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Trophic fingerprinting of Chilika, a Ramsar site and the largest lagoon of Asia using Ecopath

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ABSTRACT

The constructed mass balanced Ecopath model illustrates the trophic interactions among 22 defined functional groups of Chilika lagoon ecosystem. The estimated trophic levels (TL) in this model are in the range of 1.0 to 3.416. Elopiformes were found as the top predator with a TL value of 3.416 followed by Belonids (3.411). Zooplankton was found as the most utilized group expressing the highest ecotrophic efficiency of 0.944. Network analysis of the model indicates a mean transfer efficiencies of 8.233% from primary producers and 6.198% from detritus. The ecosystem indices: total primary production/total respiration (7.803), Finn's cycle index (1.662), mean path length (2.185), connectance index (0.460), system omnivory index (0.237), ascendancy (47.38) and overhead (52.62) were estimated by the model. The estimated pedigree index (PI) of 0.5 for the present model indicates the ecopath model of the lagoon is a robust model. The indices indicate that the Chilika lagoon ecosystem is on its developing stage and possessing a stable ecosystem with a moderate resilience capacity to overcome the perturbations.

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1. Introduction

Coastal lagoons are one of the most productive ecosystems in the world. These water bodies act as nutrient traps from the catchment area through drainage and the tidal inflow from the adjacent marine environment. Unlike the other ecosystems, the lagoon is considered as the most dynamic ecosystem having complex food web and high ecophysiological capacity of the biotic community against extremely varying environmental conditions, in space and time (Adite and Winemiller, 1997; Lalèyè et al., 2003; Villanueva et al., 2006). Their high productivity induces high biodiversity in these ecosystems offering varieties of niches for aquatic organisms (Villanueva et al., 2006). The pear-shaped Chilika lagoon present at the eastern coast of the Indian subcontinent is well known for its enormous biodiversity. Chilika is a rich fishery ground, about 200 species of Finfish and shellfish inhabit in this lagoon (Bhatta and Panda, 2007). This lagoon is considered to be one of the major capture fisheries of Odisha state in India and supports food and livelihood security to more than 0.2 million fishers and 0.8 million people living in and around it (Mohapatra et al., 2007; Mohanty et al., 2009). The fishery of the lagoon contributes around 71% of its total economic value as a direct benefit from the ecosystem (Parida et al., 2013). In between the 1990s to 2000s, the lake fishery was declining due to huge weed infestation and no seawater inflow into the lagoon. In 2000, Chilika Development Authority (CDA) had implemented the hydrological intervention by opening an artificial mouth in the ecosystem restoration programme of the lagoon (Mohanty et al., 2009) to increase the fisheries productivity. The resilient lagoon harbours more diversity and more number/volume of fish in the post-restoration scenario (Mohapatra et al., 2007; Mohanty et al., 2009).

Chilika lagoon possesses high potential in terms of both ecology and economy; hence sustainability of its multispecies resources is important. It relies upon proper management practices, especially the fishery management (Abdul and Adekoya, 2016). The comprehensive ecosystem management approach tool "Ecosystem-Based Approach to Fisheries Resources Management (EAFM)" is a better strategy than the traditional single-species stock assessment approach (Corrales et al., 2015). According to Nguyen (2012), EAFM gives a new direction for fisheries management as it focuses on management of the entire ecosystem rather than considering only on individual species. It is an approach that has been proposed as a new paradigm in fisheries management that considers the fishery, as well as other biotic, abiotic and human components of the ecosystems and their interactions (FAO, 2003).

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In EAFM, it is essential to study the behaviour of ecosystems for sustainable management practices. Sustainability of living resources can be assessed by estimating the trophic structure and flows of biomass via species interaction (prey–predator relation) using trophic models (Christensen and Pauly, 1993). Thus, in aquatic ecosystem ecological models are an essential tool to examine its functioning. Ecosystem models show the behaviour and describe the functioning of an ecosystem by providing information on factors influences, including human activities both qualitatively and quantitatively.

Ecopath with Ecosim (EwE) model is one of the widely used trophic ecosystem models for the Ecosystem-based fisheries management for the last three decades. Food web models built with Ecopath and Ecosim (EwE) are the representation of aquatic food webs and well known for providing an overview of the ecosystem's trophic state (Christensen and Walters, 2004). The EwE models show a wide application range from studying the structure and functioning of the aquatic ecosystem, assessing human activities and the impact of alien species in the ecosystem, and performing ecosystem comparison, etc. The application of EwE has resulted in policy initiatives and a variety of management actions in aquatic ecosystems (Abdul and Adekoya, 2016). Particularly, for the coastal lagoons and estuarine ecosystems, many models have been developed using EwE (Pauly et al., 1993; Abrca-Areanas and Valero, 1993; Darwall et al., 2008; Duan et al., 2009; Hossain et al., 2010; Abdul and Adekoya, 2016; Pardo et al., 2018). In the Indian context, Ecopath related studies have been restricted to fewer ecosystems. Pannikar and Khan (2008); Khan and Pannikar (2009); Pannikar et al. (2014); Banerjee et al. (2016, 2017) had studied on some Indian reservoirs; Dutta et al. (2017) on Sunderban estuary region; (Rakshit et al., 2017; Mukherjee et al., 2019) studied on Hooghly estuarine system and Vivekanandan et al. (2005) worked on decadal change of mean trophic level throughout the Indian coast. Many works have been carried out to study the ecology and the biology of specific economically important species of Chilika lagoon (Mohapatra et al., 2007; Bhatta et al., 2009; Karna and Panda, 2012; Panda et al., 2016; Karna et al., 2018). However, no study has been conducted on the ecological functioning of the lagoon integrating all the ecological groups and the interactions among themselves. As Chilika lagoon is the largest brackish water lagoon and harbours enormous biotic community, it is necessary to study its dynamics, interspecies interaction, energy flow, responses to exploitation and environmental perturbation for better understanding of ecosystem functioning, which will help in better management of the lagoon. Hence, mass-balance study using ecopath model was carried out to understand the trophic flow in the ecosystem, indicating food web interactions, energy flow pathways, the impact of functional groups and the developmental status of this lagoon ecosystem in terms of maturity and resilience.

