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Comparative study of food webs from two different time periods of Hooghly Matla estuarine system, India through network analysis

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ABSTRACT

Two mass-balanced network models of Hooghly Matla estuarine system, from two different time periods (less exploited phase → 1985–1990 and highly exploited phase → 1998–2003) have been constructed for quantitative comparison. The models are used to estimate the important biological interactions and relationships among different ecologically important groups. 20 functional groups based on species of different habitats from coastal areas in this ecosystem have been identified, including shrimps, squids, crabs, mackerel, small pelagics, demersal fishes, benthic feeders, predator fishes and trash fish. The biomass values for these components are estimated from catch production and bottom trawling surveys. The values of Ecotrophic Efficiency in the models are high (>0.5) for most groups of higher trophic levels. Interactions among different components are clearly understood from the outputs of models with a focus on energy flow. Most fish population are observed to approach high degree of exploitation with change in the overall trophic structure mainly due to top down effects. Several system statistics and network flow indices from the model outputs indicate that this estuary is facing degradation and stress resulting in some degrees of instability.

1. Introduction

The Hooghly Matla estuarine ecosystem with adjacent mangroves is one of the largest detritus based ecosystems of the world (Pillay, 1958) and has great importance in costal landscape of India. Estuarine system are of interest because the most sensitive land-water-atmosphere interactions are pronounced at these region. It provides diverse habitat for wide variety of aquatic resources of ecological and economic significance including finfish, prawn, bivalve, gastropod, fiddler crab and plankton etc. (Mitra et al., 2000, 1997; Nath et al., 2004). Beside this, like other estuaries, the Hooghly Matla system also has great significance as it supports many essential fisheries of high economic value.

But recent years have seen this ecosystem to have degraded gradually owing to the different anthropogenic factors such as overfishing, development of agriculture and sewage from aquaculture farms, expansion of human settlements (900 km^{-2}; 2001 census), establishment of Farakka barrage in the upper stream of river, construction of Kolkata-Haldia ports and climatic factors like rise in temperature, sea level, salinity and increasing frequency of severe cyclones such as Nargis, Bijli and Aila in recent years (Hazra et al., 2010, 2002). These hamper the ecological balance affecting the food web of the concerned system (Islam, 2013) .The increasing trend of fish yield over years (from 27014.5 t in 1984–93 to 64204.3 t in 1999–2003) has resulted into a drastic decline in the fish catch per unit effort (CPUE) from 189.7 kg in 1990–91 to 44 kg in 2002–03 (Mitra et al., 1997; Nath et al., 2004; Sinha, 2004). Technically this is termed as overfishing; a form of overexploitation where the amount of fish caught reduces the population below the level at which fish population can naturally sustain itself. This may happen in water bodies of any sizes from small ponds and rivers to oceans and can result in resource depletion, reduced biological growth rates, low biomass level in fish population. Futhermore, it can lead to critical situations where fish population are no longer

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able to sustain themselves and may become extinct. For example, species like *Lisa tade, Lates calcarifer* have declined and *Tenualosa toli, Chanos chanos* are totally absent in recent years (Mitra et al., 2000; Sinha, 2004). Not only that, but these situations may lead to impacts including alternation of species diversity of other trophic level, declination of mean trophic level within the system and significant habitat modification or destruction. Beside this, it affects the social and economic wellbeing of the coastal communities who depend on fish for their way of life.

Overfishing has significantly affected many fisheries around the world. As much as 85% of world's fisheries are estimated to be depleted, overexploited, fully exploited or in recovery from exploitation. For example, areas like Northeast Atlantic, the Western Indian Ocean and the Northwest Pacific ocean are in fully exploited condition (UNFAO, 2012 Statistical Year Book; UNFAO, General facts regarding world fisheries). It is a warning signal for the future of a sustainable ecosystem. Therefore, impacts of perturbations on the trophic structure of this ecosystem should be examined in order to form proper scientific management policies related to fishery and other modes of resource utilization; otherwise the system may collapse at some point in the future. Overfishing will be detrimental to the fishery industries as well as biodiversity of this system. In order to ensure sustainable and scientific fisheries management, a more holistic approach that balances both human well-being and ecological well-being are required. Modern aquatic resource management is based not only on monospecific approach but on an ecosystem approach as it includes fish as well as different organisms and different natural processes. In this regard, static mass balanced modelling approach, well-grounded with realistic data, can give answers to many salient questions for analysing ecosystem structure and function holistically. Following the comparative analysis of trophic networks between virgin and reclaimed island by Ray and Straškraba (2001) and Ray (2008), the goal of the work presented in this paper was to characterize the Hooghly Matla estuarine complex in terms of mass balanced models to obtain holistic view of the same. This study emphasized two key questions: (1) is the system gradually degrading due to overexploitation and (2) if the case is so, then how much has it degraded over years and how much is the system under stress?

To answer these questions, we constructed two mass balanced trophic network models of Hooghly estuary using Ecopath with Ecosim (EwE) software (Christensen et al., 2005) for different phases. The first model pertaining to a less exploited phase (**phase 1,** 1985–1990), and the second focused on the more exploited time phase (**phase 2,** 1998–2003). This work has three specific objectives: (1) to understand different trophic interactions (2) identification of the different pathways of energy transfer (3) investigating the current status of ecosystem efficiency in order to point the major pathway controlling the food web of this ecosystem.

2. Materials and methods

2.1. Study area

The Hooghly Matla estuarine ecosystem (HMES) is situated 21° 32′ N and 22° 40′ N; 88° 05′ E and 89° E, at an altitude 0–10 m above sea level and just south of Kolkata. It houses the estuarine phase of the River Ganges and measures 9630 km^2, out of which 4262 km^2 is intertidal area. A large saline water zone of 1892 km^2 has been selected as the current study area; this selection is done in accordance to previous study of Ganguly et al. (2006). Average surface water temperatures (27.3 °C and 28.7 °C) are obtained from (Nandy et al., 1983) and (Biswas et al., 2004) respectively for the two different phases. Maximum catches are recorded (90%) from remote places of the lower estuary, including some fishing centres such as Diamond Harbour, Kakdwip, Namkhana, Bokkhali, Jambudwip, Frasergung and Sagar Island (Mitra et al., 2000). The two time-periods under consideration are the less exploited, **phase 1** (1985–1990) and the highly exploited, **phase 2** (1998–2003). Both of the time periods are used while constructing two models for the system as the best records are available for those years (Fig. 1).

2.2. Network modelling approach

Widely used static modelling software Ecopath with Ecosim (EwE) version 6.5 (Christensen et al., 2005; Coll et al., 2009) was applied to construct the mass balanced models (a snapshot, in terms of trophic flows and biomasses at precise time periods) providing static and quantitative descriptions of studied ecosystem. It derives model parameters on the basis of two master equations, one of which ensures the balance of energy over each compartment: consumption (***Q***) = production (***P***) + respiration (***R***) + unassimilated food (***U***); and the other one describes the production term that is balanced by predation mortality, fishing mortality and other mortality due to old age.

$$P_i = Y_i + B_i M2_i + E_i + BA_i + P_i(1 - EE_i)$$

$$Or\ B_i * \left(\frac{P}{B}\right)_i * EE_i - \sum_{j=1}^{n} B_j * \left(\frac{Q}{B}\right)_j * DC_{ji} - Y_i - E_i - BA_i = 0$$

where, B_i is the biomass of prey ($\boldsymbol{i}$); $\left(\boldsymbol{\frac{P}{B}}\right)_{\boldsymbol{i}}$ is the production to biomass ratio of prey ($\boldsymbol{i}$); $\boldsymbol{M2_i}$ is total predation mortality rate for prey ($\boldsymbol{i}$) by predator ($\boldsymbol{j}$), summation term $\boldsymbol{B_i M2_i}$ signifies total predatory losses of prey ($\boldsymbol{i}$) to all predators ($\boldsymbol{j}$), that is equal to $\sum_{j=1}^{n} B_j * \left(\frac{Q}{B}\right)_j * DC_{ji}$ where $\boldsymbol{B_j}$ is the biomass of predator ($\boldsymbol{j}$); $\left(\boldsymbol{\frac{Q}{B}}\right)_{\boldsymbol{j}}$ is the consumption to biomass ratio of predator ($\boldsymbol{j}$); $\boldsymbol{DC_{ji}}$ is the fraction o prey ($\boldsymbol{i}$) by weight in the average diet of predator ($\boldsymbol{j}$); $\boldsymbol{Y_i}$ is the catch due to fishing, $\boldsymbol{EE_i}$ is the ecotrophic efficiency of ($\boldsymbol{i}$) which is the proportion of the production that it is used within the system due to consumption or is exported from the system by fishing. Assumptions were taken that there was no biomass accumulation ($\boldsymbol{BA_i}$) and net migration ($\boldsymbol{E_i}$) from this system.

