km^{-2} year^{-1}
Sum of all exports	1506.35 t km^{-2} year^{-1}
Sum of all respiratory flows	602.27 t km^{-2} year^{-1}
Sum of all flows into detritus	1959.27 t km^{-2} year^{-1}
Total system throughput	5351.00 t km^{-2} year^{-1}
Sum of all production	2352.00 t km^{-2} year^{-1}
Mean trophic level of the catch	3.01
Gross efficiency (catch/net p.p.)	0.003
Calculated total net primary production	2108.62 t km^{-2} year^{-1}
Total primary production/total respiration	3.50
Net system production	1506.35 t km^{-2} year^{-1}
Total primary production/total biomass	35.00
Total biomass/total throughput	0.011
Total biomass (excluding detritus)	60.57 t km^{-2} year^{-1}
Total catches	5.90 t km^{-2} year^{-1}
%*PPR*	19.51%
L index	0.190
P_{sust}	0
Ecopath Pedigree index	0.504
Network flow indices	
Throughput cycled (excluding detritus)	2.61
Predatory cycling index (of throughput w/o detritus)	0.18%
Throughput cycled (including detritus)	265.54 t km^{-2} year^{-1}
Finn's cycling index (of total throughtput)	4.94
Finn's mean path length	2.538
Information indices	
Ascendency	32.20%
Overhead	67.80%

to total biomass, expected to be high in an immature ecosystem, was 35.00 (Coll et al., 2007). The ratio of the standing biomass stock to the rate of biomass turnover (i.e., total biomass/total throughput) was estimated to be 0.011. The net community yield was 1,506.35 t km^{-2} year^{-1}, and the ratio of total biomass to total system production was estimated to be 0.025. Finally, the ratio of total respiration to total biomass was estimated to be 10.0.

Mixed trophic impact (MTI) analysis and keystone species identification

Direct and indirect interactions within the ecosystem, analyzed using the MTI routine, are shown in Fig. 6. This analysis showed that all groups had a negative impact on themselves due to intra-group competition. Numerous functional groups in the model were impacted by groups at the base of the food web such as phytoplankton and zooplankton. This could be related to possible bottom-up predator–prey interactions occurring in the ecosystem (Hunter & Price, 1992; Coll et al., 2007). Small pelagic fishes and the group "demersal fishes 3" showed a wide impact on numerous functional groups at higher and lower trophic levels, highlighting the importance of these groups in the ecosystem and possible wasp-waist predator–prey interactions (Cury et al., 2000).

Figure 7 shows the results of the total MTI analysis by functional group. All the fishing fleets had high negative impacts. Detritus, phytoplankton, and small pelagic fishes showed the highest positive ecosystem-level impacts arising from variations in their biomasses. By contrast, the highest negative impacts among the biological groups were attributable to large benthopelagic fishes, pelagic sharks and rays, and molluscs.

Figure 8 shows the estimated keystoneness of the functional groups in the model. Pelagic sharks and rays were identified as the keystone species in the ECSS ecosystem, based on the theory that keystone species would have keystoneness values close to or greater than zero (Libralato et al., 2006).

Fishing activity and impacts

The fishery had a trophic role equivalent to a predator with TL = 3.01 and with a gross efficiency of 0.003. Exploitation rates (F/Z) calculated for the studied area are shown in Table 2. High values of these ratios were found for various demersal and pelagic fish and invertebrates, including both target and non-target species.

The MTIs analysis highlighted the direct and indirect impacts that an increase in fishing activity by the fleet would have on the other groups (Fig. 6). Almost all the exploitation activities had significant negative impacts on most of the exploited groups. An increase in the trawl fishery would have the widest-ranging impact on all ecosystem compartments and the largest impact on most of the demersal fish groups. The negative impacts of these fishing activities were also highlighted by the total MTIs analysis (Fig. 7), where the fisheries ranked among the most negatively impacting groups in the ecosystem. However, it is noteworthy that all the fleets (except for other fisheries which treats marine turtles as the fishing target) positively impacted marine mammals, seabirds, and marine turtles, mainly by reducing the abundances of these groups' main feeding competitors. In addition, the trawl fishery also had a positive impact on those species with low catchabilities by trawl.

