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TROPHIC STRUCTURE, INTERACTIONS AND ECOSYSTEM ATTRIBUTES OF VELLAYANI LAKE, KERALA, INDIA, WITH SPECIAL REFERENCE TO FISHERIES

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Abstract: A mass balanced ecosystem model was constructed for Vellayani freshwater lake in India using Ecopath with Ecosim software. Both grazing and detrital food chains were found to be equally important. Highest omnivory index was recorded for the Indian major carps, stocked recently, indicating their effective utilization of the available niches. The ecological efficiency of the Vellayani Lake was found to be low, attributed to the lower ecotrophic efficiencies of primary producers and detritus. Quantification of Odum's attributes of ecosystem maturity showed immaturity of the lake system, which is still in development phase. Energy transfer efficiency of the lake was relatively high, which may be due to higher fishery activity on lower trophic levels, indicating fishing down the food web phenomenon. Mixed trophic impact analysis showed strong positive impact of primary producers on most of the other groups at higher trophic levels. Relatively lower overhead value obtained suggested that the lake is less resistant to perturbations including anthropogenic interferences. The present study forms a basis for future research on the changing trophic interactions within the lake in light of recent experimental introduction of Indian major carps for enhancing fish stock.

Key words: Ecopath, trophic model, ecotrophic efficiency, mass balance, energy transfer

INTRODUCTION

The explosive demographic growth in India over the past few decades coupled with burgeoning demand for drinking water and fishery resources has accelerated the deterioration of freshwater lakes. Many of the freshwater lakes have been used to increase fish production through the introduction of exotic species, without understanding the status of exploited fishery resources and the ecological efficiency of the system despite the fact that older lakes tend to possess highly specialized biodiversity, many of which may be endemic. The need to understand and quantify ecosystem behaviour and condition has come to the forefront of environmental planning and policy formulations, particularly in view of contemporary paradigm of ecosystem-based fishery management. Ecosystem models play an important role in the ecosystem approach to management of lakes and they provide inputs in identifying the properties and potential changes in complex ecosystems that cannot be identified with single-species models (Christensen and Pauly, 1998). The Ecopath with Ecosim (EwE) software (Christensen *et al*., 2005), the most widely used and tested ecosystem modelling tool, is efficient in describing trophic relationships in aquatic ecosystems and in assessing the dynamics of ecosystem functioning. The EwE is currently dominating attempts to provide information on how ecosystems are likely to respond to changes in fishery management practices and therefore suggested as a tool for designing ecosystem approach to fisheries (Plaganyi, 2007).

Traditionally modelling of aquatic ecosystems has been concentrated on lakes. The most important reason for this is that lakes are largely closed ecosystems, thus fulfilling a key requirement for modelling. A lot of modelling approaches have been carried out on tropical lakes, especially in Africa (Fetahi and Mengistou, 2007; Tsehaye and Nagelkerke, 2008; Darwall *et al*., 2010; Fetahi *et al*., 2011). In India, the first attempt at using Ecopath to model an aquatic ecosystem is the Ecopath model of Veli estuary, a bar-built estuary, along the southwest coast (Aravindan, 1993). Of late, Ecopath modelling attempts in India have been associated with the southwest (Karnataka) (Mohamed *et al*., 2005) and southeast (Parangipettai) (Antony *et al*., 2010) coasts and the two reservoirs of south India (Panikkar and Khan, 2008; Khan and Panikkar, 2009). This paper provides the first account of modelling a freshwater lake in India, the Vellayani Lake, Kerala, with the objectives to understand the trophic structure and interactions of a lacustrine ecosystem.

MATERIAL AND METHODS

Study Area

Vellayani Lake (08^{o}242 - 8^{o}262 N and 76^{o}592 - 76^{o}592 E), the second largest freshwater lake in Kerala state, India, is the major freshwater resource of southern Kerala and the leading freshwater lake in fishery production. The lake occupies an area of about 3.312 km^{-2} and has a mean depth of 1.2 m (Gopinath, 2003). The lake is believed to have its origin from the tributary of Karamana River flowing through the southern part of Kerala state and reaching Lakshadweep Sea, during Quaternary transgression (Nair, 1987). The livelihood of about 100 traditional fishermen depends on the fish resources of the lake. Since the year 2007, Kerala State Fisheries Department has started introducing the seeds of Indian major carps [*Catla catla* (Hamilton), *Labeo rohita* (Hamilton) and *Cirrhinus cirrhosus* (Bloch)] and giant freshwater prawn *Macrobrachium* rosenbergii (De Man) into the lake in order to augment fishery production. Vellayani Lake is an important wetland in south India used by waterfowls both as feeding and breeding grounds.