2.3. Functional groups and attributes

Two mass balanced EwE network models for two different time periods provide comparative and quantitative descriptions of the interactions in the trophic structure of the ecosystem. To define functional groups in the ecosystem it is necessary to identify ecologically similar species and group them together (Coll et al., 2009) in order to simplify the models. For this reason, the models though initiated with over 50 species – associated with 27 commercially important fish and several other non-fish species – are narrowed to 20 groups during the literature review process to reduce the complexity. A few species of lesser importance or with unavailable data are excluded. The EwE master equation contains four core parameters that describe the basic biology of each functional group: biomass (***B***), production to biomass ratio (***P/B***), consumption to biomass ratio (***Q/B***) and ecotrophic efficiency (***EE***). The biomass values of all functional groups are calculated in terms of carbon currency. Three out of these four parameters for each functional group are gathered from data source and are used as input in the initial model framework. Beside this, to run EwE model, the diet matrix was conceptualized and created. It describes the trophic interlinking between different functional groups and dependency of the components upon each other of this ecosystem.

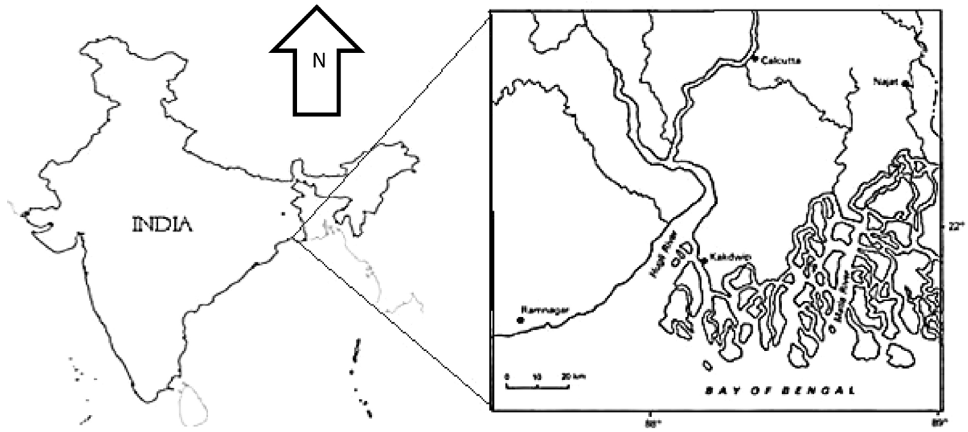

Fig. 1. A map of Hooghly Matla estuarine ecosystem in Sundarbans, India.

2.3.1. Detritus

Detritus is one of the most important inputs in EwE model due to the fact that most of the estuarine ecosystems are based primarily on detritus food chain (Day, 1989; Manickchand-Heileman et al., 2004). The detritus biomass is calculated from the empirical relationship of primary production and euphotic depth of the water body (Christensen and Pauly, 1993) using the following equation

$$logD = 0.954logPP + 0.863logE - 2.41$$

Where, $\boldsymbol{D}$ is the biomass of detritus in gCm^{-2}, $\boldsymbol{PP}$ is the primary productivity of the system ($g\,C\,m^{-2}$) and $\boldsymbol{E}$ is the euphotic depth in meters calculated from the relation $\boldsymbol{E} = \boldsymbol{2.5} \times \boldsymbol{SD}$ (Secchi depth in meters). Primary productivity for these two periods are collected and modified from literature (Bhattacharya, 2005).

2.3.2. Primary producer

Phytoplankton is considered a primary producer with the dominant groups being Bacillariophyceae or diatoms (*Coscinodiscu* spp., *Fragilari* spp. *Diatoma* spp. etc.). The biomass of this less exploited group is collected from available literatures of other studies from the same habitat area (Nath et al., 2004) and the *P/B* ratio used is adapted from (Mohamed et al., 2005).

2.3.3. Zooplankton and molluscs

Zooplankton in HMES include four major groups viz. Copepoda, Cladocera, Rotifera and Ostracoda. Among these the dominant group Copepoda includes species like *Accartiella, Acartia, Diaptomus, Pseudodiaptomus, Microstella, Cyclops* etc. Zooplankton biomass was calculated from secondary data source relative to similar ecosystem but different habitat (Nath et al., 2004; Sarkar et al., 1986) for the two time periods respectively.

Molluscs include gastropod such as *Nerita* sp., *Littorina seabra, Lambis lambis* and bivalves such as *Glaucomya* sp., Razor calm, *Terepo* sp., *Batissa inflate*. The biomass values for molluscs were estimated by the EwE models with the provided inputs of *P/B* and *Q/B* values adapted from literature (Harvey et al., 2010; Narasimham et al., 1993).

2.3.4. Prawn and crabs

The major crustacean populations of this estuary includes prawns and crabs. Prawns belong to the family Sergestidae (*Acetesindicus*), Penaeidae (*Penaeus* sp., *Metapenaeus* sp., *Solenocera* sp.) and Palaemonidae (*Exopalaemon styliferus, Macrobrachiurn* sp.); whereas the crabs include mainly *Scylla serrata, Uca* sp., *Thalassina* sp. and *Varunalitterata*. Biomass of prawns was calculated from secondary data source (Nath et al., 2004; Sinha, 2004) and that of crab was estimated by EwE model. The *P/B* and *Q/B* values of both groups are modified from the literature (S. Khan et al., 1992; Nirmale et al., 2012; Zafar et al., 1997).

2.3.5. Fish

Thirteen different groups of fish were considered in this model. Selection of fish was based on similarities in feeding habits, body size, ecological distribution and commercial importance. Primarily the groups were selected from pelagic, benthopelagic and demersal habitats. They were separated again on the basis of asymptotic length, into (1) 'small' species with length equal or less than 30 cm, (2) 'medium' with length 30–89 cm and (3) 'large' with asymptotic length of 90 cm or more. Most of the information regarding biomass value, *P/B* and *Q/B* ratios of different types of fish were taken from different available literatures and reports, single species stock assessments, fish survey data collected and published by Central Inland Fisheries Research Institute (Mitra et al., 2000, 1997; Nath et al., 2004; Sinha, 2004), Central Marine Fisheries Research Institute (Srinath et al., 2006) and Fishbase resources (Froese and Pauly, 2006). All available data are averaged for the different phases (from 1985 to 1990 and from 1998 to 2003) to remove any variation due to seasonal as well as environmental effects for the Hooghly Matla estuarine ecosystem (Christensen and Pauly, 1992). Biomass and *P/B* ratios were calculated for each fish group by using the empirical formula proposed by Beverton and Holt (2012) and Pauly (1980), and followed by Christensen et al. (2005):

$$B = \frac{Y}{F};\ F = Z - M;\ Z = \frac{P}{B} = K.\frac{L_\infty - \bar{L}}{\bar{L} - L'},$$

Where $\boldsymbol{B}$ is the biomass ($t\,km^{-2}$), $\boldsymbol{Y}$ is the annual catch yield ($t\,km^{-2}\,y^{-1}$), $\boldsymbol{F}$ is the fishing mortality ($year^{-1}$), $\boldsymbol{Z}$ is the total mortality ($year^{-1}$), $\boldsymbol{M}$ is the natural mortality ($year^{-1}$), $\boldsymbol{K}$ is the Von Bertalanffy Growth Function, $\boldsymbol{L_\infty}$ is the asymptotic length of fish (cm), $\boldsymbol{L^-}$ is the mean length of fish (cm) in population and $\boldsymbol{L'}$ is the cut off length. The values of $\boldsymbol{K}$, $\boldsymbol{L_\infty}$, $\boldsymbol{L^-}$ and $\boldsymbol{L'}$ for the different fish groups are obtained from Fishbase resources (Froese and Pauly, 2010).