Discussion

The ecological model developed in this study for the ECSS represents an important effort to integrate the available biological data from the area into a coherent framework. As the energy sources of such ecosystems, both primary production pathways and detrital pathways are important in LMEs, with each having significant impacts on the diets of groups at higher trophic levels (Pauly & Christensen, 1993, 1995). Our model of the ECSS identified the major pathways in this ecosystem belonging to each type. We estimated the herbivory/detritivory ratio in the ECSS to be 1.15, indicating that both the grazing and detrital food webs were of equal importance (sensu Dame & Christian, 2008). The EE values were high for most fish groups, but low for primary producers and detritus in the system. The low consumption rate of phytoplankton highlighted the fact that only a small proportion of phytoplankton production was grazed in the water column, with the rest going toward detritus. Similarly, due to the low consumption rate of detritus, a large portion of detritus was buried in the sediment of the system. These detrital nutrients

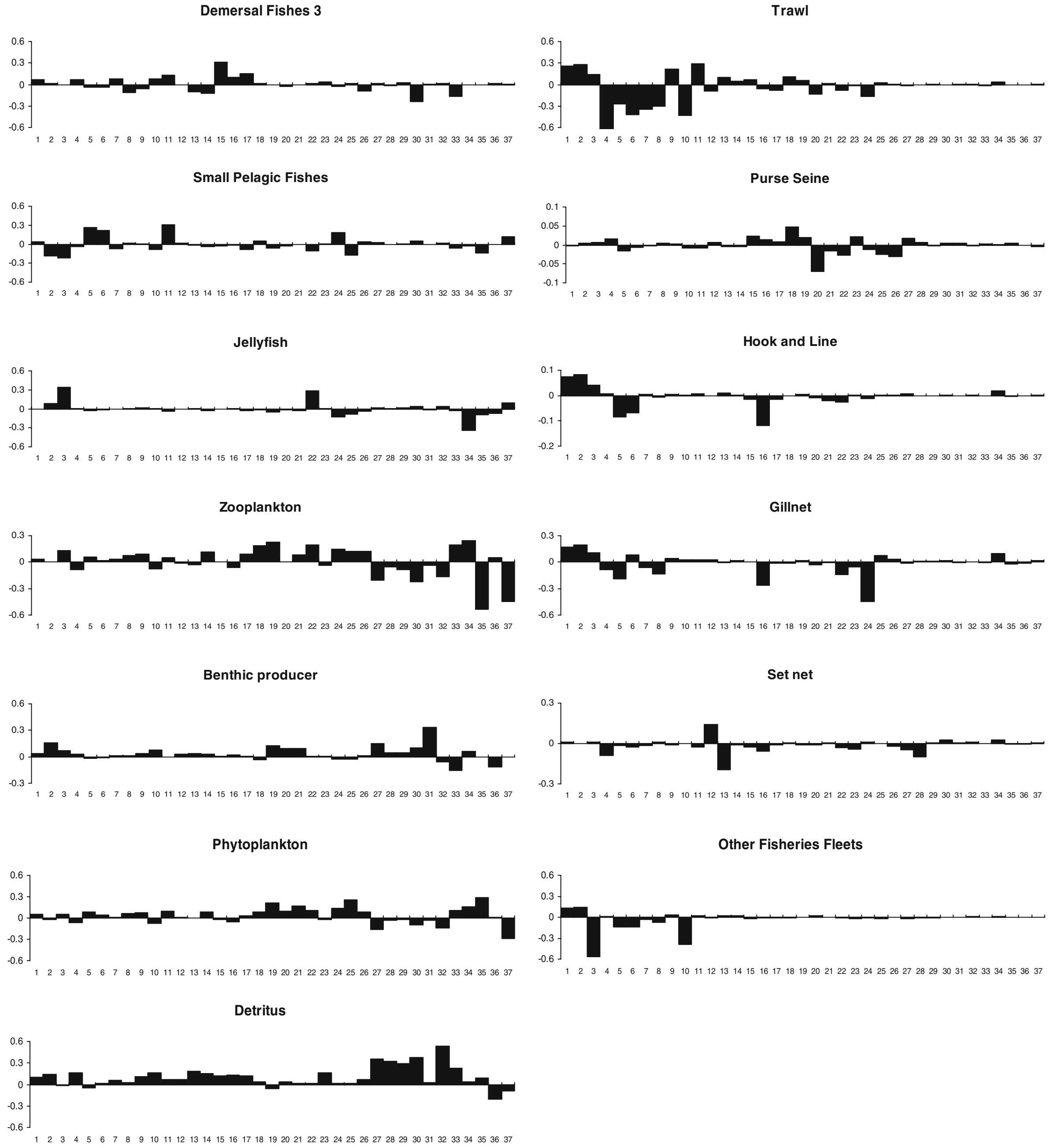


