Ecological Modelling 220 (2009) 2281–2290

Contents lists available at ScienceDirect

Ecological Modelling

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

Assessment of impacts of invasive fishes on the food web structure and ecosystem properties of a tropical reservoir in India

M. Feroz Khan*, Preetha Panikkar

Reservoir Fisheries Division, Central Inland Fisheries Research Institute, Hessarghatta Lake Post, Bangalore 560089, Karnataka, India

ARTICLE INFO

Article history:
Received 14 October 2008
Received in revised form 9 May 2009
Accepted 20 May 2009
Available online 1 July 2009

Keywords:
Mixed trophic impact
Invasive fishes
Modeling
Ascendancy
Reservoir ecosystem

ABSTRACT

A network model of trophic interactions in a tropical reservoir in India was developed with the objective to quantify matter and energy flows between system components and to study the impact of invasive fishes on the ecosystem. Structure of flows and their distribution within and between trophic levels were analysed by aggregating single flows into combined flows for discrete trophic levels. The trophic flows primarily occurred in the first four trophic level (TL) and the food web structure in this reservoir ecosystem was characterized by the dominance of low TL organisms, with the highest TL of only 3.57 for the top predator. Highest system omnivory index (SOI) was observed for indigenous catfishes (0.422), followed by the exotic fish Mozambique Tilapia (0.402). Nile Tilapia and Pearl spots show the highest niche overlap which suggests high competition for similar resources. The mixed trophic impact routine reveals that an increase in the abundance of the African catfish would negatively impact almost all fish groups such as Indian major carps, Pearl spots, indigenous catfishes and Tilapines. The other invasive fish Mozambique Tilapia adversely affects the indigenous catfishes. The most interesting observation in this study is that the most dominant invasive fish in this reservoir, the Nile Tilapia does not negatively impact any of the fish groups. In fact it positively impacts the Indian major carps. The direct and indirect effects of predation between system components (i.e. fish, invertebrates, phytoplankton and detritus) are quantitatively described and the possible influence and role in the ecosystem's functioning of the invasive fish species are discussed.

1. Introduction

Exotic species invasion is the most significant worldwide threat to native biota (Hall and Mills, 2000) and can impact ecosystems through competition with predation on native species, and by altering habitats, nutrient cycles, and energy budgets (Mack et al., 2000). Introduction of exotic species has caused extinction of native species in aquatic systems (Moreau et al., 1988; Mills et al., 1993; Pitcher and Hart, 1995; Latini and Petrere, 2004; Dudgeon et al., 2006; Villanueva et al., 2008).

Invasive species homogenize food webs by truncating the frequency distribution of species abundance, eventually turning it into an extremely skewed distribution dominated by the invader. Changes arising from invasion generally end up in local extinctions and decline in species richness. Widespread introductions of non-indigenous species have been categorized as a major cause of natural species extinction in aquatic systems (Moreau et al., 1988; Mills et al., 1993; Pitcher and Hart, 1995; Latini and Petrere, 2004; Puth and Post, 2005; Dudgeon et al., 2006). Cases where introduction of exotics have been reported beneficial are rare in aquatic ecosystems (Gottlieb and Schweighofer, 1996). The importance of considering a trophic network approach is that it can elucidate feeding relationships which occur between species in an ecological community and determine functional roles of species groups in the ecosystem (Yodzis and Winemiller, 1999). Indeed, numerous evidences suggest that food web structures are susceptible to a wide array of human activities, including species introductions or invasions (Van der Zanden et al., 1999), habitat alteration (Wootton et al., 1996) and global environmental warming (Petchey et al., 1999).

Food webs provide the framework for integrating population dynamics, community structure, species interactions, community stability, and biodiversity and ecosystem productivity. Food web interactions ultimately provide the fate and flux of every population in an ecosystem, particularly upper trophic levels of fiscal importance (May, 1973; Pimm, 1982). Additionally food webs often provide a context for practical management of living resources (Crowder et al., 1996; Winemiller and Polis, 1996). The mass-balanced Ecopath with Ecosim (EwE) model is considered as one of the effective and straightforward methods for quantifying the food web interactions and fisheries ecosystem dynamics (Christensen et al., 2000). First built for estimating biomass and food consumption of the elements of an aquatic ecosystem, EwE was combined

* Corresponding author. Tel.: +91 8028446428/23564530/9845103137.
E-mail address: ferosekhan23@gmail.com (M. Feroz Khan).