The consumption to biomass ratio (*Q/B*) for the groups are calculated following (Pauly, 1980) as

$$\log\frac{Q}{B} = -0.102 + 0.444\ \log T' - 0.115\ \log W_\infty + 0.427\ \log A$$
$$+0.577\ \log D - 0.464\ \log P$$

Where, $\boldsymbol{T'}$ is the mean ambient water temperature, $\boldsymbol{W_\infty}$ is the asymptotic weight of fish, $\boldsymbol{A}$ is the aspect ratio of height of caudal fin squared by surface area of caudal fin, $\boldsymbol{D}$ is depth ratio from tip of snout to end of caudal peduncle by maximum body depth

Table 1
Functional fish groups including species with references for the Ecopath parameters, included in modelling of the HMES.

Group	Included Species	biomass	P/B	Q/B
Cartilaginous fish	Skates or Guitarfish (*Rhinobatos* sp.), Sawfish (*Pristis microdon*), sting ray (*Himantura* sp.) and Shark (*Scoliodon laticaudus*)	Srinath et al. (2006)	Mohamed et al. (2005)	
Polynemids	*Polynemus paradiseus*, *Eleutheronema tetradactylum* (Gurjeoli)	Nath et al. (2004) and Sinha (2004)	M.G. Khan et al. (1992) and Nabi et al. (2007)	
Demersal fish	large (*Lates calcarifer*), Medium (*Sillaginopsis panijus*) or small (*Harpadon nehereus*)	Nath et al. (2004) and Sinha (2004)	Balli et al. (2011), Karmakar (2003) and M.G. Khan et al. (1992)	
Pelagic fish	Medium pelagic fish (*Rastrelliger kanagurta*) and small pelagic fish (*Setipinna* sp., *Coilia* sp.)	Nath et al. (2004) and Sinha (2004)	M.G. Khan et al. (1992) and Nabi (2007)	
Benthopelagic fish	Medium (*Trichiurus gangeticus* – Ganges hairtail) and large (*Daysciaena albida, Sciaena biauritus, Otolithoides pama*)	Nath et al. (2004) and Sinha (2004)	Chakraborty (1990), Chakraborty et al. (2000) and Reuben et al. (1997)	
Mesopelagic Fish	*Pampus argenteus* (Butter fish)	Nath et al. (2004) and Sinha (2004)	M.Z. Khan et al. (1992)	
Mullets	*Liza parsia, Liza tade*	Nath et al. (2004) and Sinha (2004)	Moorthy et al. (2003) and Rangaswamy (1975)	
Catfish	*Tachysurus jella, Mystus gulio, Plotosus canius, Pangasius pangasius, Osteogeneiosus militaris*	Nath et al. (2004) and Sinha (2004)	Raje and Dineshbabu (2008)	
Hilsa	*Tenualosa ilisha; Ilisha megaloptera; Ilisha elongate; Ilisha toil*	Nath et al. (2004) and Sinha (2004)	Amin et al. (2002) and Reuben et al. (1992)	

(***D_{max}***) and ***P*** is the relative depth of caudal peduncle i.e. the depth of caudal peduncle by $D_{\max}$. Information about the grouping of fish species is provided in the following Table 1.

2.3.6. Marine mammals

Ganges River dolphins (*Platanista gangetica*) and Irrawaddy dolphins (*Orcaella brevirostris*) were the marine mammals in this model. Due to lack of data, biomass of dolphin was calculated from (Smith et al., 2006) and kept constant across two models. The ratios are adapted from (Mohamed et al., 2005).

2.4. Feeding relationship in the food web of HMES

In static modelling approach, the diet matrix is an important input for constructing the network model as it represents the flows connecting each of the compartments that form the prey predator groups in the system. The outflow from each compartment is distributed amongst the predators of that particular group as inputs to the latter. This divison should be based upon the principle of " who eats whom and by how much" and it can be depicted in a diet matrix where the material flows from compartment *i* (prey) to compartment *j* (predator) (Fath et al., 2007). This matrix (Table 2) was developed from published data on average diet composition from feeding ecology or stomach analyses of each functional group of this ecosystem or related species of other similar ecosystems. Food composition of the predators (***DC_{ji}***) is the fraction (in weight) of every prey ***i*** in the stomach content of predator ***j***. In cases for which published information did not exist, the diet of the same species in a similar ecosystem or of another similar species was used, presuming that there are no substantial differences (Christensen et al., 2005).

2.5. Estimation of unknown parameter, mass balancing and uncertainties

In any stable system the ***EE*** values for the functional groups must be between 0 and 1, while production to consumption ratio (***P/Q***) should lie between 0.1 and 0.3 (Christensen and Pauly, 1992). To balance the models, they were modified by adjusting the input parameters of those groups with $EE > 1$ and P/Q values lie within the general acceptable range of 0.05–0.5 for most of the functional groups or compartments. In particular, parameters associated with higher uncertainty, i.e., *Q/B*, *P/B* and biomass are changed (calibrated) until acceptable runs with ***EE*** < 1 and 0.05 < ***P/Q*** < 0.5 for each group (Christensen and Walters, 2004) are obtained. The modifications to the inputs are done in accordance to (Christensen et al., 2005) with the purpose of achieving mass balance using ecological knowledge rather than solely depending on the computational algorithms embedded in the EwE software.

The modifications included minor variations in the diet matrix of some organisms. The instances where the data was not directly available for the focused system, similar data sets (pertaining to ecosystems of similar geographic location and more or less similar species composition) are used to fill in the gaps from available literature as mentioned in Table 1. Validity and dependency of the input values are then verified by running the pedigree routine for the model following (Funtowicz and Ravetz, 1990) which not only describes the data origin, but also assigns a confidence interval to each of the data sets based on their origin (Pauly et al., 2000). The pedigree index *P* is calculated based on the following formula:

$$P = \sum_{i=1}^{n} \sum_{j=1} \frac{lij}{n}$$

Where, l_{ij} is the pedigree index for model group *i* and parameter *j*, *n* is the total number of functional groups.

2.6. Application of ecological network analysis

Various ecosystem properties such as trophic level, trophic level of the catch, pathways of energy flow, primary production required are used to compare the system structure between the two phases. Odum (1969) proposed 24 ecosystem attributes, which can be used to compare the level of ecosystem development and maturity viz. the ratios like total primary production to biomass (**TPP/TB**), net primary production to respiration (**NPP/TR**), total biomass to total throughput (**TB/TST**), system omnivory index (**SOI**) etc. Higher order ecosystem indices such as throughput, ascendency, developmental capacity, Finn cycling index, etc. help in understanding different level of ecosystem maturity, stability, and resilience (Ulanowicz, 1986). Here different indices of network analysis are discussed as follows:

2.6.1. Omnivory index

Omnivory, is defined as the feeding relationship on more than one trophic level, being an important feature for evaluating maturity of ecosystems. The system omnivory index quantifies the distribution of feeding interactions among different trophic lev-

Table 2
Diet composition of the consumer groups in the Hooghly estuary.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	0.01	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
6	0.00	0.00	0.00	0.13	0.00	0.18	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
7	0.25	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8	0.00	0.10	0.05	0.00	0.00	0.01	0.00	0.00	0.42	0.00	0.06	0.00	0.27	0.35	0.00	0.00	0.00	0.00
9	0.00	0.18	0.05	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.13	0.00	0.00	0.00	0.00
10	0.11	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
11	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00
12	0.00	0.00	0.16	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
13	0.12	0.10	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00
14	0.11	0.09	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.12	0.00	0.00	0.00	0.00
15	0.31	0.32	0.00	0.05	0.00	0.07	0.00	0.18	0.20	0.01	0.00	0.02	0.05	0.06	0.02	0.00	0.00	0.00
16	0.10	0.06	0.35	0.29	0.57	0.60	0.00	0.37	0.04	0.01	0.64	0.00	0.01	0.24	0.00	0.00	0.07	0.00
17	0.00	0.00	0.02	0.00	0.28	0.00	0.00	0.00	0.00	0.06	0.25	0.00	0.06	0.00	0.00	0.00	0.00	0.00
18	0.00	0.00	0.00	0.13	0.15	0.00	0.25	0.12	0.34	0.19	0.01	0.23	0.00	0.10	0.34	0.00	0.25	0.01
19	0.00	0.00	0.01	0.13	0.00	0.02	0.39	0.23	0.00	0.00	0.00	0.19	0.00	0.00	0.21	0.35	0.02	0.45
20	0.00	0.00	0.04	0.21	0.00	0.02	0.36	0.10	0.00	0.73	0.02	0.56	0.14	0.00	0.43	0.65	0.66	0.55
Sum	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**

els through the weighted average of omnivory of the network's consumers (Libralato, 2008).