2. Materials and methods

2.1. Study area

Chilika, the largest coastal lagoon of Asia is situated along the coast of Odisha, India and lies between latitudes 19°28' and 19° 54' North and longitudes 85° 05' and 85° 38' East (Ghosh et al., 2006) (Fig. 1). It is having a water spread area of 900 km^2 during summer to 1200 km^2 during monsoon (Bhatta et al., 2009). This lagoon possesses dynamic situations with respect to the saline and freshwater regime through the inflow of freshwater from various rivers and rivulets in its northern part and the influx of seawater through outer-channel. It is a unique assemblage of marine, brackish and freshwater, which supports high productivity and huge biodiversity. The lagoon possesses a very high level of ecological importance, for which, the lagoon was declared as 1st Ramsar site of India in 1981. Apart from these, Chilika lagoon is considered as one of the hotspots of biodiversity inhabiting several endangered species listed in the IUCN Red List of Threatened species (World Bank, 2005). The lagoon also considered as one of the largest wintering refuge ground for more than one million migratory birds and has global importance of a waterfowl habitat (Balachandran et al., 2003; World Bank, 2005).

2.2. Mass balance model

This model was developed using the Ecopath with Ecosim software (version 6.5), which quantitatively described the flow of organic matter among the functional groups of the lagoon. In this study, 22 functional groups were categorized and considered for ecopath analysis (Table 1). Among the 22 groups, 15 were fish groups; two were invertebrate groups "crabs and prawns", and the rest five groups are, benthos, zooplankton, phytoplankton, aquatic plants, and detritus. These functional groups were selected based on fish catch data and available information on the diet composition of different species (Table 1).

2.3. Basic input parameters

2.3.1. Biomass

The biomass of the groups was estimated in the habitat area (t/km^2) from the equation Biomass (B) = Catch/fishing mortality (f) (Dutta et al., 2017). Catch data of the year 2010–2011 was collected from the Chilika Development Authority (CDA), Bhubaneswar. The fishing mortalities of different functional groups were calculated from old reports of CIFRI and using the Fishbase-Life history tool (www.fishbase.de) from the length–frequency data with ICAR — CIFRI for different fish species of Chilika during 2010–2017. Biomass of, zooplankton, aquatic plant and benthos were calculated from the information of (Mohanty et al., 2009). Phytoplankton biomass in terms of Chlorophyll a was taken from the report of (Mohanty et al., 2009). Then the estimated chlorophyll a (mg/l) was converted to mg/m^2 by multiplying the average chlorophyll value by the euphotic depth in metres(Abdul and Adekoya, 2016).

The detritus biomass was calculated as a function of primary production and euphotic depth by employing the relationship suggested by Christensen and Pauly (1993).

$$\mathrm{LogD} = 0.954\mathrm{logPP} + 0.863\log\mathrm{E} - 2.41$$

where D — standing stock of detritus in gC/m^2, PP — Primary productivity gC/m^2/year, E — Euphotic depth in metres.

The Carbon (C) was transformed in wet weight (WW) by assuming C: WW of 1:9 (Pauly and Christensen, 1995).

2.3.2. Production/biomass (P/B) ratio estimation:

For fish, the Production/Biomass ratios (P/B) are equivalent to the total mortality or Z value (Allen, 1971). Total mortality (Z) was calculated by the Beverton and Holt method (Beverton and Holt, 1957).

$$Z = \frac{P}{B} = K * \frac{L_\infty - L^-}{L^- - L'}$$

Where L_∞ is the asymptotic length i.e the mean size the individuals in the population would reach if they could live and grow indefinitely; K is the VBGF curvature parameter (expressing the rate at which L_∞ is approached); L^- is the mean length of fish population, computed from L′. Here L' represents the mean length at the first catch, assuming knife edge selection. The P/B ratios of phytoplankton, zooplankton, benthos and prawn were taken from information of (Dutta et al., 2017). Production per biomass ratios of aquatic plants was taken from the report of Vega-Cenedejas et al. (1993). The Z value of crab was taken from CDA-JICA report (Bhatta et al., 2009).

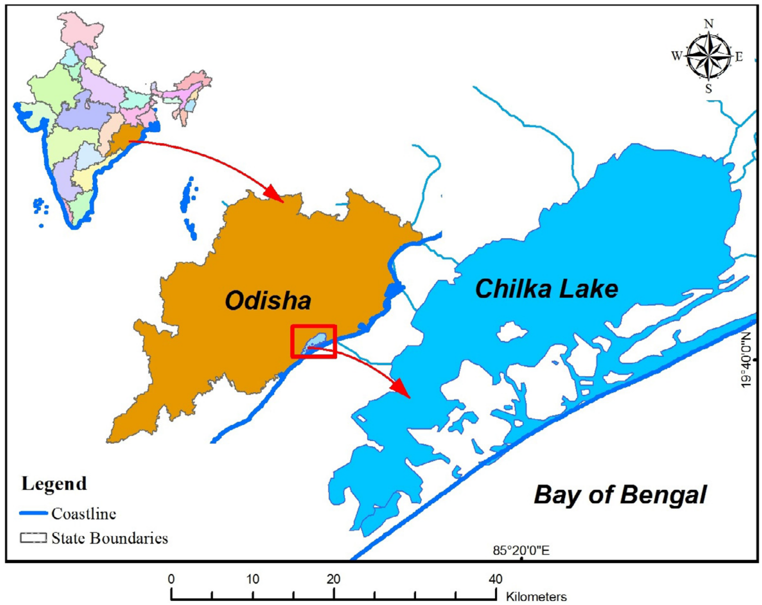

Fig. 1. Study Area Chilika Lagoon, India.

2.3.3. Consumption/biomass (Q/B):

Consumption/biomass (Q/B) was estimated for each fish group using the following empirical relationship (Palomares and Pauly, 1998).

$$\text{LogQ/B} = 7.964–0.204 \log \text{W}\infty - 1.965T' + 0.083A$$
$$+0.532h + 0.398d$$

Where W∞ — asymptotic weight (g)

T' — mean annual temperature of water body expressed in degree centigrade

A — Aspect Ratio

h — dummy variable expressing food type (1 — herbivores, 0 — detritivores & carnivores)

d — dummy variable expressing food type (1 — herbivores, 0 — detritivores & carnivores)

The Q/B of crab was taken from Lin et al. (2006). The Q/B of Prawn, Benthos, and Zooplankton were considered from Dutta et al. (2017).

2.3.4. Diet composition:

Diet composition is one of the essential input parameter for ecopath analysis. It is used to determine the trophic level calculation (Pauly and Christensen, 2000). Diets of different species and families were collected from different published literature and fishbase (Froese and Pauly, 2013) the sources were mentioned in Table 1. The diet matrix is presented in Table 5.