Ecological Groupings

The living resources in the Vellayani Lake were categorized into 17 trophic compartments for the construction of the Ecopath model. The trophic compartments included were fish-eating birds (herons, kingfishers, egrets and cormorants), pearl-spot (*Etroplus suratensis)* and other cichlids (*E. maculatus* and *Oreochromis mossambicus*), murrels (*Channa striata* and *C. marulius*), eels (*Anguilla bicolor bicolor* and *A. bengalensis bengalensis*), catfishes (*Mystus oculatus* and *Heteropneustes fossilis*), needle fishes (*Xenentodon cancila* and *Hyporhamphus xanthopterus*), gobiids (*Glossogobius giuris*), nandids (*Ambassis ambassis* and *Parambassis thomassi*), Indian major carps (*Catla catla, Labeo rohita, Cirrhinus cirrhosus*), barbs and carplets (*Puntius filamentosus*, *P. sarana* and *Amblypharyngodon microlepis*), prawns (*Macrobrachium idella* and *M. rosenbergii*), aquatic insects (coleopterans, dipterans, etc.), zoobenthos (nematodes, chironomids, snails, etc.), zooplankton (*Centropyxis*, *Brachionus*, *Daphnia*, *Cyclops*, etc.), phytoplankton (*Chlorella*, *Oscillatoria*, *Spirogyra*, *Selenastrum*, etc.), macrophytes (*Nelumbo nucifera*, *Nymphaea stellata*, etc.) and detritus.

The Ecopath Model

The Ecopath software was used to construct a mass balance model of Vellayani Lake to understand the trophic interactions of the different functional groups or trophic compartments in the lake and to figure out the flow of energy in the system. The Ecopath approach was first developed by Polovina (1984) to analyze energy flow between species or group of species based on biomass estimates and feeding relationships. This approach was subsequently refined into its present form by incorporating a variety of ecological and theoretical approaches (Christensen and Pauly, 1992; Walters *et al*., 1997; Pauly *et al.*, 2000; Christensen and Walters, 2004). The Ecopath model assumes mass balance in that production of any given prey is equal to the biomass consumed by predators plus the biomass caught plus any exports from the system. Predation mortality is the factor that links different functional groups in an ecosystem, as mortality for a prey is consumption for a predator. Once the balanced model was created, it was then used to analyze the trophic structure and ecosystem properties of Vellayani Lake.

Basic Inputs and Diet Composition

Ecopath model inputs for each trophic compartment include biomass (B) in $t.km^{-2}$, production/biomass ratio (P/B) per year, consumption/biomass ratio (Q/B) per year, ecotrophic efficiency (EE), apart from diet composition and any associated fishing mortality per year. For each functional group, three of the four parameters (B, P/B, Q/B and EE) need to be determined and entered as model input. The Ecopath parameterization routine estimates the missing parameter. EE is the most difficult one to estimate and is thus often left unknown for Ecopath.

The biomass of fishes and prawns was estimated from the experimental catch data during the present study and also from the commercial fish catch from the lake. The average biomass for each group per unit area ($t.km^{-2}$) 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. Biomass for unexploited groups like macrophytes, phytoplankton, zooplankton, zoobenthos, aquatic insects and fish-eating birds were obtained from primary data collected during the study and also from similar ecosystems (Moreau *et al.*, 2001; Panikkar and Khan, 2008).

The P/B ratio of fishes was taken as equivalent to instantaneous rate of total mortality (Z) (Pauly *et al.*, 2000) assuming 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). P/B for fish-eating birds was derived from Hustler (1997) for similar species and similar system at different habitat. For other unexploited groups, P/B was estimated directly using empirical formula or from similar models. The Q/B for fish groups was determined by using the empirical equation (Palomares and Pauly, 1998) incorporated in the Ecopath model. For other ecological groups, appropriate empirical equations available in the Ecopath or information from literature were used for determining the Q/B ratio. 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.

Diet content of fish-eating birds was derived from Piet (1998) and from the unpublished documents of amateur ornithologists associated with the group 'Waders and Warblers' located at Kerala, India. For fish groups, diet data was estimated by gut content analysis (Pillay, 1952; Natarajan and Jhingran, 1961). For a few fishes, diet data was also obtained from FishBase (www.fishbase.org) (Froese and Pauly, 2013). For aquatic insects, zoobenthos, and zooplankton groups, diet data was taken from information available from literature or from similar works. The diet data thus obtained was entered as fractions in the predator-prey diet matrix of Ecopath and used for parameterization.

Balancing the Model

The basic inputs entered were mass balanced by the Ecopath parameterization routine. On initial run, seven groups (murrels, eels, catfishes, gobiids, nandids, Indian major carps, barbs and carplets) showed ecotrophic efficiency (EE) above 1 and hence biomass and diet composition fractions of these groups were carefully calibrated coupled with application of the auto mass balance routine of Ecopath to obtain a mass balanced model.

RESULTS AND DISCUSSION

The basic input parameters and diet matrix obtained after balancing the model are listed in Tables 1 and 2. The parameterization and network routines incorporated in the Ecopath software were used to estimate different attributes of the mass-balanced trophic model.

