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Trophic network and food web characteristics in a tropical monsoonal estuary: A comparison with other estuarine systems

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A mass-balance trophic model for Zuari, a monsoon-influenced tropical Indian estuary, was constructed to understand trophic organization, to measure the ecosystem indicators and to assess the state of the ecosystem maturity and stability. Twenty-two functional groups were identified in the model starting from primary producers (trophic level = 1) to top predators (trophic level = 4.7). The estuarine food web is controlled by bottom-up control based on primary producers and detritus. Phytoplankton, zooplankton, clupeids & anchovies and heterotrophic benthos were observed as keystone species in the food web. A higher total system throughput (23333.9 t km^{-2} $year^{-1}$), and lower dimensions for recycling capacity (Finn's cycling index: 2.78 %), system omnivory index (0.25), and relative ascendency (39.9 %) were observed. Based on the ecosystem indices, Zuari estuary is relatively small, and developing ecosystem, which is resilient to the external disturbances on the system. This trophic model is the first Ecopath model for tropical monsoonal estuaries and fourth model for the estuaries along the Indian coast. The Zuari estuary model showed resemblance to the sub-tropical and tropical estuarine Ecopath models and differed from estuaries of India and temperate estuaries. This Ecopath model would be also useful for simulating the variations in trophic flows and biomass for functional groups under the impact of fishing and anthropogenic activities on the ecosystem.

[Keywords: Ecosystem maturity, Ecosystem model, Keystone species, Monsoonal estuary, Trophic organization, Zuari]

Introduction

Ecosystem Approach to Fisheries (EAF) is a strategic charter that considers structural and functional components of an ecosystem for managing fisheries[1]. EAF considers habitat features and multiple functional groups in the ecosystem, and thus, characterizes the ecological processes[2]. The major goal of EAF is to rebuild and sustain ecological habitats and biological communities in order to maintain the ecological services provided by the ecosystem to the human population[1-4]. The ecosystem features and trophic organization of food web are essential to understand sustainability of an ecosystem[2,5-7]. Ecosystem model is an efficient tool to characterize ecosystem structure and to identify its features[2]. Generally, the energy balance models have been used worldwide as tools to characterize the structure, energy fluxes between living components, trophic organization of the food web, assessment of maturity, and stability of the ecosystem[2]. There are large-scale applications of these models with dynamic simulations in aquatic ecosystem research, which includes understanding an ecosystem, the impact of anthropogenic activities, comparing various phases in its development, differentiating ecosystems and exploring policy options for EAF[8].

Estuaries provide valuable support to human population in terms of coastal protection, water purification, fisheries resources, carbon sinks, tourism opportunities and recreational services[9-11]. The diversity and abundance of aquatic communities in estuarine ecosystems have been used to quantify the ecological dynamics in the recent past[12]. However, it was realized that a comprehensive understanding of the ecological functioning and trophic organization is required to assess the integrity of estuarine ecosystems[13-15]. Estuaries along the west coast of India represent tropical estuaries under the influence of monsoon (monsoonal estuaries). The previous studies characterized fish assemblages, macro-benthos, phytoplankton and zooplankton communities individually, but none of these scientific efforts addressed to holistically integrate the findings in an ecosystem context[16-25]. Recently, three Ecopath models have been constructed for estuaries from east coast of India such as Hooghly Matlah estuary[26] and Sunderban estuary[27] from northeast coast of India and Vellar estuary from southeast coast of India[28]. However, there are no research attempts on food web based modeling of estuaries of west coast of India. Zuari estuary, one of the major ecosystems along central west coast of India, is a highly productive, macro-tidal and well-mixed estuary, and could be considered as a reference ecosystem for tropical monsoonal estuaries.

Gillnet fishing (70 vessels) provides income and livelihood to around 2000 tribal fishermen population along Zuari estuary[22]. Human settlements, effluents from agriculture and discharge from shipping and mining industries had impacted the ecosystem since the last decade[29-30]. In the estuary, these anthropogenic pressures triggered depletion in the fish catch, which affected the small-scale fisheries specifically in terms of socio-economic and nutritional security of the coastal population[16,23-24]. To the best of our knowledge, the characterization of ecosystem structure and trophic interactions for tropical monsoonal estuaries has never been studied before[31]. In this study, a trophic mass-balanced Ecopath model for a tropical monsoonal estuary, Zuari was developed to address three specific objectives: 1) to characterize the food web 2) to analyze the current status of ecosystem functioning, efficiency, maturity and stability and 3) to compare features of the estuarine model with other estuarine ecosystems.

Material and Methods

Ecosystem description

Zuari estuary is located along the west coast of India andthe mouth of the estuary is approximately 5 km wide and 5-6 m deep (Fig. 1).The mean surface water temperature is 27.6 °C and pH and salinity range between 5.6 and 8.1 and 15-34 PSU, respectively[21,30]. The estuary is under tidal influence which is of semi-diurnal in nature, with mean tidal amplitude of 2.5 m[10]. The typical tropical conditions in the estuary are favorable to high biological productivity, and thus, the diversity of phytoplankton, zooplankton, benthos and fish assemblages is very high in the estuary[10]. It is also subjected to pollution from agricultural runoff, mining, industrial effluents and tourism-based activities, especially on the southern banks[30,32,33]. Thus, Zuari can be considered as a tropical monsoonal estuary under anthropogenic stress. The area of the estuary considered in this model is under tidal influence, measuring to 39.9 km^2 (Fig. 1).

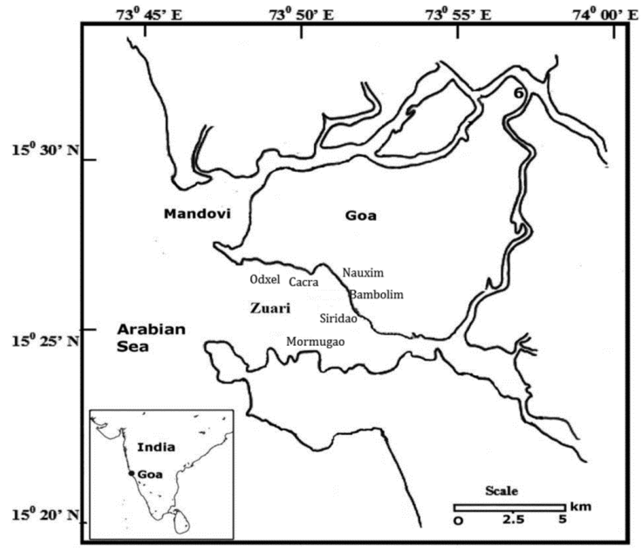

Fig. 1 — The map representing the study area, Zuari estuary, central west coast of India

Fishing fleet

The fishing fleet of the estuary includes small scale gillnet fishery, occasional mini-purse seine fishery and the trawl fishery. The major fish species caught include fish and shell fish species such as mackerel, sardine, white sardine, mullet, whitebait, moustached anchovy, silverbelly, carangid, croaker, catfish, crab and shrimps. The data on fish catch of the estuary are not regularly monitored and therefore, the fish catch and the length frequency, diet composition and length-weight data have been collected from the estuary from 2013 to 2016. The data were estimated from the fishing operations, fish landing centers and as well as from the fishermen along the estuary. The faunal species collected in this study have been described in the supporting information/ supplementary material (Table S1). Furthermore, the diet composition of various species was analyzed using the Index of Relative Importance method[34]. For constructing the mass-balanced trophic model, the basic input data (annual average for 2013 to 2016) were calculated after processing this fisheries data.