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doi:10.1016/j.ecolmodel.2009.05.020

subsequently with various approaches from theoretical ecology, proposed by Odum (1969) and Ulanowicz (1986), for the analysis of energy flows between the elements of ecosystems and to reveal the maturity and stability of ecosystems. The information derived is useful in multispecies management decision (Vasconcellos et al., 1997; Christensen and Pauly, 1998; Wolff et al., 2000; Bundy and Pauly, 2000; Moreau et al., 2001), in analyses of effects of the trophic cascade (Polis et al., 2000; Ortiz and Wolff, 2002; Schmitz et al., 2003), in verifying the relationship between stability and diversity (Hasting, 1988; Naeem and Li, 1998; Tilman, 1999).

Reservoir ecosystems are dynamic, undergoing both natural and anthropogenic change (e.g., introduction of exotic species) that can impact ecosystem processes on a continual basis. Reservoirs are considered to be a growing resource in India with enormous fish yield potential and largely support capture fisheries activities (Panikkar and Khan, 2008). These water bodies are complex systems that exhibit a range of ecological interactions.

Exotic fishes have been introduced for food fishery in all Indian reservoirs (Arunachalam, 2005). Most of the reservoirs in South India are generally dominated by exotic fishes (mostly Tilapiine species). Mozambique Tilapia, *Oreochromis mossambicus* was stocked in reservoirs of south India during the 1960s. Nile Tilapia (*Oreochromis niloticus*) and African catfish (*Clarias gariepinus*) have become popular among aquaculturists in the country (Sugunan, 2000). The effects of invasions propagate throughout ecosystem *via* direct and indirect pathways (Crooks, 2002). The extent and frequency of these disturbances make management of reservoir ecosystems challenging. These challenges can be addressed through ecosystem management approach (Christensen et al., 1996). To meet the goals of ecosystem management, we first need an understanding of ecosystem structure and function inclusive of ongoing ecological change. The effect of exotic species invasion in Indian reservoirs on the ecosystem structure is still unknown. This study is the first attempt in India to assess the impact of invasive fishes on the reservoir ecosystem through ecosystem-based approach for management of reservoir fisheries.

The objectives of this study are: (1) to document and quantify the trophic structure of the reservoir; (2) to evaluate the role of invasive species play in the reservoir ecosystem; (3) to gain insight into the properties and development status of the ecosystem (maturity).

2. Materials and methods

2.1. Study area

Kelavarapalli reservoir located in Hosur Taluk of Krishnagiri district, Tamil Nadu state, India has a total water spread area extending to 430 ha at full reservoir level. This reservoir was built in 1995 impounding South Pennar River which covers a distance of 400 km from its point of origin at Chennakeshava hills near Bangalore before joining the Bay of Bengal at Cuddalore District in Tamil Nadu (Fig. 1) This reservoir has a catchment area of 2442 km^2. The water temperature fluctuated from 21.0 °C (December 2007) to 29 °C (January 2008). The wind induced turbulence churns the water to facilitate mixing of nutrients especially in this shallow reservoir. The annual inflow and flushing rate have positive effect on the productivity of the reservoir as they have a direct bearing on the loading of organic matter and its nutrients.

2.2. Ecopath approach

The Ecopath software was used to create a static mass balance model of the Kelavarappalli reservoir. Ecopath is the core routine of the Ecopath with Ecosim (EwE), a software package based on an approach proposed by Polovina (1984) and subsequently upgraded with a variety of ecological and theoretical approaches (Christensen and Pauly, 1992; Walters et al., 1997, 2000; Pauly et al., 2000; Christensen and Walters, 2004). Ecopath allows construction of a mass balance model of a given trophic network by representing the ecosystem functional groups as interacting by means of feeding relationships and, when necessary, subjected to fishing (Christensen and Walters, 2004). Ecopath is used to establish mass balance which allows analysis of flows between trophic levels and thereby the status of the ecosystem in general via goal functions such as relative overhead and Finn's cycling index. In general, Ecopath balances production and losses for each species or species group. In the form of an equation:

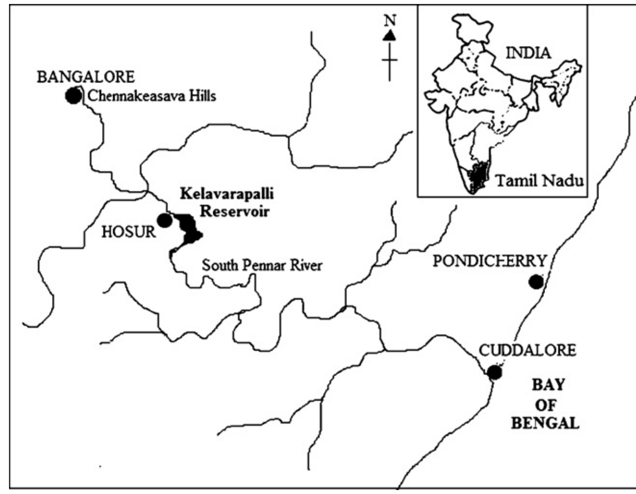

Fig. 1. Map of Kelavarapalli reservoir in Hosur, Tamil Nadu, India.