2.3.5. Pedigree analysis

Based on the information of basic input parameters for ecopath model collected, each group was assigned the colour in the software and depicted in Fig. 2. The pedigree index (PI) was calculated in ecopath model. PI indicates the robustness of the model.

2.4. Modelling approach

Ecotrophic efficiency shows, the proportion of a groups' production used in a particular ecosystem and value of EE varies from 0 to 1. For balancing the model it was ensured that the values of the ecotrophic efficiency (EE) fell below 1; if EE values showing >1 the model is not balanced, which means total energy demand exceeds the total production of the system (Christensen et al., 2005). This EE value helps for model validation and indicates how large a proportion of the production is used in the system.

A balanced model gives an overview of the ecological indicators of the ecosystem, through different analysis integrated within the Ecopath with Ecosim (EwE) software, which describes the trophic transfer, trophic flows, and impacts in between the functional groups; termed as prey and predator relationship, which may be positive or negative impacts. In Ecopath, the Mixed Trophic Impact (MTI) method shows the ecosystem interactions to study the impact analysis of the functional groups (Leontief, 1953; Hannon and Joiris, 1989; Ulanowicz and Puccia, 1990). The ratio of production/respiration (P/R) expresses the fate of assimilated food. Theoretically, this ratio can take any positive value, however, thermodynamic constraints limit the realized range of this ratio to values lower than 1. Total system throughput (sum of all flows in the system) and Finn cycling index (Finn, 1976), which denotes the proportion of the total throughput that is devoted to recycling of material, were also calculated. The overall statistics, included in Ecopath describes the function of the Ecosystem and used to assess the status of the ecosystem in terms of maturity (Odum, 1969). Other indices like system omnivory index, connectance index, ascendancy, and overhead were also calculated based on the theoretical and computational methodology (Ulanowicz, 1986) using EwE.

3. Result

3.1. Model trophic structure

In this Ecopath model, the values of Trophic Level (TL) and Ecotrophic efficiency (EE) for each functional group was calculated by the software and presented in Table 2. The trophic interactions between the 22 functional groups were aggregated within four effective trophic levels in the lagoon as shown in (Table 2). Most of the functional groups were laid within the trophic levels TL 2 and TL 3. The highest TL was estimated for Elopiformes (3.416) followed by Belonids (3.411), while the least TL was estimated for detritus, phytoplankton and aquatic plants (TL=1). For zooplankton and benthos the estimated TL were 2.01 and 2.212 respectively. For fish groups, the least TL was for tripod

Table 1
Functional groups for the Ecopath model of Chilika Lagoon.

Sl. No.	Ecological group	Family/ Species	Diet information source
1	Crab	*Scylla serrata*	Nayak et al. (2014)
2	Prawns	*Penaeus monodon* *P. indicus* *P. semisulcatus, Metapenaeus dobsoni M. Monocerous Macrobrachiumsp.*	Dutta et al. (2017)
3	Cyprinids	*Labeo rohita Catla catla Cirhinus mrigala Puntiusspp.*	Fish base
4	Tripod Fish	*Triacanthus biaculeatus*	Fish base
5	Elopiformes	*Elops machnata*	Fish base
6	Eels	FreshWater spiny eels Brackish water eels	Fish base
7	Featherbacks	*Notopterus notopterus N. chitala*	Fish base
8	Snakeheads	*Channa striatus* *C. marulius C. punctatus*	Fish base
9	Cichlids	*Etroplus suratensis*	Fish base
10	Catfish	*Plotosus canius, Arius arius Mystus gulio* *Mystussp* *Osteogeneiosus militaris*	Jhingran (1963) Karna et al. 2016
11	Croakers	*Daysciaena albida*	Jhingran (1963)
12	Gerridae	*Gerres filamentosus* *Gerresoyena*	Jhingran (1963)
13	Belonids	*Strongylura strongylura*	Fish base
14	Threadfin	*Eleutheronema tetradactylum*	Jhingran (1963), Fish base
15	Perches	*Lates calcarifer* *Rhabdosarguss arba* *Crenidens crenidens* *Datnioides polota*	Jhingran (1963) Fish base
16	Clupeids	*Nematolosa nasus* *Anadontostoma chakunda* *Tenualosa ilisha Thryssa sp. Stolephorussp.*	Jhingran (1963) Fish base Karna et al. 2014 Mukherjee et al. (2016)
17	Mullets	*Mugil cephalus* *Liza. macrolepis* *Valamugil cunnesius L.parsia* *Rhinomugil corsula* Smaller mullets	Fish base
18	Benthos	Polychaetes, Gastropods, Bivalve, Crustaceans, Amphipods, Insects, Isopods, etc.	Dutta et al. (2017)
19	Zooplankton	Copepods, Cladocera, Rotifer, Protozoa, Gastropod veliger, Mysids, Crustacean Larva, others	Dutta et al. (2017)
20	Aquatic Plant	Bottom vegetations and Sea grass (*Halophila* spp. and *Halodule* spp.)	
21	Phyto plankton	Diatom, Dinoflagellates, BGA, Green algae	
22	Detritus		

fish (2.242) followed by prawn (2.293) and Cyprinids (2.323). Ecotrophic efficiency (EE) calculated from this model ranged from 0.023 to 0.944. The highest EE value was for zooplankton, and the least for aquatic plants. High EE values were for zooplankton (0.944), Gerridae (0.775), benthos (0.693) and Cyprinids (0.537). The production/consumption (P/Q) ratios were ranged from 0.097 to 0.361.

3.2. Energy flow and transfer efficiency:

The Lindeman spine in EwE indicated pictorial information on trophic flow and flow efficiencies from primary producers, detritus and combined flows from lower trophic level to higher trophic level. In this model, flow efficiencies were fixed in five main aggregated trophic levels from TL I to TL V using Lindeman spine technique. In this model, Lindeman spine routine describes the throughputs of all functional groups by aggregating those in a structural linear food chain with five trophic levels, in which the primary producers and the detritus were placed in distinct levels. Transfer efficiency (TE) were 0.163 from TL II to TL III, 0.0553 from TL III to TL IV and 0.0446 from TL IV to TL V (Fig. 3). Lindeman spine plot of flows and biomasses also indicated that the highest proportion of fluxes in the modelled ecosystem was concentrated at TL I or at the primary producer level, which hosted over 45.91% of total system throughput (Fig. 3). Trophic efficiency model in ecopath estimated the geometric mean energy transfer of 8.233% from the primary producers, 6.198% from detritus and the total transfer efficiencies 7.373% (Table 3). The complex food web structure with the interaction among different groups and their trophic level is presented in Fig. 4.

