Regional Studies in Marine Science 61 (2023) 102861

Contents lists available at ScienceDirect

Regional Studies in Marine Science

journal homepage: www.elsevier.com/locate/rsma

Food web structure and trophic interactions of the Northern Bay of Bengal ecosystem

Sachinandan Dutta [a,b,*], Sourav Paul [c,**], Sumit Homechaudhuri [a]

[a] *Aquatic Bioresource Research Laboratory, Department of Zoology, University of Calcutta, Kolkata 700019, India*
[b] *Sultan Qaboos University, College of Agricultural and Marine Sciences, Department of Marine Science and Fisheries, Al-Khoud 123, Sultanate of Oman*
[c] *Estuarine and Coastal Studies Foundation, West Bengal, India*

A R T I C L E I N F O

Article history:
Received 8 September 2022
Received in revised form 27 December 2022
Accepted 1 February 2023
Available online 4 February 2023

Keywords:
Ecotrophic efficiency
Trophic level
Mixed trophic impact
Niche overlap
Keystone species
India

A B S T R A C T

Ecosystem models are essential for understanding the complex trophic interactions of a marine food web. An Ecopath model was built on Northern Bay of Bengal (NBoB) ecosystem considering 29 functional groups to understand the trophic interactions and ecosystem functions. Results showed that the mean trophic level of the NBoB ecosystem was 3.146. The ecotrophic efficiency of the ecosystem ranged from 0.510 to 0.995. Species such as *Arius* spp., *Tenualosa ilisha* and *Harpadon nehereus* showed higher ecotrophic efficiencies which suggested that those species were highly exploited. The total system throughput was 4163.712 t/km^2/year. Further, Finn's cycling index was 14.39% of the total ecosystem throughput and the Finn's mean path length was 3.203. The ratio of total primary production to total respiration was 1.445 and the total transfer efficiency of the NBoB ecosystem was 16.43%. Those statistics suggested that the NBoB is a highly efficient detritus-based ecosystem which is possibly in its early stage of maturity. The mixed trophic impact analysis showed that the majority of the functional groups had negatively affected the trophic interactions of the NBoB ecosystem but the detritus, phytoplankton, benthos and non-penaeid shrimps had positively affected the trophic interactions. Use of trawl and bag nets had considerable negative impacts on the various functional groups of the NBoB ecosystem. In the NBoB ecosystem elasmobranchs was the keystone group. *Upeneus* spp. and Polynemidae, and *Caranx* spp. and *Carangidae* had considerable niche overlaps in the NBoB ecosystem. Overall increases in the mean trophic level, Finn's cycling index, gross efficiency and fluctuations of the total biomass were the key indicators of the changes that the NBoB is experiencing in recent years. That may affect the trophic interactions of the NBoB foodweb; therefore, regular monitoring of the components of the food web is recommended.

1. Introduction

Complexity of a marine food web increases with its stage of maturity because in the early-stage of maturity predators are generally less diverse and variable compared to a stage when a food web reaches to its maturity (Orians, 1975; Christensen, 1995; Christensen and Pauly, 1998; Brinck and Jensen, 2017; Bossier et al., 2020). Trophic structure and functions of a marine food web are largely impacted by over-exploitation by fisheries, which in consequence may trigger trophic cascades (Lynam et al., 2017). The global mean trophic level (MTL) of fisheries landings is declining possibly as a consequence of increasing fishing pressure which is meeting the ever-increasing global demand for nutrition (Pauly et al., 1998; Halpern et al., 2008). So, adverse effects on trophic interactions of a marine food web are likely (FAO, 2001; Pikitch et al., 2004; Babcock et al., 2005; Gavaris, 2009), for example Western Indian Ocean (WIO) lost its 63.3% adult tuna biomass between 1954 and 2006, which is the highest loss on a global scale, and it even surpassed the loss of tuna biomass of Pacific (49.2%) and Atlantic (49.6%) oceans (Juan-Jordá et al., 2011). The WIO is experiencing changes of trophic structure and functions but that does not necessarily mean that the forage fish stocks of WIO are in decline (Danckwerts et al., 2014). On the contrary, from 1950 to 2018, total catches of East Indian Ocean (EIO) had shown a consistent upward trend, and during that period *Tenualosa ilisha*, *Clupea pallasi*, and *Rastrelliger kanagurta* were among the most important catch species accounting for more than 10% of total fisheries catch of the EIO (Quan et al., 2021).

* Corresponding author at: Sultan Qaboos University, College of Agricultural and Marine Sciences, Department of Marine Science and Fisheries, Al-Khoud 123, Sultanate of Oman.
** Corresponding author.
E-mail addresses: s.dutta@squ.edu.om, duttasachi@gmail.com (S. Dutta), souravpaul4@gmail.com (S. Paul).

https://doi.org/10.1016/j.rsma.2023.102861
2352-4855/

Trophic interactions of marine food webs are less understood because data availability is limited from marine biomes (Orians, 1975; Maureaud et al., 2017; Bossier et al., 2020). The majority of catch and landings data of Arabian Sea and Bay of Bengal (BoB) are essentially low resolution and poor quality. In some cases, species composition data are available, but such data are either primarily anecdotal or significantly biased towards easily recognizable species (Temple et al., 2018). Fisheries management of Arabian Sea and BoB has traditionally focused on a single species; however, that strategy has significant drawbacks because multispecies open access fisheries are common in the region (Vivekanandan, 2001). For such reasons, fisheries research is moving from a single-species evaluation and policy making to a more comprehensive multi-species and ecosystem-based approach by studying different trophic levels of a food web and trophic interactions (Link, 2002; Pikitch et al., 2004; Hilborn et al., 2005; Harvey et al., 2012).

A trophic mass-balance model provides a theoretical framework to estimate the impacts of fisheries on a marine food web and that is often used to understand the complex trophic interactions between multiple functional groups of a food web (Vasconcellos et al., 1997; Christensen et al., 2008). In order to construct any of such ecosystem model, it is important to link a species to an ecosystem, and to understand the way an ecosystem is systematically measured by complex but retraceable representations of energy flow, trophic flow, assimilation efficiency and functional response (Villanueva et al., 2006). Trophic mass-balance models could be developed by using Ecopath with Ecosim (EwE) (https://ecopath.org/) software (for ecosystem trophic mass balance analysis (Ecopath), with a dynamic modeling capability (Ecosim)) which is a free and is considered as a comprehensive modeling tool developed for better understanding and analyzing the effects of fishery management policies, establishment of marine protected areas, long-term environmental changes of marine biomes (Pauly et al., 2000; Christensen and Walters, 2004). Multiple indices could be calculated from an Ecopath model using EwE software in order to evaluate and compare the stability and the maturity of a marine food web and the direction of trophic interactions that are running within the food web (Christensen and Walters, 2004; Harvey et al., 2012). Connectance Index (CI) and System Omnivory Index (SOI) indicate the complexity of an ecosystem's inner connectivity and the stage of maturity of an ecosystem (Christensen and Pauly, 1993; Christensen and Walters, 2004). The Finn's Cycling Index (FCI) determines the degree of recycling in an ecosystem (Christensen et al., 2008). Keystone index indicates the key species of an ecosystem (Su, 2016). The proportion of prey and predatory shared between different functional groups could be calculated from the niche overlap index (Lassalle et al., 2014).

The Arabian Sea and BoB are landlocked from the north by the continental Asia (Shenoi et al., 2002) and are data poor because only a few studies (Vivekanandan et al., 2003; Dutta et al., 2017; Guenette, 2014; Ullah et al., 2012; Das et al., 2018) have ever focused on ecosystem models. Vivekanandan et al. (2003) suggested that off southwest coast of India the annual average fish catch had exceeded the estimated biomass of large and medium size predators, demersal feeders and detritivores; therefore, the catch of large zoobenthic and mesopelagic feeders such as carangids and the plankton feeders (e.g. sardines, shads, whitebaits, clupeids and scads) may increase in future. The Northern Bay of Bengal (NBoB) is a biodiverse marine ecosystem in terms of its fish assemblage (Dutta and Paul, 2021). Previous studies suggested that the NBoB has a low ecological efficiency but a high rate of energy transfer from the lower trophic levels of the food web (Dwivedi, 1993; De et al., 2011; Ullah et al., 2012). The NBoB is facing overharvesting pressure of its key fishery resources such as Hilsa shad (*T. ilisha*) (Dutta et al., 2021b), which may cause partial disappearance of one or more trophic levels leading to a trophic cascade (Chuenpagdee et al., 2006). The food web of the NBoB is mainly consist of detritivores and planktivorous organisms where phytoplankton and detritus positively affect many other functional groups (Dutta et al., 2017). Ullah et al. (2012) worked on the NBoB with 14 functional groups and reported MTL of 2.45. Dutta et al. (2017) considered 15 functional groups in their model and reported MTL of 2.716 for the NBoB ecosystem. Later, Das et al. (2018) considered 32 functional groups in their model and suggested that the NBoB ecosystem is a developing one and has MTL of 3.115, which is higher than the MTL suggested by Dutta et al. (2017) and Ullah et al. (2012). Those changes of MTL of the NBoB ecosystem in recent years have prompted us to build a steady state mass balance model on the NBoB ecosystem considering 29 functional groups. The objectives include (i) illustration of the trophic interactions and energy flow pathways, (ii) define the trophic functions using holistic ecosystem properties and flow indices, (iii) the development status (i.e., maturity) of the ecosystem (iv) estimate the proportion of prey and predators shared by various functional groups, and (v) distinguish the impact of ecological groups along with the identification of keystone species or group.

2. Methods

2.1. Study area and data collection

The study was conducted in the NBoB off West Bengal, India (see Fig. 1). The NBoB and its coastal-fringes are the nursery of innumerable coastal-marine fish species that are commercially harvested by India and Bangladesh (Islam, 2003; Sarkar and Bhattacharya, 2003). Length (cm) and weight (g) data of some of the important species (*Scomberomorus* spp., *Arius* spp., *T. ilisha, R. kanagurta*, Polynemidae and *Sardinella longiceps*) were collected monthly in 2015 from the Fraserganj fishing harbour of West Bengal, India (see Fig. 1) adjacent to NBoB. Length and weight data were used to analysis the population parameters (e.g., growth, mortality and exploitation rate). Population parameters of the other functional groups were collected from different sources (see Appendix A). Annual fish catch or yield (Y) data of 2006 to 2015 of the NBoB (see Fig. 1) were obtained from the Annual Report of 2016 of the Department of Fisheries (DoF), Government of West Bengal, India (Department of Fisheries, 2016). Those datasets were used in this study to calculate the biomass of the functional groups. Catch through gill, trawl and bag nets were considered in the study because those are the most common fishing gears (above 90% of the total catch is done by those three types of nets) used by the fishermen who fish off West Bengal, India.

2.2. Mass balance modeling approach

The EwE software version 6.5 was used to develop a mass balance model which has an equation that maintains an equilibrium between production with consumption i.e. how much mass is consumed by a prey + biomass caught (catch) + biomass accumulation + net migration in or out of the system.

$$B_i(\frac{P}{B})_i EE_i = Y_i + \sum B_j(\frac{Q}{B})_j DC_{ji} + BA_i + NM_i$$

where, B_i and B_j are the biomass of the functional group i and j; $(\frac{P}{B})_i$ is the production/biomass; EE_i is the ecotrophic efficiency of the ecosystem; $\frac{Q}{B}_j$ is the food consumption per unit biomass of j; Y_i is the fisheries yield; DC_{ji} is the fraction of j in the diet of i; BA_i is the biomass accumulation and NM_i is the net migration of the functional group. The inputs for the model are B, $\frac{P}{B}$, $\frac{Q}{B}$, Y and DC, whereas the EE is estimated by the software. The units of the model are t km^{-2} yr^{-1} wet weight for energy flow and t km^{-2} for biomass.