2.6.2. Mixed trophic impact

According to Ulanowicz and Puccia (1990) the Mixed Trophic Impact (**MTI**) routine gives an idea of how important the different groups are for the trophic interactions and also it can assess the effect of biomass change of a group (impacting) on the other groups (impacted) in a system based on the input output analysis (Hannon, 1973; Hannon and Joiris, 1989; Leontief, 1936). MTI assumes that trophic structure is constant (the basic input parameters for each trophic group are fixed in value for each model). This means that the technique cannot be used for predictive purposes, but should rather be considered as a simple form of sensitivity analysis. It is an indicator of which groups have negligible effects on others within the system, and for which there is likely to be little gained from an effort to collect additional data to refine estimates. On the other hand, it identifies groups having large trophic impacts on others, and for which it would be useful to refine estimates (Coll et al., 2009).

2.6.3. Keystoneness

All species in a system do not have equal impact on the total ecosystem functioning. Several experiments have shown that some are more important than others in maintaining the integrity of the system and are called keystone species (Paine, 1969; Power et al., 1996). These species are defined as having relatively low biomass (and hence lower food intake) with a structuring role in the food web of the system under consideration. Libralato et al. (2006) provided a method of calculating "total impact", which is a measure of the overall effect on a foodweb due to changes in the abundance of a given species or trophic group.

2.6.4. Niche overlap

Numerous niche overlap indices have been suggested by various authors to quantify how species overlap. Hurlbert (1978) and Loman (1986) summarized different methods describing their properties based on a number of hypothetical examples. When the value of overlap index equal to 0 then the two species under consideration do not share resources and a value of 1.0 indicates complete niche overlap; all intermediate values show partial overlap in resource utilization (Pianka, 1973).

3. Results

3.1. Trophic structure analysis and patterns of energy flow

In the present context, from the basic estimates (Table 3) it is found that trophic level (TL) varies from 1.0 (for primary producers and detritus) to the highest value of 3.89 (for top predators such as cartilaginous fish). Fish trophic level varies from 2.26 (Mullet) to 3.89 (Cartilaginous fish) and TL for invertebrates range from 2.01 (Zooplankton) to 2.36 (Mollusc). The average ecosystem trophic level is 2.72. Here ecotrophic efficiency values ranged from 0.0 to 1. A null *EE* (0) is found for marine mammals. For the phytoplankton group, very low *EE* value is obtained for phase 1 but it gradually increases in phase 2. When comparing the *EE* for both phases, increasing trend is found for the higher consumer group, such as medium demersal fish, mullet, large benthopelagic fish, prawn and phytoplankton. Decreasing trend is found for the detrivorous and herbivorous group such as medium mesopelagic fish, catfish, Hilsa, and zooplankton (Fig. 2). On the aspect of ecological relevancy of *EE*, it is stated that for unexploited groups like phytoplankton, Mollusca small change of *EE* in later phage does not reflect more effect on overall ecosystem status. But for the exploited groups mainly different fishes whose *EE* is nearly close to 1, small change of *EE* have the potential for adverse effect on overall ecosystem. Secondly, the fish population does not occupy single trophic level but lies in between the continuous TLs of 2.25–3.89. It is possible due to the fact that some group fish are consumed by other larger fish groups on the basis of prey-predator relationship and for that reason both increasing and decreasing trend of EE is found in this system (Fig. 3).

In terms of biomass, the system is dominated by the group associated with the bottom trophic level with maximum biomass being distributed within trophic level 1 which includes detritus and phytoplankton acting as main resource of the food web (Fig. 4). Most of the fish groups take zooplankton as prey and their biomass values (up to trophic level 3) increase in the later phase, which corresponds to a decrease in biomass values of zooplankton and also the trophic level 2. There is also an increase the biomass value of first trophic level. This suggests a top down effect, which is most common in stressed ecosystem.

Species are distributed in seven discrete trophic levels according to the Lindeman spine analysis (Fig. 5). The third trophic level, with highest transfer efficiency, plays an important role in the energy

Table 3
Basic estimates for the EwE models representing HMES for the time period 1998–2003 (phase 1) and 1985–1990 (phase 2).

Periods			1985–1990					1998–2003				
Group name		Trophic level	B	P/B year^{-1}	Q/B year^{-1}	EE	P/Q	B	P/B year^{-1}	Q/B year^{-1}	EE	P/Q
1	Marine Mammals	3.61	0.04	0.65	12.65	0.00	0.05	0.04	0.64	12.65	0.00	0.05
2	Cartilaginous fish	3.89	0.22	2.20	7.40	0.87	0.30	0.74	2.01	7.23	0.89	0.28
3	large demersal fish	3.33	0.05	2.35	7.90	0.96	0.30	0.08	4.47	15.00	0.94	0.30
4	Polynemids	2.92	0.01	6.00	20.20	0.78	0.30	0.08	4.38	14.65	0.73	0.30
5	Medium demersal fish	3.09	0.01	3.60	29.10	0.58	0.12	0.03	4.30	30.70	0.64	0.14
6	Small demersal fish	3.36	1.27	5.36	17.90	0.62	0.30	3.18	5.18	17.30	0.65	0.30
7	*Hilsa*	2.25	0.78	1.70	15.50	0.74	0.11	2.41	3.77	16.60	0.69	0.23
8	Small pelagic fish	2.74	2.90	5.98	19.98	0.94	0.30	4.17	8.68	29.00	0.99	0.30
9	Medium pelagic fish	3.39	1.10	4.92	11.60	0.90	0.42	1.90	5.12	12.10	0.90	0.42
10	Medium mesopelagic fish	2.30	0.12	3.60	12.10	0.90	0.30	1.13	1.97	6.80	0.64	0.29
11	Catfish	3.13	0.24	7.20	24.10	0.75	0.30	3.65	1.70	11.30	0.62	0.15
12	Mullet	2.26	0.21	3.70	38.70	0.91	0.10	0.19	9.50	41.50	0.96	0.23
13	Medium benthopelagic fish	3.85	2.89	2.60	8.70	0.79	0.30	2.99	4.80	16.10	0.82	0.30
14	Large benthopelagic fish	3.66	1.80	3.70	12.40	0.87	0.30	2.40	5.60	18.70	0.88	0.30
15	Molluscs	2.36	22.37	1.02	3.41	0.85	0.30	46.98	1.01	3.40	0.85	0.30
16	Prawn	2.00	5.67	9.80	32.74	0.82	0.30	10.07	11.97	39.98	0.81	0.30
17	Crab	2.32	1.19	2.76	9.30	0.96	0.30	5.31	2.76	9.30	0.96	0.30
18	Zooplankton	2.01	70.66	20.00	75.00	0.59	0.27	32.00	15.00	75.00	0.59	0.20
19	Phytoplankton	1.00	125.00	78.65		0.33		132.00	78.65		0.70	
20	Detritus	1.00	20.23			0.37		23.99			0.49	

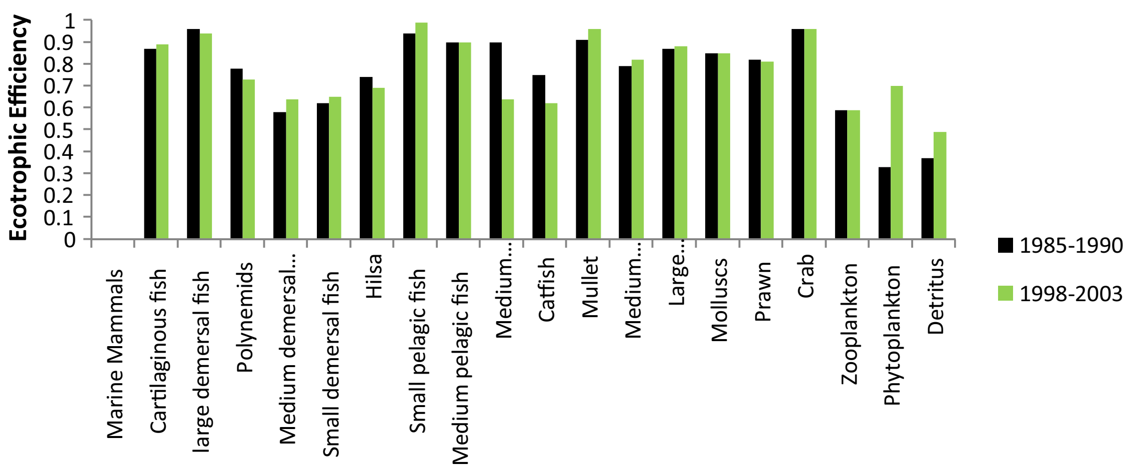

Fig. 2. Bar diagram showing comparative ecotrophic efficiency of two different periods.