$$\text{production} + \text{immigration} - \text{predation mortality} - \text{other mortality} - \text{fishery harvest} = 0.$$

Or more specifically,

$$Pi = Yi + Bi \times Mi + Ei + BAi + Pi \times (1 - EEi)$$

where Pi is the total production rate of group (i), Yi the total fishery catch rate of (i), Mi the total predation rate for (i), Bi the biomass of (i), Ei the net migration rate (emigration − immigration) of (i), BAi the biomass accumulation rate for (i), while (1 − EEi) is the 'other mortality' rate for (i).

In general, the model sets up a system with as many linear equations as there are species groups, and solves for one of four parameters (Christensen et al., 2000). Necessary model inputs for each group include biomass (*B*) in t km^{-2}, production/biomass ratio (*P*/*B*) per year, consumption/biomass ratio *Q*/*B*) per year, ecotrophic efficiency (EE), diet composition, and any associated fishing mortality per year. EE is the proportion of total production and mortality that is accounted for by the model. The opposite of EE (i.e. 1 − EE) is unexplained mortality. Although accurate estimates of all parameters for each functional species group lead to greater confidence in model outputs, only three of the four (*B*, *P*/*B*, *Q*/*B*, and EE) primary inputs are necessary. EE is generally not specified, but is often estimated during model balancing if reasonable estimates of the other three parameters (*B*, *P*/*B*, and *Q*/*B*) are available.

The balanced state was assumed to be reached when realistic estimates of the unknown parameters were obtained and there was a consistent view of the energy flow between the different compartments in the model (Gamito and Erzini, 2005). The balanced model was then used to analyze the food web structure and ecosystem properties of this reservoir.

2.3. Input data and sources

In this study, we used 14 functional groups. The selection of fish and some macroinvertebrate groups was based on the most abundant families and on economic importance. Other invertebrate groups were selected because of their importance in the diet of fish groups. Two groups of primary producers (phytoplankton and macrophytes) and a detritus group were also included in the model. Data used in this work mostly come from our investigations in the reservoir. All rates and biomasses were expressed as wet weight and standardized for a year to the area of the reservoir system. The biomass of fish groups was calculated based on the experimental fishing conducted at the reservoir and also from the commercial fish catch. The biomass for unexploited groups like phytoplankton, zooplankton, zoobenthos, dipterans, macrophytes, benthic algae and fish eating birds for the periods were obtained from our field studies and also from similar ecosystems (Moreau et al., 2001; Panikkar and Khan, 2008).

For non-exploited fish, production by biomass (*P*/*B*) was calculated by using the empirical equation by Pauly (1980). The *P*/*B* ratio is equivalent to the instantaneous rate of total mortality (*Z*) used by fisheries biologists (Allen, 1971). For some species *Z* is estimated using length-converted catch curve method of Pauly (1983). A software package known as FiSAT (Gayalino et al., 1996) is used as it contains a routine for length-converted catch curve method. The production/biomass (*P*/*B*) ratios for groups with data were estimated using the empirical (regression) models incorporated in the Ecopath with Ecosim (EwE) software (www.ecopath.org) and from FishBase (http://www.fishbase.org). *P*/*B* for fish eating birds was derived from Panikkar and Khan (2008) for same species and similar ecosystem. *Q*/*B* of fishes were calculated using the empirical formula, developed by Pauly (1991) relating mean annual temperature, body size, and morphometric aspects of the body and the caudal fin (Table 1).

Diet composition of consumers was represented in a prey–predator matrix that contains the fraction of the diet of each predator contributed by each prey (Table 2). Diet composition of fish eating birds was derived from Piet (1998). The model parameters were calibrated to obtain for all the groups ecotrophic efficiency (EE) values less than 1 and gross efficiency values (GE = *P*/*Q*) within 0.1 and 0.3 (Christensen et al., 2000).

Table 1
Input parameters for the Ecopath model of Kelavarapalli reservoir.