Basic analysis

Ecotrophic efficiency (EE) is the fraction of the production that is used in the system, i.e., either passed up the food web, used for biomass accumulation, migration or export. It is a dimensionless factor that ranges between 0 and 1 (Christensen *et al.*, 2005). The EE values of different trophic compartments of Vellayani Lake varied considerably (Table 2). The values approached 1 for major consumers of the system. Murrels and eels showed very high EE values (0.996 and 0.912 respectively), which suggests that the fishes included in this group are heavily exploited. All the fish groups have higher EE values, which indicate their higher exploitation rate and the need for formulating conservation measures for a sustainable fishery in the lake. Detritus has the lowest EE value (0.015), suggesting that negligible amount of export is taking place comparing the huge import into the detritus group. The EE values of primary producers also are on the lower side (macrophytes, 0.050; phytoplankton, 0.617), indicating their excess supply in the system and contribution to detritus in unutilized form, which is comparable with the observations of Khan and Panikkar (2009) in Kelavarapalli reservoir of India.

Table 1. Input parameters and balanced output of Vellayani Lake, India

Trophic Compartments	TL	B ($t.km^{-2}$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	EE	P/Q
Fish-eating birds	*3.44*	0.029	0.33	0.84	*0*	*0.393*
Pearlspot & other cichlids	*2.16*	10.995	4.454	15.474	*0.728*	*0.288*
Murrels	*3.19*	3.125	0.675	6.74	*0.996*	*0.1*
Eels	*3.33*	2.995	0.615	5.99	*0.912*	*0.103*
Catfishes	*3.24*	1.116	1.34	12.764	*0.855*	*0.105*
Needle fishes	*3.04*	3.25	2.095	16.181	*0.791*	*0.129*
Gobids	*3.05*	3.824	0.955	9.429	*0.83*	*0.101*
Nandids	*2.62*	4.293	4.5	16.672	*0.742*	*0.27*
Indian major carps	*2.68*	3.97	1.115	10.593	*0.724*	*0.105*
Barbs and carplets	*2.29*	5.283	3.925	17.022	*0.707*	*0.231*
Prawns	*2.5*	1.125	25.2	90.12	*0.868*	*0.28*
Aquatic insects	*2.02*	6	18	38.75	*0.659*	*0.465*
Zoobenthos	*2.17*	5.6	11.86	*47.441*	0.95	0.25
Zooplankton	*2.18*	10.2	63	*252*	*0.772*	0.25
Phytoplankton	*1*	1.225	3647.02	-	*0.617*	-
Macrophytes	*1*	279	10	-	*0.05*	-
Detritus	*1*	24.32	-	-	*0.015*	-

(Values estimated by Ecopath are shown in italics)

P/Q ratios were low for most of the fish groups. This might be due to low density of their prey and the necessity for these fishes to use more energy for hunting their prey which are available only at low densities (Villanueva *et al.*, 2008). Carnivorous fish groups like murrels, eels, and catfishes have surprisingly low gross efficiency values, which might be due to the scarcity of their possible prey in terms of biomass per volume unit (Khan and Panikkar, 2009).

Key indices for each trophic compartment of the lake are summarized in Table 3. For each group, Flow to Detritus (FtD) consisted of the egested non-assimilated food, sedimentation for phytoplankton and sources of 'other mortality' like death due to old age, diseases, etc., which is expressed by (1 – EE) (Christensen *et al.*, 2005). The FtD for the Vellayani Lake was computed as 5316.754 $t.km^{-2}.yr^{-1}$. This higher value may be attributed to the progressively lesser mean depth (1.2 m) of the lake. The primary producers contribute more than 80% of the total flow to detritus in the Vellayani lake system. The FtD of each ecological group in an ecosystem is directly proportional to their biomass in the system and hence the value was found to be maximum for the primary producers and minimum for the top consumers of the lake, viz., fish-eating birds. Top predatory fish groups of the lake also were found to be contributing lesser to the total FtD of the system. The net food conversion efficiency (NE) is calculated as the production divided by the assimilated part of the food. NE was observed maximum for aquatic insects (0.581), followed by the fish-eating birds (0.491). Among the fish groups, NE was found highest for cichlids (0.360) and minimum for murrels (0.125).

The omnivory index (OI) is calculated as the variance of the trophic level of a consumer's prey groups. When the value of OI is zero, the consumer in question is specialized, i.e., it feeds on a single trophic level. A larger value indicates that the consumer feeds on many trophic levels (Christensen *et al.*, 2005). It is a factor that demarcates the degree of network formation in an ecosystem (Christensen and Pauly, 1993) and an indicator to analyse the effect of each fish on food web structure. Highest OI in the Vellayani Lake was observed for the Indian major carps (0.380), indicating that the newly introduced carps effectively exploit the niches available in the ecosystem, winning the competition with indigenous fish.