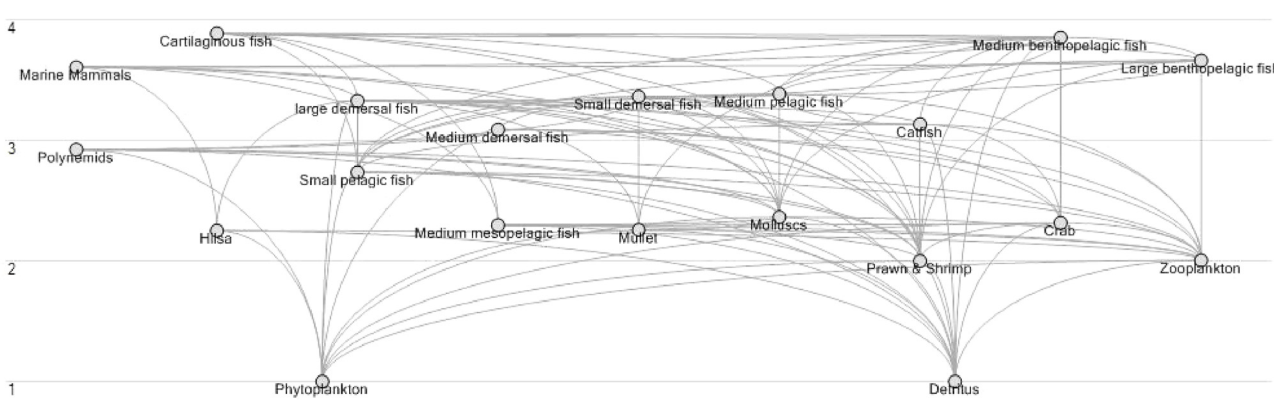

Fig. 3. Flow diagram of the HMES where the nodes represent the components, curved lines show food web connectivity and horizontal straight lines represent the trophic levels.

transfer (prey and predator) in both the phases. The Lindeman spine shows that the trophic level 1 consisting of phytoplankton and detritus is responsible for most of the energy flow or total system throughput out of which the maximum part is transferred by the latter. This finding is also reflected by the distribution of biomass as observed from both the models. Not only that, the

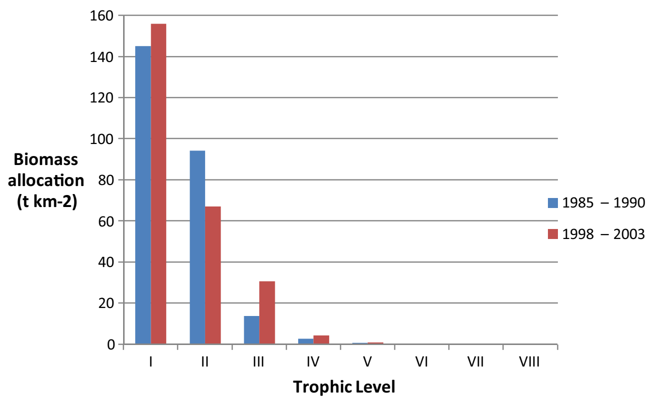

Fig. 4. Comparison of distribution of biomass among discrete trophic levels between two periods.

transfer efficiency from primary producers and detritus to next trophic levels are 9.887% and 10.45% respectively for phase 1 and 14.42% and 14.98% respectively for phase 2 (calculated from EwE software). Here it is indicated that both gazing pathway as well as detrital pathway are almost equally important in this estuary. This fact has been mentioned as it is somewhat contradictory to most available literature where the detrital pathway is shown to be of prime importance. Differences were found when comparing the Lindeman spine for the two models. Mean transfer efficiency increased from 10.21% to 14.74% in phase 2 (Fig. 5). Among all groups, the maximum primary production is required by zooplankton, followed by medium benthopelagic fish, small pelagic fish and molluscs. From the PPR (primary production required) values of the EwE model, it is clear that, in the phase 2 all consumer groups require more primary production to support their biomass than the previous phase 1.

3.2. Mixed trophic impact

Like any estuarine ecosystem, in the present context the positive impact of phytoplankton is greatest on their major consumers, like zooplankton, *Hilsa*, small pelagic fish but has negative impact on detritus. Fig. 6 highlights these observations where the bold lines indicate negative impact and solid line indicate the positive impact. Other invertebrates (particularly benthos) molluscs, prawns exert negative impacts on mesopelagic fish which have similar dietary composition (detritus), but have pronounced positive impacts on maximum predator fish in the system. All the functional groups except detritus have a negative impact on themselves reflecting increased intragroup competition for resources.

3.3. Niche overlap

There is evidence of strong prey niche overlaps occurring between prawn and zooplankton in HMES, which indicates that both of them serve as food (prey) for predators with almost similar preference (here the prey index value of prawn and zooplankton is almost close to 1; see point 16, 18 in Fig. 7) and strong predator overlap index is seen in between catfish and medium benthopelagic fish (here the predator index value of prawn and zooplankton is almost close to 1; see point 11, 13 in Fig. 7) and it corresponds that both of them serve as predator upon preys with almost similar preference.