3.3. Mixed trophic impacts:

The mixed trophic impacts among the functional groups of Chilika lagoon is presented in (Fig. 5). The impact magnitude (+ve and –ve) is represented by the +ve and –ve values on a colour

Table 2
Basic Input and output (in bold) of functional groups as estimated by Ecopath for the tropical Lagoon Ecosystem of Chilika, India.

Species/ Group	Trophic level	Biomass (t/km^2)	Production/ Biomass (/year)	Consumption/ Biomass (/year)	Ecotrophic efficiency	Production/ consumption
Crab	**2.696**	0.530	2.900	14.000	**0.386**	**0.207**
Prawns	**2.293**	2.920	5.140	20.580	**0.225**	**0.250**
Cyprinids	**2.323**	0.254	3.100	20.000	**0.537**	**0.155**
Tripod Fish	**2.242**	0.117	1.380	5.500	**0.295**	**0.251**
Elopiformes	**3.416**	0.002	1.760	13.900	**0.211**	**0.127**
Eels	**3.306**	0.045	1.500	7.900	**0.413**	**0.190**
Feather backs	**2.700**	0.212	1.510	9.900	**0.184**	**0.153**
Snakeheads	**3.037**	0.089	1.990	7.600	**0.434**	**0.262**
Cichlids	**2.581**	0.252	2.260	15.800	**0.248**	**0.143**
Catfish	**2.891**	0.868	1.340	7.900	**0.425**	**0.170**
Croakers	**3.247**	0.422	1.450	10.600	**0.116**	**0.137**
Gerridae	**2.722**	0.233	3.490	36.000	**0.775**	**0.097**
Belonids	**3.411**	0.088	1.850	12.200	**0.365**	**0.152**
Threadfin	**3.346**	0.202	1.030	4.500	**0.408**	**0.229**
Perches	**3.221**	0.760	1.500	7.100	**0.052**	**0.211**
Clupeids	**2.596**	1.858	3.100	15.000	**0.340**	**0.207**
Mullets	**2.424**	1.500	2.800	20.000	**0.221**	**0.140**
Benthos	**2.212**	10.940	9.000	60.000	**0.693**	**0.150**
Zooplankton	**2.010**	2.900	48.000	133.000	**0.944**	**0.361**
Aquatic Plants	**1.000**	350.100	12.500	0.000	**0.023**	
Phyto plankton	**1.000**	7.830	134.270	0.000	**0.388**	
Detritus	**1.000**	308.217			**0.094**	

Table 3
Transfer efficiencies from different trophic level.

Source/Trophic level	II	III	IV	V	VI
Producer	21.44	5.547	4.692	2.673	3.146
Detritus	10.90	5.496	3.975	2.770	3.222
All flows	16.26	5.530	4.457	2.701	3.169

Proportion of total flow originating from detritus: 0.49
Transfer efficiencies (calculated as geometric mean for TL II–IV)
From primary producers: 8.233%
From detritus: 6.198%
Total: 7.373%

Fig. 2. Pedigree assignments in ecopath model for each functional groups of Chilika Lagoon.

scale. The magnitude of green colour signifying effective -ve impact and magnitude of red colour indicating effective +ve Impact. The impact plot is showing the interaction among the functional groups. Threadfins on Elopiformes, perches on catfish and croakers on Gerridaeis indicating strong negative impacts in MTI analysis. Phytoplankton on zooplankton, perches on Elopiformes, phytoplankton on Clupeids and croakers on catfish indicating strong +ve impact. Most of the species are impacting negatively on their own group in MTI analysis. Crabs are impacting negatively to croakers and Featherback; however, showing a positive impact on Cyprinids and Gerridae. Featherback and Snakeheads are impacting negatively to Cyprinids. Perches are impacting negatively to prawns in the ecosystem. The fish groups like tripod fish and Cichilids are not affecting much to other groups of finfish and shellfish. Clupeids and mullets are negatively impacted by perches and catfishes respectively. In the lower trophic levels, zooplankton had negative impact on aquatic plant, phytoplankton and the zooplankton itself. The benthos group is acting as a negative impacting group for detritus, aquatic plants, zooplankton, benthos, etc., whereas it was acting as a positive impacting group

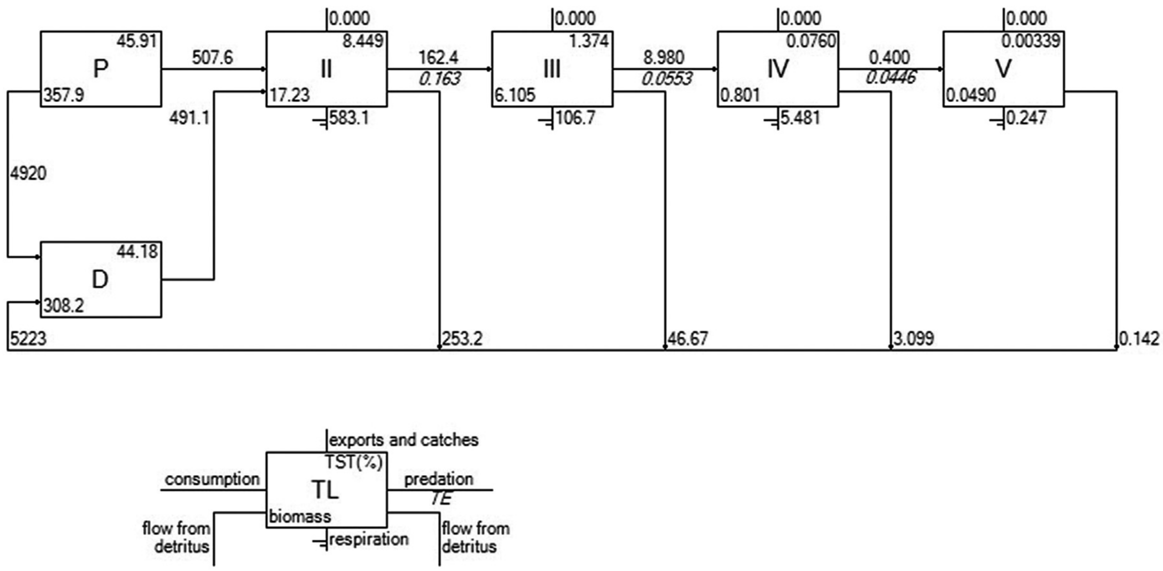

Fig. 3. Lindeman spine Flow network of Organic matter and transfer efficiency for the Chilika lagoon Ecosystem in different trophic level.