Ecological groups	Biomass ($t\,km^{-2}$)	*P*/*B*	*Q*/*B*
Fish eating birds	0.560	0.33	0.840
African catfish	0.069	2.14	10.800
Indigenous catfishes	0.140	2.900	4.750
Snake heads	0.050	2.670	7.600
Mozambique Tilapia	0.933	2.800	6.200
Nile Tilapia	10.990	3.600	31.300
Pearl spots	0.130	2.800	12.890
Major carps	3.143	9.400	16.500
Dipterans	6.000	18.000	38.750
Zoobenthos	10.100	4.210	21.050
Zooplankton	33.000	45.800	99.800
Macrophytes	63.600	97.350	–
Phytoplankton	32.000	188.600	–
Detritus	24.000		–

P/*B* is the production/biomass ratio and *Q*/*B* is the consumption/biomass ratio.

2.4. Ecological groups

2.4.1. Fish eating birds

This group includes Indian cormorant, *Phalocrocorax fuscicollis*, great cormorants, *Phalocrocorax carbo*, painted storks *Mycteria leucocephala*, king fishers, *Ceryle rudis*, etc. These are top predators in this reservoir ecosystem and they feed on catfishes, snakeheads, tilapia cichlids, etc.

2.4.2. African catfish

C. gariepinus, popularly known as African catfish is a voracious predator and feeds across trophic levels. People consider this fish as a menace to the whole freshwater ecosystem. The Fisheries Department of some state governments in India have banned the culture of this fish, but in Tamil Nadu state where Kelavarappalli reservoir is located this fish is not under banned list. *C. gariepinus* has entered this reservoir from culture ponds adjacent to river South Pennar during rain and floods. Though undesired by many, this fish fetch higher price than tilapia as there is market for it in certain areas in this state.

2.4.3. Indigenous catfishes

Indigenous catfishes include *Ompok bimaculatus*, *Aorichthys aor*, *Aorichthys seenghala* and *Mystus gulio*. This group is caught occasionally in gill nets. Most of these fishes are voracious feeders. Some of these fishes are caught mainly by hook and lines.

2.4.4. Snakeheads

Channa marulius, *Channa striata* and *Channa punctatus* are the major species in this group. These are air-breathing fishes and they are mainly caught using hook and lines. These are much preferred food fishes in this area and have good demand. They are mainly piscivorous and voracious feeders

2.4.5. Mozambique Tilapia

Mozambique Tilapia, *O. mossambicus* is one among the dominant fishes in South Indian reservoir ecosystem and it feeds mainly on detritus, dipterans, zooplankton and zoobenthos. No major shifts in

Table 2
Diet matrix of Kelavarapalli reservoir ecosystem.

Prey/predator		1	2	3	4	5	6	7	8	9	10	11
1	Fish eating birds											
2	African catfish											
3	Indigenous catfishes	0.340	0.254									
4	Snake heads	0.130	0.012									
5	Mozambique Tilapia	0.160	0.058									
6	Nile Tilapia	0.300	0.230									
7	Pearl spots	0.150	0.156									
8	Major carps	0.640	0.148									
9	Dipterans		0.142	0.298	0.289	0.328						
10	Zoobenthos				0.093	0.013						
11	Zooplankton			0.042	0.012	0.129	0.210	0.174	0.147	0.350	0.288	
12	Macrophytes			0.066		0.032	0.034	0.246	0.214			0.294
13	Phytoplankton			0.214		0.002	0.254	0.128	0.297	0.129	0.169	0.456
14	Detritus			0.380	0.244	0.496	0.502	0.452	0.342	0.521	0.543	0.250

diet composition in this fish were observed. This fish is a voracious feeder and survives extreme conditions. It has co-existed with Nile Tilapia and African catfish in this reservoir and lives across the depth profile from pelagic to benthic niches.

2.4.6. Nile Tilapia

This is the most dominant fish in this reservoir and available throughout the year. *O. niloticus* grows faster and reaches bigger sizes in short span of time. The littoral areas of Kelavarappalli reservoir are full of nests of Nile Tilapia and they breed during south-west monsoon (July–September). The fish mainly feeds on detritus. The zooplankton, phytoplankton and macrophytes also were recorded occasionally from the gut of Nile Tilapia. There is a heavy demand especially from local poor people as this fish is affordable to the lowest income group in this area.

2.4.7. Pearl spots

Etroplus suratensis and *Etroplus maculatus* form the main species and the former is dominant among Pearl spots. They mainly feed on detritus and occupy the same niche as that of *O. mossambicus*. These fishes are very popular food fishes but their biomass is very low in this reservoir.

2.4.8. Major carps

The Indian major carps are the most sought after inland fishes in the country. *Catla catla*, *Labeo rohita* and *Cirrhinus mrigala* are the three important species widely available across the country but these fishes do not breed in the reservoir ecosystem. These fishes are stocked in Indian reservoirs for enhancement of fish production. Kelavarappalli reservoir is also regularly stocked with these carps, but these fishes are not reflected in the desired level of minimum 5 kg per coracle unit in the fishery. These fishes feed on zooplankton, phytoplankton, zoobenthos, detritus, etc.

