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Trophic Web Structure and Ecological Network Analysis of Sasthamkotta Lake, A Ramsar Site in Kerala, India

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Abstract

A mass balanced trophic model was constructed for Sasthamkotta Lake, a Ramsar site in Kerala, India to study the energy flows and species interactions among fourteen key functional groups in the lake. The functional groups considered were fish-eating birds, cichlids, murrels, eels, catfishes, needlefishes, gobiids, nandids, barbs, zoobenthos, zooplankton, phytoplankton, macrophytes and detritus. The model was constructed using Ecopath with Ecosim software. All the fish groups recorded high ecotrophic efficiencies, suggesting exploitation pressure on these groups. Flows based on aggregated trophic levels revealed the importance of primary producers to higher trophic levels. The overall transfer efficiency of the lake was found to be 13.6%. The gross ecological efficiency of Sasthamkotta Lake was found to be low. The mixed trophic impact analysis showed the strong positive impact of primary producers on higher trophic levels. The total primary production/respiration ratio was high, indicating the Sasthamkotta Lake has not attained ecological maturity and is in a developmental stage.

Keywords: Ecopath modelling, Trophic relationship, Ecotrophic efficiency, Production/Respiration ratio, Ecological maturity, Functional groups, Tropical freshwater lake

1. Introduction

Due to the ever-increasing population, living aquatic resources of the world in general and that of India, in particular, are under constant pressure (Raghavan *et al.*, 2016; Dudgeon, 2019; Albert *et al.*, 2020). This has resulted in accelerated ecological deterioration of freshwater lakes on one side and over-exploitation of fishery resources on the other hand (FAO, 2018), often seriously impacting the livelihood of fishers and global initiatives to achieve standards set for responsible fisheries (Lynch *et al.*, 2020). Indiscriminate fishing practices may result in loss or change of biodiversity at different trophic levels, and therefore it is important to study the interactions between species in ecosystems and the implications of fishing in ecosystem functioning in order to frame effective management strategies. Fish groups play a critical role as consumers in aquatic ecosystems. Fisheries management strategies are moving away from single-species management, towards an ecosystem-based approach (Dame and Christian, 2006), more specifically ecosystem-based fisheries management (EBFM) (Stefansson *et al.*, 2019).

In ecosystem-based fisheries management, prey and predators cannot be managed independently. Therefore, a proper understanding of the trophic structure of the ecosystem is essential for fishery assessment and management. Ecosystem models help in integrating such complex interactions between the various components of an ecosystem, thereby helping ecosystem managers to prepare a sustainable conservation plan (Hollowed *et al.*, 2000). The Ecopath model has been used to describe the structure and dynamic functions of trophic levels, energy flows and ecological potential of aquatic ecosytems, including lakes (Christensen and Walters, 2004; Fetahi and Mengistou, 2007; Gubiani *et al.*, 2011; Mensah *et al.*, 2019). This model has been extensively applied to evaluate the trophic structure and system functions of lakes in Africa (Moreau, 1995, 1997; Sarvala *et al.*, 1999; Fetahi and Mengistou, 2007; Villanueva *et al.*, 2008; Darwall *et al.*, 2010; Mensah *et al.*, 2019) and in lakes and reservoirs of India (Khan and Panikkar, 2009; Biju Kumar *et al.*, 2015; Khan *et al.*, 2015).

The Sasthamkotta Lake, located in Kollam District of Kerala, India, is the largest freshwater lake of the state, is one among the 26 wetlands identified in the country for intensive conservation and management by the Ministry of Environment and Forests, Government of India, under the National Wetland Conservation Programme. In the year 2002, Sasthamkotta wetland was declared as a Ramsar Site (Ramsar, 2020). The designation of this Ramsar site was based on the fact that it is the largest freshwater lake in Kerala state and form the major drinking water source of about 500,000 people in the marginal areas and it supports rich fish fauna that supports livelihood of people (Chackacherry *et al.*, 2010). The fisheries of Sasthamkotta Lake are of significant socio economic importance, providing direct and indirect livelihood to hundreds of fishermen, with about 30 species (Girijakumari *et al.*, 2011). Accordingly, the objective of the present study was to develop a mass balance trophic model of Sasthamkotta Lake using the ecological modeling software Ecopath with Ecosim (EwE) to illustrate the energy pathways and trophic interactions of the food web and to analyse the maturity of the ecosystem.