Fig. 6 Mixed trophic impact analysis of dermersal fishes 3, small pelagic fishes, jellyfish, zooplankton, benthic producer, phytoplankton, detritus, and fishing fleets of the East China Sea Shelf model. Positive and negative effects on the biomass of each group were represented above and below each line, respectively. *Note*: *1* marine mammals, *2* seabirds, *3* marine turtles, *4* demersal sharks and rays, *5* pelagic sharks and rays, *6* hairtails (A), *7* hairtails (J), *8* large croakers, *9* small croakers, *10* flatfishes, *11* lizardfishes, *12* demersal fishes 1, *13* demersal fishes 2, *14* demersal fishes 3, *15* snappers, *16* groupers, *17* bigeyes, *18* large reef-associated fishes, *19* small reef-associated fishes, *20* large benthopelagic fishes, *21* small benthopelagic fishes, *22* pomfrets, *23* threadfin bream, *24* large pelagic fishes, *25* small pelagic fishes, *26* cephalopods, *27* crabs, *28* shrimps, *29* molluscs, *30* benthic crustaceans, *31* echinoderms, *32* polychaetes, *33* other invertebrates, *34* jellyfish, *35* zooplankton, *36* benthic producer, and *37* phytoplankton. The *y*-axis represents the impact strength, *x*-axis represents the numbers of functional groups that are being impacted