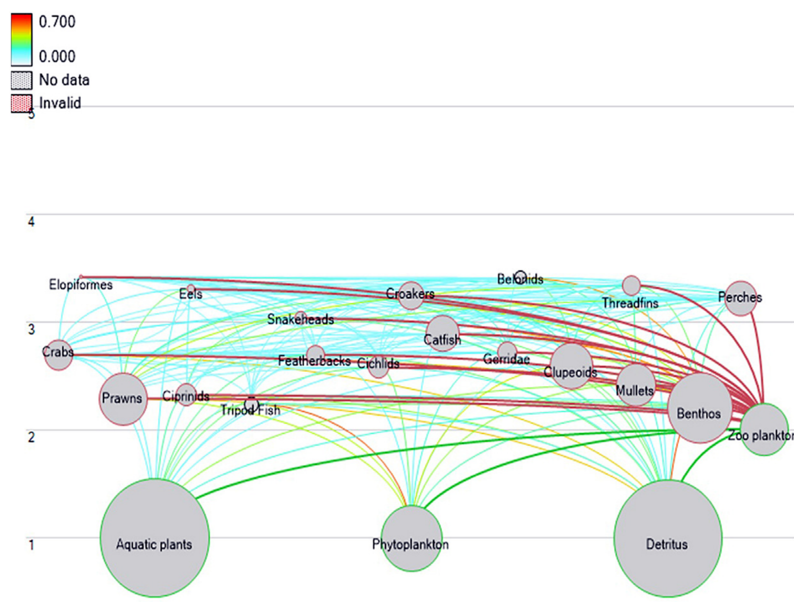

Fig. 4. Flow diagram of the Chilika lagoon Ecosystem.

for Belonids, Threadfins, tripods, crabs, etc. The phytoplankton, detritus and aquatic plants positively impacted on almost all groups.

3.4. Ecosystem properties:

The summary of ecosystem properties of the Chilika lagoon is presented in Table 4. The sum of all consumption, sum of all exports, sum of all respiratory flows, sum of all flows into detritus and total system throughput were 1207.424 t/km^2/year, 4731.993 t/km^2/year, 695.591 t/km^2/year, 5223.0934 t/km^2/year, and 11858.1 t/km^2/year, respectively. The system throughput is the sum of all internal and external inputs to system components, or the sum of all outputs (endogenous flows, exports, and respirations) of all the compartments and also represents the size of the entire system in terms of flow (Kay et al., 1989). Flows into detritus share the highest percentage of throughput followed by all exports. The sum of all productions was 5697.932 t/km^2/year. The total primary production (TPP) and total respiration ratio (TPP/TR) and the Total primary production and total biomass ratio (TPP/B) were 7.803 and 14.204 respectively. Total biomass and total system throughput (B/TST) was 0.032 per year. The Finn's cycling index was 1.62% of total throughput and Finn's mean path length was 2.185. The connectance index (CI) and system omnivory index (SOI) were found to be 0.460 and 0.237 respectively in the system. The overhead and the ascendancy index for this ecosystem were 52.62 and 47.38. The pedigree index of the system is 0.5. The calculated Shannon diversity index was 0.456 for the Chilika lagoon.

4. Discussion

The Ecotrophic efficiency (EE) acts as a prime constituent of any mass balanced model, denoting the proportion of the functional group utilized within the system. The calculated EE value for this ecosystem was high for the zooplankton and fish

Table 4
Summary of Ecosystem properties of Chilika Lagoon.

Parameters	Value	Units
Sum of all consumption	1207.424	t/km^2/year
Sum of all exports	4731.993	t/km^2/year
Sum of all respiratory flows	695.591	t/km^2/year
Sum of all flows into detritus	5223.095	t/km^2/year
Total system throughput	11858.100	t/km^2/year
Sum of all production	5697.932	t/km^2/year
Calculated total net primary productivity	5427.584	t/km^2/year
Total primary production/total respiration	7.803	
Total primary production/Total biomass	14.204	
Total biomass/total throughput	0.032	/year
Connectance Index	0.460	
System Omnivory Index	0.237	
Overhead	52.62	
Ascendancy index	47.38	
Finn's cycling index was	1.662	% of total throughput
Finn's mean path length	2.185	
Ecopath pedigree index	0.5	
Shannon diversity index	0.456	

Table 5
Diet composition matrix.

	Prey/Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	Crab	0.01	0	0	0	0.05	0.05	0	0.005	0.005	0.005	0.005	0.005	0.0005	0	0.07	0	0	0	0
2	Prawn	0.06	0	0	0	0.1	0.21	0.05	0.005	0.005	0.01	0.2	0.005	0.094	0.29997	0.25	0	0	0	0
3	Cyprinids	0.001	0	0	0	0	0.05	0.09	0.19	0	0.01	0	0	0.011	0	0	0	0	0	0
4	Tripod fish	0.001	0	0	0	0.01	0.005	0.01	0.01	0	0	0.001	0	0.0005	0	0.001	0	0	0	0
5	Elopiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0	0	0	0
6	Eels	0.001	0	0	0	0	0	0	0.01	0	0.001	0	0	0.0005	0.001	0.001	0	0	0	0
7	Featherbacks	0.0045	0	0	0	0.01	0.005	0	0.01	0	0.001	0.001	0	0.005	0	0	0	0	0	0
8	Snakeheads	0.005	0	0	0	0.01	0.003	0.01	0	0	0.001	0.001	0	0.0005	0	0.001	0	0	0	0
9	Cichlids	0.005	0	0	0	0.05	0.005	0.01	0.01	0	0	0.002	0	0.005	0.005	0.01	0	0	0	0
10	Catfish	0.001	0	0	0	0	0.005	0	0.01	0	0	0	0	0.0005	0.049995	0.08	0	0	0	0
11	Croakers	0.005	0	0	0	0	0.005	0.005	0.005	0	0.001	0	0	0.005	0.001	0.001	0	0	0	0
12	Gerridae	0.0005	0	0	0	0.15	0.05	0	0.005	0	0.005	0.1	0	0.0005	0.09999	0.005	0	0	0	0
13	Belonids	0	0	0	0	0.01	0	0	0	0	0	0	0	0.05	0	0.001	0	0	0	0
14	Threadfins	0.001	0	0	0	0.01	0.005	0.005	0.005	0	0.001	0.005	0	0.005	0	0.005	0	0	0	0
15	Perches	0.001	0	0	0	0.1	0.05	0	0.005	0	0	0.005	0	0.005	0.0001	0	0	0	0	0
16	Clupeids	0	0	0	0	0.05	0.1	0	0	0	0.01	0.135	0	0.2	0.126987	0.17	0	0	0	0
17	Mullets	0	0	0	0	0.1	0.002	0	0	0	0.035	0.025	0	0.15	0.149985	0.051	0	0	0	0
18	Benthos	0.414	0.2	0.1	0.2	0.1	0.34	0.2	0.445	0.35	0.47	0.35	0.3	0.467	0.209979	0.154	0.2	0.1	0.05	0
19	Zooplankton	0.05	0.05	0.2	0	0.2	0.05	0.2	0.1	0.14	0.2	0.1	0.34	0	0.005	0.05	0.35	0.3	0.15	0.01
20	Aquatic Plants	0.05	0.05	0.15	0.2	0	0.055	0.17	0.005	0.2	0.005	0	0.05	0	0	0.025	0.05	0.25	0.1	0.05
21	Phytoplankton	0	0.3	0.3	0.55	0	0	0.05	0	0.2	0.045	0	0.1	0	0	0.025	0.35	0.25	0.15	0.7
22	Detritus	0.39	0.4	0.25	0.05	0.05	0.01	0.2	0.18	0.1	0.2	0.07	0.2	0	0.049995	0.1	0.05	0.1	0.55	0.24
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