2.4.9. Dipterans

Midges, *Tendipes*, etc. constituted the dipteran population. Aquatic dipterans play important role in the food web ecology and in supporting fish population. Approximately 10% of all dipteran species are aquatic in their larval stage. Eggs and pupae of these species are also aquatic, whereas adults are always terrestrial (Narf, 1997).

2.4.10. Zoobenthos

Zoobenthos consisted of benthic deposit feeders such as dipteran larvae, nematodes, gastropods, bivalve mollusks, oligochaetes, coleopteran larvae, etc. The dipteran larvae and molluscs constituted the bulk of the biota. The other groups that occurred in low density were oligochaetes, trichopterans and coleopterans.

2.4.11. Zooplankton

The zooplanktonic community is dominated by Copepods (*Diaptomus*, *Cyclops* and to a lesser extent, cladocerans (*Ceriodaphnia*, *Moina*) though seasonal density variations can be observed. Protozoans represented by *Arcella*, *Centropyxis*; Rotifers (*Brachionus*, *Keratella*), etc. also constituted the zooplankton in this reservoir.

2.4.12. Phytoplankton

Chlorophyceae represented mainly by *Scenedesmus* dominated the phytoplankton community followed by myxophyceae represented by *Microcystis*. This group also consisted of Bacillariophyceae (*Navicula*, *Cymbella*).

2.4.13. Macrophytes

This reservoir has a very high density of macrophytes. The marginal areas of the reservoir have *Hydrilla* spp. and *Chara* spp. while deeper zones harbour V*allisneria* spp. Macrophytes offer substrata for a wide array of insects, molluscs and other invertebrate fauna, and thereby contribute to the species diversity of a water body. Submerged weeds provide shelter for minnows and weed fishes, which compete with major carps for food (Sugunan, 1995). The floating vegetation utilizes the incident solar radiation for its photosynthesis and makes it unavailable to the phytoplankton communities.

2.4.14. Detritus

The detritus mass was estimated using an empirical relationship derived by Pauly et al. (1993) that relates detritus biomass to primary productivity and euphotic depth.

$$\log_{10} D = -2.41 + 0.954 \log_{10}\mathrm{PP} + 0.863 \log_{10} E$$

where D is the standing stock of detritus ($\mathrm{g\,cm^{-2}}$), PP is primary productivity ($\mathrm{g\,cm^{-2}\,year^{-1}}$), and E is the euphotic depth (m). This resulted in a detritus biomass of $0.5\,\mathrm{t\,km^{-2}}$. Here, bacteria were considered part of the detritus compartment.

2.5. Model analysis

Since this is a steady state model, biomass remains unchanged and all parameters were normalized to unit surface area using wet weight for biomass and fishery catch ($\mathrm{g\,m^{-2}}$), while flows and rates were expressed on an annual basis. The criterion used for balancing the model was ecotrophic efficiency (EE). Trophic level of consumer groups is calculated as the weighted average of the trophic levels of their prey, using the consumption of each prey item as weighting factor (Christensen et al., 2004). Inversely, flows between model groups can be fractionated according to the trophic level they originate from (Ulanowicz, 1995; Christensen et al., 2004) to construct a linearized food chain, referred to as a Lindeman spine. Transfer efficiencies between trophic levels can be calculated and the method allows comparing “spines” from different ecosystems and model structures.

The mixed trophic impact (MTI) routine (Majkowski, 1982 in Blanchard et al., 2002) in EwE was used to evaluate critical trophic interactions between groups in the ecosystems and also to assess the impact of the exotic fishes on other indigenous fishes.

We have also included a set of commonly used indices for comparing ecosystem properties in our study. In particular, Odum (1971) postulated that the ratio between total primary productivity and total system respiration (TPP/TR) would approach unity in mature system, whereas systems in development would be characterized by smaller ratios. Total primary production per total biomass (TPP/TB) has also been used to indicate system maturity (Odum, 1971; Christensen, 1995). Systems in “developmental phase” have high TPP/TB ratios, while “mature” ones tends to have lower TPP/TB ratio, associated with high biomass or lower production rate (Christensen, 1995). Similarly, the total biomass per total system throughput ratio (TB/TST) tends to be low in the developmental phase of an ecosystem and increase in values as the system matures and conserves energy by storing it in its components (Odum, 1971; Ulanowicz, 1986).