Fig. 7 Total predicted impact of each group upon all the other groups

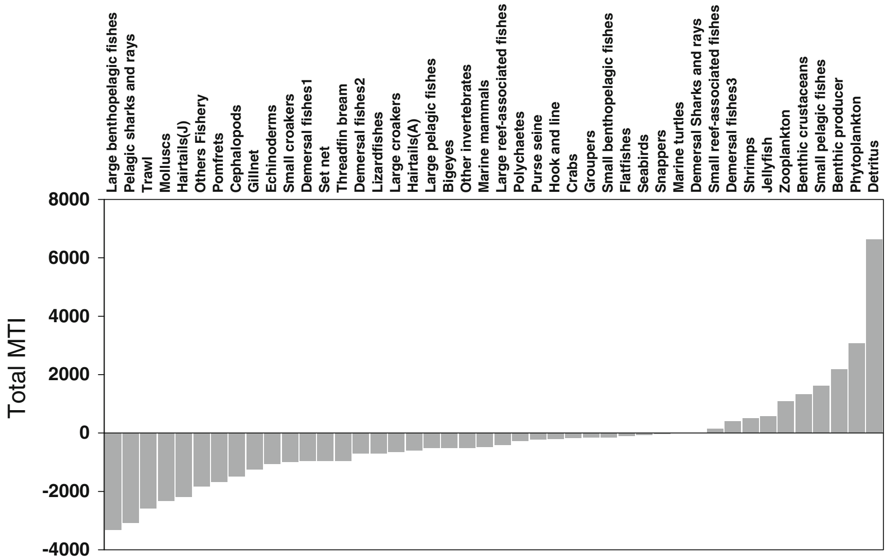
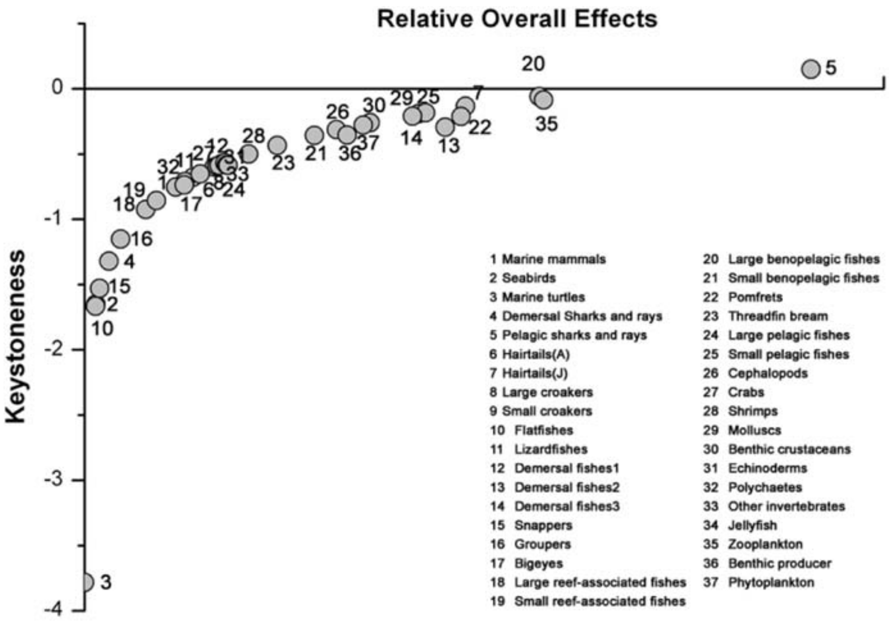


Fig. 8 Keystoneness index and overall effects of each functional group from the East China Sea Shelf model. Keystone groups are those with higher overall impacts and a higher keystoneness index



tended to continually pollute the system, leading to eutrophication that in turn might contribute to the occurrence of red tide every spring (Chen & Shen, 1998; Xu et al., 2003). Calculated transfer efficiencies were within the range of values reported in the literature (Pauly & Christensen, 1995). The relatively high trophic efficiencies in the ECSS ecosystem highlighted a good coupling between benthic and pelagic invertebrates and their predators (Coll et al., 2006; Libralato et al., 2006).

More than 90% of the fishery was mainly focused on trophic levels 2, 3, and 4 (see Fig. 6). The mean trophic level of catch (TLc) in the ECSS ecosystem in 2000 was estimated to be 3.01 (Table 4), which is much lower than the mean trophic level of catch of 3.5 that prevailed in 1965 (Chao et al., 2005). This was mainly due to the collapse of traditional fisheries that had targeted demersal species at higher TLs, as well as to the expansion of new fisheries targeting species at lower TLs (Jackson et al., 2001; Mayers &

Worm 2003). This agreed with previous studies which showed depletion of large predatory demersal fishes in the ECSS (Chao et al., 2005; Yan et al., 2006). However, the TLc did increase slightly from 2.8 in 1995 to 3.01 in 2000. This is likely explained by the recovery of some stocks in response to a closed area policy (Yan et al., 2004b, 2006; Cheng et al., 2006). The gross efficiency of the ECSS fisheries was high (0.003) when compared with the fisheries of other modeled systems, and also when viewed against the global mean of 0.0002 reported for fisheries worldwide (Christensen et al., 2005). High ecotrophic efficiencies and total mortality rates and low natural predation mortalities for fishable groups all suggested that the ecosystem was highly constrained by the fishery. Moreover, high *%PPR* value and *L* index (compared with other ecosystem model reviewed by Libralato et al., 2008 and Coll et al., 2008) and low P_{sust} indicators of fishing intensity identified the degree of overexploitation of the ECSS ecosystem.