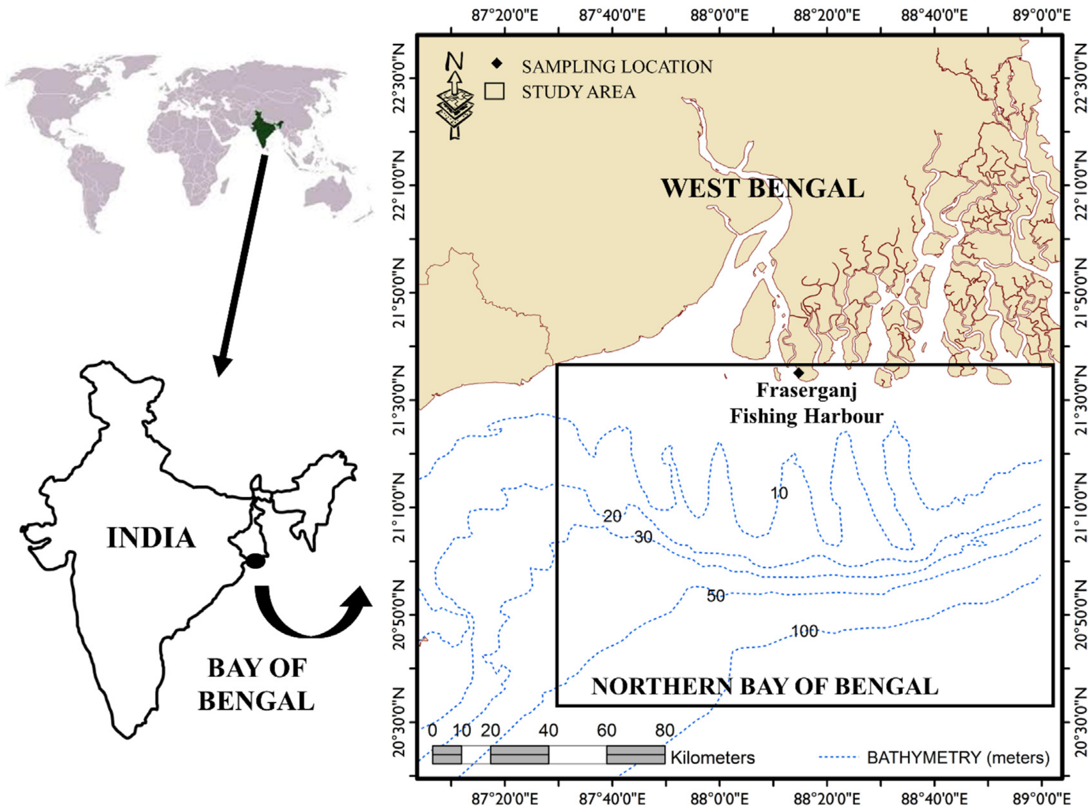

Fig. 1. Map of the study area and sampling site in the Northern Bay of Bengal off West Bengal, India with bathymetry contour.

2.3. Functional groups

Twenty-nine functional groups were considered in the model out of which 28 were living groups and one detritus group. Phytoplankton group was considered as the producers of the NBoB ecosystem. Elasmobranchs, coastal tunas, *Harpodon nehereus*, Sciaenidae and *Arius* spp. were considered as the top predators of the ecosystem. Table 1 described the NBoB ecosystem model consists of 29 functional groups and input parameters of the model. The functional groups were identified based on their ecological and biological similarities such as feeding habits, habitats, growth and so on. For each functional group, key parameters (see Appendix A) and diets (see Appendix B) were compiled from the previously published literatures and reports.

2.4. Model analysis and indices

Diet composition studies focused on fish and invertebrates are rare for the NBoB; therefore, literatures that focused on same (or similar) species of elsewhere in the tropics had to be considered (see Appendix A) along with the information available in the FishBase (Froese and Pauly, 2021). Biomass (B), Production/ Biomass ratio $\left(\frac{P}{B}\right)_i$ and Consumption/Biomass ratio $\left(\frac{Q}{B}\right)_i$ were obtained either from the previously published literature or by using length, weight and growth data fitted to empirical equations (Pauly et al., 2000; Palomares and Pauly, 1998). Growth and mortality of the *Scomberomous* spp., *Arius* spp., *T. ilisha, R. kanagurta*, Polynemidae and *Sardinella longiceps* were calculated from the length frequency analysis.

Biomass of each functional group was estimated from the equation of Biomass (B) = Yield (Y)/ Fishing mortality (F) (Gulland, 1971). Biomass of the benthos was collected from the Holmgren (1994). Reference biomass of zooplankton and phytoplankton groups were taken from Mustafa (2003). Detritus biomass was estimated using an empirical equation based on primary production and depth of the photic zone (Pauly et al., 1993):

$$\mathrm{Log}_{10}D = -2.41 + 0.954 * Log_{10}(PP) + 0.863 * Log_{10}(E)$$

where PP is the primary productivity (i.e., gC/m^2/year) and E is the depth (m) of the euphotic zone. The average euphotic depth of the study area was 15 m. The carbon (C) was transformed in wet weight by assuming a ratio of 1:9 (Pauly and Christensen, 1995).

The Production/ Biomass ratio was calculated from the Beverton and Holt (1957) equation of total mortality *(Z = P/B)* following the Von Bertalanffy Growth Function (VBGF).

$$Z = \frac{P}{B} = K * \frac{L\infty - \bar{L}}{\bar{L} - L'},$$

where $L\infty$ is the asymptotic length, i.e., the mean size of the individuals of a population would reach if those individuals live and grow indefinitely; K is the VBGF curvature parameter (i.e., rate at which $L\infty$ is approached); and $\bar{L}$ is the mean length of the fish population. Here, L' represents the mean length of the first catch assuming knife-edge selection. $\bar{L}$ must be > L'. The P/B ratios of the phytoplankton and zooplankton were taken from the Guenette (2014) and the Vivekanandan et al. (2003), respectively.

Consumption is the intake of food by a functional group over a considered time period and in the Ecopath model it is generally taken as a ratio of consumption over biomass (Q/B). Absolute consumption computed by Ecopath is generally expressed in 't km^{-2} year^{-1}' but the Q/B is a ratio so it is unit less. The Q/B was calculated following the equation

$$\log(Q/B) = 7.964 - 0.204 \log W\infty - 1.965T' + 0.083A + 0.532h + 0.398d \text{ (Palomares and Pauly, 1998)}$$

where W∞ is the asymptotic weight (g), *T'* is an expression for mean annual temperature of the water body, expressed using *T'*

Table 1
Input data of the Ecopath model built on the Northern Bay of Bengal ecosystem off West Bengal, India considering different functional groups.

Sl no	Functional groups	Landing	Bi	P/B	Q/B	P/Q
1	Elasmobranchs	0.372	0.930	0.613	-	0.2
2	Coastal tunas	0.006	0.080	0.513	-	0.2
3	*Harpadon nehereus*	0.874	0.387	4.560	15.255	–
4	*Scomberomorus* spp.	0.030	0.180	3.390	11.831	–
5	*Arius* spp.	1.510	1.110	1.895	6.691	–
6	*Lates* spp. and *Lutjanus* spp.	0.566	0.760	1.690	5.690	–
7	Sciaenidae	1.285	0.710	2.610	9.542	–
8	Muraenesox	0.011	0.089	0.472	-	0.2
9	*Tenualosa ilisha*	0.934	0.680	3.524	22.410	–
10	Leiognathidae	0.052	0.380	2.950	27.434	–
11	*Upeneus* spp.	0.011	0.270	4.510	15.481	–
12	*Hemiramphus* spp.	0.013	0.470	3.596	12.059	–
13	*Rastrelliger kanagurta*	0.561	0.483	3.500	17.796	–
14	Mugilidae	0.456	0.980	2.880	11.899	–
15	Polynemidae	0.059	0.210	4.210	17.640	–
16	*Caranx* spp.	0.136	0.630	2.035	10.735	–
17	Carangidae	0.383	0.695	2.220	7.950	–
18	Stromateidae	0.511	0.500	1.950	9.655	–
19	*Sardinella longiceps*	0.263	1.270	4.980	38.929	–
20	Engraulidae	0.366	1.300	3.555	19.910	–
21	Trichiuridae	0.227	0.320	1.860	9.549	–
22	Penaeid shrimps	0.515	0.910	5.750	17.138	–
23	Non-penaeid shrimps	0.250	0.710	13.430	25.336	–
24	Marine crust crab	0.018	0.882	4.690	17.701	–
25	Squid and cuttlefish	–	1.300	3.977	16.537	–
26	Benthos	–	13.745	8.605	-	0.3
27	Zooplankton	–	10.000	40.000	119.700	–
28	Phytoplankton	–	13.000	100.000		–
29	Detritus	–	36.537			–

Landings (t/km^2/year); Bi = Initial biomass (t/km^2); P/B = Production/Biomass (/year); Q/B = Consumption/Biomass (yr^{-1}); P/Q= Production/Consumption (yr^{-1}).

= 1000/Kelvin (Kelvin = °C + 273.15), A is the aspect ratio, h is a dummy variable expressing food type (1 for herbivores, 0 for detritivores and carnivores), and d is a dummy variable that also express type of food (i.e. 1 for detritivores, 0 for herbivores and carnivores). The Q/B of the zooplankton was taken from the Ullah et al. (2012). The Q/B of elasmobranchs, coastal tunas, muraenesox and benthos were estimated from the input of P/Q value.

Diets of different species and families were collected from the published literature and reports and from Fishbase (Froese and Pauly, 2021) (see Appendix A) and a diet matrix of the functional groups was built (see Appendix B).

The ecotrophic efficiency (EE) is the proportion of the production that is used within the ecosystem (Christensen and Pauly, 1998). The values of EE range from 0 to 1 and an EE value may approach 1 for a group that faces considerable predation pressure (Christensen et al., 2008). In a few cases EE could be > 1, which specifies that total energy demand surpasses the total production of the system (Christensen et al., 2008). To achieve a balanced model (i.e., $EE_i \leq 1$ for all the groups i) a value greater than 1 ($EE \geq 1$) necessitates the examination of data inconsistencies, adjustment of biomass, P/B ratio, and diet composition, beginning with the factors judged less reliable (Blanchard et al., 2002; Guenette, 2014).

A model is considered balanced when: (i) realistic estimates of the missing parameters are calculated (EE < 1), (ii) values of P/Q or gross efficiency of food conversion is generally between 0.1 and 0.35 for most of the functional groups except the fast growing groups which often have higher values of P/Q and the top predators which generally have lower values of P/Q (iii) respiration/biomass (R/B) ratios are generally high for the small organisms and low for the top predators (iv) respiration/food assimilation (R/A) ratios are often less than 1 and the top predators generally have higher R/A ratios compared to the lower trophic groups (v) net efficiency of food conversion is often less than 1 for all the functional groups (vi) Production/Respiration (P/RA) < 1.0. (Christensen et al., 2008; Heymans et al., 2016). In some cases, the EE of the functional groups could be >1, which indicates the demand of a functional group is too high to be sustainable (Christensen et al., 2008). A high value of the EE also means "other mortality" of that functional group is low, but the predation or fishing mortality is high (Christensen et al., 2008). In order to balance the EwE model properly the input parameters are generally adjusted in a manner that the EE does not exceed 1 (Harvey et al., 2012). The model is later balanced manually by adjusting the biomass, P/B ratios, and diet compositions (Christensen and Walters, 2004).

The Mixed Trophic Impact (MTI) analysis was carried out on the EwE software by using the Leontief (1951) matrix routine (Ulanowicz and Puccia, 1990; Libralato et al., 2006). The MTI emphasizes the nutritional interconnections among the different functional groups and explores direct and indirect effects among those functional groups through a complete food web analysis (Christensen and Walters, 2004) and returns a value range −1 to 1.

Keystone species or group could be identified from the MTI analysis (Valls et al., 2015). Presently, keystone index of Libralato et al. (2006) has been used. Keystone species could be recognized by plotting the relative overall effect (εi), which is derived from the MTI (m_{ij}), against the keystoneness (KS_i). The overall effect (ε_i) is defined as:

$$\varepsilon_i = \sqrt{\sum_{j \neq i}^{n} {m_{ij}}^2}$$

where, m_{ij} is derived from the MTI analysis as the product of all net impacts for all the possible pathways of the food web that connect prey i and predators j. The keystone value (KS_i) of a functional group was calculated as:

$$KS_i = log\left[\varepsilon_i(1 - p_i)\right]$$

Table 2
The modified input and output parameters of the Ecopath model of the Northern Bay of Bengal ecosystem off West Bengal, India.