	Impacted																					
Impacting	Crabs	Prawns	Ciprinids	Tripod Fish	Elopiformes	Eels	Featherbacks	Snakeheads	Cichlids	Catfish	Croakers	Gerridae	Belonids	Threadfins	Perches	Clupeoids	Mullets	Benthos	Zoo plankton	Aquatic plants	Phytoplankton	Detritus
Crabs	-0.166	-0.054	0.254	0.096	0.016	-0.106	-0.388	-0.233	-0.172	-0.110	-0.341	0.236	-0.004	0.059	0.113	0.054	0.030	-0.015	0.003	0.004	0.001	0.007
Prawns	-0.021	-0.102	-0.005	-0.077	-0.086	0.170	0.056	-0.039	-0.073	-0.122	0.129	-0.124	0.005	0.154	0.093	-0.108	-0.033	-0.090	0.038	0.030	-0.039	0.016
Ciprinids	0.001	0.003	-0.078	-0.050	0.009	0.007	0.063	0.155	-0.018	0.008	-0.018	0.010	0.005	-0.008	-0.004	0.004	-0.001	-0.006	-0.003	-0.003	0.000	0.002
Tripod Fish	0.001	0.000	-0.006	-0.005	0.011	0.003	0.008	0.006	-0.002	0.000	-0.001	0.001	0.000	-0.001	-0.001	0.000	0.000	-0.001	0.000	-0.001	-0.001	0.001
Elopiformes	0.022	0.014	0.006	0.005	-0.020	-0.002	-0.020	-0.009	0.002	0.037	-0.005	-0.007	0.001	0.017	-0.045	0.019	-0.002	-0.003	0.001	0.002	-0.001	0.001
Eels	0.097	0.060	-0.020	0.023	-0.096	-0.014	-0.099	-0.029	0.064	0.186	-0.045	-0.011	0.020	0.090	-0.231	0.087	0.010	-0.017	0.003	0.007	-0.003	0.008
Featherbacks	-0.017	-0.007	-0.353	-0.392	0.094	0.073	0.013	-0.326	-0.136	-0.021	-0.115	0.092	0.002	-0.080	0.035	0.023	0.020	0.000	-0.003	-0.001	0.002	0.000
Snakeheads	-0.005	0.006	-0.235	-0.083	0.029	-0.241	-0.110	-0.012	-0.033	-0.031	-0.016	0.017	-0.002	-0.017	0.021	0.002	0.007	0.000	0.001	0.002	0.000	0.000
Cichlids	-0.028	-0.005	-0.012	-0.011	0.050	0.004	0.022	0.012	-0.001	-0.003	0.008	-0.006	-0.001	-0.003	0.001	-0.004	0.000	-0.010	0.004	-0.002	-0.002	0.006
Catfish	-0.113	-0.029	-0.103	0.034	0.068	-0.215	-0.028	-0.035	-0.002	-0.111	-0.042	0.000	-0.036	-0.089	0.129	-0.061	-0.234	-0.007	0.017	0.021	-0.003	0.003
Croakers	0.176	-0.093	0.057	0.023	0.096	-0.089	-0.181	-0.073	0.065	0.301	-0.150	-0.567	-0.001	-0.222	-0.322	-0.102	-0.048	0.008	0.012	0.002	-0.002	-0.003
Gerridae	-0.039	-0.018	-0.009	-0.003	0.057	0.039	0.008	0.009	0.016	0.036	0.098	-0.083	-0.005	0.070	-0.050	-0.014	-0.013	-0.017	0.000	0.009	0.004	0.010
Belonids	0.017	0.008	0.005	0.023	0.017	-0.016	-0.056	0.007	0.001	0.028	-0.041	0.033	-0.468	-0.017	-0.034	-0.028	-0.080	0.000	0.006	0.005	-0.002	-0.001
Threadfins	-0.003	-0.077	0.004	-0.003	-0.970	-0.027	0.026	0.018	-0.028	-0.116	-0.030	-0.098	-0.010	-0.052	0.036	-0.053	-0.109	0.018	0.002	0.000	0.001	-0.008
Perches	-0.412	-0.246	-0.051	-0.160	0.367	0.042	0.269	0.125	-0.221	-0.632	0.103	-0.015	-0.072	-0.365	-0.218	-0.337	-0.019	0.066	-0.011	-0.026	0.012	-0.030
Clupeoids	-0.037	-0.047	0.006	-0.017	-0.011	0.080	0.007	-0.001	-0.036	-0.068	0.104	-0.091	0.083	0.032	0.066	-0.084	-0.036	-0.032	-0.026	0.018	0.006	0.029
Mullets	-0.020	-0.019	-0.002	-0.004	-0.032	-0.020	-0.008	0.000	-0.029	-0.018	0.007	-0.036	0.065	0.112	0.031	-0.043	-0.053	-0.022	-0.033	-0.049	0.012	0.018
Benthos	0.071	-0.031	-0.096	0.148	-0.105	0.052	-0.163	0.122	0.080	0.135	0.064	-0.091	0.117	0.037	-0.037	-0.033	-0.183	-0.464	-0.378	-0.263	0.127	-0.320
Zoo plankton	-0.025	-0.146	-0.082	-0.287	0.162	-0.022	0.046	0.010	-0.027	0.110	0.043	0.118	-0.002	-0.035	-0.027	0.065	0.029	-0.016	-0.339	-0.115	-0.429	-0.106
Aquatic plants	0.024	0.019	0.069	0.119	0.022	0.076	0.156	-0.023	0.157	-0.003	-0.011	0.050	0.032	0.025	0.027	0.032	0.220	0.037	-0.012	-0.043	-0.007	-0.028
Phytoplankton	-0.0559	0.132	0.175	0.299	0.101	0.0693	0.109	0.0517	0.134	0.0613	0.117	0.0892	0.0603	0.0527	0.0555	0.307	0.196	0.0208	0.4	-0.117	-0.288	-0.1
Detritus	0.282	0.239	0.117	-0.0475	0.0487	-0.00339	0.00223	0.118	-0.0162	0.137	0.0191	0.173	0.0603	0.0812	0.139	-0.0338	-0.0576	0.246	-0.035	-0.16	-0.0458	0