Ecosystem maturity generally declined with the depletion of the older, longer-lived species that had accumulated large amounts of biomass when the system was still relatively underexploited. This is evidenced by a comparison of various system indices against Odum's attributes of ecosystem maturity (Table 4; Odum, 1969; Christensen, 1995). Comparing indices for the ECSS with those for other shelf ecosystems (Christensen, 1995; Okey & Pugliese, 2001), we found that the ECSS system had a relatively higher primary production to respiration ratio, a greater ratio of system production to biomass, a less diverse trophic network, a smaller Finn's cycling index, shorter path lengths, and, lastly, lower system overheads. All these characteristics of the ECSS suggest a comparatively immature ecosystem, with less resilience in the face of perturbations than is seen for other shelf systems (Odum, 1969; Vasconcellos et al., 1997).

The declining maturity and growing instability of the ecosystem may increase its volatility and that of its fisheries (Pauly et al., 1998). Potential indications of such a shift can be found in the progressive dominance of the ecosystem's pelagic domain and in the increasing dependence of its fisheries on lower trophic level species. Of particular concern, fish populations became dominated by juveniles after intensive fishing removed a large proportion of the adult biomass (Zheng et al., 2003; Chao et al., 2005; Cheng et al., 2006). Such truncation of the age–class structure of fish populations may further intensify their variability and the variability of the system in which they reside (Hsieh et al., 2006; Cheung, 2007).

Various functional groups in the model were impacted by the groups at the base of the food web. Some important impacting groups in this regard included zooplankton and benthic crustaceans. These impacts denote bottom-up control within the ecosystem (Hunter & Price, 1992). The wide-ranging impact that "demersal fishes 3" had on numerous groups at both higher and lower TLs highlighted the likely importance of these species in the ecosystem, by way of the wasp-waist flow control they appeared to contribute (Cury et al., 2000). We identified only marginal top-down control of forage fish by predator populations. This was consistent with the long-term, intensive fishing activities in the region that substantially reduced the biomass of top predators (Bearzi et al., 2004).

A large increase in jellyfish blooms in the Yangtze Estuary of the ECSS has occurred over the last 10 years (Yan et al., 2004a; Cheng et al., 2005). Jellyfish blooms in estuaries worldwide can have substantial effects on plankton communities and fish populations because jellyfish are consumers of zooplankton and ichthyoplankton (Xian et al., 2005). Although there are little available data that the jellyfish blooms are responsible for the changes on the oceans and coastal habitats, the impacts of jellyfish blooms on the fisheries sources were identified through the MTI analysis. Jellyfish were mainly impacted by plankton groups (phytoplankton and zooplankton) which were their direct and indirect prey and this suggested that jellyfish species were subject to bottom-up control (Pauly et al., 2009).

Pelagic sharks and rays have been identified as keystone species in many modeled ecosystems (Libralato et al., 2006). These high-impact groups tend to exert strong top-down effects. In the ECSS, pelagic sharks and rays had the highest value of keystoneness (0.148). These results were similar to those of the preliminary Hong Kong (South China Sea) models constructed by Cheung et al. (2002) and Buchary et al. (2002). Furthermore, the total MTI analysis ranked large benthopelagic fishes and pelagic sharks and rays as having the largest and second-largest negative impacts on the ecosystem, respectively, and zooplankton as having the largest positive impact (Fig. 7).