Functional groups

Twenty-two functional groups were defined on the basis of the similarity in size, population parameters and diet contents (Table 1). The functional groups

Table 1 — Functional groups defined for Zuari estuary

SN	Group	SN	Group
1	Birds (BD)	12	Clupeids and anchovies (oil sardine, white sardine, lesser sardines, rainbow sardine, moustached anchovies, bony breams, tardoore, shads, whitebaits and golden anchovy) (CA)
2	Dolphins (DO)	13	Crabs (swimming crabs, mud crab and other crabs) (CR)
3	Large pelagics (barracudas, seer fishes) (LP)	14	Shrimps (penaeid shrimps and stomatopods) (SR)
4	Rays and skates (sting rays and guitar fish) (RS)	15	Benthic omnivores (mullets, soles, tongue soles and gobies) (BO)
5	Cephalopods (squids, cuttlefishes and octopus) (CEP)	16	Heterotrophic benthos (gastropods and bivalves) (HB)
6	Benthopelagics (queenfish, horse mackerel, carangids and ribbonfishes) (BP)	17	Sessile benthos (polychaetes and hydrozoans) (SB)
7	Large benthic carnivores (groupers, snappers, seabass and threadfins) (LBC)	18	Jellyfish (JF)
8	Medium benthic carnivores (silver sillago, catfishes, croakers, flatheads, bamboo shark, grunts, lizard fish, wrasse, bream, sweetlips, sicklefish, eels and scat) (MBC)	19	Zooplankton (copepods, ostracods, bivalve larvae, cirripeds, cladocerans, mysids, euphausiids, amphipods, chaetognaths, and fish larvae) (ZP)
9	Piscivores (fullbeak and halfbeak) (PS)	20	Benthic producers (algae) (BPR)
10	Small benthic carnivores (glassy perchlets, false trevally, pufferfish, tiger perches, silverbellies and silverbiddies) (SBC)	21	Phytoplankton (diatoms, dinoflagellates and blue green algae) (PP)
11	Mackerel (Indian mackerel) (MA)	22	Detritus (DET)

identified were birds (BD), dolphins (DO), large pelagics (LP), rays and skates (RS), cephalopods (CEP), benthopelagics (BP), large benthic carnivores (LBC), medium benthic carnivores (MBC), piscivores (PS), small benthic carnivores (SBC), mackerel (MA), clupeids &anchovies (CA), crabs (CR), shrimps (SR), benthic omnivores (BO), heterotrophic benthos (HB), sessile benthos (SB), jellyfish (JF), zooplankton (ZP), benthic producers (BPR), phytoplankton (PP) and detritus (DET). The functional groups were described after considering the trophic models constructed for the Arabian Sea off Karnataka[35] and similar models developed from other estuarine ecosystems of the world[31,36-37].

Data pedigree and pedigree index

In mass-balanced trophic models, the pedigree of input data is an index that assesses the source of an input data (i.e., primary or secondary data)[2]. Therefore, a ‘pedigree’ was assigned to each input data based on the source of the data (and thus the degree of uncertainty associated with it). For this, the key criterion used was that the primary data of an input parameter calculated from the modeled ecosystem using empirical equations is better than the data collected from secondary sources of information (Table S2). The individual index values for functional groups were used to estimate a composite pedigree index, which ranges from 0 (for non-local data) to 1 (for local data).

Estimates of parameters

In order to construct mass-balanced model for an ecosystem, four of the five input parameters (1. biomass (B), 2. production/biomass (P/B), 3. ecotrophic efficiency (EE), 4. consumption/biomass (Q/B), and 5. diet matrix) should be available for each functional group. Thus, the model can estimate the unknown basic input parameter and generally, ‘EE’ is kept as the unknown parameter. Apart from these, fish catch data were also provided as an input for the model. Estuaries are dynamic ecosystems with a lot of movement of species between the sea and estuary. These movements of species are profoundly affected by salinity changes[29,36]. Experimental fishing showed that there were differences in biomass for various functional groups on the basis of salinity profiles[22]. Based on these differences in biomass, a proportion was derived and used for immigration and emigration rates for all the functional groups and provided as an input for the model (Table S3). Biomass accumulation rates were not estimated for the functional groups and the value for this index was assumed as zero. After collecting the species-wise information for basic input, all data were compiled for functional groups by estimating the mean values weighted by the relative biomass of the groups.

Among the functional groups, the biomass of fishery groups was estimated from the equation of Gulland (1971), ‘B = Y/F’, where ‘Y’ is the mean

Table 2 — Final modified diet matrix of the Zuari estuary. The fraction of one functional group by another is expressed as a fraction of the total diet.

Prey / predator	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
BPR	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.060	0.040	0.180	0.080	0.000
SBC	0.036	0.000	0.000	0.000	0.000	0.190	0.060	0.000	0.111	0.220	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
JF	0.017	0.050	0.000	0.000	0.030	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
BD	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
DO	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LP	0.000	0.000	0.090	0.050	0.040	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
RS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
CEP	0.000	0.000	0.030	0.190	0.057	0.000	0.060	0.060	0.134	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
BP	0.006	0.000	0.220	0.230	0.150	0.080	0.002	0.040	0.004	0.000	0.100	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LBC	0.000	0.000	0.040	0.140	0.040	0.014	0.005	0.006	0.037	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
MBC	0.000	0.000	0.060	0.200	0.060	0.002	0.004	0.022	0.150	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PS	0.000	0.000	0.160	0.040	0.170	0.001	0.002	0.084	0.022	0.006	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
MA	0.000	0.000	0.030	0.000	0.180	0.000	0.004	0.085	0.003	0.002	0.150	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
CA	0.008	0.050	0.070	0.030	0.200	0.003	0.230	0.150	0.065	0.005	0.710	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
CR	0.080	0.000	0.000	0.000	0.018	0.010	0.001	0.100	0.130	0.120	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SR	0.160	0.000	0.050	0.020	0.004	0.060	0.170	0.142	0.160	0.290	0.003	0.000	0.008	0.110	0.040	0.006	0.000	0.000	0.000
BO	0.136	0.000	0.030	0.000	0.012	0.300	0.132	0.190	0.150	0.280	0.000	0.000	0.000	0.080	0.020	0.004	0.000	0.000	0.000
HB	0.140	0.000	0.000	0.000	0.000	0.200	0.220	0.020	0.000	0.006	0.000	0.000	0.006	0.300	0.120	0.190	0.040	0.000	0.000
SB	0.182	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.108	0.140	0.230	0.238	0.040	0.000
ZP	0.005	0.850	0.000	0.000	0.000	0.000	0.100	0.001	0.000	0.002	0.017	0.164	0.349	0.082	0.350	0.060	0.127	0.000	0.000
PP	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.720	0.582	0.000	0.000	0.008	0.095	0.008	0.750
DET	0.230	0.000	0.020	0.000	0.039	0.140	0.010	0.090	0.034	0.050	0.010	0.116	0.055	0.320	0.270	0.462	0.320	0.872	0.250
Import	0.000	0.000	0.200	0.100	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

(BD-birds, DO-dolphins, LP-large pelagics, LBC-large benthic carnivores, MBC-medium benthic carnivores, BP-benthopelagics, CEP-cephalopods, RS-rays and skates, PS-piscivores, SBC-small benthic carnivores, JF-jellyfish, CR-crabs, SR-shrimps, BO-benthic omnivores, HB-heterotrophic benthos, SB-sessile benthos, MA-mackerel, CA-clupeids and anchovies, ZP-zooplankton, BPR-benthic producers, PP-phytoplankton, DET-detritus)

annual catch of the functional group, and 'F' is the fishing mortality coefficient, calculated by deducting natural mortality coefficient (M) from total mortality coefficient (Z). The biomass values reported in earlier research studies from Zuari estuary were used for HB, SB, ZP, BPR and PP[18-19,29]. The biomass estimates for DO and BD were collected from similar reports from estuarine ecosystems[35,38]. For the DET group, the standard empirical equation was used for the estimation of biomass using primary productivity (mg C m^{-2} $year^{-1}$) and euphotic layer depth (in meters)[39]. The primary productivity (7500 mg C m^{-2} $year^{-1}$) and euphotic depth estimates (5m) from earlier reports were used for estimating the biomass of DET group[18,29]. The P/B value is corresponding to the coefficient of total mortality ('Z') under the assumption of steady state[2]. Therefore, 'Z' values were estimated for various species using the length converted catch curve method in FiSAT[40]. For some species for which length-frequency data were not collected, the estimates available from FishBase were used[41]. Q/B estimates for the functional groups were valued using the standard empirical formula given in earlier reports[39].