Table 2. Diet matrix of Vellayani Lake ecosystem, India

Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Fish-eating birds														
Pearlspot & other	0.243		0.25	0.54	0.313	0.114		0.00086		0.009				
Murrels	0.00057				0.000042									
Eels			0.004		0.006									
Catfishes						0.008								
Needle fishes	0.239	0.003	0.038	0.058	0.037					0.004				
Gobiids				0.016	0.036	0.008								
Nandids	0.052		0.144	0.148	0.173	0.026	0.027							
Indian Major Carps				0.025	0.031			0.003						
Barbs and carplets	0.408	0.004	0.248	0.196		0.011		0.0001	0.025					
Prawns		0.02		0.001	0.076	0.206	0.103	0.012	0.082	0.006				
Aquatic insects	0.057	0.026	0.25	0.017	0.197	0.138	0.176	0.462		0.006	0.11			
Zoobenthos		0.015			0.028	0.209	0.072	0.038	0.148	0.145	0.215	0.012		
Zooplankton		0.064			0.031	0.101	0.498	0.065	0.3	0.075	0.119	0.005	0.145	0.15
Phytoplankton		0.792				0.156	0.088	0.412	0.341	0.575	0.496	0.453	0.661	0.85
Macrophytes		0.07					0.023	0.007	0.044			0.516	0.014	
Detritus		0.006	0.066		0.072	0.023	0.013		0.059	0.18	0.06	0.014	0.18	
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 3. Flow to detritus (FtD), net efficiency (NE) and omnivory index (OI) of Vellayani Lake, India

	FtD ($t.km^{-2}.yr^{-1}$)	NE	OI
Fish-eating birds	0.015	0.491	0.125
Pearlspot & other cichlids	47.369	0.36	0.175
Murrels	4.22	0.125	0.162
Eels	3.75	0.128	0.07
Catfishes	3.066	0.131	0.213
Needle fishes	11.941	0.162	0.274
Gobiids	7.833	0.127	0.176
Nandids	19.3	0.337	0.28
Indian major carps	9.63	0.132	0.38
Barbs and carplets	24.063	0.288	0.267
Prawns	24.027	0.35	0.32
Aquatic insects	83.306	0.581	0.023
Zoobenthos	56.46	0.313	0.172
Zooplankton	660.646	0.313	0.176
Phytoplankton	1709.939	-	0
Macrophytes	2651.189	-	0
Detritus	0	-	0.225

Summary Statistics and Ecosystem Maturity

The summary statistics of the Vellayani Lake Ecopath model is summarised in Table 4. Total system throughput (TST) is the sum of all flows in the system, estimated as the sum of the four flow components: sum of all consumption, sum of all exports from the system, sum of all respiratory flows and 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 comparison of flow networks. The TST of Vellayani Lake was computed as 16,260 $t.km^{-2}.yr^{-1}$. This is lower than the TST of Veli estuary (Aravindan, 1993) of South India, modelled using Ecopath. Significantly higher values for TST had been reported for Wyra and Kelavarappalli reservoirs of South India (Panikkar and Khan, 2008; Khan and Panikkar, 2009).

Table 4. Summary of system statistics obtained from Vellayani Lake, India

Parameter	Value	Units
Sum of all consumption	3685.574	$t.km^{-2}.yr^{-1}$
Sum of all exports	5263.877	$t.km^{-2}.yr^{-1}$
Sum of all respiratory flows	1993.72	$t.km^{-2}.yr^{-1}$
Sum of all flows into detritus	5316.754	$t.km^{-2}.yr^{-1}$
Total system throughput	16260	$t.km^{-2}.yr^{-1}$
Sum of all production	8212	$t.km^{-2}.yr^{-1}$
Mean trophic level of the catch	2.59	
Gross efficiency (catch/net p.p.)	0.003862	
Calculated total net primary production	7257.6	$t.km^{-2}.yr^{-1}$
Total primary production/total respiration	3.64	
Net system production	5263.88	$t.km^{-2}.yr^{-1}$
Total primary production/total biomass	21.219	
Total biomass/total throughput	0.021	
Total biomass (excluding detritus)	342.03	$t.km^{-2}$
Total catches	28.028	$t.km^{-2}.yr^{-1}$
Connectance Index	0.395	
System Omnivory Index	0.205	
Finn's cycling index	2.52	% of TST
Finn's mean path length	2.24	-

Gross efficiency (GE) of fishery is computed as the sum of all realized fisheries catches relative to the total primary production (Christensen *et al*., 2005). This ratio will have a wide range between different systems, with high values for systems with a fishery harvesting fish low in the food web and low values in systems whose fish stocks are underexploited, or where the fishery is concentrated on apex predators. The Vellayani Lake has a low ecological efficiency. Ecological efficiency is a measure of the amount of energy transferred between trophic levels. It usually ranges from 0.05 to 0.2, i.e., 80-95% of the energy are lost at each transfer in the food chain (Lampert and Sommer, 1997). The Ecopath model calculated a GE value of 0.003862 for the lake. This is lower when compared to that of Veli estuary of India (0.0119; Aravindan, 1993) and other tropical lakes like Lake George (0.0057; Moreau *et al*., 1993a) and Lake Victoria (0.0082; Moreau *et al*., 1993b) in Africa. It should be noted that the calculated GE value of Vellayani 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 fish groups in the lake. The low ecological efficiency of the Vellayani Lake ecosystem may be attributed to the lower values of EE for the primary producers and detritus in the lake.