	Functional groups	Trophic level	Biomass (t km^2)	Production/ Biomass (/year)	Consumption/ Biomass (/year)	Ecotrophic efficiency	Production/ Consumption (/year)	Flow to detritus (t/km^2/year)	Net efficiency	Omnivory index	Throughput (t/km^2/year)	Production/ respiration
1	Elasmobranchs	**4.182**	0.930	0.613	**3.064**	**0.919**	0.200	**0.616**	**0.250**	**0.211**	**2.756**	**0.333**
2	Coastal tunas	**3.900**	0.080	0.513	**2.566**	**0.885**	0.200	**0.046**	**0.250**	**0.293**	**0.205**	**0.333**
3	*Harpadon nehereus*	**3.495**	0.387	4.560	15.255	**0.992**	**0.299**	**1.194**	**0.374**	**0.062**	**5.904**	**0.597**
4	*Scomberomorus* spp.	**3.718**	0.180	3.390	11.831	**0.988**	**0.287**	**0.433**	**0.358**	**0.113**	**2.13**	**0.558**
5	*Arius* spp.	**3.529**	1.110	1.895	6.691	**0.995**	**0.283**	**1.497**	**0.354**	**0.466**	**7.427**	**0.548**
6	*Lates* spp. and *Lutjanus* spp.	**3.604**	0.760	1.690	5.690	**0.950**	**0.297**	**0.930**	**0.371**	**0.094**	**4.324**	**0.591**
7	Sciaenidae	**3.809**	0.710	2.610	9.542	**0.825**	**0.274**	**1.679**	**0.342**	**0.172**	**6.775**	**0.520**
8	Muraenesox	**3.493**	0.089	0.472	**2.358**	**0.945**	0.200	**0.044**	**0.250**	**0.417**	**0.21**	**0.333**
9	*Tenualosa ilisha*	**2.300**	0.680	3.524	22.410	**0.993**	**0.157**	**3.064**	**0.197**	**0.243**	**15.24**	**0.245**
10	Leiognathidae	**2.697**	0.380	2.950	27.434	**0.631**	**0.108**	**2.499**	**0.134**	**0.377**	**10.42**	**0.155**
11	*Upeneus* spp.	**2.828**	0.270	4.510	15.481	**0.964**	**0.291**	**0.880**	**0.364**	**0.439**	**4.18**	**0.573**
12	*Hemiramphus* spp.	**2.642**	0.470	3.596	12.059	**0.978**	**0.298**	**1.170**	**0.373**	**0.341**	**5.668**	**0.594**
13	*Rastrelliger kanagurta*	**2.833**	0.483	3.500	17.796	**0.988**	**0.197**	**1.739**	**0.246**	**0.441**	**8.639**	**0.326**
14	Mugilidae	**2.304**	0.980	2.880	11.899	**0.990**	**0.242**	**2.359**	**0.303**	**0.280**	**11.66**	**0.434**
15	Polynemidae	**3.066**	0.210	4.210	17.640	**0.894**	**0.239**	**0.835**	**0.298**	**0.243**	**3.704**	**0.425**
16	*Caranx* spp.	**3.122**	0.630	2.035	10.735	**0.979**	**0.190**	**1.380**	**0.237**	**0.243**	**6.763**	**0.311**
17	Carangidae	**3.162**	0.695	2.220	7.950	**0.987**	**0.279**	**1.124**	**0.349**	**0.236**	**5.525**	**0.536**
18	Stromateidae	**2.809**	0.500	1.950	9.655	**0.976**	**0.202**	**0.989**	**0.252**	**0.330**	**4.827**	**0.338**
19	*Sardinella longiceps*	**2.356**	1.270	4.980	38.929	**0.962**	**0.128**	**10.127**	**0.160**	**0.269**	**49.44**	**0.190**
20	Engraulidae	**2.790**	1.300	3.555	19.910	**0.976**	**0.179**	**5.288**	**0.223**	**0.347**	**25.88**	**0.287**
21	Trichiuridae	**3.293**	0.320	1.860	9.549	**0.964**	**0.195**	**0.633**	**0.243**	**0.024**	**3.056**	**0.322**
22	Penaeid shrimps	**2.444**	0.910	5.750	17.138	**0.986**	**0.336**	**3.195**	**0.419**	**0.296**	**15.6**	**0.722**
23	Non-penaeid shrimps	**2.444**	0.710	13.430	25.336	**0.983**	**0.530**	**3.757**	**0.663**	**0.296**	**17.99**	**1.964**
24	Marine crust crab	**2.754**	0.882	4.690	17.701	**0.893**	**0.265**	**3.565**	**0.331**	**0.478**	**15.61**	**0.495**
25	Squid and cuttlefish	**3.051**	1.300	3.977	16.537	**0.729**	**0.241**	**5.698**	**0.301**	**0.471**	**21.5**	**0.430**
26	Benthos	**2.314**	13.745	8.605	**28.684**	**0.510**	0.300	**136.763**	**0.375**	**0.269**	**394.3**	**0.600**
27	Zooplankton	**2.111**	10.000	40.000	119.700	**0.657**	**0.334**	**376.575**	**0.418**	**0.111**	**1197**	**0.717**
28	Phytoplankton	**1.000**	13.000	100.000		**0.655**		**448.944**		**0.000**	**1300**	
29	Detritus	**1.000**	36.537			**0.616**				**0.401**	**1017**	

Values marked in **Bold** are calculated by the EwE software.

where, p_i is the contribution of the functional group to the total biomass of the food web.

The SOI is defined on the basis of the omnivory index (OI) of each food web component. It indicates the variance of trophic levels and formulated as:

$$OI_i = \sum_{j=1}^{n} (TL_j - (TL_i - 1))^2 * DC_{ij}$$

So, from the OI of each functional group the SOI could be calculated following the equation:

$$SOI = \frac{\sum_{i=1}^{n} [OI_i * \log(Q_i)]}{\sum_{i-1}^{n} \log(Q_i)}$$

where Q_i is the food intake of each consumer (Christensen and Walters, 2004; Libralato, 2008).

The CI can be calculated by the following equation

$$CI = \left[\frac{\sum_{j \neq k}^{n} C_{ijk}}{\frac{n_i(n_i-1)}{2}} \right] (100)$$

C_{ijk} = joining between patch j and k (0 = unjoined, 1 = joined) of the corresponding patch type (i), based on a user specified threshold distance. n_i = number of patches in the landscape of the corresponding patch type (class). The CI and the SOI are two indices that represent the complexity of the internal interconnection within the ecosystem and help in characterizing an ecosystem's maturity and are likely to be higher in mature environments (Christensen, 1995; Lira et al., 2018).

The FCI (Finn, 1976) exploits the Leontief matrix to evaluate the quantity of material cycling within an ecosystem. The formula is:

$$FCI = \sum_{i=1}^{n} \frac{S_i}{TST} \frac{l_{ii} - 1}{l_{ii}}$$

where l_{ii} is the ith coefficient along the diagonal of the Leontief matrix, S_i = inflow to the ith compartment and TST = total system throughput. The FCI and Finn's mean path length (FML) are used to measuring the degree of recycling in a system (Xu et al., 2011).

Niche overlap is the proportion of prey and predators shared by various functional groups. Pianka (1973) proposed the use of the index of overlap resulting from the Lotka–Volterra equation competition coefficients. The index, O_{jk}, could be derived for two species/groups j and k, from

$$O_{jk} = \sum_{i=1}^{n} \frac{(P_{ji} * P_{ki})}{\sqrt{(\sum_{i=1}^{n} P_{ji}^2 * P_{ki}^2)}}$$

where, P_{ji} and P_{ki} are the proportions of the resource i used by species j and k, respectively. The index is symmetrical, and it assumes a scale of 0 (no overlap) to 1 (identical diet or predator compositions). If the index value is greater than 0.6 than it indicates significant niche overlap between two functional groups (Pianka, 1973).

3. Results

The model derived output data were summarized in Table 2. The cluster analysis divided the 29 functional groups of the NBoB model into 4 major classes (Fig. 2). Class 1 was composed of producers i.e., phytoplankton and detritus (Fig. 2). Class 2 included top predators i.e., elasmobranchs, coastal tunas, muraenesox, Sciaenidae, *Harpadon nehereus*, *Scomberomous* spp. *Arius* spp., *Lates* spp. and *Lutjanus* spp. (Fig. 2). Class 3 was a combination of the primary consumers and Class 4 was a mixture of the secondary consumers (Fig. 2).

3.1. Trophic levels and trophic efficiency

Trophic levels (TL) of the different functional groups (see Table 2) ranged from 1 to 4.182 (Fig. 3). The EE ranged between 0.510 and 0.995; however, for the majority of the functional groups the EE values were close to 1 (Table 2). The Leiognathidae had the lowest EE (i.e., 0.631) among the fish groups. The benthos had the lowest EE (i.e., 0.510) among the non-fish groups (Table 2). High EE values were evident for *Arius* spp., *T. ilisha* and *H. nehereus* (Table 2).

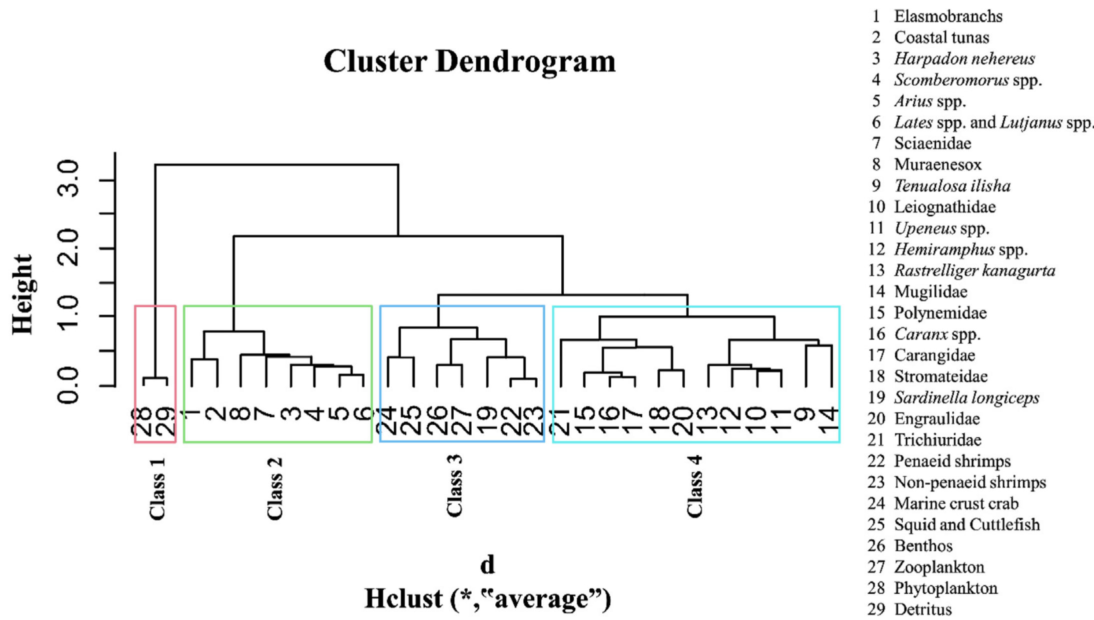

Fig. 2. Hierarchical cluster analysis of the trophic level of different functional groups of the Ecopath model built on the Northern Bay of Bengal ecosystem off West Bengal, India.

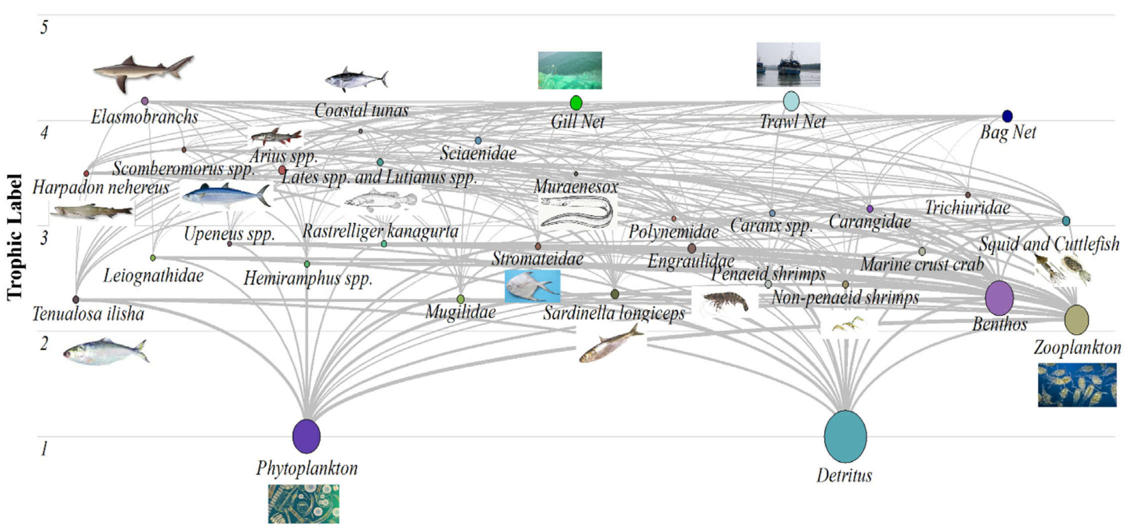

Fig. 3. Trophic interactions of the Ecopath model of the Northern Bay of Bengal ecosystem off West Bengal, India.