Mass balancing the model

Diet compositions for various functional groups (Table 2) have been estimated based on the gut content analysis in this study (for 85 species where number of samples were more than 60) and also from secondary sources of information available such as FishBase and SeaLifeBase[41]. For DO and BD, the import (diet component outside the ecosystem) was also considered as a part in the diet matrix, assuming frequent movements for these groups outside the estuary (Table 2). After compiling the diet composition data on various species, data were pooled for functional groups on the basis of relative biomass for each species within a functional group. With all these inputs, the model was balanced for the period from 2013 to 2016 in Ecopath and the primary criterion for mass balancing the model was that EE_i

should lie between 0 and 1. Besides, the value of respiration, 'R_i' should not be negative and the respiration/ biomass ratio $(R/B)_i$ should be proportional to the activity levels of the group, with high values for small sized groups. In addition, the values of P/Q were also checked for all the functional groups to ensure that this index ranges from 0.1 to 0.3 for the majority of the functional groups.

To balance any trophic model, some adjustments would be required in the basic input data. During the modeling process, values for those input data with low pedigree index (highest degree of uncertainty) were modified first. In this study, adjustments were made in the biomass, Q/B values and diet composition. In order to sustain predation, adjustments in biomass were found to be necessary for specific consumer groups. Therefore, biomass values were adjusted for SBC, LP, CEP, BP, MBC, PS, MA, CA, CR, SR and ZP. The estimated values for Q/B were found to be unrealistically low for some of the functional groups. Therefore, the values for Q/B were adjusted for SBC and CEP. The data collected on diet composition of the species from primary and secondary sources were considered as reliable estimates. However, rational modifications were necessary in the diet composition of SR, CR, CA, BP, SBC and MBC with reference to the trophic models developed for the southwest coast of India and Fish-Base[35,41-42]. For SR, the proportions of ZP and DET were increased in their diet content. Similarly, the proportions of SB and DET were increased in the diet of CR. The proportions of ZP and PP were increased in the diet content of CA. The diet component, DET, was also included in the diet composition of BP. The diet composition of SBC was adjusted with the inclusion of prey item, CR. For the functional group MBC, the proportion of CR was reduced and the proportions of SR and BO were increased in their diet composition. For JF, a proportion for CA was also included in the diet composition. These iterations using modifications in biomass, Q/B and diet composition were continued until reasonable and acceptable estimates of EE_i, R_i, P/Q and $(R/B)_i$ were obtained.

Performance indicators

To assess the ecological structure of the ecosystem, indices such as total system throughput (TST), gross efficiency of the fishery (GE), net primary production (NPP), trophic level of functional groups and system omnivory index (SOI) were used[2]. The mass-balanced ecosystem models yield a single trophic flow diagram, which represents all flows and biomasses in the ecosystem. 'Lindeman spine' flow chart was used to measure the transfer efficiencies between various trophic levels[43]. Further, the keystone species index (KSI) was used to identify important functional groups that significantly affect the food web dynamics[2]. For this, the overall impact is plotted against KSI to identify keystone species (species that has an important role in the food web with low biomass) and the dominant groups (groups which are important in the food web with large biomass) in the ecosystem. To analyze the maturity and stability of the ecosystem, indices such as net system production (NSP), Finn's cycling index (FCI), ascendency (AS), mean path length (MPL), primary production/ respiration (PPR/R), primary production/biomass (PPRB), system omnivory index (SOI) and system overhead (SO) were used (Table S4). The description of various ecosystem performance indicators are presented in Table 3.

Appraisal among estuaries

The Ecopath model was compared to the ecosystem features of 10 other estuarine Ecopath models developed for tropical estuaries (3 models), and coastal ecosystems along Indian coast (2 models) and five other estuarine models (1 tropical, 2 sub-tropical and 2 temperate) around the world. We selected a total of 13 variables related to the ecosystem structure (FG, SC, SE, SR, SD, and SP), maturity (PPR/R, NSP, PP/B, SOI, FCI, AS) and stability (FCI, AS, SO) of the ecosystems to compare the different ecosystems. We adapted the method reported in earlier studies[31], in which the metadata of Ecopath models constructed for estuaries (21 models) around the world were compared. Following the screening methods proposed in earlier reports, FG, SC, SE, SR, SD, SOI, FCI, and SO were selected for multivariate analysis[31,44-45]. These attributes were normalized using logarithmic transformation and the SC, SE, SR and SD were divided by TST to standardize the size of the ecosystem[31,37,44-45]. We analyzed the variable groupings and ecosystems using Principal Component Analysis and Cluster analysis[37,44-45]. Further, the variables of the ecosystem models were compared using a Non-parametric multivariate analysis of variance (PERMANOVA) at 5 % significance level with factors as clusters obtained in the former analyses[37,44-45]. The statistical methodologies were carried out using PAST software[46].

Table 3 — Performance indicators used for comparison of ecosystems

Performance indicator	Definition	Significance
Functional group (FG)	A group of single species, individuals of same size/age or ecologically related species	The number and type of functional groups determines the diversity of ecosystem
Sum of all consumption (t km^{-2} year^{-1}) (SC)	Total consumption within the ecosystem	Structure of the ecosystem
Sum of all exports (t km^{-2} year^{-1}) (SE)	Total exports from the ecosystem	Structure of the ecosystem
Sum of all respiratory flows (t km^{-2} year^{-1}) (SR)	Total respiratory flows within the ecosystem	Structure of the ecosystem
Sum of all flows into detritus (t km^{-2} year^{-1}) (SD)	Total flows to detritus within the ecosystem	Structure of the ecosystem
Sum of all production (t km^{-2} year^{-1}) (SP)	Summation of all production	Structure of the ecosystem
Total system throughput (t km^{-2} year^{-1}) (TST)	Total consumption + total export + total respiration + total flows to detritus) in an ecosystem	It provides an idea about size of the system
Mean trophic level of the catch (MTL)	Weighted mean value of all trophic levels in the catch	It gives the exploitation level of fish groups in the system, if it is high, then the level of exploitation is low
Gross efficiency of the fishery (GE)	Ratio between the total fish catch and NPP	Represent the exploitation of fish groups in an ecosystem and this index will be higher ecosystems harvesting fish groups low trophic levels
Net system production (t km^{-2} year^{-1}) (NSP)	Total primary production − total respiration	Maturity of the ecosystem, it will be high in immature ecosystems and close to zero in mature ones
Total catch (t km^{-2} year^{-1}) (C)	Summation of catch of all fish groups	It gives the fish productivity within the ecosystem
Total biomass (exc. detritus) (t km^{-2} year^{-1}) (B)	Total biomass of all functional groups except detritus	It gives the carrying capacity within the ecosystem
Total primary production/B (PPR/B)	Total primary production/total biomass	Maturity of the ecosystem, In mature ecosystems, the ratio will be low
Total primary production/respiration (PPR/R)	Total primary production/total respiration	Maturity of the ecosystem, This index demonstrates values greater than unity in immature ecosystems
Total biomass/TST (B/TST)	Total biomass /TST	Maturity of the ecosystem, maximum values (close to 1) will be observed for mature ecosystems
System omnivory index (SOI)	Average omnivory indices of all consumers weighed by the logarithm of each consumer's food intake	Maturity of the ecosystem, it yields higher values in mature ecosystems (> 0.5)
Mean path length (MPL)	Average ecological distance between various pathways	Maturity of the ecosystem, higher values denote maturity of ecosystems
Finn's cycling index (FCI)	The fraction of flows of TST recycled	Maturity and stability of an ecosystem, higher values show that more mature and resilient ecosystems
Ascendency (%) (AS)	This measures the extent of balance of food web in an ecosystem. It is contrast to system overhead	Maturity of the ecosystem, higher values for this index indicate, maturity of the system (> 50 %)
System overhead (%) (SO)	Energy in balance for an ecosystem. It is contrast to Ascendency	Stability of an ecosystem, in stable and resilient ecosystem, the value will be high (> 50 %)
Ecopath pedigree index (PI)	The pedigree of input data showing the origin of an input data	This index provides the extent of validity of the model based on the input data. If the model is based on local data, the index will be more than 0.6