Fig. 5. The Mixed trophic impact plot of functional groups of the Chilika lagoon. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

groups; however, it showed lower value for primary producers viz. phytoplankton and aquatic plants and also detritus. It indicates a small proportion of primary producers (phytoplankton and aquatic plant) are utilized in this system. The low EE value of detritus also indicates that a less fraction of detritus is consumed in the system; whereas, the remaining were incorporated in sediment and exported out of the system. Similar types of results were observed in Danshuei River estuary ((Lin et al., 2007); Pearl river Delta (Xu et al., 2011); coastal waters of Bight of Benin, Nigeria (Abdul and Adekoya, 2016). The higher detritus accumulation in the system is buried as sediment and then decomposed by micro heterotrophs (Nixon et al., 1986). The excess amount of detritus could lead to eutrophication, if the resilience property of a lake does not cope with the detritus load (Villanueva et al., 2008). The least observed value of EE (0.023) of aquatic plants in this study might be attributed to its minimal consumption (utilization) of aquatic plants by other functional groups. The high production of the aquatic vegetation in this ecosystem and its less consumption in the system had created ecosystem menace, resulted in lower fish catch in the past (Mohapatra et al., 2007). Fish groups like perches and croakers exhibited lower calculated EE values 0.052 and 0.116 respectively. The low EE value indicated a lesser number of available predators for these trophic groups. However, the higher EE value of other fishes indicated the readily available predators for those groups (Christensen et al., 2000). The zooplankton had the highest EE value in this study, which indicates zooplankton being consumed by the majority of the groups and has a high rate of utilization. Similar types of observations were reported by Abdul and Adekoya (2016) in coastal waters of Bight of Benin, Nigeria and Haputhantr et al. (2008) in the shallow coastal ecosystem of Sri Lanka.

Trophic level (TL) of any organism depends on its feeding habit and the TL considered as the key concept of ecosystem models and an index of fishing impact in the ecosystem (Pauly and Christensen, 2000). The mean trophic level of fish landings is considered as an index of sustainable exploitation of resources (Dutta et al., 2017). A decline in mean trophic level has been observed in many ecosystems due to over-exploitation of higher trophic level organisms from the ecosystem (Pauly et al., 2002; Essington et al., 2006). In this study, the estimated highest TL (3.416) was similar to the calculated TL of top predator (3.5) by Vivekanandan et al. (2003) in the south-west coast of India. The TL of an organism depends on its prey and predators and their abundance in the system. This study also showed that zooplankton (TLII) played a significant role in this food web; being the direct consumer of phytoplankton, it serves as the main food supplier for the higher TL fishes. Most of the fishes were placed in between TL II to TL III in the food web of Chilika. This indicates that the fisheries of Chilika are targeted at lower trophic level fishes, as the top predators biomass and catch are less.

The transfer efficiency (TE) represents the proportion of flow from a given trophic level to its successive discrete trophic level. Its estimation is vital for the assessment of an ecosystem due to its influencing factor on the food web structure and the fish yield (Gaedke and Straile, 1994). The TE value generally decreases with the subsequent increase of trophic level. In this model, TE value has decreased from lower to higher trophic levels; similar to the observations in Northern Hangzhou Bay by Xu et al. (2011). The calculated mean transfer efficiency (7.634%) of this model was lower than the mean transfer efficiency of 10% reported by Lindeman (1942) but it falls within the value reported by Pauly and Christensen (1995). In Curonian Lagoon, low transfer efficiency (6.0) was reported by Tomczak et al. (2005). Coll et al. (2008) and Shannon et al. (2009) had also reported the higher productive ecosystems like upwelling ecosystems show low transfer efficiency. Hence, the lower TE value in Chilika lagoon might be resulted due to improper utilization of primary producers.

The mixed trophic impact plot describes the importance and the interactions among the trophic groups (Pannikar et al., 2014; Li et al., 2009). The negative impact by the impacting group is because of competitions for the same food or they prey upon the impacted group. The +ve impact because either the species are not competing for food or the impacting group prey upon the competing species and/or predators of the impacted group. In this model, the lower trophic organisms including the detritus possess a positive impact on almost all higher trophic level organisms by facilitating foods, whereas the others showed scattered impact. The positive impact of detritus with all other groups indicated its importance in the ecosystem. Also, it is revealed that the higher trophic level organisms are impacted negatively by the lower level organisms like phytoplankton, zooplankton and the detritus. This is because of the competition for similar food by the higher-level organisms and analogous to the observations made by Hunter and Price (1992).

Ecosystem statistics give an overview of any ecosystem properties. The summarized ecosystem statistics of Chilika lagoon have characterized its status of maturity. The total system throughput (TST) of this system was 11,858.31 t/km^2/year, which is higher than the reported value of Lake Kivu (6086 t/km^2/year) by Villanueva et al. (2008); but lower than Hangzhou Bay (19,323 t/km^2/year) (Lin et al., 2004) and Kuoshey Bay (29,692 t/km^2/year) (Xu et al., 2011). The high value of TST might be because of higher productivity with high nutrient inflow from the catchment area to the lagoon.