3.2. Summary statistics of the model

The sum of all consumption, exports, respiratory flows and the sum of all flows into detritus were 1846.741 t/km^2/year, 400.342 t/km^2/year, 899.608 t/km^2/year and 1017.021 t/km^2/year, respectively (Table 3). The TST of NBoB ecosystem was 4163.712 t/km^2/year (Table 3). The MTL of the NBoB ecosystem was 3.146. The SOI had a value of 0.276 and the CI was 0.269. The ratio of total primary production/ total respiration (TPP/TR) was 1.445. The ratio of TPP to total biomass (TPP/B) was 24.537 and the ratio of total biomass/total throughput (B/TST) was 0.013 t/km^2/year. The FCI was 14.39% of the TST and the FML was 3.203.

3.3. Transfer efficiency of the model

Two main food chains, a detritus-based food chain and a grazing food chain were identified (Fig. 4). The biomass of the primary producers was 13.00 t km^{-2} y^{-1} and the biomass of the detritus was 36.54 t km^{-2} y^{-1}. The energy flow along the grazing food chain was 851.1 t km^{-2} y^{-1} and through the detritus food chain was 626.1 t km^{-2} y^{-1} (Fig. 4). TL I was made of primary producers and detritus, both of which were considered while analyzing the energy flows associated with all functional groups (Fig. 4). The total ecosystem transfer efficiency (TE) was 16.43%. The TE of primary producers (16.28%) was lower than the TE of detritus (16.63%) (Table 4). TE increased from TL II to TL V then declined TL VI onwards (Table 4). The highest value (i.e., 21.21) of the TE was observed at TL V of all flows (Table 4).

3.4. Mixed Trophic Impact analysis

The MTI of the most functional groups were influenced by the functional groups that form the base of the food web such as detritus, phytoplankton and benthos (Fig. 5). Elasmobranchs, *Arius* spp., squid and cuttlefish, zooplankton, *H. nehereus*, *Scomberomous* spp., *Lates* spp. and *Lutjanus* spp., Sciaenidae and coastal tunas have negatively impacted the trophic interactions of NBoB

Table 3
System statistics of the Ecopath model of the Northern Bay of Bengal ecosystem off West Bengal, India.

Parameter	Value	Units
Sum of all consumption	1846.741	t/km^2/year
Sum of all exports	400.342	t/km^2/year
Sum of all respiratory flows	899.608	t/km^2/year
Sum of all flows into detritus	1017.021	t/km^2/year
Total system throughput	4163.712	t/km^2/year
Sum of all production	1877.784	t/km^2/year
Mean trophic level of the catch	3.146	
Gross efficiency (catch/net p.p.)	0.007	
Calculated total net primary production	1300.000	t/km^2/year
Total primary production/total respiration	1.445	
Net system production	400.392	t/km^2/year
Total primary production/total biomass	24.537	
Total biomass/total throughput	0.013	t/km^2/year
Total biomass (excluding detritus)	52.981	t/km^2
Total catch	9.408	t/km^2/year
Connectance Index	0.269	
System Omnivory Index	0.276	
Shannon diversity index	2.306	
Finn's cycling index	14.39	% of total throughput
Finn's mean path length	3.203	none

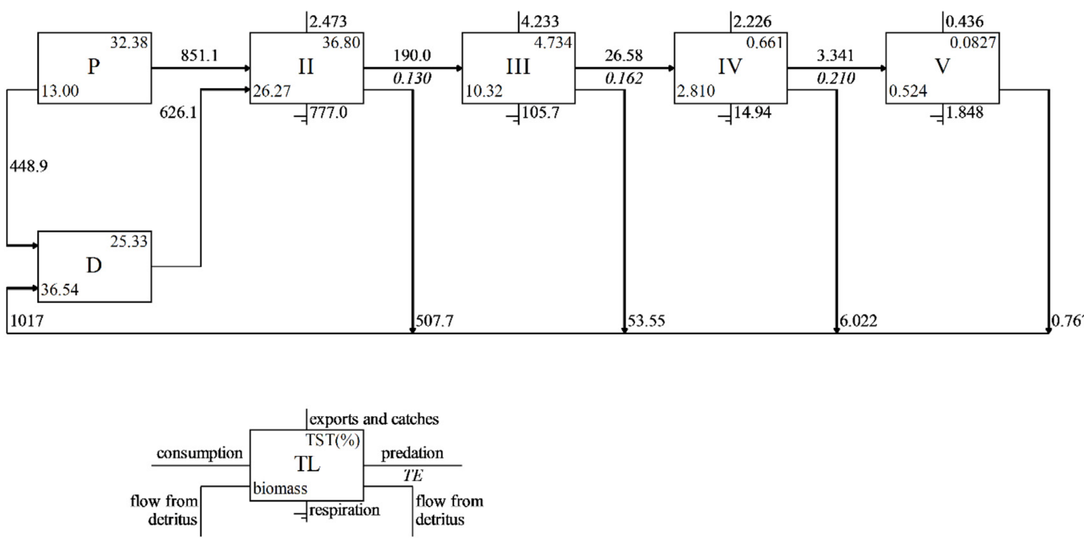

Fig. 4. The trophic flows transmitted between the trophic levels of the Ecopath model of the Northern Bay of Bengal ecosystem off West Bengal, India. P: primary producers; D: detritus; TST: total system throughput; TL: trophic level; TE: transfer efficiency. Units: t/km^2/year.

Table 4
Transfer efficiency (calculated as geometric mean for TL II–IV) of different trophic levels of the Ecopath model of the Northern Bay of Bengal ecosystem off West Bengal, India.

Source \Trophic level	II	III	IV	V	VI	VII
Producer	13.09	15.77	20.88	21.29	20.03	18.79
Detritus	12.95	16.82	21.11	21.08	19.82	18.74
All flows	13.03	16.21	20.98	21.21	19.95	18.77
Proportion of total flow originating from detritus: 0.43						
From primary producers: 16.28%						
From detritus: 16.63%						
Total: 16.43%						

ecosystem (Fig. 5). Cannibalism had a significant negative influence among zooplankton. Trawl nets had the highest negative impact on the whole ecosystem (Fig. 5). The MTI index showed majority of the 29 functional groups had negatively affected the trophic interactions of the NBoB ecosystem (Fig. 6). The highest total negative impact was showed by Sciaenidae (−1.653) followed by the *Arius* spp. (−1.591), zooplankton (−1.518), elasmobranchs (−1.428). Functional groups such as the detritus (total MTI is 3.834), phytoplankton (total MTI is 3.090), benthos (total MTI is 0.391) had shown positive impacts on the other functional groups of the NBoB ecosystem (Fig. 6).

3.5. Keystone index

The key functional group of the NBoB ecosystem was the elasmobranchs (KS = −0.098). Among the higher trophic level keystone indices of Sciaenidae, *Arius* spp., squid and cuttlefish and *H. nehereus* were −0.157, −0.238, −0.292 and −0.343, respectively. Among the lower trophic levels, the keystone indices of

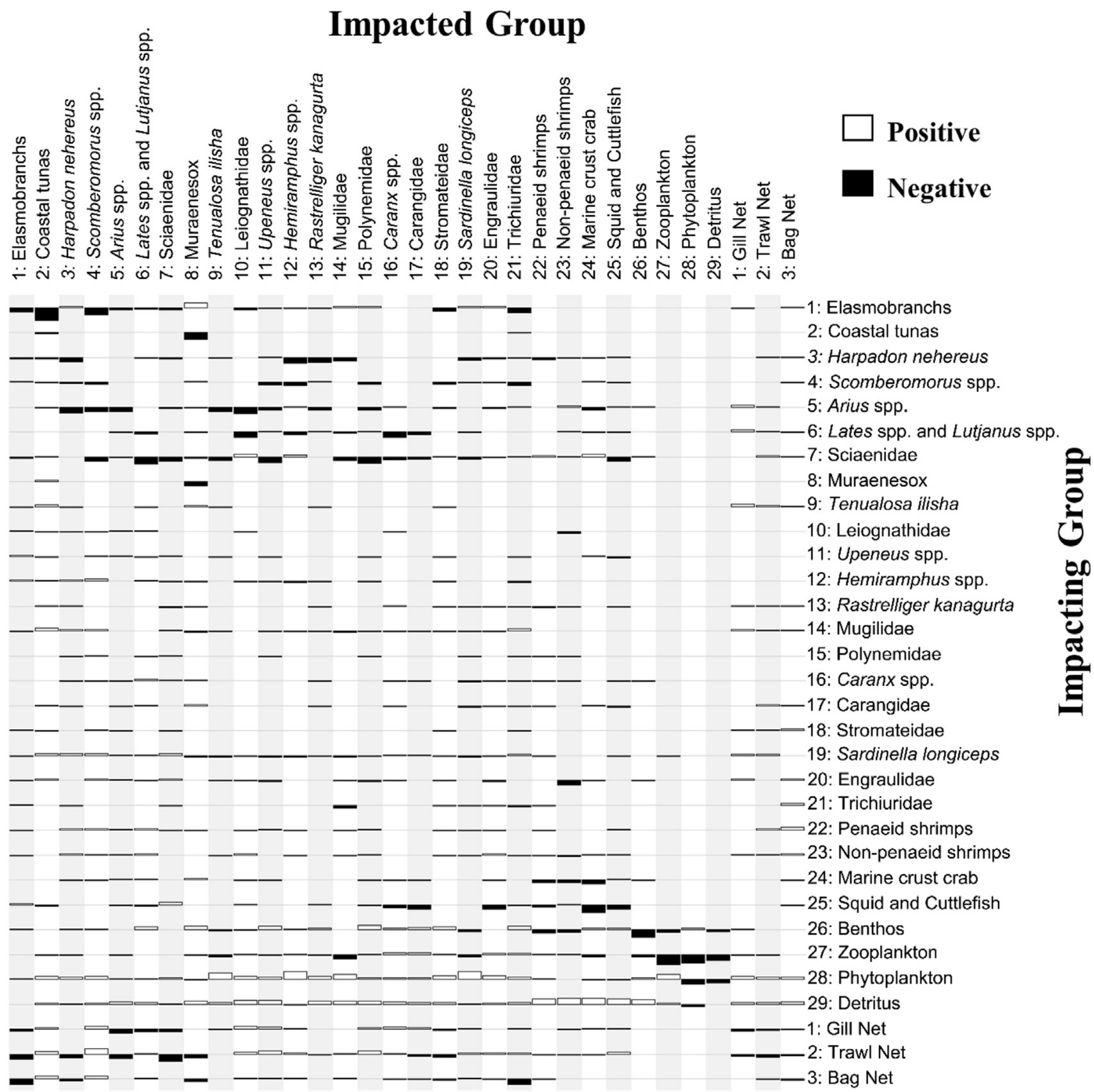

Fig. 5. Mixed Trophic Impact observed in the Ecopath model of the Northern Bay of Bengal ecosystem off West Bengal, India.

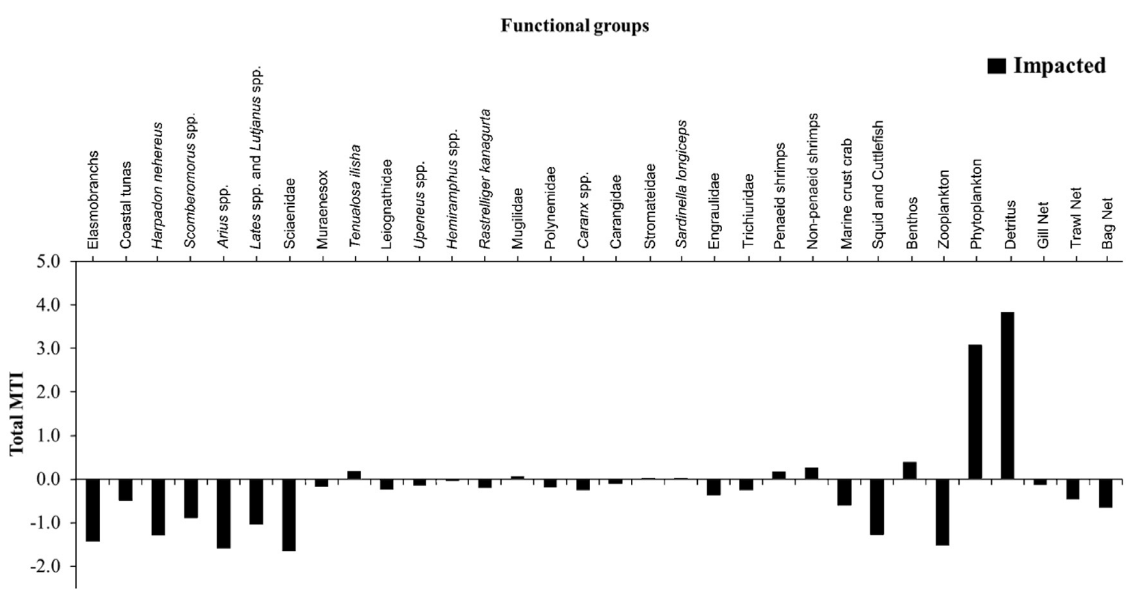

Fig. 6. Total positive and negative impacts of different functional groups on the Northern Bay of Bengal ecosystem off West Bengal, India.