"Everything existing in the universe is the fruit of chance and necessity," as Democritus is alleged to have observed. The study of ecosystems integrates many fields of scientific research (including physical, chemical, and biological disciplines) and relies on a whole spectrum of data types, each with its own degree of variability and uncertainty. This, coupled with the complexity of the interactions within ecosystems, makes predicting them difficult. However, the application of ecosystem models, such as EwE, allows us to obtain a relatively lower degree of overall variability, and to thereby arrive at more reasonable results in line with the true values of the parameters sought. Even so, it remains difficult to consistently reach the same conclusions when using different constructions for the functional groups in the model, and this is one of the current reasons why ecosystem-based management cannot be fully applied to fishery science. On the other hand, with the increasing number of applications of EwE, defining an ecosystem model reference point for EwE functional group construction ($\mathrm{EMRP}_{\mathrm{EwEfc}}$) has become one of the main challenges. By organizing species into functional groups using multivariate statistical analysis, previous studies have tried to reduce the impact of variability without changing the community structure of modeled ecosystems (Opitz 1996; Coll et al., 2006, 2007). We believe that the combination of ecosystem modeling and multivariate statistical methods such as factor and cluster analyses should be helpful to the creation of an $\mathrm{EMRP}_{\mathrm{EwEfc}}$ and to the establishment of a standard reference point for ecosystem comparisons.

Conclusion

The present model constitutes the first mass-balance model constructed to characterize shelf and upper slope exploited ecosystems from the East China Sea, and it represents an important effort to integrate the available biological data from the area in a coherent format. Deficiencies in available biological data have been identified. Further efforts to better characterize the key elements of the ecosystem, such as the trophic data of functional groups, would be an important step toward the characterization of the ecosystem. The data were also scarce in landing and discard data. Thus, although the pedigree index of the model was high and the sensitivity analysis proved the robustness of the model, the continuous incorporation of new empirical data from the region into the model would improve its results.

The ecotrophic efficiencies and mortality rates suggested that the ecosystem is highly constrained by predators (natural predators and the fishery). Although predation has been proved to occur in marine ecosystems even under heavy fishing (Christensen & Pauly, 1993; Coll et al., 2006), fishing mortality was very high for some modeled groups, in agreement with results on growth and recruitment overfishing of some demersal and pelagic resources (Zheng et al., 2003; Lin et al., 2006a, b). At the same time, the intermediate low development of the ecosystem in terms of Odum's theory of ecosystem development (Odum, 1969, 1971; Christensen, 1995) was, at least partially, related to high fishing intensity and further supported by a high gross efficiency ratio, high primary production required to sustain the fishery, and the low trophic level of catch (Pauly & Christensen, 1995; Pranovi et al., 2003). In addition, fishing impact per fleet indicated large impacts on the principal components. The low trophic level of the catch, characterizing the ECSS ecosystem (Pauly et al., 1998) and ratified in this study, is also in line with the long history of exploitation in the ECSS (Chao et al., 2005).

Like most studies of similar nature, deficiencies in available biological and fisheries data might influence the quality of this study. Further efforts to better characterize key elements of the ecosystem, such as the ecological efficiency of some functional groups, the aspect ratio of fishes, and the biomass of some of the fish groups and detritus, could be an important step toward the improvement of the input data and the characterization of the ecosystem. Data are also scarce in estimating Illegal unreported and unregulated (IUU) fisheries catches. Because the information is not available, they were not considered in this study. This study shows the importance of collecting information on the discard and IUU catch in modeling an ecosystem. Although the quality of input data might be an issue for this study and the pedigree index of the model was high, the sensitivity analysis did suggest that the modeling results are robust. Besides, though the result of keystone species identification was reasonable compared with other similar ecosystems, further studies should also be carried out to testify the results of keystone species identification in the Ecosim dynamic simulation (Thomas Okey from Fishery Center of UBC, personal communication).

Ecological modeling can be an important tool allowing the inclusion of trophic interaction dynamics in the assessment and management of marine resources within the context of the precautionary approach and an adaptive management process. The present model provides the basis to further develop dynamic simulations in order to understand the extent to which fishing activities, the environment, and other anthropogenic factors are driving marine resources in the area and to describe the configuration of trophic interactions (Walters et al., 1997; Christensen & Walters, 2004). The output of different management strategies can then be studied.

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