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2. Materials and Methods

2.1 Study area

Sasthamkotta Lake (9°0' - 9°5' North 76°35' - 76°46' East), located in Kunnathur Taluk of Kollam District in Kerala (Fig. 1), at an elevation of 33 m above MSL, has a total catchment area of about 12.69 km^2, average depth of 6.53 m, and total storage capacity of 22.4 km^2 (Divya and Mophin, 2018). The lake is a major drinking water source of people in Kollam district. Sasthamkotta Lake is also a very important wetland in south India used by waterfowls both as feeding and breeding grounds (Chackacherry *et al*., 2010).

2.2 Ecopath Modelling Approach

The complex ecological systems can be potentially understood by applying an ecosystem approach, which encompasses all species of the system and their trophic interactions. Ecopath with Ecosim (version 5.1) is a static modelling approach, which is a tool to understand the trophic structure of an ecosystem, considering functional groups from different trophic levels. Being a static model, Ecopath uses a series of linear equations to quantify the network flows within a system, further analysed by ecological network analysis indices.

The Ecopath modelling approach was first developed by Polovina (1984) to analyze energy flow between groups of species based on feeding interactions and biomass estimates. This approach was later refined incorporating a variety of ecological and theoretical approaches (Christensen and Pauly, 1992; Walters *et al*., 1997, 2000; Pauly *et al*., 2000; Christensen and Walters, 2004). The Ecopath model attains mass balancing in that production of any given prey is equal to the sum of the biomass consumed by predators, the biomass caught, and any exports from the system. The most important factor which links different ecological groups in an ecosystem is the predation mortality because mortality for prey is the consumption for a predator. Ecopath balances production and losses for each species or species groups in the form of an equation:

$P_i = Y_i + B_i \,.\, M_i + E_i + BA_i + P_i(1-EE_i)$

Where P_i = total production rate of i; Y_i = total catch rate of i; B_i = biomass of the group;

M_i= total predation rate of i; E_i= net migration rate (emigration minus immigration); BA_i = biomass accumulation rate for i; and $(1-EE_i)$ = other mortality rate of i.

This equation can be re-written as follows and becomes the basic equation of Ecopath:

$B_i \,.\, (P/B)_i \,.\, EE_i = Y_i + \Sigma\, (B_j).(Q/B)_j \,.\, DC_{ij}$

Where, B_i = the biomass of prey group i;

P/B_i =production /biomass ratio of group i;

EE_i =ecotrophic efficiency, Y_i =its yield or fishery catch; B_j =the biomass of predator group j; Q/B_j= the food consumption per unit biomass of j, and DC_{ij} = the fraction of i in the diet of j.

2.3 Functional groups and input parameters

Ecologically similar species of the biological assemblages were grouped together to identify the functional components of the ecosystem (Coll *et al*., 2015) and fourteen functional groups were considered for constructing the trophic model of the Sasthamkotta Lake, of which eight groups included fishes. Fish-eating birds were considered as the top predator of the lake ecosystem. The different functional groups and their species composition are shown in Table 1.

Biomass (B) in tonnes/km^2, production/biomass ratio (P/B) per year, consumption/biomass ratio (Q/B) per year, ecotrophic efficiency (EE), and diet composition (DC) are the main input parameters of the Ecopath model. For constructing a mass-balanced model, diet composition and at least three of the four parameters (B, P/B, EE, and Q/B) should be provided as the basic input for each functional group. The Ecopath parameterization algorithm estimates