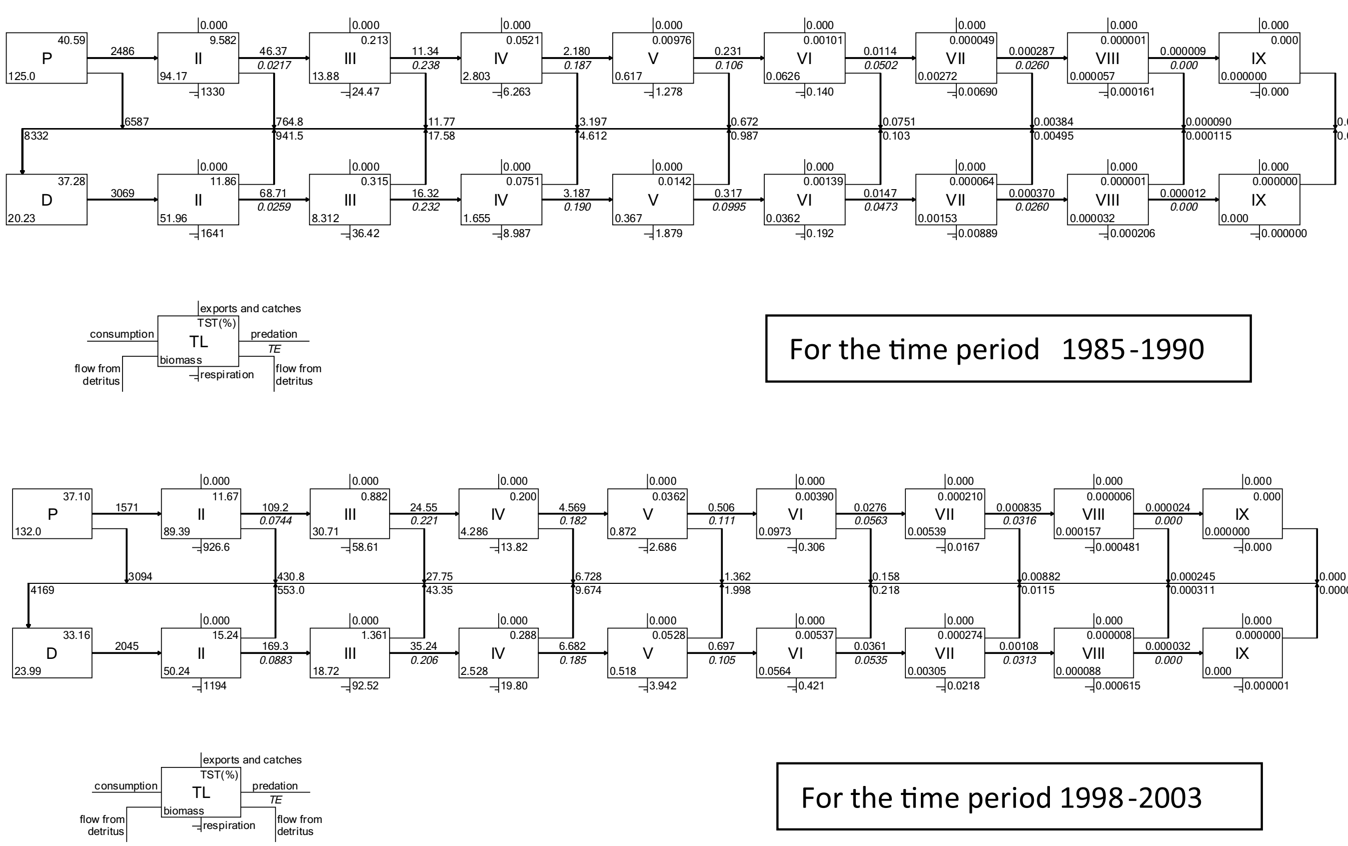

Fig. 5. Comparison of patterns of energy flow by Lindeman spine between two phases.

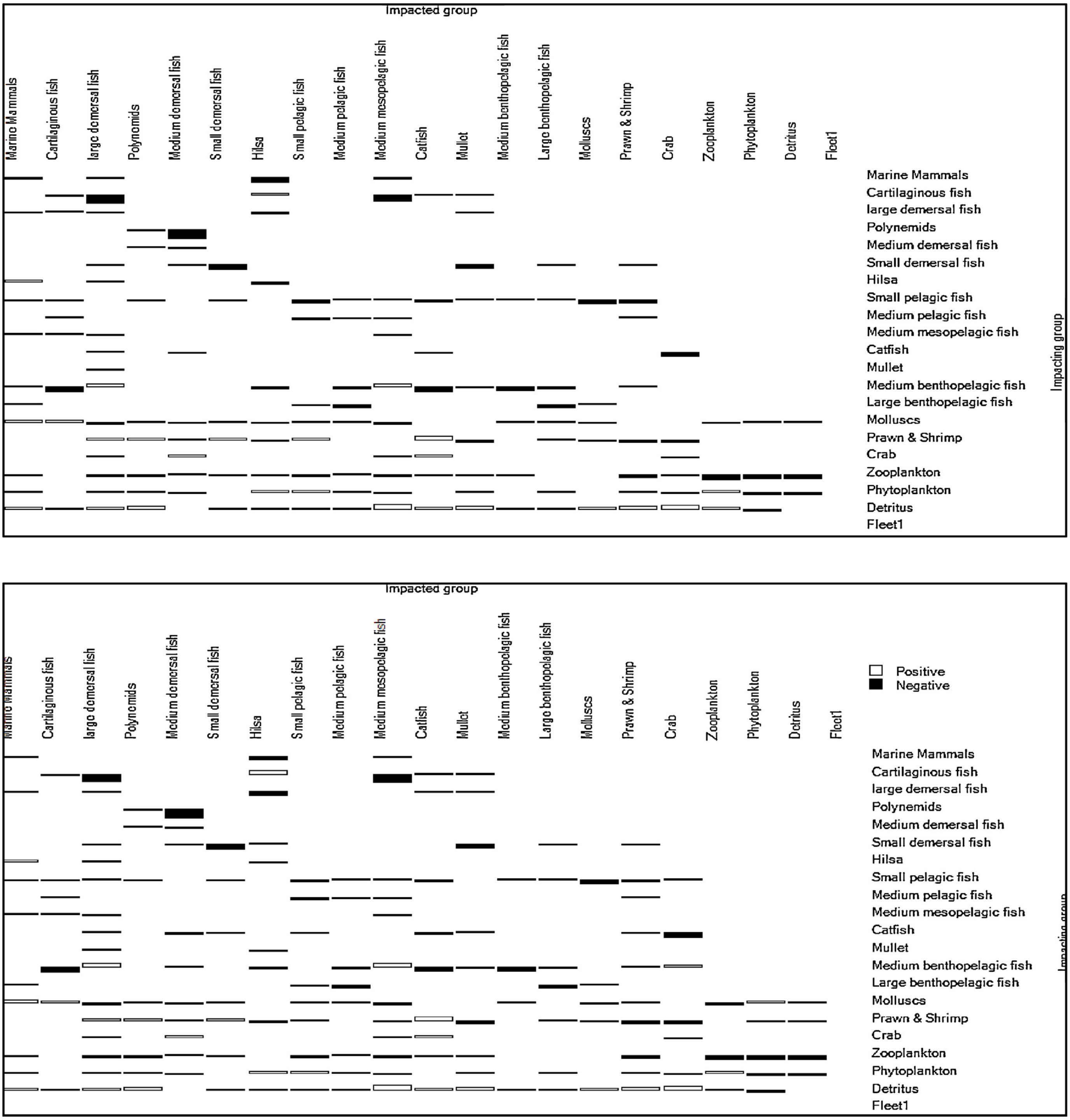

Fig. 6. The mixed trophic impact graph shows the direct and indirect impact of each group.

3.4. Keystone species

Cartilaginous fish are observed to have the most relative total impact (***RTI***) in the system (1.0) for both of the time periods and thus can be considered as keystone species in the system according to Libralato et al. (2006). *RTI* value of marine mammals decrease and that of the large demersal fish increases in later phase thus indicating the important role of large demersal fish in stability of system in later phase than in the previous; thus becoming more important in the keystoneness ranking compared to the marine mammals. Results also underline the important role of lower trophic level organisms like zooplankton, prawn and small pelagic fish in the system in terms of total effects and keystoneness during both phases. In the following Table 4, the functional groups of the system for both phases are ranked in repect to their relative index values. Dispite the individual differences observed, a Wilcoxon Signed Rank test indicates no statistially significant differences in the keystonnenss distributions (W = 197, p = 0.6404).