The maturity of an ecosystem can be quantified using Odum's attributes of ecosystem maturity (Christensen, 1995). The Ecopath model calculates several of these attributes and can be made use to assess an ecosystem to be in a mature or developing phase, by comparing with other ecosystems. Odum (1969) demonstrated that the ratio of total primary production and total respiration (TPP/TR) describes the maturity of an ecosystem. In the early stages of development of an ecosystem, the rate of primary production exceeds the rate of community respiration, so that the TPP/TR ratio is greater than 1. However, in a mature or "climax" ecosystem, TPP/TR approaches 1, as the energy fixed tends to be balanced by the energy cost of maintenance (viz., community respiration). Thus the TPP/TR ratio presents an excellent functional index of the relative maturity of the system. The TPP/TR ratio of the Vellayani Lake was 3.640, indicating that the lake ecosystem has not attained maturity and is still in a developmental stage or a young ecosystem. This higher value of TPP/TR may be attributed to important part of production of many trophic compartments in the system being not completely utilized.

Net system production (NSP), another attribute of maturity, is the difference between total primary production and total respiration. The NSP will be higher in immature systems and close to zero in mature ones. The Vellayani Ecopath model calculated an NSP value of 5263.880 $t.km^{-2}.yr^{-1}$. This very high value indicates the immaturity of this lake ecosystem. The ratio between the total primary production and total biomass (TPP/TB) also indicates the maturity of the system. Biomass accumulates as the system develops, thus leading to a lower TPP/TB ratio. A high value of 21.219 in the lake reaffirms that the system is still in a developing phase and has not attained maturity. The total biomass/total throughput ratio is used to assess the total biomass supported by the available energy and is expected to increase with ecosystem maturity. The observed value of 0.021 indicates that the lake is in a developmental stage.

The system omnivory index (SOI) and the connectance index (CI) are also used as parameters describing ecosystem maturity and are expected to be higher in mature ecosystems (Odum, 1971). The SOI of Vellayani Lake was observed to be 0.205, 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 at 0.395, suggesting a high diversity of trophic compartments that can be naturally expected in biodiverse tropical lakes. All these unequivocally support the immaturity of the Vellayani Lake, supporting the recent geological origin of the lake (Nair, 1987).

Network Analysis

Trophic structure and transfer efficiency of the Vellayani Lake are shown in the flow diagram constructed for the lake by Ecopath (Fig. 1). The aggregation of biomass and energy flows among different trophic levels (TLs) of the lake resulted in seven trophic levels. Majority of the trophic flows occurred in the first four trophic levels with TL1 contributing near to 77%. The flows in the remaining

TLs were relatively low. 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 (3.44). Trophic levels of the fish groups ranged from 2.16 to 3.33. The mean trophic level of the commercial fish catch from the lake was estimated to be 2.59, justifiable as the fishery of the lake mainly concentrates on pearl-spot (*Etroplus suratensis*) and other cichlids, barbs and carplets, and nandids. The low mean trophic level may be attributed to the absence of specialized top predators and a shorter food chain (Fetahi and Mengistou, 2007). Both grazing and detrital food chains were found to be important in Vellayani Lake. Energy flows from detritus contributed about 33% of the total system throughput of the lake. The main source of flow to detritus was the primary producers (phytoplankton and macrophytes), which contributed about 82% of the total flow (Fig. 1).

The trophic transfer efficiencies (TE) between successive discrete TLs can be calculated as the ratio between the sum of the exports from a given TL, plus the flow that is transferred from the TL to the next, and the throughput on the TL (Christensen *et al.*, 2005). The TE between different trophic levels of the Vellayani Lake is illustrated in Fig. 2. The TE of Vellayani Lake ecosystem was calculated to be 18.4%. 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, indicating fishing down food web phenomenon proposed by Pauly *et al*. (1998) for aquatic ecosystems. The transfer efficiencies include the ratio of total flow originating from the detritus to the total flow originating from both primary producers and detritus. This ratio, which may be viewed as an index of the importance of detritus in a system, is the quantitative form of yet another of Odum's (1969) measures of ecosystem maturity.