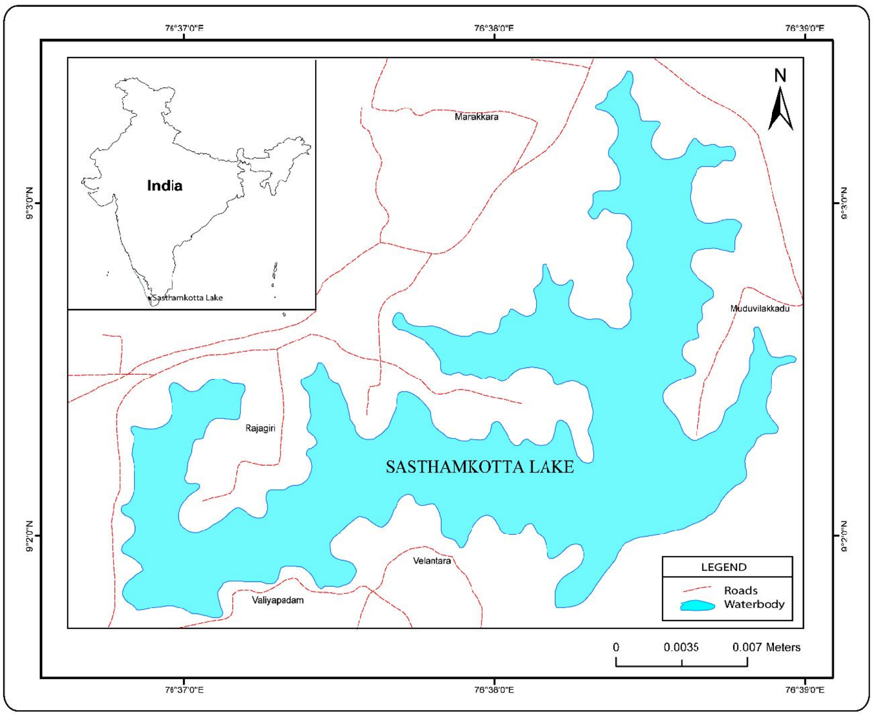

Fig. 1. Map of Sasthamkotta Lake, Kollam district, Kerala

Table 1. Functional groups and their species composition for Sasthamkotta Lake trophic model

No.	Functional Group	Biotic components
1	Fish-eating birds	Herons, kingfishers, egrets
2	Cichlids	*Etroplus suratensis, Pseudetroplus maculatus, Oreochromis mossambicus*
3	Murrels	*Channa striata, C. marulius*
4	Eels	*Anguilla bicolor bicolor, A. bengalensis bengalensis*
5	Catfishes	*Mystus oculatus, Heteropneustes fossilis*
6	Needle fishes	*Xenentodon cancila, Hyporhamphus xanthopterus*
7	Gobiids	*Glossogobius giuris*
8	Nandids	*Ambassis ambassis, Parambassis thomassi*
9	Barbs	*Dawkinsia filamentosa, Systomus sarana*
10	Zoobenthos	Nematodes, chironomids, snails
11	Zooplankton	*Brachionus, Daphnia, Cyclops*, etc.
12	Phytoplankton	*Oscillatoria, Spirogyra, Scenedesmus, Chlorellum*, etc.
13	Macrophytes	*Limnocharis flava, Salvinia molesta*, etc.
14	Detritus	

the missing parameter. Since EE is considered the most difficult parameter to estimate, it is often left to the algorithm to calculate.

Fishes

The biomass of fish groups was estimated from the experimental catch data from March 2010 to February 2011 and also from the commercial fish catch from the lake. Sample collection was made using the locally used gears like gillnet, cast net and hook and line. The average biomass for each group per unit area (tonnes/km^2) was estimated from the equation of Gulland (1971), B = Y/F, where Y is the average annual yield of each group and F the fishing mortality. The production/biomass (P/B) ratio of fishes was taken as equivalent to the instantaneous rate of total mortality (Z) (Pauly *et al.*, 2000) assuming a steady state of the ecosystem (Allen, 1971). The Z values were estimated for all fish species using the length-converted catch curve routine incorporated in the FiSAT software (Gayalino *et al.*, 1996). Q/B is the annual food consumption/biomass ratio of each group. For fish groups, it was determined by using the empirical equation (Palomares and Pauly, 1998) incorporated in the Ecopath model.

$$\text{Log } (Q/B) = 7.964 - 0.204\log W_{inf} - 1.965T + 0.083A + 0.532h + 0.398d$$

Where W_{inf} is the asymptotic weight (g); T an expression for the mean annual temperature of water body, expressed using T = 1000/K (K = ^oC + 273.15); A is aspect ratio (A = h^2/s) of the caudal fin of fish, given height of caudal fin (h) and surface area of caudal fin (s); h is a dummy variable expressing food type (1 for herbivores and 0 for detritivores and carnivores) and; d is also a dummy variable also expressing food type (1 for detritivores and 0 for herbivores and carnivores).

Fish-eating birds

P/B for fish-eating birds was derived from Hustler (1997) for similar species and similar system at different habitat. All other inputs for this functional group were taken from a tropical reservoir system (Moreau *et al.*, 2000).

Zoobenthos and zooplankton

The zoobenthos of the Sasthhamkotta Lake included nematodes, chironomids and snails. The zooplankton community comprised primarily of *Brachionus, Daphnia*, and *Cyclops*. For zoobenthos, gross food conversion efficiency (P/Q) was assumed as 25% and ecotrophic efficiency was taken as 95% after Fetahi and Mengistou (2007) to calculate the minimum P/B and Q/B ratios. Similarly, for zooplankton, P/Q was assumed as 95% to calculate the Q/B ratio. The Annual average of fresh weight (t.km^{-2}) was used as the biomass input for zoobenthos and zooplankton.