Results

Mass-balanced model and ecological structure

The mass balancing of the trophic model for Zuari was carried out by adjusting the input parameters such as Biomass, Q/B and diet composition for various functional groups. The modified diet matrix of functional groups was used as an input for the model (Table 2). The estimate of Ecopath pedigree index provided a reasonably good estimate of 0.59. The input values and output estimates of the mass-balanced model are given in Table 4. Primary producer groups (BPR and PP) shared majority of the ecosystem biomass excluding detritus. Among fishery groups, BO, CA, SR and SBC presented highest biomass estimates. The trophic network for Zuari clearly indicated that majority of the trophic flows have accumulated at the base of the trophic network (Fig. 2). There were two major paths (from PP and

Table 4 — Estimates of parameters of the Zuari model. The parameters estimated by the model are shown in italics and earlier estimates for input variables are in parentheses.

Ecological Group	TL	B	P/B	Q/B	EE	P/Q
DO	*4.66*	0.004	0.07	16.22	*0.000*	*0.004*
BD	*4.34*	0.002	0.08	58.02	*0.000*	*0.001*
LBC	*4.04*	0.118	4.50	12.20	*0.953*	*0.369*
LP	*3.97*	0.02 (0.011)	2.40	8.20	*0.884*	*0.293*
MBC	*3.75*	0.42 (0.396)	3.90	10.80	*0.991*	*0.361*
BP	*3.64*	0.34 (0.206)	3.10	9.60	*0.993*	*0.323*
RS	*3.57*	0.005	1.70	7.30	*0.706*	*0.233*
CEP	*3.56*	0.84 (0.70)	4.20	7.90 (5.7)	*0.995*	*0.532*
PS	*3.46*	0.37(0.25)	2.30	9.30	*0.969*	*0.247*
SBC	*3.19*	0.85(0.45)	5.20	20.53 (15.2)	*0.997*	*0.253*
JF	*3.02*	1.41	4.86	28.50	*0.904*	*0.171*
CR	*2.94*	0.79(0.68)	6.70	20.50	*0.990*	*0.327*
SR	*2.77*	1.92 (1.18)	6.80	24.20	*0.988*	*0.281*
BO	*2.58*	4.200	3.20	11.30	*0.900*	*0.283*
HB	*2.43*	22.50	3.40	16.70	*0.482*	*0.204*
CA	*2.37*	2.30(1.49)	7.30	26.30	*0.960*	*0.278*
MA	*2.16*	0.40(0.12)	6.80	20.20	*0.573*	*0.337*
SB	*2.04*	16.20	9.80	45.00	*0.872*	*0.218*
ZP	*2*	6.50 (4.62)	25.50	240.00	*0.758*	*0.106*
BPR	*1*	150.60	12.80	0.00	*0.068*	
PP	*1*	85.60	96.20	0.00	*0.152*	
DET	*1*	600.00			*0.118*	

TL: trophic level, B: biomass (t km^{-2} year^{-1}), P/B: production/biomass (year^{-1}), Q/B: consumption/biomass (year^{-1}), EE: ecotrophic efficiency, P/Q: production/consumption or gross efficiency of food conversion (year^{-1}), BD-birds, DO-dolphins, LP-large pelagics, LBC-large benthic carnivores, MBC-medium benthic carnivores, BP-benthopelagics, CEP-cephalopods, RS-rays and skates, PS-piscivores, SBC-small benthic carnivores, JF-jellyfish, CR-crabs, SR-shrimps, BO-benthic omnivores, HB-heterotrophic benthos, SB-sessile benthos, MA-mackerel, CA-clupeids and anchovies, ZP-zooplankton, BPR-benthic producers, PP-phytoplankton, DET-detritus

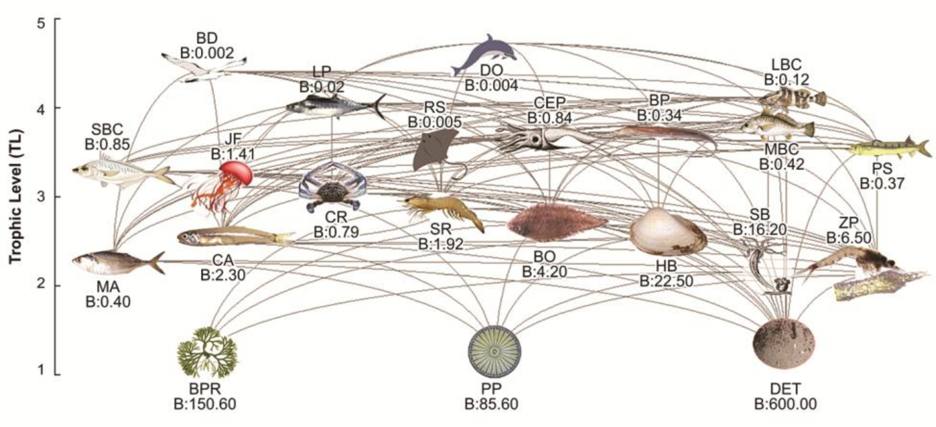

Fig. 2 — Trophic flow diagram of the Zuari estuarine food web (BD-birds, DO-dolphins, LP-large pelagics, LBC-large benthic carnivores, MBC-medium benthic carnivores, BP-benthopelagics, CEP-cephalopods, RS-rays and skates, PS-piscivores, SBC-small benthic carnivores, JF-jellyfish, CR-crabs, SR-shrimps, BO-benthic omnivores, HB-heterotrophic benthos, SB-sessile benthos, MA-mackerel, CA-clupeids and anchovies, ZP-zooplankton, BPR-benthic producers, PP-phytoplankton, DET-detritus), 'B' represents the biomass (t km^{-2} year^{-1}) for each functional group.

DET) in the ecosystem and trophic flows from DET and PP together contributed about 80 % of the total flows (Fig. 2). The trophic flows were accumulated at the base of the trophic food web where ZP and PP were the main food sources. Therefore, the main pathway in this ecosystem appeared is through PP and ZP to primary and secondary carnivores. Similarly, the detritus-based pathway was channeled through benthic groups (SB and HB) and BO to benthic carnivores and BP (Fig. 2). The highest trophic levels or the top predators in the ecosystem were DO, BD, LBC, LP and MBC (Table 3). Among fishery groups, LBC, LP, MBC, BP, RS and CEP have occupied the highest trophic levels, whereas, MA, CA, BO, SR and CR occupies the lowest trophic levels (Table 3). Generally, EE was very high for JF, SB, ZP and for fishery groups (except RS and MA) (Table 3). BPR, DET, PP, HB, DO and BD demonstrated low values of EE (Table 4). The mean trophic level of the catch from the estuary was found to be 2.91 (Table 5).