In this model, the sum of all flows into detritus constitutes a 44% share in the total system throughput, which is good for Chilika ecosystem as the detritus is helpful for the planktonic production and increasing the ecosystem productivity (Giordani et al., 1992).

The ratio of total primary productivity to total respiration (TPP/TR) is an indicator of the ecosystem's maturity (Odum, 1969). Persad and Webber (2009) have also described that, in a matured ecosystem, the above-mentioned ratio tends to approach 1. However, Christensen and Pauly (1993) described that in an early developing stage of an ecosystem, the production exceeds respiration and in an organically polluted ecosystem the respiration exceeds production. In this study, the calculated TPP/TR (7.809) was >1, which indicates the ecosystem is in a developmental stage (not fully matured), the estimated ratio can be comparable to 6.325 of a coastal estuarine ecosystem of Bight of Benin, Nigeria (Abdul and Adekoya, 2016). The higher ratio might be due to the dynamic nature of the estuarine characteristics of Chilika lagoon like the Bight of Benin as freshwater inflow and influx of seawater happening continuously and hampering the maturing process.

In an ecosystem, if the ratio of total primary production and total biomass (TPP/TB) is low, then it possesses a tendency of biomass accumulation in it (Pannikar et al., 2014). The TPP/TB value of Chilika (14.204) is lower than the TPP/TB value of mature ecosystem of coastal waters of Sunderban of West Bengal (38.85) (Dutta et al., 2017) and Hooghly estuarine system, India (39.61 as described by (Rakshit et al., 2017). The values are comparable to the ratio of the most mature Wyra reservoir of India (16.24) (Pannikar and Khan, 2008). The high TPP/TR ratio and the low TPP/TB ratio in this model might be the result of improper utilization of primary producers in the ecosystem.

Finn's cycling index (FCI) indicates the proportion of total flow recycled in the system compared to the total system throughput. Finn's cycle also referred to as a stress and maturity indicator of an ecosystem, as it indicates the ecosystem's ability to maintain its structure and integrity through its positive feedback mechanism (Ulanowicz, 1986; Monaco and Ulanowicz, 1997; Vasconcello et al., 1997). Ecosystem's maturity is expressed with high Finn's cycling Index (FCI) (Abdul and Adekoya, 2016). Taylor et al. (2008) had reported that high utilization of primary productivity and detritus is responsible for the higher degree of cycling index of an ecosystem. The estimated FCI value 4.35% of its TST of Chilika lagoon is higher than the reported values of Nanwan bay (3.5) (Liu et al., 2009), Southern Benguela (Shannon et al., 2009) and lower than Hooghly-Matlah estuary, India (Rakshit et al., 2017; Mukherjee et al., 2019). The low FCI could be a result of the low utilization of its aquatic plants and detritus. The detritivore community in the ecosystem is less to consume all the detritus produced by the system. Chilika lagoon is less mature than, Hooghly-Matlah estuarine system, which indicates Chilika ecosystem may take a comparatively longer time to recover from a perturbation than a matured system.

The Connectance Index (CI) and the System Omnivory Index (SOI) are two important indices of Ecopath analysis. They generally reflect the complexity of inner linkages among the organisms in the ecosystem. The SOI is the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake, whereas the CI is the ratio of the number of actual links to the number of possible links for a given food web (Christensen and Walters, 2004). The SOI and the CI are positively correlated to the maturity of the system as with increasing in maturity, the food chains are turns to web-like structure from its linearity as the system mature (Odum, 1971; Christensen, 1995). The computed SOI value (0.241) of Chilika is higher than the reported value 0.19 of Northern and Central Adriatic Sea (Coll et al., 2006), 0.162 of Rabisankar Reservoir (Pannikar et al., 2014) and similar to the SOI value 0.288 in the coastal waters of Nigeria (Abdul and Adekoya, 2016) and 0.24 in Hooghly-Matlah estuarine system (Rakshit et al., 2017). The calculated CI (0.463) is higher than the reported CI values 0.31 of Gulf of Paria ecosystem (Manickchand-Heileman et al., 2004) and 0.32 of Coastal waters of Nigeria (Abdul and Adekoya, 2016). It signifies the wider feeding variety and web pattern of trophic relationships and more interdependency among the functional groups in this ecosystem.

The pedigree index of the present model (0.5) is more than the estuarine system of Nigeria (0.36) (Abdul and Adekoya, 2016) and Hooghly estuarine system (0.197) (Dutta et al., 2017). The pedigree index (PI) signifies the validity of the ecopath model used in the study. In this present study, the ecopath model prepared for the Chilika lagoon is robust.

The overhead of an ecosystem indicates the difference between the capacity and ascendency of the system (Christensen, 1995; Christensen and Pauly, 1995) and reflects the system's "strength in reserve" to overcome unexpected perturbations (Ulanowicz, 1986). Odum (1969) described that a system with high ascendency will be highly developed and much diversified, however a system with high overhead is more resilient and has more strength in reserve. The present result of overhead (52.62%) is lower than the Hooghly estuarine system (70%) (Rakshit et al., 2017) and Bight of Benin estuarine system, Nigeria (57.7%) (Abdul and Adekoya, 2016). The present overhead indicates the food web of Chilika can recover from some unexpected disturbances but at a lower level than Hooghly estuarine system and Bight of Benin estuarine system of Nigeria.

5. Conclusion

This ecopath model of Chilika is a baseline model, which has integrated all the available biological data of this coastal lagoon ecosystem and gave crucial information on the functioning of the ecosystem. The PI indicates the present model is robust. Further addition of new information upon this model could be helpful to deliberate a fruitful result for the management of this lagoon ecosystem. The network analysis of this model indicates that Chilika lagoon is developing towards its maturity and possessing a better level of stability towards the external perturbation. Further to address the better fisheries management strategies in multispecies ecosystem of Chilika through the simulation "Ecosim" module, this study can be used as the baseline information.

CRediT authorship contribution statement

Prajna Ritambhara Behera: Investigation, Writing - original draft. **Pranaya Kumar Parida:** Writing - original draft, Writing - review & editing. **Subodh Kumar Karna:** Investigation. **Rohan Kumar Raman:** Investigation. **V.R. Suresh:** Writing - original draft. **Bijay Kumar Behera:** Writing - review & editing. **Basanta Kumar Das:** Conceptualization, Supervision, 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.

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