Primary producers

The phytoplankton biomass was estimated from the determination of photosynthetic pigment (chlorophyll-a) concentration (Parsons *et al.*, 1984) and productivity by Winkler's light and dark bottle method (Strickland and Parsons, 1968). Fresh weight of macrophytes taken from 50 x 50 cm quadrate was taken as an estimate of their biomass. The primary productivity of macrophytes was measured by changes in biomass values; the method referred to as harvest method (Trivedy and Goel, 1984).

Detritus

The detrital biomass was calculated as a function of primary production and euphotic depth by employing the empirical relationship suggested by Christensen *et al.* (2005):

$$\text{Log } D = 0.954\log PP + 0.863\log E - 2.41$$

Where, D= detrital biomass (gC/m^2/year), PP= gross primary production (in gC/m^2/year) and E= euphotic depth in meter.

Euphotic depth was estimated from the Secchi depth transparency measurement (Talling and Lemoalle, 1998). To change the detritus biomass to wet weight, carbon to wet weight ratio of 10% was employed (Jones, 1979).

2.4 Diet composition

Diet composition for fish groups was estimated by gut content analysis. From each functional group, representative specimens were examined for gut contents, and their volume was measured using water displacement method (Qasim, 1972). The occurrence and relative importance of the prey were investigated by calculating their percentage by volume in the stomachs. Diet data was also taken from FishBase (www.fishbase.org; Froese and Pauly, 2013) for fish groups lacking primary data on diet content. Diet composition of fish-eating birds was adopted from Piet (1998) and also from the unpublished documents of 'Waders and Warblers,' the amateur ornithologists' group. For zoobenthos and zooplankton groups, diet data was taken from information available from the literature or from similar works. The data thus obtained was entered into the Ecopath predator-prey diet matrix as fractions of one, for parameterization.

2.5 Trophic model balancing

The inputs entered were mass balanced using the Ecopath parameterization routine. On initial run of the software, four functional groups - eels, catfishes, nandids and barbs - showed EE value above 1. Generally, a manual alteration of the input data can be exercised to balance the model (Christensen *et al*., 2005), based on ecological knowledge and reasoning, rather than running the computer algorithm alone. The biomass and diet compositions of these functional groups were slightly and carefully calibrated in order to derive the mass-balanced model (Piroddi *et al*., 2015).

3. Results and Discussion

The basic input variables and diet matrix obtained from the balanced model of the lake are listed in Tables 2 and 3. The different parameterization and network routines of the Ecopath software were used to estimate different ecosystem attributes of the mass-balanced trophic model.

3.1 Ecotrophic efficiency and gross efficiency

The ecotrophic efficiency (EE), a dimension-less factor, is the fraction of the production that is used in the system, that is either passed up in the food web, used for biomass accumulation, migration or export. It generally ranges between 0 and 1 (Christensen *et al.*, 2005). There was considerable variation in the EE values among different functional groups of Sasthamkotta Lake (Table 2). Cichlids and Nandids showed very high EE values (0.996 and 0.983), which suggests heavy exploitation of the fishes included in this group (Piroddi *et al*., 2015). The observation that the EE values for all the fish groups were high throw light into formulating measures for checking the higher exploration rate and also designing conservation strategies for the sustainable fishery in the lake. The lowest EE value (0.007) was shown by the detritus group, suggesting a negligible amount of export of detritus taking place in the system. The lower EE values of phytoplankton (0.614) indicate their surplus supply in the system and contribution to detritus in unutilized form, which is comparable with the observations of similar ecosystems (Khan and Panikkar, 2009; Biju Kumar et al., 2015).

The P/Q ratio or the gross efficiency was found to be low for most of the fish groups. This might be attributed to the low prey density and the necessity to use more energy for hunting their prey (Villanueva et al., 2008). The lower gross efficiency values for carnivorous fish groups might be due to the scarcity of their possible prey in terms of biomass per volume unit (Khan and Panikkar, 2009).

3.2 Key indices

Assuming that there is no biomass accumulation and net migration from the system, the Ecopath model for the Sasthamkotta Lake computes three key indices - flow to detritus (FtD), net food conversion efficiency (NE) and omnivory index (OI) (Table 4). For each functional group, the FtD comprises of the egested non-assimilated food, sedimentation for phytoplankton and sources of other mortality factors like death due to old age, diseases, etc., which can be expressed as (1–EE) (Christensen et al., 2005). A higher FtD value of 2786.074 t/km^2/year computed may be attributed to the moderate mean depth (6.53 m) of the lake. The primary producers contributed the major bulk of the total flow to detritus, which is directly proportional to their biomass.