The system omnivory index (SOI) is defined as the average omnivory index (variance of trophic levels of the consumers prey) of all consumers weighted by the logarithm of each consumer’s food intake. The system omnivory index therefore characterizes the diversity of consumer–prey relationships (Pauly et al., 1993). Niche overlap is measured by using a symmetrical index derived from the one proposed by Pianka (1973) based on competition coefficients of the Lotka–Volterra equation (Volterra, 1931) and derived from the Jaccard similarity index (Harris, 1968). It is used to describe mainly the trophic aspect of niche partitioning. An index value close to 0 indicates that two groups have a low resemblance in terms of food consumed and vice versa for a value close to 1 (Christensen et al., 2005).

Trophic aggregation per discrete trophic level, sensu Lindman (1942), is based on an approach suggested by Ulanowicz (1995). This routine facilitates calculation of flows per TL based on diet compositions by reversing the routine for calculation of fractional trophic levels quoted above. More particularly, the transfer efficiencies between the successive discrete trophic levels are calculated as the ratio between the sum of the exports plus the flow that is transferred from one trophic level to the next, and the throughput at this trophic level (Christensen et al., 2005).

The gross efficiency of the fishery (GEF) is computed as the ratio between the total catch and the total primary production in the system. The value will be higher for systems with a fishery harvesting fish belonging mainly to low TLs than for systems whose fisheries concentrate on high TLs. Therefore, this index may increase with fisheries 'development' as defined by Pauly et al. (1998).

Ecopath also links flow indices like: (a) the total system ascendency, considered a measure of the average mutual information and used for describing ecosystem flow characteristics (Christensen, 1994); (b) the total system throughput, that is the sum of all flows (Ulanowicz and Norden, 1990); (c) the Finn's cycling index (Finn, 1976) which considers the fraction of the ecosystem throughput that is recycled; (d) the path length, defined as the average number of groups that an inflow or outflow passes through.

Flow indices are valuable techniques for illuminating exotic species impacts at the whole-system level while at the same time allowing for inspection of impacts at the level of species or even life stage (Jaeger, 2006).

The following indices were calculated by Ecopath total system throughput, which is the sum of the total of all flows occurring in the system; and the Finn cycling index, which is the proportion of the total throughput that is devoted to recycling of material (Finn, 1976). Ascendancy (A) is the key index that characterizes the level of development and maturity of a system, since it takes into account both the dimension (TST) and the organization (information, I) of flows (Ulanowicz, 1986). The complement to ascendancy is system overhead, the cost to an ecosystem of circulating matter and energy (Monaco and Ulanowicz, 1997). As suggested by Mann et al. (1989), the system-wide effects of eutrophication can be indexed using a combination of A and TST, comparing the change of flows in the whole ecosystem during and after eutrophication. Eutrophication may be defined at the ecosystem level as an increase in A due to a rise in TST that more than compensates for a concomitant fall in I (Ulanowicz, 1986). Relative ascendancy (A/C) is the fraction of possible organization that is actually realized (Ulanowicz, 1986), and is negatively correlated with maturity (Christensen, 1995).

A number of statistics describing an ecosystem as a whole have been included into Ecopath and were used to assess the status of the ecosystem in terms of maturity (Odum, 1969) and for comparison with other similar ecosystems. Summary statistics are totals of consumption, exports, respiration, flows to detritus, primary production. The connectance index is the ratio of the number of existing trophic links with respect to the number of possible links. The mean trophic level (TL) of the catch was calculated as the mean of TLs of groups included weighted by the contribution to total catch.

3. Results

Two groups of primary producers – phytoplankton and macrophytes – were the sources of carbon and energy for the reservoir food web. This reservoir had dense macrophyte growth and probably contributed strongly to the total primary production. Because of their high *P*/*B* ratio, macrophyte production was not channeled into the food webs directly as shown by the low ecotrophic efficiency.

Table 3
Parameters calculated for the Kelavarapalli ecosystem model.

Ecological groups	TL	EE	*P*/*Q*	FtD	NE	OI
Fish eating birds	3.57	0.000	0.393	0.279	0.491	0.142
African catfish	3.42	0.000	0.198	0.267	0.248	0.058
Indigenous catfishes	2.72	0.903	0.611	0.157	0.763	0.422
Snake heads	3.01	0.531	0.351	0.138	0.439	0.347
Mozambique Tilapia	2.59	0.042	0.452	3.656	0.565	0.402
Nile Tilapia	2.21	0.010	0.119	105.739	0.149	0.166
Pearl spots	2.17	0.543	0.217	0.492	0.272	0.144
Major carps	2.15	0.005	0.570	39.916	0.712	0.125
Dipterans	2.35	0.021	0.465	152.171	0.581	0.228
Zoobenthos	2.29	0.003	0.200	84.789	0.250	0.205
Zooplankton	2.00	0.146	0.459	1948.852	0.574	0.000
Macrophytes	1.00	0.160	–	5200.139	–	0.000
Phytoplankton	1.00	0.276	–	4367.277	–	0.000
Detritus	1.00	0.111	–	0.000	–	0.175

TL is the mean trophic level, EE is the ecotrophic efficiency, *P*/*Q* is the production/consumption ratio, FtD is the flow to detritus ($t\,km^{-2}\,year^{-1}$), NE is the net efficiency and OI is the omnivory index.