Table 5 — Performance indices and general features for Zuari estuary compared to models for other ecosystems (the values in bold represent the variables with comparatively higher values for Zuari estuary; the underlined values for variables represent comparatively lower values for Zuari estuary)

Performance indicator	Zuari estuary, India (ZU)	SW coast of India (SW)[42]	Karnataka coast of Arabian Sea (KA)[35]	Río de la Plata estuary (RD)[50]	Pearl River estuary, China (PR)[38]	Gironde estuary, France (GR)[36]	Canche estuary, France (CC)[37]	Ogun estuary, Nigeria (OG)[47]	Hooghly Matla estuary, India (HM)[26]	Vellar estuary, India (VE)[28]	Sunderban estuary, India (SBN)[27]
Ecosystem type	Tropical monsoonal	Open Sea	Open Sea	Sub-tropical	Sub-tropical	Temperate	Temperate	Tropical	Tropical	Tropical	Tropical
Size (Km^2)	39.9	-	27000	70500	43000	625.3	7.8	26	156250	-	2590
Discharge (m^3 s^{-1})	145.4	-	-		1000	900	11	-	400	15	56
Depth (m)	6	100	100	25	100	4.5	6.9	10	15	5	15
Period	2013-2016	1994-1996	1999-2001	2005-2007	1998	-	-	-	1998-2003	2004	2011-2012
Functional groups (number) (FG)	22	11	24	37	26	18	15	14	20	14	15
Sum of all consumption (t km^{-2} $year^{-1}$) (SC)	2920.77	7242.6	5421	3654.64	4969.9	937.82	366.837	5639.8	4009.51	16782.05	2346.2
Sum of all exports (t km^{-2} $year^{-1}$) (SE)	8925.53	13.84	904	19506.64	3139.8	2411.53	5747.113	12,598.80	2124.3	3383.42	423.97
Sum of all respiratory flows (t km^{-2} $year^{-1}$) (SR)	1393.86	6765.7	3190	2010.05	1681.6	401.92	122.279	2365.8	2313.11	8916.57	1321.54
Sum of all flows into detritus (t km^{-2} $year^{-1}$) (SD)	10093.77	60.01	2005	20511.66	5452.1	2813.45	5869.392	13781.3	4168.85	15272.56	1128.86
Total system throughput (t km^{-2} $year^{-1}$) (TST)	23333.94	14083.44	11522	45683	15243	6698.7	12227.9	34385.8	12615.76	44355	5220.57
Sum of all production (t km^{-2} $year^{-1}$) (SP)	10633.64	9553.7	5243	21760	5812	635.22	4106.2	17110.6	11276.31	16810	2300.92
Mean trophic level of the catch (MTL)	2.91	3.61	3.04	2.95	2.31	-	-	2.12	2.72	2.93	2.71
Gross efficiency (catch/net p.p.) (GE)	0.003	0.001	0.002	0.001	0.004	-	-	-	-	0.001	0.001
Net primary production (t km^{-2} $year^{-1}$) (NPP)	10162.4	9090.9	4095	20810	4821.4	409.77	4058.1	-	10381.8	12300	1745.51
Total primary production/total respiration (PPR/R)	7.29	1.34	1.28	10.46	2.86	1.05	22.06	6.32	4.49	1.37	1.32
Net system production (t km^{-2} $year^{-1}$) (NSP)	8768.53	2325.2	904	18821	3139.8	17.91	3866.4	12598.8	8068.7	3383.42	423.96
Total primary production/total biomass (PP/B)	34.4	57.22	29.99	81.14	18.13	21.52	100.57	82.6	41.57	49.12	38.85
Total biomass/total throughput (TB/TST)	0.012	0.01	0.012	0.005	0.02	0.001	0.003	0.005	0.01	0.006	0.009
Total biomass (excluding detritus) (t km^{-2} $year^{-1}$) (TB)	295.39	158.87	136	256.2	265.8	19.08	40.23	181.13	257.35	250.39	44.93
Total catch (t km^{-2} $year^{-1}$) (TC)	31.3	15.12	6.57	-	3.49	-	-	-	-	-	1.69
System Omnivory Index (SOI)	0.29	0.1	0.29	0.22	0.33	0.12	0.04	0.29	0.24	0.21	0.35
Total number of pathways (TPW)	20342	-	13110	-	-	-	-	41	-	-	-
Mean path length (MPL)	2.21	-	8.81	-	2.31	-	-	2.78	2.84	-	10.59
Finn's cycling index (%) (FCI)	2.78	5.76	6.03	0.82	2.72	3.99	0.8	2.29	8.4	2.88	2.99
Number of discrete trophic levels (TL)	10	-	10	6	-	-	-	6	9	-	
System transfer efficiency (%) (TE)	16.4	-	13.4	9.4	-	-	7	6.8	14.7	-	
Ascendency (%) (AS)	39.9	-	33	53	33.5	48	53.6	42.3	30	-	
System Overhead (%) (SO)	60.1	-	67	47	66.5	52	46.4	57.7	70	-	
Ecopath pedigree Index (PI)	0.59	-	0.52	0.61	-	-	-	-	0.54	-	0.19

Trophic flows, interactions and important functional groups

Lindeman spine analysis identified ten trophic levels (TL) in the estuary and the first TL is divided into primary producers (PP and BPR) and DET (Fig. 3). The flows from primary producers and DET components to higher TLs were 1386 t km^{-2} year^{-1} and 1195 t km^{-2} year^{-1}, respectively. Higher TLs showed greater transfer efficiency (%) accompanied by the lowest flows to DET. Transfer efficiencies were reduced from TL V (0.3 %), VI (0.29 %), VII (0.27 %) to IX (0.21 %). Geometric transfer efficiencies from DET and PP were 15.8 % and 17 %, respectively. The mean trophic transfer efficiency reported for the estuary was 16.4 %. The trophic flows and flows to DET were concentrated from TL I to IV and there was a sharp decline in the flow at higher TLs. The total system throughput (TST) was concentrated in the first TL with 88 % of the total TST. On the basis of KSI, the most important functional groups in the estuary were PP, ZP, CA and HB (Fig. 4).

Ecosystem flows, maturity and stability indicators

The basic ecosystem parameters including flow indices for Zuari are described in Table 5. The ecosystem indicators such as TST, NSP, SE and SD were very high. On the other hand, the estimated levels of consumption and respiratory flows were found to be on a lower scale (Table 5). The count of pathways in the estuarine trophic network was 20342. A very high estimate for NSP and lower estimates for FCI (2.78), SOI (0.29) and MPL (2.26)

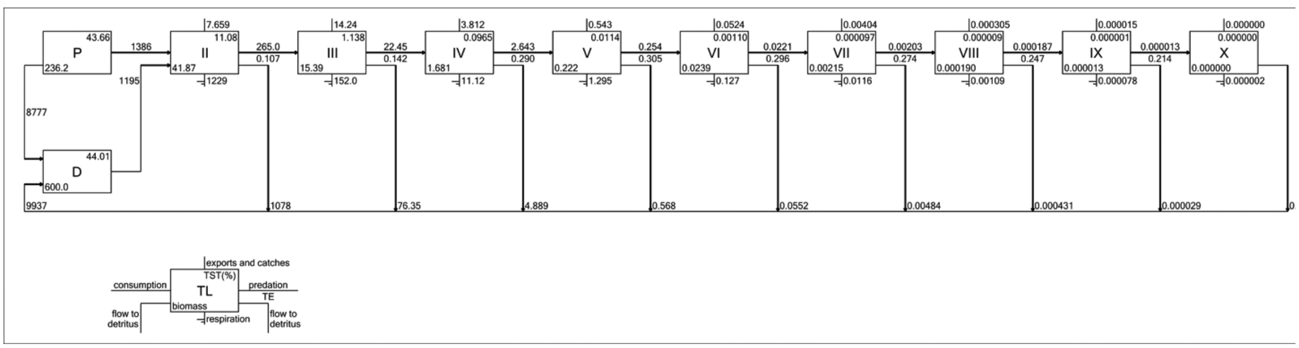

Fig. 3 — Lindeman spine of Zuari model and trophic level 1 has two components: primary producers (P) and detritus (D). TE: transfer efficiency (%), TST - total system throughput. Values are in t km^{-2} year^{-1}.