The net food conversion efficiency (NE) is the ratio of the production of a functional group to the assimilated part of the food. NE was observed maximum for fish-eating birds (0.468). Among the fish groups, NE was found highest for cichlids (0.372).

The omnivory index (OI) of a system calculates the variance of the trophic level of a consumer's prey groups. When OI is zero, the consumer is specialized, i.e., it feeds on a single trophic level. A higher value indicates that the consumer feeds on more than one trophic levels

Table 2. Input parameters and balanced output of Sasthamkotta Lake trophic model

Trophic Compartments	TL	B (t/km^2)	P/B (/year)	Q/B (/year)	EE	P/Q
Fish-eating birds	*3.74*	0.00014	0.213	0.569	0	*0.374*
Cichlids	*2.31*	7.304	2.872	9.662	*0.996*	*0.297*
Murrels	*3.37*	2.271	0.539	4.362	*0.952*	*0.124*
Eels	*3.33*	1.916	0.512	2.261	*0.938*	*0.226*
Catfishes	*3.55*	1.393	2.389	8.168	*0.949*	*0.292*
Needle fishes	*3.55*	0.89	2.362	8.115	*0.936*	*0.291*
Gobiids	*3.06*	0.881	0.801	3.776	*0.933*	*0.212*
Nandids	*3.11*	1.585	1.812	7.141	*0.983*	*0.254*
Barbs	*2.91*	3.269	1.992	7.065	*0.949*	*0.282*
Zoobenthos	*2.59*	6.118	*2.75*	*11.001*	0.95	0.25
Zooplankton	*2.28*	9.335	63	*252*	*0.972*	0.25
Phytoplankton	*1*	1.384	2217	-	*0.614*	-
Macrophytes	*1*	108	10	-	*0.007*	-
Detritus	*1*	18.56	-	-	*0.019*	-

(Values estimated by Ecopath are shown in italics)

Table 3. Diet matrix showing proportional diet composition of functional groups of Sasthamkotta Lake trophic model

	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	Fish-eating birds														
2	Cichlids	0.421		0.466	0.817	0.612	0.434						0.421		0.466
3	Murrels	0.03				0.022	0.008						0.03		
4	Eels			0.003		0.02									0.003
5	Catfishes	0.007		0.002	0.00048								0.007		0.002
6	Needle fishes	0.094	0.007	0.046	0.017	0.034							0.094	0.007	0.046
7	Gobiids			0.005		0.009	0.027								0.005
8	Nandids	0.041				0.073	0.211						0.041		
9	Barbs	0.407		0.157	0.096	0.17	0.184	0.025	0.031				0.407		0.157
10	Zoobenthos		0.027	0.186		0.026	0.026	0.332	0.43	0.251				0.027	0.186
11	Zooplankton		0.191	0.02	0.026	0.017	0.055	0.38	0.287	0.4	0.463	0.218		0.191	0.02
12	Phytoplankton		0.61	0.02	0.026	0.017	0.055	0.197	0.243	0.325	0.406	0.767		0.61	0.02
13	Macrophytes		0.04	0.013				0.02	0.01	0.025	0.058			0.04	0.013
14	Detritus		0.125	0.083	0.018			0.045			0.073	0.016		0.125	0.083
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1

(Christensen *et al.*, 2005). The OI demarcates the degree of network formation in an ecosystem (Christensen and Pauly, 1993) and functions as an indicator to analyse the effect of each fish on food web structure. Highest OI value was observed for Nandids (0.439), indicating its effective exploitation of the niches available in the Sasthamkotta Lake ecosystem.

3.3 Summary statistics

The summary statistics of Sasthamkotta Lake Ecopath model is given in Table 5. The total system throughput (TST), which is the sum of all flows in the system, is estimated as the sum of the four flow components – total consumption, total exports from the system, total respiratory flows and the sum of all flows into the detritus. TST represents the size of the entire system in terms of flow (Ulanowicz, 1986) and is an important parameter for comparing energy flow networks in an ecosystem. The TST of Sasthamkotta Lake was computed as 9495 t/km^2/year. This was found to be much lower than the TST of Veli-Akkulam Lake, Kerala (Aravindan, 1993; Regi, 2014). Significantly higher values for TST had been reported for Wyra and Kelavarappalli reservoirs of South India (Panikkar and Khan, 2008; Khan and Panikkar, 2009).