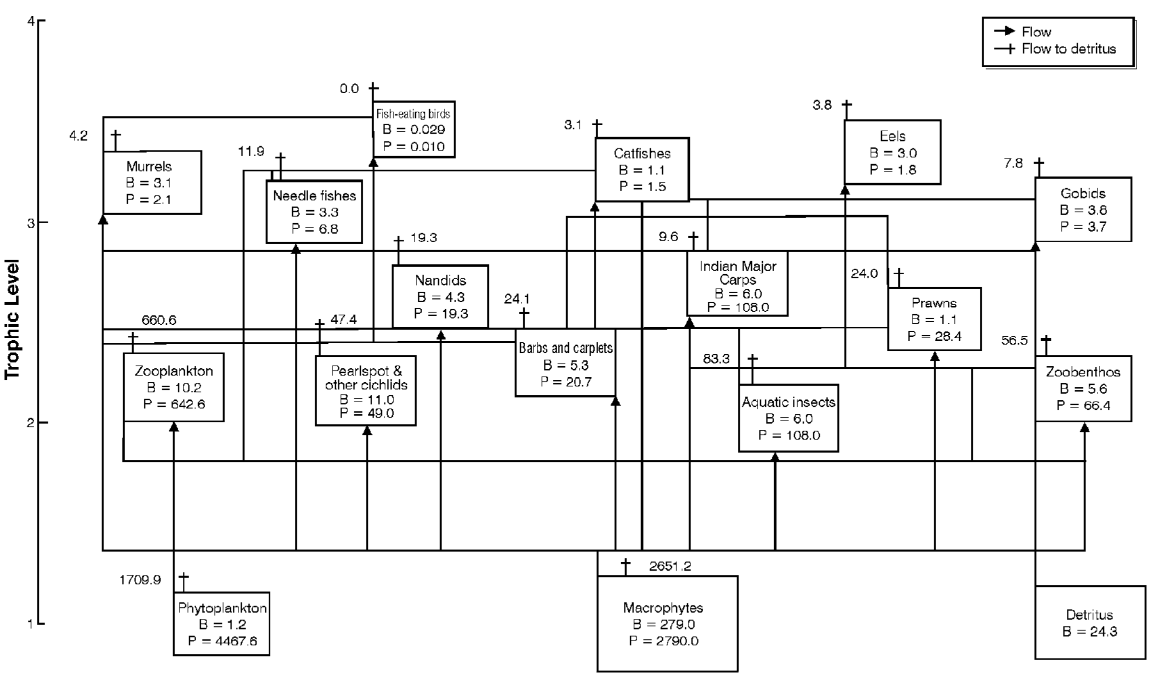

Fig. 1. Flow diagram showing trophic flows in Vellayani Lake, India. Flows are expressed in $t.km^{-2}.yr^{-1}$

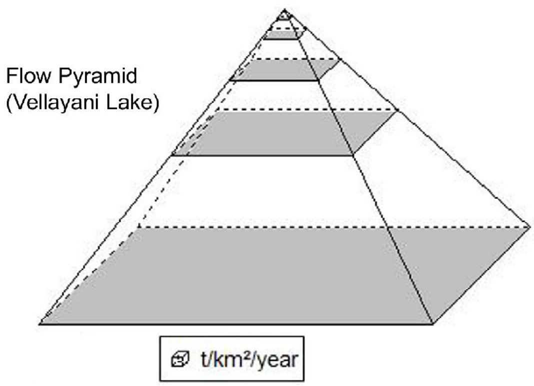

Fig. 2. Flow pyramid representing energy flow in Vellayani Lake, India

Mixed trophic impact (MTI) of Ecopath (Ulanowicz and Puccia, 1990) shows the direct and indirect influence of abundance variations of any species group on all other groups considered. The MTI plot of Vellayani Lake is shown in Fig. 3. The bars rising above the horizontal (shaded black) indicate positive effects, while the bars dropping below the horizontal (shaded grey) indicate negative impacts. The sizes of bars reflect relative response. The Fig. 4 shows a very strong bottom-up trophic control observed in the lake, as an increase in abundance of primary producers, both phytoplankton and macrophytes, have a strong positive impact on most of the other groups at higher TLs. The impact of primary producers was highest for their direct consumers, viz., zooplankton and pearl-spot and other cichlids. The impact of zooplankton biomass variations was found to be less important compared to the phytoplankton group. Increase in biomass of predatory fishes of the lake, viz., murrels and eels, may cause a negative effect on most of the other fish groups. Most of the trophic compartments have a negative impact on themselves and this may show competition within the groups for the same food resources (Christensen *et al*., 2000).

Flow indices such as ascendency and overhead have been shown to be related to stability and maturity of an ecosystem (Christensen, 1995). Ascendency is a measure of average mutual information in a system (Ulanowicz and Norden, 1990). A comparatively higher value of ascendency (39.872%) was observed in the Vellayani Lake system. Overhead is a measure of energy in an ecosystem that is available to resist perturbations (Christensen, 1995). The relative overhead value of 60.128% is lower when compared to the trophically modelled Wyra and Kelavarapalli reservoirs of India (Panikkar and Khan, 2008; Khan and Panikkar, 2009). This implies that the Vellayani Lake is less resistant to perturbations including