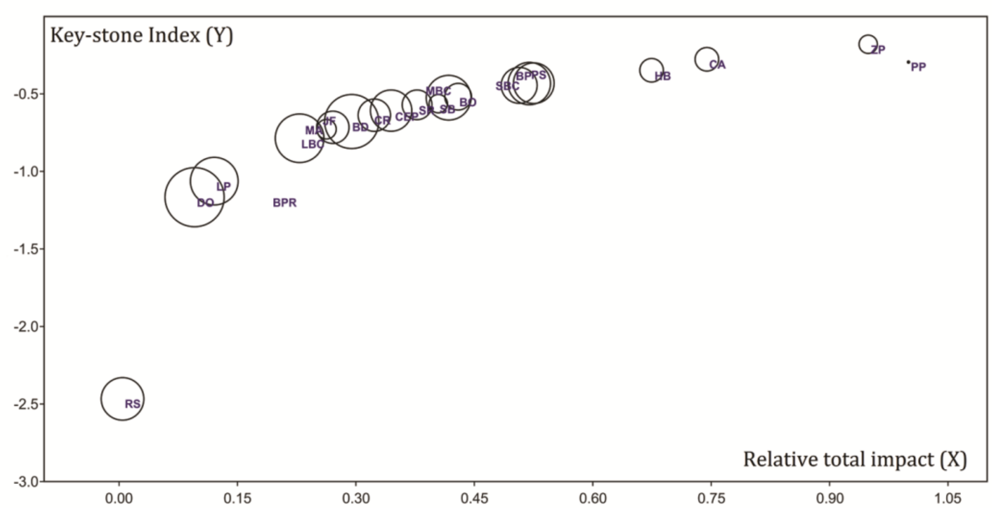

Fig. 4 — Keystone species index (KSI) and relative total impact (RTI) of various ecological groups in Zuari estuary (RS- rays and skates, DO- dolphins, LP-large pelagics, BPR-benthic producers, LBC-large benthic carnivores, MA-mackerel, JF-jellyfish, BD-birds, CR-crabs, CEP-cephalopods, SR-shrimps, SB-sessile benthos, MBC-medium benthic carnivores, BO-benthic omnivores, SBC-small benthic carnivores, BP-benthopelagics, PS-piscivores, HB-heterotrophic benthos, CA-clupeids and anchovies, ZP-zooplankton and PP-phytoplankton).

indicated the immature and developing nature of the estuary (Table 5). Higher rates were observed for PPR/R and PPR/B, which also reflects the immature status of the ecosystem. A high value for SO (61.7 %) and low estimate for AS (Supp. Table 5) suggest that the estuary has strength in reserve to resist and recover from unexpected disturbances in the ecosystem.

Multivariate analysis of ecosystem variables

Based on the ecosystem properties of 11 Ecopath models (Table 5), the PCA and cluster analysis discriminated three groups (clusters) differentiating the models from tropical estuaries, temperate estuaries, and estuaries along Indian coast (except Zuari) (Fig. 5). The first (56.6 %) and second (17.8 %) principal components explained 74.4 % of the total variability in the ecosystem variables across the Ecopath models (Table 6). The variables, SC, SE, SR, SD, and FCI influenced the variability within the first component, whereas, SOI and FG loaded significantly on the second component. A total of three significantly different groups of ecosystems were identified on the basis of Nonparametric multivariate permutational analysis of variance (PERMANOVA, Pseudo-F = 16.32; p = 0.006). The first cluster included two tropical (ZU and OG) and two sub-tropical estuaries (RD and PR) (Fig. 5). The second cluster was identified exclusively for the temperate estuaries (CC and GR). The third cluster consisted of other tropical estuaries from Indian coast (SBN, HM and VE) and open sea ecosystem off Karnataka (KA). The first cluster, including Zuari, demonstrated a positive correlation with FG, SE and SD and negative correlation with SR, SC and FCI. This cluster showed highest values of FG, SE, SOI and SD. The second/temperate cluster showed lowest values for SO, FC and SOI (Fig. 5). Third cluster for tropical estuaries from east coast of India indicated highest values for SO, FCI, FC and SR.

Table 6 — Eigen values (correlation) and variance explained by the first two components. The values in italics denote the variables loaded on the respective axis.

Variable	Principal component 1	Principal component 2
Eigen value	5.09	1.6
Variance (%)	56.6	17.8
Variable loadings		
FG	-0.36	1.57
SC	1.11	0.08
SE	-1.15	0.00
SR	1.10	-0.51
SD	-1.11	0.42
SOI	0.21	1.63
FCI	0.84	0.21
SO	0.89	0.92

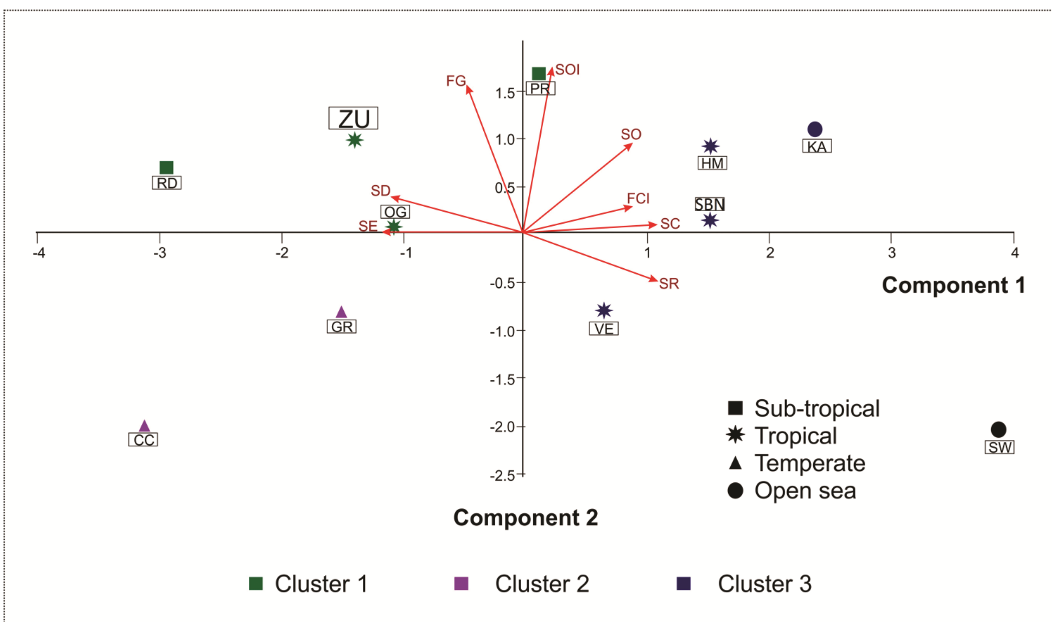

Fig. 5 — Principal component analysis bi-plot for 11 estuarine Ecopath models on the basis of ecosystem variables. Green, Purple and Blue colors indicate Cluster 1, Cluster 2 and Cluster 3 respectively. FG: number of functional groups; SC: total consumption; SE: total exports; SR: total respiration; SD: total flows to detritus; FCI: Finn's cycling index; SOI: system omnivory index; SO: system overhead. ZU: Zuari; RD: Rio de la Plata; OG: Ogun; PR: Pearl River; CC: Canche; GR: Gironde; HM: Hooghly-Matlah; KA: Karnataka; SBN: Sunderban; VE: Vellar; SW: Southwest coast of India