Gross efficiency (GE) of fishery is calculated as the sum of all realized fishery catches relative to the total primary production (Christensen *et al.*, 2005). The GE ranges widely between different systems, with high values for those with a fishery harvesting fish low in the food web, and low values in systems whose fish stocks are less exploited, or where the fishery has been concentrated on top predators (Christensen *et al.*, 2000; Antony *et al.*, 2010). The Sasthamkotta Lake is estimated to have a low ecological efficiency (0.002209). Ecological efficiency is a measure of the amount of energy transferred between trophic levels and generally ranges from 0.05 to 0.2. This means that 80-95% of the energy is lost at each transfer in the food chain (Lampert and Sommer, 1997). The GE of Sasthamkotta Lake is lower when compared to similar ecosystems in India (Regi, 2014; Biju Kumar *et al.*, 2015) and other tropical lakes like Lake George (Moreau *et al.*, 1993a) and Lake Victoria (Moreau *et al.*, 1993b) in Africa. It should be taken into account that the calculated ecological efficiency of Sasthamkotta Lake is much higher than the weighted global average of about 0.0002; the higher fishery GE indicates the excessive fishing pressure exerted on the different fish groups in the lake. The lower values of EE for the primary producers and detritus in the lake may also account for the calculated low ecological efficiency.

3.4 Ecosystem maturity indices

Quantification of ecosystem maturity can be done using Odum's attributes of ecosystem maturity (Odum, 1969; Christensen, 1995). Several attributes calculated by the mass-balanced Ecopath model can be used to assess the maturity status of an ecosystem, upon comparison with other ecosystems. The ratio of total primary production to total respiration (TPP/TR) describes the maturity of an ecosystem. The rate of primary production exceeds the rate of community respiration in the early stages of development of an ecosystem, making the TPP/TR ratio greater than 1. When the ecosystem matures, the TPP/TR approaches 1, as the energy fixed tends to be balanced by the energy cost of maintenance. Thus, the TPP/TR ratio represents an excellent functional index of the relative maturity of the ecosystem. The TPP/TR ratio of the Sasthamkotta Lake was 2.952, which indicates that the lake ecosystem is a young ecosystem, not attained maturity, and is still in a developmental stage. This higher value of TPP/TR may be attributed to incomplete utilization of the major part of production of many functional groups in the system.

Net system production (NSP), the difference between total primary production and total respiration, is another attribute of maturity. The NSP will be close to zero in mature ones, while higher values will be recorded for immature systems. The Sasthamkotta Ecopath model calculated NSP value of 2743.257 t/km^2/year, which indicates the immaturity of this lake ecosystem. The total primary production and total biomass (TPP/TB) ratio is another indicator for the maturity of the system. As the system develops, the biomass accumulates, thus leading to a lower TPP/TB ratio. A higher value of 28.739 in the lake reaffirms that the system is still in a developing phase. The total biomass/total throughput ratio, which (0.015) is used to assess the total biomass supported by the available energy and is expected to increase with ecosystem maturity, was found to be lower in the lake (0.015), which also supports the view that Sasthamkotta Lake is in a developing stage.

Other parameters that describe ecosystem maturity are the system omnivory index (SOI) and the connectance index (CI), which are expected to be higher in mature ecosystems (Odum, 1971). The SOI of Sasthamkotta Lake was found to be 0.328, indicating a low degree of omnivory in the system. The CI, the ratio of actual links between groups to the number of theoretically possible links, was estimated as 0.414, which suggests a high diversity among functional groups, as expected in biodiversity-rich tropical lakes.

3.5 Trophic structure

The biomasses of different functional groups and the energy flow between them can be represented in mass-balanced trophic models as a single flow diagram (Christensen *et al*., 2000). The trophic interactions taking place between different functional groups of the Sasthamkotta Lake are shown in Fig. 2. The aggregation of biomass and energy flows among different trophic levels (TLs) of the lake resulted in seven trophic levels, which is typical of tropical lakes (Fetahi and Mengistou, 2007, Darwall *et al*., 2010, Biju Kumar *et al*., 2015). Majority of the trophic flows occurred in the first three trophic levels, with more than 75% concentrated in the first trophic level. The lake was found to be dominated by organisms occupying lower trophic levels; the highest TL observed was for the top predator of the system, viz., fish-eating birds (3.74). Trophic levels of the fish groups ranged from 2.31 to 3.55. The mean trophic level of the commercial fish catch from the lake was estimated to be 3.08. Both grazing and detrital food chains were found to be important in the lake. Energy flows into the detritus contributed about 29% of the total system throughput of the lake. The main source of flow to detritus was found to be the primary producers (phytoplankton and macrophytes).