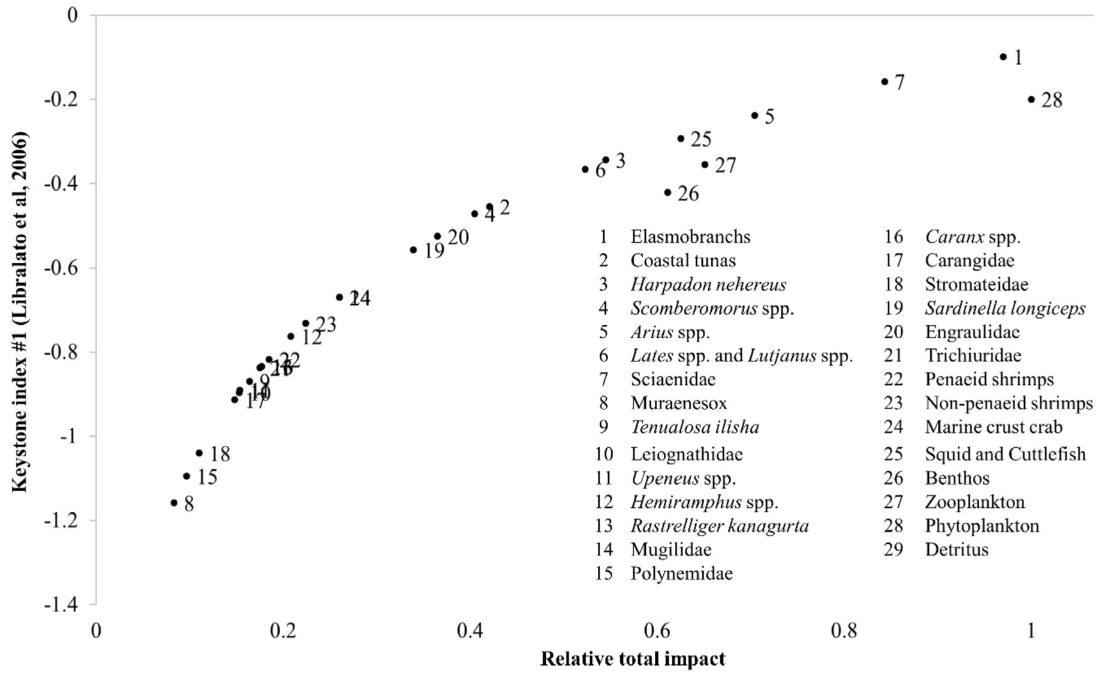

Fig. 7. Keystone index of functional groups of the Ecopath model built on the Northern Bay of Bengal ecosystem off West Bengal, India.

phytoplankton, zooplankton and benthos were −0.199, −0.354 and −0.421, respectively (Fig. 7). Phytoplankton had the highest relative total impact (RTI) in the NBoB ecosystem (1.0) followed by elasmobranchs (0.97), Sciaenidae (0.843), *Arius* spp. (0.704), zooplankton (0.651), and squid and cuttlefish (0.625) (Fig. 7).

3.6. Niche overlaps

Upeneus spp. and Polynemidae, and *Caranx* spp. and Carangidae showed the highest levels of niche overlaps in terms of their predators and preys (Fig. 8). *Arius* spp. and Engraulidae; *H. nehereus* and marine crust crab; *H. nehereus* and Stromateidae and *Scomberomorus* spp. and Carangidae, showed limited niche overlaps (Fig. 8). Polynemidae and Trichiuridae; non-penaeid shrimps and benthos; penaeid shrimps and Benthos showed low values of predator overlap index but high values of the prey overlap index (Fig. 8). Elasmobranchs and Sciaenidae, *T. ilisha* and Polynemidae; *H. nehereus* and *R. kanagurta* had high values of the predator overlap index but low values of the prey overlap index (Fig. 8).

4. Discussion

4.1. Ecotrophic efficiency and mean trophic level

Ecotrophic efficiency of a functional group is a measure of the proportion of the production that is utilized by the next trophic level through direct predation or fishing (Heymans et al., 2016). Leiognathidae and Sciaenidae had the lowest EE among all the fish groups of the NBoB ecosystem. It is possible that they have fewer predators and are less exploited by the fisheries in the region. The benthos and detritus have considerably lower EE values among the non-fish groups of the NBoB. *Arius* spp., *T. ilisha* and *H. nehereus* had high EE values. In terms of high EE values of functional groups (small pelagic, penaeid shrimp), results have similarities with Mustafa (2003) and Ullah et al. (2012) who worked in the NBoB.

The results showed that the MTL of the NBoB ecosystem was 3.146. The MTL of NBoB increased in comparison to the previous studies conducted by Ullah et al. (2012), Dutta et al. (2017) and Das et al. (2018) (see Table 5). Predation and fishing of different target species affect the stability, complexity and maturity of an ecosystem (Hattab et al., 2013), which are possibly affecting the trophic interactions of the NBoB and its MTL. *T. ilisha* is a highly exploited fish in India and Bangladesh (Dutta et al., 2021a) and *H. nehereus* is highly predated by itself (cannibalism). Traditionally fishers of the NBoB region did not fish higher trophic levels and the top predators (e.g., elasmobranchs, coastal tunas and Sciaenidae), fishers rather targeted species that are essentially small pelagic. In recent years, however, there has been a noticeable increase in fish movement towards the NBoB, which is linked to ocean warming which may impact different trophic levels of the food web (Burrows et al., 2014). An important new pattern of winter fishing in the NBoB region is the transition from small pelagic to demersal fishing (Dutta et al., 2014a). Further with the advancement of boats and fishing techniques a section of fishers has even started targeting top predators, which might be affecting the MTL of the NBoB.

4.2. Summary statistics of the model

Results showed that the B/TST of NBoB was 0.013 t/km^2/year. The B/TST ratio generally remains small during the developmental stage of an ecosystem, and it increases according to ecosystem maturity (Odum, 1969; Christensen, 1995). Results have similarities with Bohai Sea, China which too is at its early stage of maturity (Rahman et al., 2019). The TPP/TR value is generally small for ecosystems that are in the early stage of their maturity and have less variety and number of predators (Christensen and Pauly, 1993). In the current study TPP/TR was 1.445 possibly because the biomass of detritus is high in NBoB ecosystem. The Bangladesh part of the NBoB ecosystem has a TPP/TR ratio of 1.351 (Ullah et al., 2012); therefore, it is plausible that the NBoB ecosystem is still in its early stage of maturity. In the present study, the detritus flow (16.63%) is more than the producer's flow, which shows the significance of the detritus food chain in the NBoB ecosystem. The gross efficiency of the fishery (catch/net

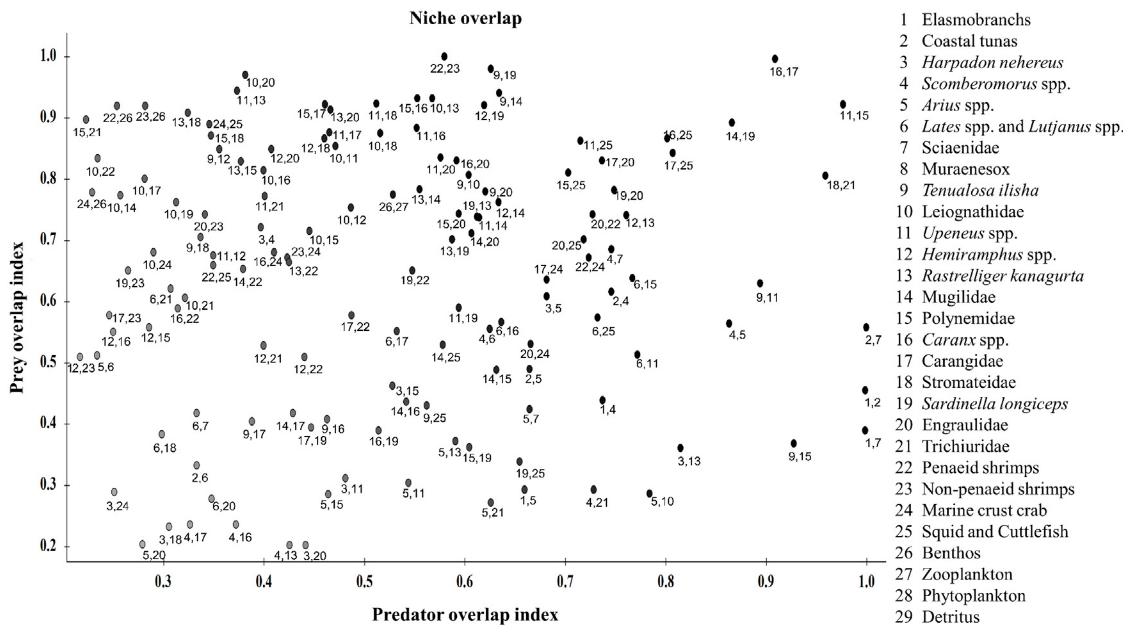

Fig. 8. Niche overlap derived from the Ecopath model of the Northern Bay of Bengal ecosystem off West Bengal, India. The prey and predator overlap index scale cut-off has been set to 0.2.

Table 5
Comparison of present Ecopath model with the previous Ecopath models of the Northern Bay of Bengal (NBoB) ecosystem off West Bengal, India.

Ecosystem	Authors	Number of functional groups	MTL	Throughput	Net system production	Omnivory index	Gross efficiency	FCI	Mean path length	B/TST	TPP/TR	Maturity
Northern Bay of Bengal (NBoB)	Ullah et al. (2012)	14	2.45	2628	264.235	0.224	0.0015	10	2.583	0.026	1.351	Developing stage
	Dutta et al. (2017)	15	2.716	5220.574	423.962	0.352	0.001	10.59	2.991	0.009	1.321	Lower level of maturity
	Das et al. (2018)	32	3.115	4307.745	223.555	0.248	0.003	11.09	9.13	0.0196	1.2	Developing stage
	Present study	29	3.146	4163.712	400.392	0.276	0.007	14.39	3.203	0.013	1.445	Early stage of maturity

MTL = Mean Trophic Level; FCI = Finn's Cycling Index; B/TST = total biomass/total throughput; TPP/TR = total primary production / total respiration.

primary production) from the NBoB is high (0.007) compared to the global mean of 0.0002 (Christensen et al., 2008). In the present study, FCI is 14.39% which indicates that the NBoB is yet to reach its maturity and stability. The FCI of the present study is higher than those of the previous studies conducted in the NBoB (Ullah et al., 2012; Dutta et al., 2017; Das et al., 2018) (see Table 5). The SOI had a value of 0.276. Results suggested that the consumers of the NBoB ecosystem feed on the different trophic levels. A low CI value (i.e., 0.269) of the NBoB ecosystem possibly suggests its early stage of maturity and limited trophic interactions where predators are competing for the similar prey groups. Such a condition of an ecosystem was also observed by Srithong et al. (2021) who focused on Andaman Sea of Thailand.

4.3. Transfer efficiency of the NBoB ecosystem

In general, trophic flows and biomass indicate pelagic compartment (plankton and small pelagic fish) dominated the NBoB ecosystem. The increasing TE values from TL II to TL V explained the efficiency of the food chain; however, the TE declined from TL VI, which is consistent with the Lindeman's theory (Lindeman, 1942). The total TE is 16.43%, higher than the 10% presumed by Lindeman (1942), which is a reasonable approximation of the average TE of aquatic ecosystems (Pauly and (Christensen, 1995)). The mean TE of the Bangladesh part of the NBoB is lower (i.e. 5.9%) (Ullah et al., 2012) than the current results. Das et al. (2018) documented a mean TE of 16.9% for the Indian part of the NBoB ecosystem and such is close to the present result. A High mean TE is not unusual for Jimo coastal ecosystem of China which had a mean TE of 17.6% (Su, 2016) and the Gulf of Mexico ecosystem had a mean TE of 11.4% (Geers et al., 2016). Such a result possibly suggests high-energy fluxes to the TL and a better efficiency of the NBoB ecosystem in transferring energy through the different food chains. It is possible that in recent years species composition predation pressure and fishing practices of the NBoB ecosystem are undergoing changes (Dutta et al., 2014a,b; Bachok et al., 2004; Dutta and Paul, 2021), which in consequence may be affecting the material recycling process of the NBoB making that process more efficient than the past.