Discussion

Estuaries function as an important link between the freshwater and marine ecosystems, characterised by their significant ecological and socio-economic relevance[9,16,21,31]. The trophic mass balance model built for Zuari estuary incorporates biological and ecological data and renovates the data into ecosystem features such as trophic structure and functioning of a tropical estuary. The Zuari model supplements the existing trophic models developed along the Indian coast[26-28,35,42] and estuarine ecosystem models developed around the world[31]. Thus, this model can be recognized as the basic reference model for tropical monsoonal estuaries.

Zuari estuary Ecopath model

The Ecopath model developed for the estuary was, to the greatest extent, based on the original data. Primary data was used to estimate the biomass of several functional groups especially the fishery resources. In the absence of original data for other functional groups (HB, SB, ZP, BPR, PP, DET, DO and BD), the data were gathered from secondary sources from the same ecosystem or from similar ecosystems[18-19,29,35,38-39]. The validity of the model was assessed through the PREBAL routine, which recognizes the discrepancies of the input data[2]. In ecosystem models, the Ecopath pedigree index provides the extent of validity of the model based on the input data. Generally, the pedigree index range from 0.13 (low) to 0.74 (high) for ecosystem models[31,52]. For Zuari estuary, a reasonably good estimate of 0.59 was obtained as the pedigree index (Table 5) from the present study.

The primary producer groups (PP and BPR) and detritus shared majority of the biomass in Zuari estuary, followed by invertebrates (HB, SB, SR, JF, CEP and CR) and fish groups (BO, CA, SBC, MBC, MA, PS, BP, LBC, LP and RS). The EE values obtained were very high for commercially fished functional groups and ZP because they were under high risk of predation. Therefore, these groups played a significant role in the estuarine food web. The heavy effluent export following the southwest monsoon accumulates organic debris in the estuarine system[29]. Therefore, the detritus biomass, which is the summation of *in-situ* organic debris and export, was extremely high in Zuari estuary. For detritus group, a low value of EE implies that only a small proportion of the detritus biomass was utilized, and the rest accumulated into the sediment or exported out of the system. The EE values for functional groups in this study were in agreement with the findings from the Sunderban estuary[27], Canche estuary[37], Pearl River Delta[38] and Ogun estuary[47]. However, the trends in EE were contrasting to the values obtained for other estuarine ecosystems of India[26.28]. The high value of EE for ZP is observed in estuaries including Zuari, as they are preferred food items for many of the functional groups whereas, lower estimates have been reported from the Vellar estuary and Hooghly Matlah estuary[26.28]. The values of EE were found to be zero for apex predators (dolphins and birds) as none of the other group predate them in estuarine ecosystem.

Ecosystem flow indices and network analysis

TST in Zuari estuary was higher compared to all the Ecopath models from Indian coast (Table 5). The combined effect of multiple factors such as an increase in primary productivity under heavy freshwater effluent discharge, nutrient export from agricultural runoff (rice cultivation and Horticulture), mining rejects and industrial effluents, intense fishing activity with higher levels of multiple fleet fishing effort, increase in fishing mortality for top predator groups and high flow towards detritus would have increased the TST in the estuary[16,24,29]. Zuari receives an annual freshwater discharge of 9 km^3 with a highest rate of flushing (145.4 $m^3\ s^{-1}$) and at the same time, the ecosystem is also subjected to eutrophication through pollution from industrial, domestic and tourism activities. The high inflow of freshwater effluents and eutrophication could result in heavy organic nutrient loading[48] and cause high primary productivity and TST in Zuari estuary (Table 4). These observations are in agreement with the reports from other estuarine ecosystems[31]. GE for the Zuari estuary is comparatively higher (0.003) because of the highly productive and high turnover nature of the estuary (Table 2). GE would be higher for ecosystems with a fishery harvesting low trophic level fish groups[2]. Mean trophic level value of the catch i.e. less than 3.0 (2.9) for Zuari estuary indicated that the higher trophic levels are intensely exploited.

The trophic flow diagram and Lindeman spine indicated that DET and PP are the major sources of food positively impacting all functional groups in Zuari estuary. In the Lindeman spine, the functional groups of the estuary were confined to ten trophic levels. The transfer efficiencies (TE) from primary producers and detritus were found to be very high compared to the other ecosystem models (Table 5). In

Zuari estuary, most of the trophic groups including the predatory groups (LP, BP, LBC, MBC and PS) comprise sub-adults, adults and juvenile groups[16,24]. Therefore, these groups are able to predate on various trophic levels, more specifically on the lower trophic groups such as PP, DET, ZP, HB and CA, leading to a complex estuarine food web. Since the predation of lower trophic levels is shared by multiple trophic levels, the trophic flows were concentrated at lower levels (PP and DET) of the food web. The TE increased from TLII to TL V, and furthermore, it showed a gradual declining trend. Such increase in TE is reported in trophic models for estuarine ecosystems and would be a result of the conversion in energy used as it is changed from one form to another[37-38,47].

The Zuari estuarine food web showed two major pathways which are based on primary producers and detritus, indicating a bottom-up control of the food web. The mean TE was highest, when compared to Ecopath models from other estuaries such as Hooghly Matlah estuary, India (14.7 %), Sirinhaem estuary, Brazil (11.8 %)[31], Caete estuary, Brazil (9.8 %)[49], Rio de la Plata estuary, Uruguay (9.4 %)[50], Canche estuary, France (7 %)[37] and Ogun estuary, Nigeria (6.8 %)[47]. Generally, the ecosystems with high primary productivity; demonstrate low mean TE because of the inefficient utilization of primary productivity[37,47]. The higher values of TE for this ecosystem might be a result of the high transfer efficiency observed from TL II to V. Trophic level (TL) of consumer groups ranged from 2 to 4.7, in which fishery groups demonstrated a wider range (2.16 to 4.04) compared to other estuaries from India (Table 5). The wide range of TLs shows that, there is a large-scale immigration of marine migrant species into the estuary, which makes it a functionally diverse ecosystem[25].

Keystone species and trophic pathways

In estuarine ecosystems of low fish species diversity, predatory fish groups have been found to be the keystone species, which control the lower trophic levels (top-down control) through predation pressure. The top-down control food webs have been observed in estuaries along east coast of India, with top predators as the keystone groups[26-27]. Zuari estuary is highly diverse estuary in terms of species richness, trophic level and diversity[25]. PP, ZP, CA and HB were the keystone groups in this estuary and these groups form the major links for transferring energy from the base trophic levels to higher levels. A very high NPP in Zuari estuary could support rich biomass of ZP. In tropical monsoonal estuaries, the diverse estuarine phytoplankton and zooplankton population comprise of marine, brackishwater and freshwater plankton groups in substantial densities[29]. They support various consumer groups along the estuarine gradient. In estuaries, ZP is considered to be the most important link in the trophic food web connecting primary producers and consumer groups[37]. Similarly, being a consumer of plankton, CA formed an important link between lower and higher TL. HB functions as a major link between detritus and benthic carnivores and omnivores. Diversity and biomass of benthos groups are also considered as indicators of estuarine health[19]. Benthos group along with their diversity and adaptability to various habitats, provides food sources for most of the benthic carnivore species. The results from this study also indicated that CA and HB plays a significant role in the trophic network, transferring energy from PP and detritus to higher TLs. From this study, it is underlined that, the lower TL groups like PP, ZP, benthos and planktivorous fishes are identified as keystone species in tropical monsoonal estuaries.