3.6 Transfer efficiencies

The transfer efficiencies (TE) between successive discrete trophic levels are the ratios between the sum of the exports from a given trophic level, plus the flow that is transferred from that level to the next, and the throughput on the trophic level (Christensen *et al*., 2005). The transfer efficiencies between different trophic levels of the Sasthamkotta Lake are shown in Fig. 2. The overall transfer efficiency of Sasthamkotta Lake ecosystem was computed by the EwE software to be 13.6%. This is higher than the general average of 10.1% (Pauly and Christensen, 1995) and significantly more than that observed in the Wyra reservoir (6.3 and 7.0%) of India (Panikkar and Khan, 2008). This relatively high TE of the lake may be due to higher fishery activity on lower TLs (Pauly *et al*., 1998). The transfer efficiencies include the ratio of total flow originating from the detritus to the total flow originating from both primary producers and detritus. The transfer efficiency may be viewed as an index of the importance of detritus in a system, which is the quantitative form of yet another of Odum's (1969) measures of ecosystem maturity.

3.7 Mixed Trophic Impact

The mixed trophic impact (MTI) routine incorporated in the Ecopath software (Ulanowicz and Puccia, 1990)

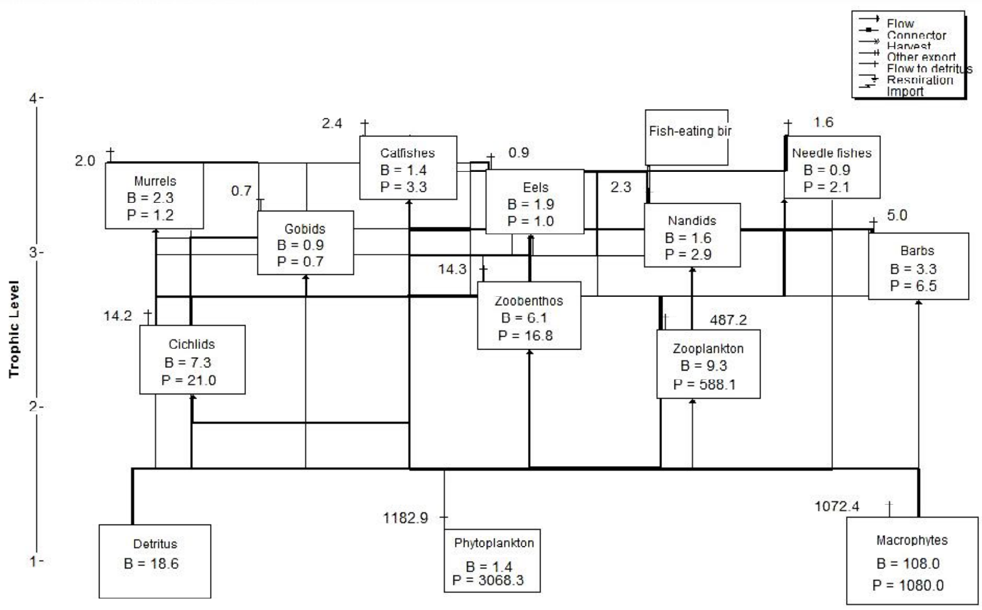

Fig. 2. Flow diagram showing trophic flows in Sasthamkotta Lake. Flows are expressed in t/km^2/year