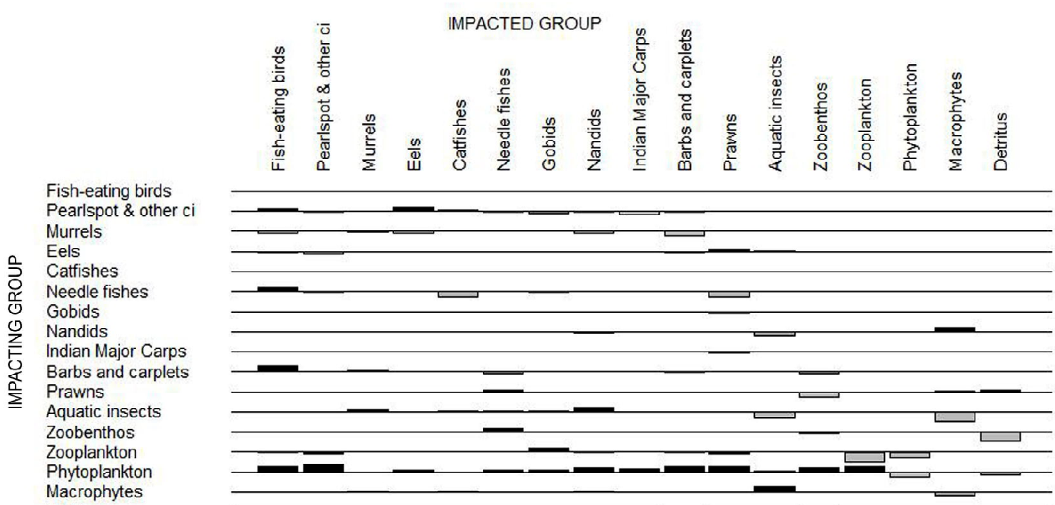

Fig. 3. Mixed trophic impacts of the functional groups in Vellayani Lake showing the trophic impacts. Positive impacts are shown above each baseline in dark columns, while negative impacts are shown below the baseline

anthropogenic interferences. Finn's cycling index was 2.52% of the total system throughput and the mean path length was 2.240, which further corroborate the developing stage of Vellayani Lake.

CONCLUSIONS

The whole-lake ecosystem analysis of the Vellayani Lake was carried out using the Ecopath with Ecosim model. The analysis showed that both grazing and detrital food chains are equally important in the lake. The system showed low ecological efficiency and the demand on the top predatory fishes like murrels, eels and catfishes is high, which is reflected on higher EE values for these groups. Maturity analysis using various parameters confirmed that the Vellayani Lake has not attained maturity and is a developing ecosystem. 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 Vellayani Lake ecosystem was relatively high, which may be attributed to fishing down the food web phenomenon. Study of flow indices also showed the less mature status of the system. The relative overhead value was lower, indicating less resistance of the lake ecosystem to perturbations. In the present study, we considered the property of the Vellayani Lake ecosystem in a given time period and did not quantify the dynamics of the ecosystem. Recently Indian major carps have been introduced in the lake in order to augment fishery production from the lake. In this context, followup studies using the Ecopath model would be prudent in future to assess the impacts of these stockings on other trophic compartments of the lake. This will be the focus of our future research.

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REFERENCES

Allen, K.R. 1971. Relation between production and biomass. *J. Fish. Res. Board Can.*, 28: 1573–1581.

Antony, P.J., Dhanya, S., Lyla, P.S., Kurup, B. M. and Ajmal Khan, S. 2010. Ecological role of stomatopods (mantis shrimps) and potential impacts of trawling in a marine ecosystem of the southeast coast of India. *Ecol. Modell.*, 221: 2604–2614.

Aravindan, C.M. 1993. Preliminary trophic model of Veli Lake, southern India. In: Christensen, V. and Pauly, D. (Eds.), *Trophic models of aquatic ecosystems*. ICLARM, Philippines, p. 87–89.

Christensen, V. 1995. Ecosystem maturity: towards quantification. *Ecol. Modell.*, 77: 3–32.

Christensen, V. and Pauly, D. 1992. *A guide to the Ecopath software system* (version 2.1). ICLARM, Manila, 72 pp.

Christensen, V. and Pauly, D. 1993. Flow characteristics of aquatic ecosystems. I In: Christensen, V. and Pauly, D. (Eds.), *Trophic models of aquatic ecosystems*. ICLARM, Philippines, p. 338–352.

Christensen, V. and Pauly, D. 1998. Changes in models of aquatic ecosystem approaching carrying capacity. *Ecol. Appl.*, 8: S104–S109.

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

Christensen, V., Walters, C.J. and Pauly, D. 2000. Ecopath with Ecosim: A user's guide, October 2000, Fisheries Center, University of British Columbia, Vancouver and ICLARM, Malaysia.

Christensen, V., Walters, C. and Pauly, D. 2005. Ecopath with Ecosim: a user's guide. Fisheries Centre Report, Fisheries Center, University of British Columbia, Vancouver, Canada, 130 pp.

Darwall, R.T.W., Allison, H.E., Turner, F.G. and Irvine, K. 2010. Lake of flies or lake of fish? A trophic model of Lake Malawi. *Ecol. Modell.*, 221: 713–727.

Froese, R. and Pauly, D. 2013. FishBase [available on website URL: http://www.fishbase.org/].

Fetahi, T. and Mengistou, S. 2007. Trophic analysis of Lake Awasa (Ethiopia) using mass balance Ecopath model. *Ecol. Modell.*, 201: 398–408.

Fetahi, T., Schagerl, M., Mengistoua, S. and Libralatoc, S. 2011. Food web structure and trophic interactions of the tropical highland lake Hayq, Ethiopia. *Ecol. Modell.*, 222: 804-813.

Gayalino F.C. Jr., Sparre, P. and Pauly, D. 1996. The FAO-ICLARM Fish Stock Assessment Tools (FiSAT) User's Guide. FAO Computerized Information Series (Fisheries No. 7). FAO, Rome, 126 pp.