Ecosystem maturity

A bottom-up trophic organization was foundin the estuarine food web of Zuari, with flows concentrating on the lower trophic levels. Higher estimates for TE, TST, NSP, PP/R, PP/B and low values for FCI and MPL were observed in the estuarine food web. These observations suggest that the ecosystem is far from maturity as described by Odum[2]. Therefore, in terms of ecological indicators, Zuari estuary is an immature system similar to other estuarine systems of the world[36]. FCI and MPL are cycling indices, which represent the ability of an ecosystem to maintain its structure and status of maturity[2]. In matured ecosystems, the utilization of primary production and detritus is very high, which leads to greater degree of recycling and higher values of FCI. FCI also determines the length of cycling in ecosystems, and the diverse and highly productive ecosystems follow longer cycles. The metadata on estuarine Ecopath models show that the values of FCI and MPL range from 0.19 to 24.8 and from 1.7 to 4.5, respectively[31]. The values for FCI (2.78) and MPL (2.2) were found to be low in Zuari estuary, and similar observations for these indices were reported from other temperate and tropical estuaries[31].

In mature ecosystems, primary production rate equals respiratory flows, which reduces PP/R ratio[2]. Similarly, a lower estimate for PP/B is observed in mature ecosystems, due to biomass accumulation over the primary production. PP/R and PP/B ratios were significantly higher for Zuari estuary (7.29), and comparable to the values of PP/R in tropical estuaries and higher than the values for other estuaries and open sea ecosystems from India (Table 5). The greater value for PP/R in Zuari estuary could be due to the poor utilization of the high primary productivity and detritus (huge organic load)[29]. A trophic organization based on primary producers and detritus was observed with high values for TE, TST, NSP and PP/R and low values for FCI and MPL in Zuari estuary. This denotes that the estuary is conclusively at an immature and developing stage.

Ecosystem stability and complexity

SOI, AS, and SO determine the stability, integrity and complexity of an ecosystem. SOI increases with the maturity of an ecosystem, as the food web will be more complex in mature systems. For Zuari estuary, SOI was comparatively low, which shows that the majority of the functional groups are specialist feeders (Table 5). However, the SOI was found to be higher in Zuari estuary compared to other estuaries from temperate, tropical and sub-tropical ecosystems and other estuarine ecosystems from India as well (Table 5). Since, tropical monsoonal estuaries support high diversity of fish species, which supports a complex food web and most of these species likely to be opportunist feeders, and thereby, exhibit comparatively higher values of SOI[29]. From an ecosystem point of view, AS determine the dependence of the ecosystem on external factors. High ratios of AS indicate that the ecosystem is subjected to eutrophication through nutrient enrichment[2]. For Zuari estuary, these ratios were found to be low and denote a developing ecosystem with an intermediate to complex level of trophic organization. The tropical estuaries and coastal ecosystems are highly productive and dynamic and most of these ecosystems are in immature or developing stages[31]. Zuari estuary, being a tropical monsoonal estuary is in the early phase of maturity. The values of SO will be higher in tropical estuaries when compared to temperate counterparts[31]. In monsoonal estuaries, the dynamics of freshwater discharge regulate its stability and assimilative capacity[51]. Zuari estuary receives approximately 9 km^3 of annual freshwater mostly during the monsoon phase at an average rate of 145.4 $m^3\ s^{-1}$(ref. 10). The monsoonal estuaries could remain in mesotrophic condition and possess enormous assimilative capacity for effluents and pollutants. Hence, although the estuary is immature in terms of the ecosystem indices, a high system overhead (SO) value for Zuari estuary shows that it has an adequate strength in reserve to overcome disturbances in the system.

Clustering of estuarine models

The data analyzed for clustering and multivariate analysis were collected from selected tropical, sub-tropical and temperate estuarine Ecopath models[31] and from available estuarine and open sea ecosystem models along the Indian coast. In many of the models, the data on all the performance indicators listed in Table 5 were not available. Therefore, as described in earlier reports, the analysis of the indicators across various Ecopath models was really a challenging task. The ecosystem features of tropical and sub-tropical estuaries have been found to be similar in terms of reasonably high export rates, detritus flow, and SOI. SOI was found to highest for tropical and sub-tropical estuaries compared to temperate estuaries (Table 5). SOI depends on the complexity of trophic network (the higher the complexity, the higher the SOI), and number of ecological compartments (the higher the numbers, the higher the SOI); and the majority of the tropical/sub-tropical ecosystems represent moderate to complex food web. The subjective analysis of diet contents and too much dependence on secondary data sources for diet contents could lead to loss of multiple feeding interactions between the trophic levels[52]. For example, the SOI value was found to be reasonably high (0.35) for Sunderban estuary with lesser number of functional groups[27]. FCI was found to lowest for majority of the ecosystems, which shows that all these ecosystems are immature. Tropical and sub-tropical estuaries showed the highest values for SO compared to temperate estuaries. Therefore, the tropical estuaries possess high stability and capacity to resist external disturbances within its ecosystem. The Ecopath model for southwest coast of India seems to be an outlier in the analysis and it differed from general patterns with very low estimates for functional groups, flows to detritus and exports.

Conclusion

The ecological features of the Zuari estuary were found to be similar with tropical/subtropical estuaries around the world. However, the tropical monsoonal estuary differed from tropical estuaries from east coast of India and other temperate estuaries. Zuari estuary is an immature, developing, highly productive and highly diverse ecosystem under anthropogenic stress, and seems to be steady in energy transfer and trophic organization of functional groups. Zuari estuary is in a non-climax state and seems to be ecologically stable, and resilient to natural and anthropogenic disturbances because of the monsoonal estuarine hydrography, primary productivity and diverse fish communities.The multiple flushing during southwest monsoon purifies the monsoonal estuary and thus, the estuary could remain in mesotrophic condition and possess enormous assimilative capacity for effluents and pollutants. This study is a substantial addition to the available knowledge on trophic modeling of highly diverse tropical monsoonal estuaries, improving the understanding of the role of ecological interactions. While considering Ecopath models developed for estuarine ecosystems, there were absence of many important ecological indicators for most of the estuaries. These inconsistencies in the estuarine models indicate that there is still further scope for improving these models. Therefore, studies on the ecosystem structure of estuaries should invariably focus on collecting original data from the ecosystem, use of modern techniques such as acoustic surveys, underwater visual census and stable isotope analysis to make valid conclusions on the ecosystem functioning. The model could be further improved to account for the seasonal and spatial considerations using Ecosim and Ecospace modules. Thus, this model will be helpful in developing strategic framework through analysis of various fisheries management plans and possible impacts at the ecosystem level.

Supplementary Data

Supplementary data associated with this article is available in the electronic form at http://nopr.niscair.res.in/jinfo/ijms/IJMS_49(05)774-789_SupplData.pdf

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Conflict of Interest

The authors declare that they have no conflicts of interest for the work reported in this paper

Author Contributions

SGB, CSK, and ZPU**:** Conceptualization, Methodology, Sampling; SGB**,** JAK**,** and ZPU: Data collection, Writing- Original draft preparation; and MKS and FP: Software analysis, Writing- Reviewing and Editing.

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