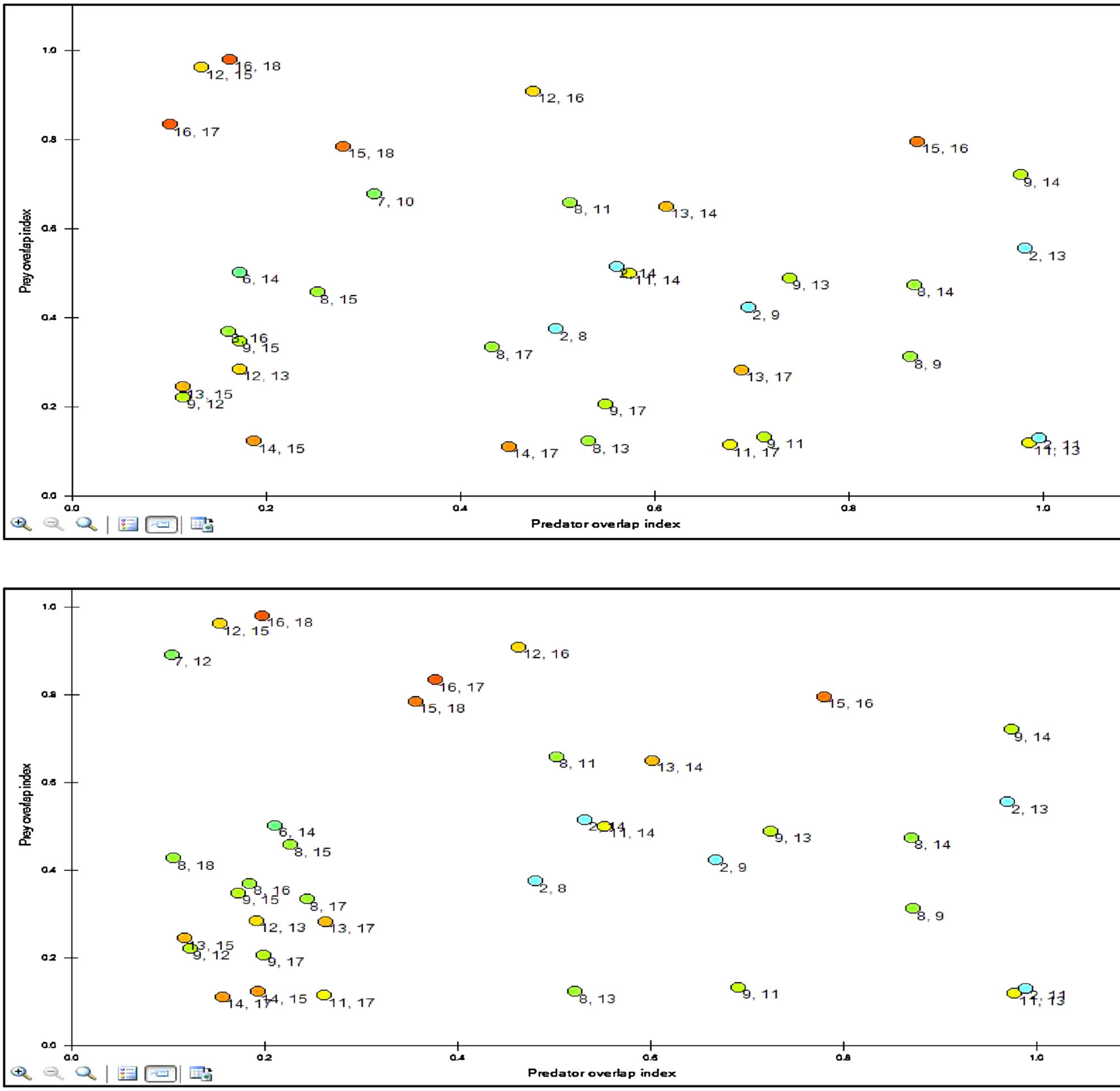

Fig. 7. Niche overlap plot for the time periods 1985–1990 and 1998–2003 respectively.

Table 4
Keystone index of the system for two different time periods.

Group	Relative total impact for time period 1985–1990.	Relative total impact for time period 1998–2003.
Cartilaginous fish	1	1
Medium benthopelagic fish	0.875	0.838
Polynemids	0.87	0.769
Prawn	0.7	0.612
Zooplankton	0.645	0.559
Small pelagic fish	0.612	0.512
Marine Mammals	0.555	0.288
Molluscs	0.505	0.477
Small demersal fish	0.451	0.398
Phytoplankton	0.41	0.374
Catfish	0.407	0.517
Large benthopelagic fish	0.355	0.316
Crab	0.296	0.253
Medium pelagic fish	0.256	0.213
large demersal fish	0.249	0.412
Hilsa	0.229	0.211
Medium mesopelagic fish	0.141	0.125
Mullet	0.141	0.129
Medium demersal fish	0.0545	0.0476

3.5. System statistics for the Hooghly Matla estuarine ecosystem

The balanced Ecopath models prepared for the Hooghly estuary show an Ecopath pedigree index value of 0.541 and a measure of fit of 2.649 (Table 5). This suggests that the model is well suited for the system under consideration. Beside this, in Table 3 All of the *EE* values of the functional groups are less than 1 and most of the *P/Q* values are within the acceptable range of 0.05 and 0.3 except a few thus meeting the criterion for a balanced model (Christensen et al., 2005). According to the summary statistics calculated here, *TPP/TB* ratios are 40.34 and 41.56 and *TPP/TR* are 3.22 and 4.49 for phase 1 and phase 2 respectively indicating the gradual degradation of the system over time. According to the summary statistics, the *TB/TST* value is 0.020 for phase 1 and 0.011 for phase 2 suggesting that the ecosystem shows degradation in the later phase. A slight increase of system omnivory index is observed from phase 1 (0.236) to phase 2 (0.239). Omnivory index (***OI***) is zero for prawn suggesting that it feeds on a single trophic level i.e. it is most specialized group in the system. It can be noted that there are some peculiarities for the prawn component for this system; prawn is generally a diverse feeder and thus generally have higher omnivory index. These peculiarities can be explained by further focussed study in the future. Large value for medium benthopelagic fish (0.837) indicates their large feeding spectrum (highest omnivorous animal in the HMES). Marine mammals, cartilaginous fish, small demersal fish, large benthopelagic fish with a high *OI* value (>0.3) suggests that they have the most diverse diets.

3.6. Stability and resilience indices

At a community scale, throughput is dominated by phytoplankton and detritus and then gradually decreases towards upper trophic level. Phase 1 of the HMES ecosystem has a *TST* of 22390.260 t km^{-2} year^{-1}, and phase 2 shows TST of 12615.76 t km^{-2} year^{-1}, which is a 44% reduction. Relative ascendency decreased from 36.32% to 30%, and the 6.32% difference was gained in the relative system overhead (63.68%–70%). Recycling was lower in phase 1 than phase 2 (FCI was 7.747% and 8.396%, respectively).

4. Discussion

4.1. Trophic structure of the ecosystem

In the HMES, a strong competition for similar resource type among most of the economically important fish is observed. Average ecosystem trophic level (2.72) is quite similar with Campeche Sound estuary, Gulf of Mexico (TL = 2.6; Rejón, 2004) where local economy is mainly based on fisheries. High ecotrophic efficiencies of most of the fish group suggests that these groups are highly predated within the ecosystem or exploited by fisheries leaving almost no individuals to die from natural mortality thus adding relatively small flow to the detritus pool. A null EE (0) for dolphin suggests that it has no predators and also is not otherwise utilized. On comparing the two different periods, an increase in biomass of top predators (most of fishes) appears to result in the decrease of biomass in second trophic level, most specifically zooplankton. There is also a biomass increase for the lower trophic level group (such as phytoplankton, detritus) that appears to be due to top-down effect. It is most common on estuary where most of top predators (fishes) are expoited through overfishing.

The increased biomass of most of fish can be explained by the following. Initially when fishing pressure is increased for a species, the initial biomass of that particular population decreases but at the same time available resource for the remaining population might increase due to lower intraspecific competition. It leads to optimal growth of the remaining population and this tends to replenish that particular population. But due to continuous exploitation the average body size and age of fish stock decreases as most of these individuals are caught before they could attain maturity. On consideration of following biomass equation $\boldsymbol{B = Y/F}$, overall biomass of most of the fish species is seen to increase in phase 2 due to increase of the catchment (*Y*) of most of fishes as well as remaining fish population (Mitra et al., 1997; Nath et al., 2004). But this increase only happens for few years. The ecotrophic efficiency of fish groups increases and approaches 1 (maximum value of exploitation). It is the indication of degradation of ecosystem due to fishing pressure (overfishing).

From the *PPR* values, it also appears that all of the groups require more primary production to support biomass of each compartment in phase 2 than phase 1, but this is most pronounced for zooplankton. It indicates the higher degree of expolation, specifically on top predator fishes in phase 2 due to overfishing and according to top down effect, utilization pressure on the primary producer increases gradually but the biomass of the phytoplankton group also increases. This result may seem contradictory to the notion of top-down effect related to overfishing, but the fish population does not occupy single trophic level but lies in between the continuous TLs of 2.25–3.89. As a result some groups of fish may be consumed by other larger fish groups (prey-predator relationship). Thus, the overfishing effect is not the sole factor for explaining the top-down effect in this case. To compensate this utilization pressure, the model exhibits an increase of mean transfer efficiency from 10.21% in phase 1–14.74% in phase 2. Respiration flows also decrease between the two phases, which balanced the energy budget of each trophic level.