4.4. Mixed trophic impact and keystone index

Both the detritus and phytoplankton groups have significant positive impacts on the other functional groups of the NBoB ecosystem which demonstrates its bottom-up structure. The MTI analysis suggests that the NBoB food web is highly impacted by the functional groups that mostly belong to the lower trophic levels. For example, detritus had positive impacts on the benthos, penaeid and the non-penaeid shrimps, marine crust crab, squid

Table A.1
Growth parameters, mortality and exploitation rate of different fish species under the present functional group of the Ecopath model of the Northern Bay of Bengal ecosystem off West Bengal, India along with the list of references for diet composition.

Sl no	Family/Genus/Species	Common name	L∞ (cm)	K (/year)	A	B	Z (/year)	F (/year)	M (/year)	E	References	References for diet composition
1	Elasmobranchs	Sharks, Skates, Rays	207.40	0.19	0.004790	3.09	0.72	0.40	0.32	0.56	FishBase	Rao (1964), FishBase
2	Coastal tunas	Coastal Tunas	192.40	0.37	0.006000	3.19	1.58	1.04	0.54	0.66	FishBase	Rohit et al. (2010), Nootmorn et al. (2008), Bachok et al. (2004);
3	*Harpadon nehereus*	Bombay Duck	43.40	0.81	0.002400	3.05	4.33	3.03	1.30	0.70	Balli et al. (2011)	Ghosh (2014)
4	*Scomberomorus* spp.	Seer fish	66.15	1.20	0.029400	2.98	3.39	2.54	0.85	0.75	Present Study	Devaraj (1999), Bachok et al. (2004);
5	*Arius* spp.	Sea Cat fish	42.00	0.66	0.018100	2.82	1.40	0.75	0.65	0.54	Present Study	FishBase
6	*Lates* spp., *Lutjanus* spp.	Parches	143.00	0.10	0.019600	2.92	1.69	1.43	0.26	0.85	FishBase	Bachok et al. (2004);
7	Sciaenidae	Croakers	145.30	0.14	0.012800	2.94	2.61	1.81	0.80	0.69	Ghosh et al. (2010)	Rao (1964); FishBase
8	Muraenesox	Eels	203.40	0.06	0.003180	2.78	0.32	0.18	0.14	0.56	FishBase	Chaudhuri et al. (2012, 2014);
9	*Tenualosa ilisha*	Hilsa Shad	53.34	0.83	0.017900	2.87	3.15	2.44	0.71	0.77	Present Study	Dutta et al. (2014b)
10	Leiognathidae	Silver Bellies	21.10	0.32	0.014790	3.01	1.62	0.79	0.98	0.49	FishBase	FishBase
11	*Upeneus* spp.	Goat fish	21.40	0.63	0.004100	3.43	3.21	1.84	1.37	0.57	FishBase	Prabha and Manjulatha (2008)
12	*Hemiramphus* spp.	Half Breaks	46.90	0.34	0.002310	3.00	1.46	0.75	0.71	0.51	FishBase	FishBase
13	*Rastrelliger kanagurta*	Indian Mackerel	29.19	0.94	0.000001	3.42	3.35	2.44	0.91	0.73	Present Study	Sivadas and Bhaskaran (2009)
14	Mugilidae	Mullets	59.00	0.20	0.020000	2.96	0.98	0.53	0.45	0.54	FishBase	FishBase
15	Polynemidae	Indian Solomon	60.90	1.06	0.000004	3.11	4.21	3.16	1.05	0.75	Present Study	Rao (1964)
16	*Caranx* spp.	Kala Bangada	91.90	0.24	0.031800	2.93	1.03	0.56	0.47	0.54	FishBase	Rao (1964), Bachok et al. (2004);
17	Carangidae	Bangada										Rao (1964), Bachok et al. (2004);
18	Stromateidae	Butter fish, Pomfret	34.86	0.74	0.006400	3.12	1.93	1.19	0.74	0.62	FishBase	FishBase
19	*Sardinella longiceps*	Indian oil sardine	20.37	1.20	0.000020	2.84	3.53	2.35	1.18	0.67	Present Study	Purusothaman et al. (2014).
20	Engraulidae	Anchovies	28.50	0.07	0.000010	2.93	2.68	1.37	1.30	0.51	Fernandez and Devaraj (1987)	Chaudhuri et al. (2012, 2014);
21	Trichiuridae	Hair tail Ribbon Fish	131.00	0.34	0.000550	3.05	1.26	0.71	0.55	0.56	FishBase	Chaudhuri et al. (2012, 2014), Rohit et al. (2015)
22	Penaeid shrimps		35.70	1.21			5.13	3.11	2.02	0.61		Thomas (1972, 1980)
23	Non-penaeid shrimps		3.11	3.19	0.000012	2.91	13.43	2.56	10.87	0.19	Deshmukh (1993)	FishBase
24	Marine crust crab		17.87	1.20	0.000042	3.06	4.69	2.85	1.84	0.61	Dash et al. (2013)	FishBase
25	Squid and Cuttlefish		17.40	0.74			1.43	0.74	0.69	0.52	Kasim (1993)	FishBase

L∞ = asymptotic length; K = growth coefficient; Z = total mortality; M =natural mortality; F = fishing Mortality; E = exploitation rate; FishBase = Froese and Pauly (2021).

and cuttlefish. Phytoplankton had positive impacts on zooplankton and on the pelagic fish groups such as *S. longiceps*, *Hemiramphus* spp. and *T. ilisha*. A similar finding was reported by Das et al. (2018) in the NBoB, Vega-Cendejas and Arreguın-Sánchez (2001) in a coastal lagoon of Yucatan Peninsula of Mexico, Xu et al. (2011) in northern Hangzhou Bay of China, and Su (2016) in Jimo coastal ecosystem of China.

In the NBoB ecosystem, elasmobranchs and phytoplankton are the key predators and producers, respectively. The identification of elasmobranchs and the phytoplankton as keystone complex of the NBoB ecosystem is associated with the fact that those groups hold the whole ecosystem as a top predator and as a producer, respectively. Those groups also have the greatest influence in the food web in relation to their biomasses. Phytoplankton form the keystone group of the North Coast-Central Java ecosystem (Buchary, 1999). Coll et al. (2006) identified micro and meso-zooplankton and phytoplankton as the keystone functional groups of the lower TL whereas dolphins are recognized as a keystone group of the higher TL in the northern and central Adriatic Sea. Essekhyr et al. (2019) identified pelagic sharks, large demersal sharks and rays and small demersal sharks and rays as keystone groups of the Moroccan Atlantic coast.

4.5. Niche overlap

Upeneus spp. and Polynemidae, and *Caranx* spp. and *Carangidae* had shown high levels of niche overlaps in this study, which possibly suggest competition for similar food items and habitat (Pianka, 1974). The maximum predatory overlap among the small pelagic fishes of the NBoB possibly suggest their diverse prey preferences that vary with their size class and the available food supplies in different trophic levels of an ecosystem (Rashed-Un-Nabi and Ullah, 2012). Navia et al. (2007) observed that the shrimps (penaeid and stomatopods) and the benthic fish were the main diets of elasmobranchs; further the diet breadth and overlap of elasmobranchs were relatively low in the Pacific Ocean off Colombia. In the recent years, presence of *S. longiceps* and *R. kanagurta* increased in the BoB (Vivekanandan et al., 2016).

4.6. Exploitation impacts on the NBoB food web

Landing statistics of the West Bengal (India) suggest, *Arius* spp., Sciaenidae, *T. ilisha* and *H. nehereus* are among the most important coastal-marine fisheries of the region (Dutta et al., 2016). Top predators such as sharks, rays, tunas, *Scomberomous* spp. were traditionally less in the NBoB but in recent years the local fishermen are increasingly catching them from the NBoB without modifying their traditional gears. The MTI analysis suggest that in the NBoB ecosystem, trawl and bag nets had more negative impacts on the functional groups compared to the gill net. Fishing gears such as bottom trawling and bag net, small mesh size, illegal catch of juveniles and gravid females of a few highly priced fish species and unregulated bycatch are the major problems that are adversely affecting the NBoB ecosystem (Dutta et al., 2016; Das, 2018; Begum et al., 2020). It is plausible that the use of non-selective fishing gears has damaged the underwater habitat of the

Table B.1
Diet matrix of the functional groups of the Ecopath model of the Northern Bay of Bengal ecosystem off West Bengal, India.

	Prey\predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1	Elasmobranchs	0.020	0.010																									
2	Coastal tunas	0.010	0.010																									
3	*Harpadon nehereus*			0.030	0.050	0.080																						
4	*Scomberomorus spp.*	0.100	0.020			0.020		0.020																				
5	*Arius spp.*	0.100				0.040																						
6	*Lates spp. and Lutjanus spp.*	0.060	0.040					0.070																				
7	Sciaenidae	0.080	0.080																									
8	Muraenesox		0.090						0.050																			
9	*Tenualosa ilisha*	0.050	0.090	0.020		0.080		0.080	0.150																			
10	Leiognathidae	0.050				0.040	0.050																					
11	*Upeneus spp.*	0.070			0.090	0.040		0.070																				
12	*Hemiramphus spp.*	0.080	0.100	0.100	0.150	0.030	0.060																					
13	*Rastrelliger kanagurta*	0.040	0.070	0.080		0.060											0.010	0.007										
14	Mugilidae		0.130	0.110	0.070	0.030	0.050	0.100														0.130						
15	Polynemidae	0.020	0.030		0.050	0.030		0.050																				
16	*Caranx spp.*	0.030	0.030				0.090	0.060	0.080																	0.010		
17	Carangidae	0.030	0.030				0.060	0.050	0.100																	0.020		
18	Stromateidae	0.090	0.020		0.050	0.010																						
19	*Sardinella longiceps*		0.120	0.200	0.150	0.090	0.100	0.180						0.040		0.050	0.080	0.070				0.100				0.010		
20	Engraulidae		0.070	0.070	0.100	0.100	0.050	0.110	0.060					0.030			0.020	0.030				0.050				0.050		
21	Trichiuridae	0.080	0.060		0.050																							
22	Penaeid shrimps			0.120	0.040	0.050	0.070					0.020		0.040		0.050	0.040	0.040				0.070			0.050	0.050		
23	Non-penaeid shrimps			0.120	0.050	0.040	0.090				0.100	0.010		0.050		0.070	0.060	0.040			0.100				0.100	0.050		
24	Marine crust crab					0.080	0.080		0.100																0.050	0.090		
25	Squid and cuttlefish	0.090			0.100		0.060	0.210	0.060			0.050		0.030			0.030	0.053								0.030		
26	Benthos			0.150	0.050	0.060	0.240		0.290		0.150	0.350	0.150	0.220	0.130	0.450	0.320	0.320	0.320		0.170	0.370			0.300	0.260	0.070	
27	Zooplankton									0.270	0.320	0.200	0.400	0.220	0.120	0.210	0.300	0.320	0.350	0.320	0.380	0.280	0.400	0.400	0.050	0.160	0.200	0.100
28	Phytoplankton									0.460	0.180	0.170	0.450	0.190	0.450	0.070			0.230	0.510	0.200		0.100	0.100			0.230	0.590
29	Detritus					0.120			0.110	0.270	0.250	0.200		0.180	0.300	0.100	0.140	0.120	0.100	0.170	0.150		0.500	0.500	0.450	0.270	0.500	0.310

countless marine species that belong to the lower trophic levels of the NBoB ecosystem, which in consequence may be a threat to the existence of many top consumers (Das, 2018). In the Bay of Bengal Large Marine Ecosystem, illegal, unreported and unregulated (IUU) catches were estimated only for Myanmar (∼9% larger than the reported catch) and Sri Lanka (40% unreported of the total reconstructed catch) (Harper et al., 2011). In the NBoB, India and Bangladesh are the two major fishing countries that hardly have reports of their IUUs and discards. The IUUs, overfishing and insufficient 'Monitoring Control and Surveillance (MCS)' are the key threats attached to open access fisheries in the region (Dutta et al., 2016; Behera et al., 2017; Akester, 2019; Begum et al., 2020; Dutta et al., 2021b). Increases in the community's mean trophic level, total flow to detritus, FCI and fluctuations of biomass are the key indicators of the changes that the NBoB is undergoing. In order to gain a stronger and mechanistic understanding of those changes and effects on the NBoB, studies of functional traits are required to narrow down the complex trophic interactions of the core quantifiable aspects of the NBoB (O'Brien et al., 2018). In that regard, the mixed trophic matrix allows for the inclusion of both the direct and indirect trophic interactions (Libralato et al., 2006) that might be ongoing in the NBoB. The present NBoB ecosystem model (Ecopath) is a steady state one, however, it can be further used for replicating the dynamic (Ecosim) changes of the NBoB; therefore, regular monitoring of the different functional groups is recommended.