Gopinath, S. 2003. Structure and diversity of fish assemblages and their dynamics in Vellayani Lake. Ph.D. Thesis, University of Kerala, India, 310 pp.

Gulland, J.A. 1971. Estimation of mortality rates. Annex to Arctic Fisheries Working Group Report, ICES C.M. Doc. 3 (mimeogr.)

Hustler, K. 1997. The ecology of fish-eating birds and their impact on the inshore fisheries of Lake Kariba. In: Moreau, J. (Ed.), *Advances in the ecology of Lake Kariba*, University of Zimbabwe Publications, Zimbabwe, p. 196–218.

Khan, M.F. and Panikkar, P. 2009. Assessment of impacts of invasive fishes on the food web structure and ecosystem properties of a tropical reservoir in India. *Ecol. Modell*. 220: 2281–2290.

Lampert, W. and Sommer, U. 1997. *Limnology: the ecology of lakes and streams.* Translated by Haney, J.F., Oxford University Press, New York.

Mohamed, K. S., Zacharia, P. U., Muthiah, C., Abdurahiman, K. P. and Nayak, T. H. 2005. A trophic model of the Arabian Sea ecosystem off Karnataka and simulation of fishery yields for its multigear marine fisheries. Special Publication, Central Marine Fisheries Research Institute, Cochin, India, 80 pp.

Moreau, J. V., Christensen, V. and Pauly, D. 1993a. A trophic ecosystem model of Lake George, Uganda. In: Christensen, V. and Pauly, D. (Eds.), *Trophic models of aquatic ecosystems*. ICLARM, Philippines, p. 124–129.

Moreau, J. V., Ligtvoet, W. and Palomares, M. L. D. 1993b. Trophic relationship in the fish community of Lake Victoria, Kenya, with emphasis on the impact of Nile perch (*Lates niloticus*). In: Christensen, V. and Pauly, D. (Eds.), *Trophic models of aquatic ecosystems*. ICLARM, Philippines, p. 114–152.

Moreau, J., Mavuti, K. and Daufresne, T. 2001. A synoptic Ecopath model of biomass flows during two different static ecological situations in Lake Nakuru (Kenya). *Hydrobiologia*, 458: 63–74.

Nair, M. M. 1987. Coastal geomorphology of Kerala. *J. Geol. Soc. India*, 29: 450-458.

Natarajan, A. V. and Jhingran, A. C. 1961. 'Index of preponderance'-a method of grading the food elements in the stomach analysis of fishes. *Indian J. Fish.*, 8: 54-59.

Odum, E. P. 1969. The strategy of ecosystem development. *Science*, 104: 262–270.

Odum, E.P. 1971. *Fundamentals of ecology*. W.B. Saunders Co., Philadelphia, 574 pp.

Palomares, M.L. and Pauly, D. 1998. Predicting food consumption of fish populations as functions of mortality, food types, morphometrics, temperature and salinity. *Mar. Freshw. Res.*, 49: 447–453.

Panikkar, P. and Khan, M. F. 2008. Comparative mass balanced trophic models to assess the impact of environmental management measures in a tropical reservoir ecosystem. *Ecol. Modell.*, 212: 280–291.

Pauly, D. and Christensen, V. 1995. Primary production required to sustain global fisheries. *Nature*, 374: 255–257.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. and Torres F. Jr. 1998. Fishing down marine food webs. *Science*, 279, 860–863.

Pauly, D., Christensen, V. and Walters, C.J. 2000. Ecopath, Ecosim and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES J. Mar. Sci.* 57: 697–706.

Piet, G. J. 1998. Impact of environmental perturbations on a tropical fish community. *Can. J. Fish. Aquat. Sci.*, 55: 1842–1853.

Pillay, T. V. R. 1952. A critique of the methods of study of food of fishes. *J. Zool. Soc. India*., 4: 1885-200.

Plaganyi, E. E. 2007. Models for an ecosystem approach to fisheries. FAO fisheries technical paper, No. 477, FAO, Rome, 108 pp.

Polovina, J. J. 1984. Model of a coral reef ecosystem, part I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs*, 3: 1–11.

Tsehaye, I. and Nagelkerke, A. J. L. 2008. Exploring optimal fishing scenarios for the multispecies artisanal fisheries of Eritrea using a trophic model. *Ecol. Modell.*, 212: 319–333.

Ulanowicz, R. E. 1986. *Growth and development: ecosystem phenomenology*. Springer Verlag, New York, 203 pp.

Ulanowicz, R. E. and Norden, J. S. 1990. Symmetrical overhead in flow and networks. *Int. J. Systems Sci.*, 21: 429–437.

Ulanowicz, R. E. and Puccia, C. J. 1990. The mixed trophic impact routine. *Coenose*, 5: 7–16.

Villanueva, M. C., Isumbisho, M., Kaningini, B., Moreau, J. and Micha, J. 2008. Modelling trophic interactions in Lake Kivu, what roles do exotics play? *Ecol. Modell.*, 212: 422–438.

Walters, C., Christensen, V. and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish Biol. Fisher.*, 7: 139–172.