3.1. Comparison of ecotrophic efficiencies (EE)

Ecotrophic efficiency, the proportion of the production that is consumed by predators or exported, varied considerably in this tropical reservoir ecosystem. As shown in Table 3, low values of ecotrophic efficiency were observed for phytoplankton (0.276) and zooplankton (0.146). This shows that these groups are underexploited. The EE value of macrophytes (EE = 0.160) was very low adding considerable amount of biomass to the detritus box in this model (Fig. 2). Detrital biomass ($24\,t\,km^{-2}$) was calculated taking only primary productivity of phytoplankton into consideration. A significant amount of macrophytes (and periphyton) primary productivity was not included in the biomass calculation. Hence lower detritus biomass is reported in this reservoir than other tropical lakes (L. Turkana $-415\,t\,km^{-2}$, Kolding, 1993), but similar to L. George ($10\,t\,km^{-2}$, Moreau et al., 1993) and Wyra reservoir ($10\,t\,km^{-2}$) in India (Panikkar and Khan, 2008). A high value of EE is noted for Pearl spots (0.543) and Snake heads (0.531). Ecotrophic efficiencies of fish groups are variable. For the two groups of Tilapiine fish, EE is quite low (EE = 0.042 and 0.010), suggesting a very limited exploitation and predation in the lake. The maximum EE value is recorded for indigenous catfishes (0.903), because these fish are exploited and predated.

3.2. The gross efficiencies

The *P*/*Q* ratios (Table 3) are lowest for Nile Tilapia and this might be due to the low density of their prey. Highest *P*/*Q* values observed for indigenous catfishes could be attributed to their carnivorous habits. Ichthyophagous fish *C. gariepinus* has surprisingly low *P*/*Q* values which could be related to the scarcity of their possible prey in terms of biomass per volume unit.

3.3. System omnivory index and niche overlap

The system omnivory index (SOI) of the ecological groups is presented in Table 3. Highest SOI was observed for indigenous catfishes (0.422), followed by the exotic fish Mozambique Tilapia (0.402). This can be attributed to their large feeding spectrum and distribution in the reservoir. The carnivorous fishes, snakeheads also showed a high SOI (0.347). These fishes also had higher TLs which indicate more complexity in this part of the food web. The other exotics, African catfish and the Nile Tilapia had SOI of 0.058 and

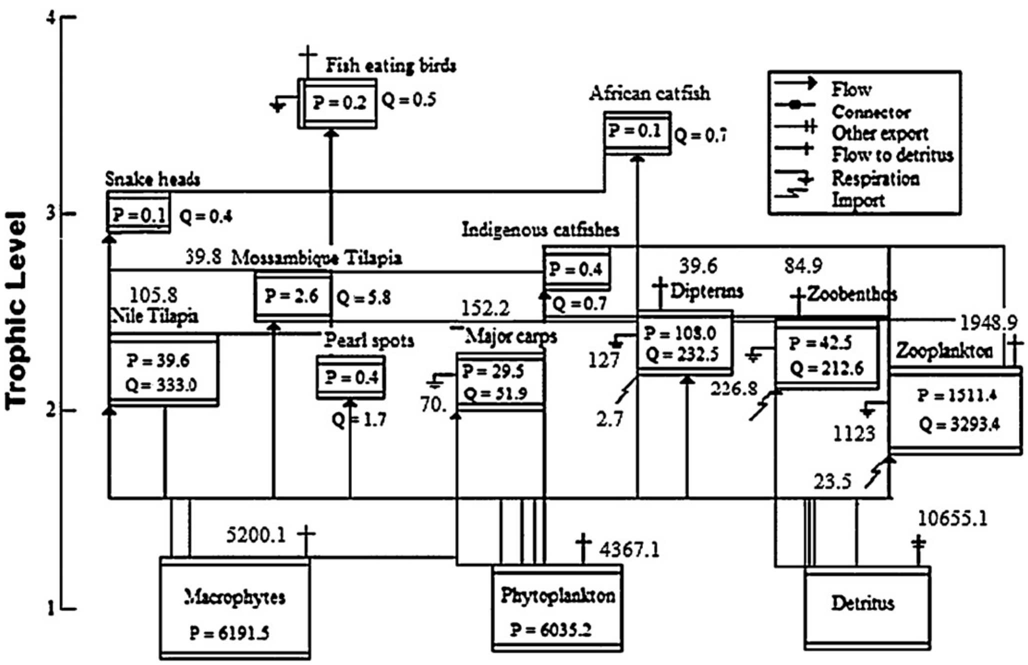

Fig. 2. Trophic model of Kelavarapalli ecosystem indicating trophic flows expressed in t km^{-2} year^{-1} (P—production, Q—consumption). Box sizes represent relative abundance. Each box is aligned with its respective trophic levels.