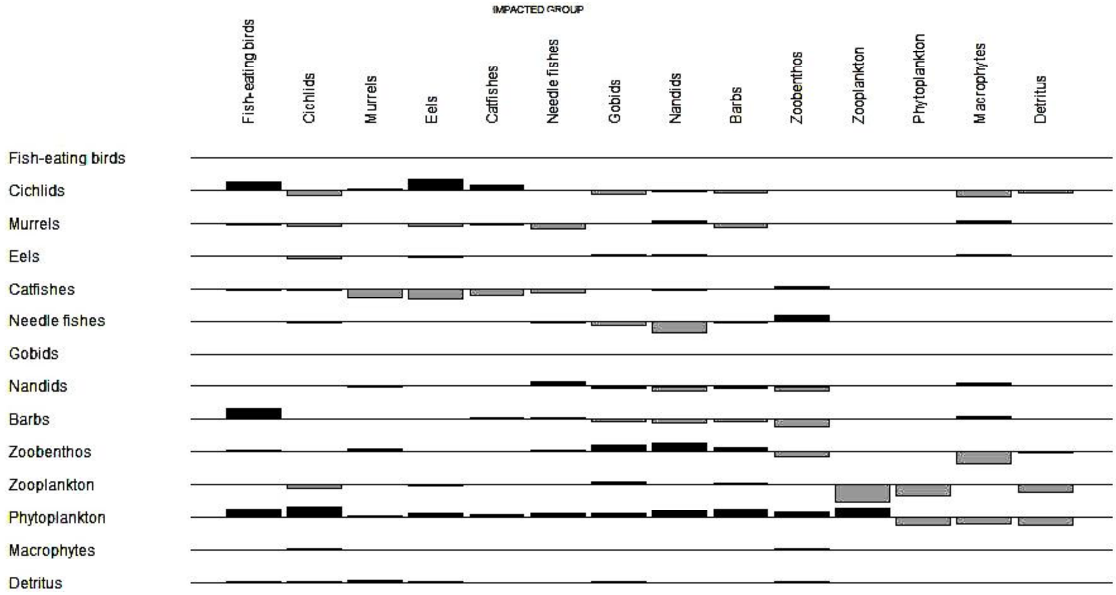

Fig. 3. Mixed trophic impacts of the functional groups in Sasthamkotta Lake

represents the direct and indirect influence of abundance variations of any functional group on all other groups considered. The MTI plot of Sasthamkotta Lake is shown in Fig. 3. The bars rising above the horizontal (shaded black) indicate positive effects, whereas the bars dropping below the horizontal (shaded grey) indicate negative impacts, and the sizes of the bars reflect relative response. A very strong bottom-up trophic control was observed in the lake, as an increase in abundance of primary producers has a strong positive impact on most of the other groups at higher TL. The impact of zooplankton biomass variations was found to be negligible. The biomass increases of carnivorous fishes like catfishes, eels and murrels may cause a negative impact on most of the other fish groups. Most of the functional groups have negative impacts on themselves, which may be attributed to the competition within the groups for the same food resources (Christensen *et al.*, 2000).

Table 4. Key indices of Sasthamkotta Lake trophic model (FtD - flow to detritus, NE - net efficiency, OI - omnivory index)

Functional groups	FtD (t/km2/year)	NE	OI
Fish-eating birds	0	0.468	0.175
Cichlids	14.193	0.372	0.333
Murrels	2.041	0.154	0.346
Eels	0.928	0.283	0.136
Catfishes	2.445	0.366	0.186
Needle fishes	1.579	0.364	0.265
Gobiids	0.712	0.265	0.425
Nandids	2.312	0.317	0.439
Barbs	4.95	0.352	0.46
Zoobenthos	14.302	0.313	0.406
Zooplankton	487.236	0.313	0.278
Phytoplankton	1182.949	-	0
Macrophytes	1072.427	-	0
Detritus	0	-	0.271

Table 5. Summary of system statistics computed for Sasthamkotta Lake trophic model

Parameter	Value	Units
Sum of all consumption	2560.882	t/km²/year
Sum of all exports	2743.257	t/km²/year
Sum of all respiratory flows	1405.071	t/km²/year
Sum of all flows into detritus	2786.074	t/km²/year
Total system throughput	9495	t/km²/year
Sum of all production	4792	t/km²/year
Mean trophic level of the catch	3.08	
Gross efficiency (catch/net p.p.)	0.002209	
Calculated total net primary production	4148.328	t/km²/year
Total primary production/total respiration	2.952	
Net system production	2743.257	t/km²/year
Total primary production/total biomass	28.739	
Total biomass/total throughput	0.015	
Total biomass (excluding detritus)	144.347	t/km²
Total catches	9.165	t/km²/year
Connectance Index	0.414	
System Omnivory Index	0.328	

4. Conclusions

The trophic network analysis of the Sasthamkotta Lake was carried out using the Ecopath with Ecosim model. The lake ecosystem showed low ecological efficiency, and the fishing demand on the top predatory fishes like eels and catfishes is high, which is reflected on higher EE values for these groups. The model also suggests the equal importance of both grazing and detrital food chain in the trophic structure of the lake. Maturity analysis using various parameters showed that the Sasthamkotta Lake is a system that is in a developing stage and has not attained maturity. The mixed trophic impact analysis established a very strong bottom-up trophic control in the lake and the abundance in biomass of the primary producers has a positive effect on most of the other groups. The energy transfer efficiency of the lake ecosystem was relatively high, which may be attributed to fishing at lower trophic levels. The ecosystem dynamics of Sasthamkotta Lake during the given time period was only taken into consideration in this study, and periodic follow-up studies using the Ecopath model are suggested to assess the anthropogenic impacts on this very important freshwater lake of Kerala.

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