CRediT authorship contribution statement

Sachinandan Dutta: Conceptualization, Funding acquisition, Methodology, Software, Formal analysis, Writing – original draft. **Sourav Paul:** Conceptualization, Investigation, Writing – review & editing. **Sumit Homechaudhuri:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

Authors are grateful to the fishermen for their support in the data collection process. Dr. Dutta is thankful to the Science and Engineering Research Board (SERB), Government of India for awarding the National Post-Doctoral Fellowship (PDF/2016/000640) for conducting this work. Dr. Dutta is grateful to College of Agricultural and Marine Sciences, Sultan Qaboos University, Muscat, Oman, for research and administrative supports. Authors are grateful to Professor Michel Claereboudt for editing the manuscript. Dr. Dutta and Prof. Homechaudhuri are thankful to the Head of the Department of Zoology, University of Calcutta, for research facilities and administrative supports. Dr. Paul thanks the Estuarine and Coastal Studies Foundation for providing research facilities to him.

Appendix A

See Table A.1.

Appendix B

See Table B.1.

References

Akester, M.J., 2019. Productivity and coastal fisheries biomass yields of the northeast coastal waters of the Bay of Bengal large marine ecosystem. Deep Sea Res. II: Top. Stud. Oceanogr. 163, 46–56.

Babcock, E.A., Pikitch, E.K., McAllister, M.K., Apostolaki, P., Santora, C., 2005. A perspective on the use of spatialized indicators for ecosystem-based fishery management through spatial zoning. ICES J. Mar. Sci. 62, 469–476.

Bachok, Z., Mansor, M.I., Noordin, R.M., 2004. Diet composition and food habits of demersal and pelagic marine fishes from Terengganu waters, east coast of peninsular Malaysia. NAGA, WorldFish Center Q. 27 (3–4), 41–47.

Balli, J.J., Chakraborty, S.K., Jaiswar, A.K., 2011. Population dynamics of Bombay Duck *Harpadontidae nehereus* (Ham, 1822) (Teleostomi/Harpadontidae) from Mumbai waters, India. Ind. J. Geo-Mar. Sci. 40 (1), 67–70.

Begum, A., Sarker, S., Uzzaman, M.S., Shamsuzzaman, M.M., Islam, M.M., 2020. Marine megafauna in the northern Bay of Bengal, Bangladesh: Status, threats and conservation needs. Ocean. Coast. Manag. 192 (105228).

Behera, P.R., Ghosh, S., Muktha, M., Kumar, M.S., Dev, J.M., 2017. Species composition and temporal variation of trawl by-catch in fishing grounds off northern Andhra Pradesh, Western Bay of Bengal. Indian J. Geo-Mar. Sci. 46 (10), 2037–2045.

Beverton, R.J.H., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations. Chapman and Hall, London, p. 533, (facsimile reprint, 1993).

Blanchard, J.L., Pinnegar, J.K., Mackinson, S., 2002. Exploring Marine Mammal-Fishery Interactions Using 'Ecopath with Ecosim': Modelling the Barents Sea Ecosystem. Sci. Ser. Tech Rep., 117, CEFAS Lowestoft, p. 52.

Bossier, S., Nielsen, J.R., Neuenfeldt, S., 2020. Exploring trophic interactions and cascades in the Baltic Sea using a complex end-to-end ecosystem model with extensive food web integration. Ecol. Model 436 (109281).

Brinck, K., Jensen, H.J., 2017. The evolution of ecosystem ascendency in a complex systems based model. J. Theoret. Biol. 428, 18–25.

Buchary, E., 1999. Evaluating the Effect of the 1980 Trawl Ban in the Java Sea, Indonesia (Doctoral Dissertation). University of British, Columbia.

Burrows, M.T., Schoeman, D.S., Richardson, A.J., Molinos, J.G., Hoffmann, A., Buckley, L.B., Moore, P.J., Brown, C.J., Bruno, J.F., Duarte, C.M., Halpern, B.S., 2014. Geographical limits to species-range shifts are suggested by climate velocity. Nature 507 (7493), 492–495.

Chaudhuri, A., Mukherjee, S., Homechaudhuri, S., 2012. Diet composition and digestive enzymes activity in carnivorous fishes inhabiting mudflats of Indian Sundarbans estuaries. Turk. J. Fish. Aquat. Sci. 12, 265–275.

Chaudhuri, A., Mukherjee, S., Homechaudhuri, S., 2014. Food partitioning among carnivores within feeding guild structure of fishes inhabiting a mudflat ecosystem of Indian Sundarbans. Aquat. Ecol. 48 (1), 35–51.

Christensen, V., 1995. Ecosystem maturity-towards quantification. Ecol. Model. 77 (1), 3–32.

Christensen, V., Pauly, D., 1993. Trophic models of aquatic ecosystems. In: ICLARM Conference Proceedings Vol. 26, first ed. International Center for Living Resources Management, Manila, Philippines.

Christensen, V., Pauly, D., 1998. Changes in models of aquatic ecosystems approaching carrying capacity. Ecol. Appl. 8 (sp1), S104–S109.

Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: Methods, capabilities and limitations. Ecol. Model. 172, 109–139.

Christensen, V., Walters, C.J., Pauly, D., Forrest, R., 2008. Ecopath with Ecosim Version 6, User's Guide, Lenfest Ocean Futures Project. University of British Columbia, Vancouver.

Chuenpagdee, R., Liguori, L., Preikshot, D., Pauly, D., 2006. A public sentiment index for ecosystem management. Ecosystems 9 (3), 463–473.

Coll, M., Palomera, I., Tudela, S., Sardà, F., 2006. Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. J. Mar. Syst. 59 (1), 63–96.

Danckwerts, D.K., McQuaid, C.D., Jaeger, A., McGregor, G.K., Dwight, R., Corre, M.Le., Jaquemet, S., 2014. Biomass consumption by breeding seabirds in the western Indian Ocean: Indirect interactions with fisheries and implications for management. ICES J. Mar. Sci. 71 (9), 2589–2598.

Das, M., 2018. Environmental impact of trawling on the continental shelf of Bay of Bengal. Sustain. Water Resour. Manag. 4 (4), 1091–1104.

Das, I., Hazra, S., Das, S., Giri, S., Chanda, A., Maity, S., Ghosh, S., 2018. Trophic-level modelling of the coastal waters of the northern Bay of Bengal, West Bengal, India. Fish. Sci. 84 (6), 995–1008.

Dash, G., Dash, S.S., Koya, M., Sreenath, K.R., Mojjada, S.K., Zala, M.S., Pradeep, S., 2013. Fishery and stock assessment of the three-spot swimming crab *Portunus sanguinolentus* (Herbst, 1783) off veraval, Gujarat. Ind. J. Fisher 60 (4), 17–25.

De, T.K., De, M., Das, S., Chowdhury, C., Ray, R., Jana, T.K., 2011. Phytoplankton abundance with cultural eutrophication at the land-ocean boundary of Sunderbans, NE Coast of Bay of Bengal, India. J. Environ. Stud. Sci. 1 (3), 169–180.

Department of Fisheries, 2016. A Handbook of Fisheries Statistics 2015-16 (2016) Directorate of Fisheries. Department of Fisheries, Government of West Bengal.