4.2. Keystone of the ecosystem and mixed trophic impact study

Cartilaginous fish have a high keystoneness index like other ecosystems such as Bay of Biscaya (Ainsworth et al., 2001), Eastern tropical Pacific (Watters et al., 2003), Floreana of Galapagos (Okey et al., 2004) and Hong Kong (Buchary et al., 2002). Results from the keystoneness analysis highlight the importance of the medium-low trophic levels, such as zooplankton, prawn, small pelagic fish in the functioning of these systems, which may be due to their essential role in capturing energy during consumption of plankton and making it available to the higher trophic levels. These results are well aligned with the *MTI* results. The medium-low trophic levels transfer energy from the bottom of the food chain to the top and occupy the central positions in this food web. These results are quite similar with coastal and semi-enclosed marine environments such as Northern and Central Adriatic Sea (Coll et al., 2007), Georgia Strait (Jarre-Teichmann and Christensen, 1998; Pauly et al., 1998; Walters et al., 2005), Chesapeake Bay (Baird and Ulanowicz, 1989), Bolinao reef (Aliño et al., 1993) and Gulf of Thailand (Christensen, 1998; Walters et al., 2005).

Results of *MTIs* routine illustrate the importance of lower trophic level groups, particularly detritus in the ecosystem, indicating a degree of 'bottom-up' control in the ecosystem. The positive impact of phytoplankton is greatest on their major consumers. The analysis of mixed trophic impact shows that most of the fishery resource species are important trophic components in the system, with strong impacts on the other components as predators, prey or competitors (Neira et al., 2004). The trophic cascade can be found in the present context, i.e. predators have negative impact on their prey but has an indirect positive impact on prey of their prey (top down control). For example, large benthopelagic fish has negative impact on polynemids, small pelagic fish and crab but indirect positive impact on phytoplankton that is consumed by small pelagic fish and crab.

Table 5
System statistics, flows and higher-order indices of Hooghly Matla estuary for the time period 1985–1990 and 1998–2003.

Parameter/ecosystem indices	Unit	Phase 1 (1985–1990)	Phase 2 (1998–2003)
Sum of all consumption	$t\,km^{-2}\,year^{-1}$	5743.80	4009.51
Sum of all exports	$t\,km^{-2}\,year^{-1}$	5262.76	2124.3
Sum of all respiratory flows	$t\,km^{-2}\,year^{-1}$	3051.45	2313.11
Sum of all flows into detritus	$t\,km^{-2}\,year^{-1}$	8332.25	4168.85
Total system throughput	$t\,km^{-2}\,year^{-1}$	22,390.26	12615.76
Sum of all production	$t\,km^{-2}\,year^{-1}$	11374.84	11276.31
Calculated total net primary production	$t\,km^{-2}\,year^{-1}$	9831.25	10381.80
Total primary production/total respiration		3.22	4.49
Net system production	$t\,km^{-2}\,year^{-1}$	6779.81	8068.7
Total primary production/total biomass		40.34	41.57
Total biomass/total throughput	$year^{-1}$	0.02	0.01
Total biomass (excluding detritus)	$t\,km^{-2}$	236.53	257.35
System Omnivory Index		0.24	0.24
Ecopath Pedigree index		0.54	0.54
Measure of fit, t*		2.65	2.65
Ascendancy	Flowbits	22287 (36.32%)	12993 (30%)
Throughput	$t/km^2/year$	22390.26	126165.760
Overhead	Flowbits	39077 (63.68%)	30324 (70%)
Development capacity		61365	43317
Throughput cycled (excluding detritus)	$t/km^2/year$	39.61	42.65
Predatory cycling index(excluding detritus)	% of throughput	0.69	0.99
Throughput cycled (including detritus)	$t/km^2/year$	1735	1059
Finn's cycling index	% of throughput	7.75	8.4
Finn's mean path length		2.69	2.84
Finn's straight through path length(excluding detritus)		1.86	1.83
Finn's straight through path length(including detritus)		2.48	2.61

4.3. Impact of overfishing on the ecosystem

In this system, mean trophic level of catches (3.12) is quite similar with South Brazil Bight coastal ecosystem (2.99; Gasalla and Rossi-Wongtschowski, 2004). Mean trophic level of fishes (>3) is greater than the average ecosystem trophic level (2.71) indicating that most of fishes occupy top position of estuarine food web and most of are captured and utilized by fishing. So the available resource for next trophic level (including marine mammals and cartilaginous fish) for predation is reduced. A constant fishing pressure is thus observed on this ecosystem and the trophic structure of this ecosystem is badly impacted by such overfishing. As a consequence, it can be assumed that whole ecosystem will decline in the near future if sustainable fisheries management is not applied. Further, overfishing can change the fishery target of this system as well as the trophic structure. For example, removal of top predator fish such as small demersal fish, medium benthopelagic fish from higher trophic levels of the food web, result into alterations of food web structure by increasing the biomass of their prey such as *Hilsa*, small pelagic fish and other forage fish. So fishing target is shifted from fish-eating, high trophic level fish to plankton-feeding, small, lower trophic level fishes and invertebrates, which will start to dominate the fishery catches in the near future.

4.4. Trends of change in ecosystem efficiency

Comparison of network indices for the same ecosystem at two different phases, implies a difference of functioning at two different time periods. The change in indices of ecosystem maturity for phase 1 and 2 follow the expectations of Odum (1969) for an impacted system.

The observed 3% increase in *TPP*/*TB* and 39% increase in *TPP*/*TR* indicate that the system is slowly degrading. In addition, the 45% decrease in *TB*/*TST* dalso suggests that the ecosystem functioning has declined. Usually the smaller the amount of material or energy flowing through the system, the smaller is the throughput, which is another character of system degradation. In this system, we observed a decrease in the sum of all exports, flows into detritus, total system throughput, sum of all productions, sum of all consumptions and respiratory flows. Based on these indicator differences, we conclude that phase 2 is less mature than phase 1 of the HMES.

The ascendency decrease (from 36.32% to 30%) also suggests that the system is under stress in phase 2, which is likely due to overfishing. However, the linked increase in system overhead (from 63.68% to 70%) indicates that the food web may be able to better resist perturbations and recover from unexpected disturbances. The relative ascendancy (36%) of phase 1 is quite similar in Campeche Sound (45%) (Rejón, 2004) and in Gulf of Paria (42%) (Manickchand-Heileman et al., 2004), which indicate that previously this system was of relatively high productive nature. The relative ascendancy (30%) of phase 2 is more similar to the Veracruz continental shelf system (31.6%) (Cruz-Escalona et al., 2007). According to Wulff and Ulanowicz (1989) when an ecosystem is stressed, its relative amount of cycling increases but on the other hand Jørgensen et al. (2000) reported that an increase in *FCI* is a sign of system growth and development According to (Goerner et al., 2009) as a system approaches maturity, its ability to deal with stress decreases. These ideas are somewhat contradictory to each other and is one of the uncertainities of ENA analysis and is a scope for future study. In this ecosystem, *FCI* increases by 8% which again suggests that phase 2 is under a more stressed situation than that of phase 1. This increase in recycling may be due to a homeostatic response to maintain the resources in circulation in the disturbed system (Wulff and Ulanowicz 1989). Considering the phase 2 *FCI*, we observe that the system appears less mature than the Gulf of Mexico (14.8; Vidal Hernandez, 2000) but more mature than Campeche Sound (4.47; Rejón, 2004) and Alvarado Lagoon shelf system in Veracruz (4.1; Cruz-Escalona et al., 2007).

5. Conclusion

Modelling the trophic structure of the HMES with adjacent mangroves for two different time periods let us quantify the biomass of standing stocks and the exchanges of matter and energy between system components for the two time periods. Species are distributed over seven discreet trophic levels (Lindeman spine) with the trophic level 3 playing an important role in the energy transfer either through prey or predator interactions. Strong competition is found among groups aggregating around trophic level 3. Due to fishing down the food web, we expect that landings of these fish will decrease in near future which may affect the food web. Several whole system statistics and network flow indices from the model output indicate that overexploitation result into stressful situation and increase in the degree of instability of this ecosystem. Lastly it can be concluded that the model output improves our understanding of the predator–prey interactions among different components in this system and provide us with a summary of the trophic structure of an exploited ecosystem with a focus on energy flow.

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