Deshmukh, V.D., 1993. Status of non-penaeid prawn fishery of India and stock assessment of *Acetes indicus* Milne Edwards off Maharashtra. Ind. J. Fish. 40, 50–62.
Devaraj, M., 1999. Food and feeding habits of the king seer *Scomberomorus commerson* (Lacepede) in the seas around the Indian Peninsula. J. Mar. Biol. Assoc. Ind. 40, 69–90.
Dutta, S., Al-Abri, I., Paul, S., 2021a. Bio-economic trends of Hilsa (*Tenualosa ilisha*) fishery: Perspectives of transboundary management between India and Bangladesh. Mar. Pol. 128 (104483).
Dutta, S., Chakraborty, K., Hazra, S., 2016. The status of the marine fisheries of West Bengal coast of the northern Bay of Bengal and its management options: A review. Proc. Zool. Soc. 69 (1), 1–8.
Dutta, S., Chakraborty, K., Hazra, S., 2017. Ecosystem structure and trophic dynamics of an exploited ecosystem of Bay of Bengal, Sundarban Estuary, India. Fish. Sci. 83, 145–159.
Dutta, S., Giri, S., Dutta, J., Hazra, S., 2014a. Blackspotted croaker, *Protonibea diacanthus* (Lacepède, 1802): A new dimension to the fishing pattern in West Bengal, India. Croat. J. Fish 72 (1), 41–44.
Dutta, S., Maity, S., Bhattacharyya, S.B., Sundaray, J.K., Hazra, S., 2014b. Diet composition and intensity of feeding of *Tenualosa ilisha* (Hamilton, 1822) occurring in the Northern Bay of Bengal, India. Proc. Zool. Soc. 67 (1), 33–37.
Dutta, S., Orlov, A., Hazra, S., 2021b. Population biology and exploitation status of four commercially important marine fishes of the northern Bay of Bengal. India. Iran. J. Fish Sci. 20 (1), 62–83.
Dutta, S., Paul, S., 2021. Temporal variability of economic fish assemblage of the Northern Bay of Bengal in relation to its environment. Iran. J. Ichthyol. 8 (2), 104–113.
Dwivedi, S.N., 1993. Long-term variability in the food chains, biomass yield, and oceanography of the Bay of Bengal ecosystem. Large Mar. Ecosyst.: Stress, Mitig. Sustain. 43–52.
Essekhyr, H., Khalil, K., Damsiri, Z., Derhy, G., Elkalay, K., 2019. Trophic interactions in the coastal ecosystem of Morocco: An ecopath approach. Commu. Ecol. 20 (2), 161–171.
FAO, 2001. Towards ecosystem-based fisheries management. In: The Reykjavik Conference on Responsible Fisheries in the Marine Ecosystem. 1-4 October 2001, FAO and Government of Norway, Reykjavik, Iceland, p. 11.
Fernandez, I., Devaraj, M., 1987. Estimates of *Coilia dussumieri* population along the Northwest coast of India using cohort analysis. Ind. J. Fish. 34 (4), 423–432.
Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. J. Theoret. Biol. 56, 363–380.
Froese, R., Pauly, D. (Eds.), 2021. FishBase. World Wide Web electronic publication, https://www.fishbase.org, (06/2021).
Gavaris, S., 2009. Fisheries management planning and support for strategic and tactical decisions in an ecosystem approach context. In: Ecosystem Approach to Fisheries: Improvements on Traditional Management for Declining and Depleted Stocks, Annual Meeting of the North Pacific Marine Science Organization. In: Fish. Res., vol. 100, pp. 6–14.
Geers, T.M., Pikitch, E.K., Frisk, M.G., 2016. An original model of the northern Gulf of Mexico using ecopath with ecosim and its implications for the effects of fishing on ecosystem structure and maturity. Deep Sea Res. II: Top. Stud. Oceanogr. 129, 319–331.
Ghosh, S., 2014. Fishery, reproductive biology and diet characteristics of Bombay Duck *Harpadon nehereus* from the Saurashtra Coast. Ind. J. Geo-Mar. Sci. 43 (3), 418–426.
Ghosh, S., Mohanraj, G., Asokan, P.K., Dhokia, H.K., Zala, M.S., Bhint, H.M., Anjani, S., 2010. Fishery and population dynamics of *Protonibea diacanthus* (Lacepede) and *Otolithoides biauritus* (Cantor) landed by trawlers at Vanakbara, Diu Along the West Coast of India. Ind. J. Fish. 57 (2), 15–20.
Guenette, S., 2014. An Exploratory Ecosystem Model of the Bay of Bengal Large Marine Ecosystem. Phuket, Thailand, Bay of Bengal Large Marine Ecosystem Project (BOBLME, p. 69, (BOBLME-2014-Ecology-09).
Gulland, J.A., 1971. The Fish Resources of the Ocean. West By fleet, Survey, Fishing News (Books), Ltd., for FAO, p. 255, Revised edition of FAO Fisheries Technical Paper. 97, 425.
Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., et al., 2008. A global map of human impact on marine ecosystems. Science 319, 948–952.
Harper, S., O'Meara, D., Booth, S., Zeller, D., Pauly, D., 2011. Fisheries catches for the Bay of Bengal Large Marine Ecosystem since 1950. Bay of Bengal Large Marine Ecosystem Project (BOBLME).
Harvey, C.J., Williams, G.D., Levin, P.S., 2012. Food web structure and trophic control in central Puget sound. Estuar. Coasts 35, 821–838.
Hattab, T., Lasram, F.B.R., Albouy, C., Romdhane, M.S., Jarboui, O., Halouani, G., Cury, P., Le Loc'h, F., 2013. An ecosystem model of an exploited southern mediterranean shelf region (Gulf of Gabes, Tunisia) and a comparison with other mediterranean ecosystem model properties. J. Mar. Syst. 128, 159–174.
Heymans, J.J., Coll, M., Link, J.S., Mackinson, S., Steenbeek, J., Walters, C., Christensen, V., 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. Ecol. Model. 331, 173–184.
Hilborn, R., Orensanz, J.M.L., Parma, A.M., 2005. Institutions, incentives and the future of fisheries. Phil. Trans. R. Soc. B 360, 47–57.
Holmgren, S., 1994. An Environmental Assessment of the Bay of Bengal Region. Bay of Bengal Programme, Madras, p. 240, BOBP/REP/67.
Islam, M.S., 2003. Perspectives of the coastal and marine fisheries of the Bay of Bengal, Bangladesh. Ocean Coast. Manag. 46 (8), 763–796.
Juan-Jordá, M.J., Mosqueira, I., Cooper, A.B., Freire, J., Dulvy, N.K., 2011. Global population trajectories of tunas and their relatives. Proc. Nat. Acad. Sci. USA 108, 20650–20655.
Kasim, H.M., 1993. Population dynamics of the cuttlefish *Sepia elliptica* Hoyle in Saurashtra waters. J. Mar. Biol. Assoc. Ind. 35, 80–86.
Lassalle, G., Pasqual, J.S.N., Boët, P., Rochet, M.J., Trenkel, V.M., Niquil, N., 2014. Combining quantitative and qualitative models to identify functional groups for monitoring changes in the Bay of Biscay continental shelf exploited foodweb. ICES J. Mar. Sci. J. Du Conseil 71 (1), 105–117.
Leontief, W., 1951. Input Output Economics. Oxford University Press, New York.
Libralato, S., 2008. System omnivory index. In: Jørgensen, S.E., Fath, B.D. (Eds.), Ecol. Indic. pp. 3472–3477.
Libralato, S., Christensen, V., Pauly, D., 2006. A method for identifying keystone species in food web models. Ecol. Model. 195 (3), 153–171.
Lindeman, R.L., 1942. The trophic– dynamic aspects of ecology. Ecology 23, 399–418.
Link, J.S., 2002. What does ecosystem-based fisheries management mean. Fisheries 27 (4), 18–21.
Lira, A., Angelini, R., Le Loc'h, F., Ménard, F., Lacerda, C., Frédou, T., Frédou, F.L., 2018. Trophic flow structure of a neotropical estuary in northeastern Brazil and the comparison of ecosystem model indicators of estuaries. J. Mar. Syst. 182, 31–45.
Lynam, C.P., Llope, M., Möllmann, C., Helaouët, P., Bayliss-Brown, G.A., Stenseth, N.C., 2017. Interaction between top-down and bottom-up control in marine food webs. Proc. Natl. Acad. Sci. 114 (8), 1952–1957.
Maureaud, A., Gascuel, D., Colléter, M., Palomares, M.L., Du Pontavice, H., Pauly, D., Cheung, W.W., 2017. Global change in the trophic functioning of marine food webs. PLoS One 12 (8), e0182826.
Mustafa, M.G., 2003. Trophic model of the coastal ecosystem in the waters of Bangladesh, Bay of Bengal, pp. 263–280. In: Silvestre, G., Garces, L., Stobutzki, I., Ahmed, M., Valmonte-Santos, R.A., Luna, C., Lachica-Aliño, L., Munro, P., Christensen, V., Pauly, D. (Eds.), Assessment, Management and Future Directions of Coastal Fisheries in Asian Countries. WorldFish Center Conference Proceedings, Vol. 67. pp. 1–120.
Navia, A.F., Mejía-Falla, P.A., Giraldo, A., 2007. Feeding ecology of elasmobranch fishes in coastal waters of the Colombian Eastern Tropical Pacific. BMC Ecol. 7 (1), 1–10.
Nootmorn, P., Sumontha, M., Keereerut, P., Jayasinghe, R.P.P.K., N., Jagannath., Sinha, M.K., 2008. Stomach content of the large pelagic fishes in the Bay of Bengal. p. 13, IOTC-2008-WPEB-11.
O'Brien, B.S., Mello, K., Litterer, A., Dijkstra, J.A., 2018. Seaweed structure shapes trophic interactions: A case study using a mid-trophic level fish species. J. Exp. Mar. Biol. Ecol. 506, 1–8.
Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.
Orians, G.H., 1975. Diversity, stability and maturity in natural ecosystems. In: Unifying Concepts in Ecology. Springer, Dordrecht, pp. 139–150.
Palomares, M.L.D., Pauly, D., 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. Mar. Freshw. Res. 49 (5), 447–453.
Pauly, D., Christensen, V., 1995. Primary production required to sustain global fisheries. Nature 374, 255–257.
Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, Jr., F., 1998. Fishing down marine food webs. Science 279 (5352), 860–863.
Pauly, D., Christensen, V., Walters, C., 2000. ECOPATH, ecosim, and ecospace as tools for evaluating ecosystem impact of fisheries. ICES J. Mar. Sci. 57, 697–706.
Pauly, D., Soriano-Bartz, M.L., Palomares, M.L.D., 1993. Improved construction, parametrization and interpretation of steady-state ecosystem models. In: Christensen, V., Pauly, D. (Eds.), Trophic Models of Aquatic Ecosystems. ICLARM Conference Proceedings, Vol. 26. pp. 1–13, 390 p.
Pianka, E.R., 1973. The structure of lizard communities. Annu. Rev. Ecol. Syst. 4 (1), 53–74.
Pianka, E.R., 1974. Niche overlap and diffuse competition. Proc. Natl. Acad. Sci. 71 (5), 2141–2145.
Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., Sainsbury, K.J., 2004. Ecosystem-based Fishery management. Science 305 (5682), 346–347.

Prabha, Y.S., Manjulatha, C., 2008. Food and feeding habits of *Upeneus vittatus* (Forsskal, 1775) from Visakhapatnam coast (Andhra Pradesh) of India. Int. J. Zool. Res. 4 (1), 59–63.
Purusothaman, S., Silambarasan, A., Jayaprabha, N., Murugesan, P., 2014. Feeding strategies and diet composition of oil sardine *Sardinella longiceps* Valenciennes 1847 in the trawl by catches off Parangipettai, Southeast Coast of India. Asian Fish. Sci. 27, 137–148.
Quan, L., Xue, S., Zhou, F., Xinjun, C., 2021. Evaluation of sustainable utilization of fishery resources in the eastern Indian ocean based on the mean trophic level. 海洋学报 43 (8), 118–127.
Rahman, M.F., Qun, L., Xiujuan, S., Chen, Y., Ding, X., Liu, Q., 2019. Temporal changes of structure and functioning of the Bohai Sea ecosystem: Insights from ecopath models. Thalassas: Int. J. Mar. Sci. 35 (2), 625–641.
Rao, K.S., 1964. Food and feeding habits of fishes from trawl catches in the Bay of Bengal with observations on diurnal variation in the nature of the feed. Ind. J. Fish. 11 (1), 277–314.
Rashed-Un-Nabi, M., Ullah, M.H., 2012. Effects of set Bagnet fisheries on the shallow coastal ecosystem of the Bay of Bengal. Ocean Coast. Manag. 67, 75–86.
Rohit, P., Rajesh, K.M., Sampathkumar, G., Sahib, K., 2015. Food and feeding of the ribbonfish *Trichiurus lepturus* Linnaeus off Karnataka, south-west coast of India. Ind. J. Fish. 62 (1), 58–63.
Rohit, P., Rao, G.S., Ram Mohan, K., 2010. Feeding strategies and diet composition of yellowfin tuna *Thunnus albacares* (*Bonnaterre*, 1788) caught along Andhra Pradesh, East Coast of India. Ind. J. Fish. 57 (4), 13–19.
Sarkar, S.K., Bhattacharya, A.K., 2003. Conservation of biodiversity of the coastal resources of Sundarbans, Northeast India: An integrated approach through environmental education. Mar. Poll. Bull. 47 (1–6), 260–264.
Shenoi, S.S.C., Shankar, D., Shetye, S.R., 2002. Differences in heat budgets of the near-surface Arabian Sea and Bay of Bengal: Implications for the summer monsoon. J. Geophys. Res. Oceans 107 (C6), 5-1-5-14.
Sivadas, M., Bhaskaran, M.M., 2009. Stomach content analysis of the Indian mackerel *Rastrelliger kanagurta* (Cuvier) from Calicut. Kerala. Ind. J. Fish. 56 (2), 143–146.
Srithong, N., Jensen, K.R., Jarernpornnipat, A., 2021. Application of the ecopath model for evaluation of ecological structure and function for fisheries management: A case study from fisheries in coastal Andaman Sea, Thailand. Reg. Stud. Mar. Sci. (101972).
Su, M., 2016. Preliminary analysis of the Jimo Coastal ecosystem with the ecopath model. J. Ocean Uni. China (6), 1–17.
Temple, A.J., Kiszka, J.J., Stead, S.M., Wambiji, N., Brito, A., Poonian, C.N., Amir, O.A., Jiddawi, N., Fennessy, S.T., Pérez-Jorge, S., Berggren, P., 2018. Marine megafauna interactions with small-scale fisheries in the southwestern Indian ocean: A review of status and challenges for research and management. Rev. Fish. Biol. Fish. 28 (1), 89–115.
Thomas, M.M., 1972. Food and feeding habits of *Penaeus monodon* fabricius from Korapuzha estuary. Ind. J. Fish. 19, 202–204.
Thomas, M.M., 1980. Food and feeding habits of *Penaeus semisulcatus* de Haan at Mandapam. Ind. J. Fish. 27, 130–139.
Ulanowicz, R.E., Puccia, C.J., 1990. Mixed trophic impacts in ecosystems. Coenoses 5, 7–16.
Ullah, M.H., Rashed-Un-Nabi, M., Al-Mamun, M.A., 2012. Trophic model of the coastal ecosystem of the Bay of Bengal using mass balance ecopath model. Ecol. Model. 225, 82–94.
Valls, A., Coll, M., Christensen, V., 2015. Keystone species: Toward an operational concept for marine biodiversity conservation. Ecol. Monogra. 85 (1), 29–47.
Vasconcellos, M., Mackinson, S., Sloman, K., Pauly, D., 1997. The stability of trophic mass-balance models of marine ecosystems: A comparative analysis. Ecol. Model. 100 (1–3), 125–134.
Vega-Cendejas, M.E., Arreguın-Sánchez, F., 2001. Energy fluxes in a mangrove ecosystem from a coastal lagoon in Yucatan Peninsula. Mexico. Ecol. Model. 137 (2–3), 119–133.
Villanueva, M.C., Lalèyè, P., Albaret, J.J., Lae, R., de Morais, L.T., Moreau, J., 2006. Comparative analysis of trophic structure and interactions of two tropical lagoons. Ecol. Model. 197 (3–4), 461–477.
Vivekanandan, E., 2001. Ecosystem Considerations for Managing Marine Fisheries in the Indian Ocean. Coastal Communities and the Indian Ocean's Future, Chennai, India, 9–13 October 2001. http://hdl.handle.net/1834/868.
Vivekanandan, E., Hermes, R., O'Brien, C., 2016. Climate change effects in the Bay of Bengal large marine ecosystem. Environ. Dev. 17, 46–56.
Vivekanandan, E., Srinath, M., Pillai, V.N., Immanuel, S., Kurup, K.N., 2003. Trophic model of the coastal fisheries ecosystem of the southwest coast of India, p. 281–298. In: Silvestre, G., Garces, L., Stobutzki, I., Ahmed, M., Valmonte-Santos, R.A., Luna, C., Lachica-Aliño, L., Munro, P., Christensen, V., Pauly, D. (Eds.), Assessment, Management and Future Directions for Coastal Fisheries in Asian Countries. WorldFish Center Conference Proceedings, Vol. 67. p. 1 120.
Xu, S., Chen, Z., Li, S., He, P., 2011. Modeling trophic structure and energy flows in a coastal artificial ecosystem using mass-balance ecopath model. Estuar. Coast. 34 (2), 351–363.