0.166, respectively which can be related to their feeding flexibility. Our results indicate that these fishes adjust their trophic behavior to the availability of their prey organisms in habitats where they are already acclimated. The higher SOI of Mozambique Tilapia compared to Nile Tilapia can be attributed to their higher trophic plasticity that enables dietary shifts from plant or detrital matter to animal matter (Ulyel, 1991; Kaningini et al., 1999; Villanueva et al., 2008).

High values of SOI for groups sharing the same type of food can be associated with estimates of niche overlaps. Fig. 3 shows that Nile Tilapia and Pearl spots show the highest overlap which suggests high competition for similar resources. African catfish and Mozambique Tilapia have the lowest overlap which expresses divergent preferences in terms of resources consumed (Fig. 3). Nile Tilapia had slight overlap with Mozambique Tilapia and indigenous catfishes.

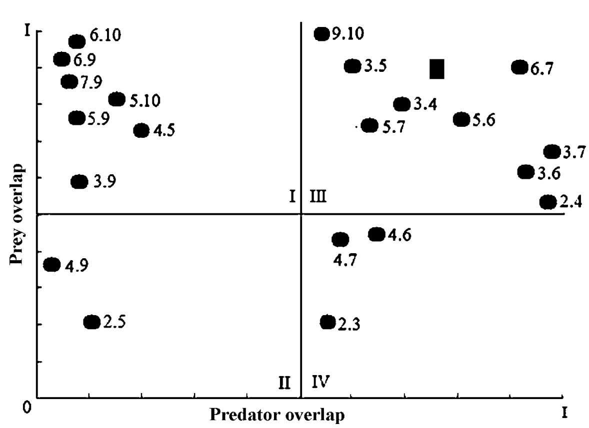

Fig. 3. Prey vs. predator niche overlap plot. Groups in the lower left of the figure have no overlap and are quite independent for both preys and predators. Groups on the upper right corner have a high overlap for both predators and preys. The numbers represents the system compartments as follows: (2) African catfish; (3) Indigenous catfishes; (4) Snake heads; (5) Mozambique Tilapia; (6) Nile Tilapia; (7) Pearl spots; (8) Major carps; (9) Dipterans; (10) Zoobenthos.

3.4. *Mixed trophic impact*

Ecopath gives the mixed trophic impacts within the ecosystem, which is shown in Fig. 4. Mixed trophic impact (MTI) allows assessing the impact that changes in biomass of a group will have on the biomass of the other groups in an ecosystem trophically (Christensen and Walters, 2004). An initial condition that should be considered for this routine is that diet composition of each functional group does not change, despite possible variations in abundance of their various preys. An increased abundance of fish groups of high TLs (about three or more) would have various levels of negative impacts on other groups. This is particularly the case for invasive fishes, the African catfish. An increase in the abundance of this fish would negatively impact almost all fish groups such as Indian Major carps, Pearl spots, indigenous catfishes and Tilapines. The other invasive species Mozambique Tilapia adversely affects the indigenous catfishes. The most interesting observation in this study is that the invasive species Nile Tilapia does not negatively impact any of the fish groups. In fact it shows positive impact on Indian major carps (Fig. 4) and this species adversely affect non-fish groups that would generate a positive impact on most groups including fish groups. The impact of zooplankton biomass variations would be less important compared to the phytoplankton group. As a prey, a group causes a positive impact on its predators. As a direct predator, it has a negative impact on its prey. Phytoplankton and detritus have positive impact on most other groups. The impact was greatest on their direct predators. For instance, the impact of phytoplankton was greatest for zooplankton, zoobenthos and planktivorous fishes in this reservoir. This shows that 'bottom up' control exists in the reservoir ecosystem.

3.5. *Trophic aggregation*

The results of the aggregation of biomass and energy flows among trophic levels (TLs) showed the presence of six trophic levels. Flows in TL I involved the groups of phytoplankton, macrophytes and detritus. The TL II included zoobenthos, some other carnivorous or omnivorous fish groups, as well as the group of major carps and

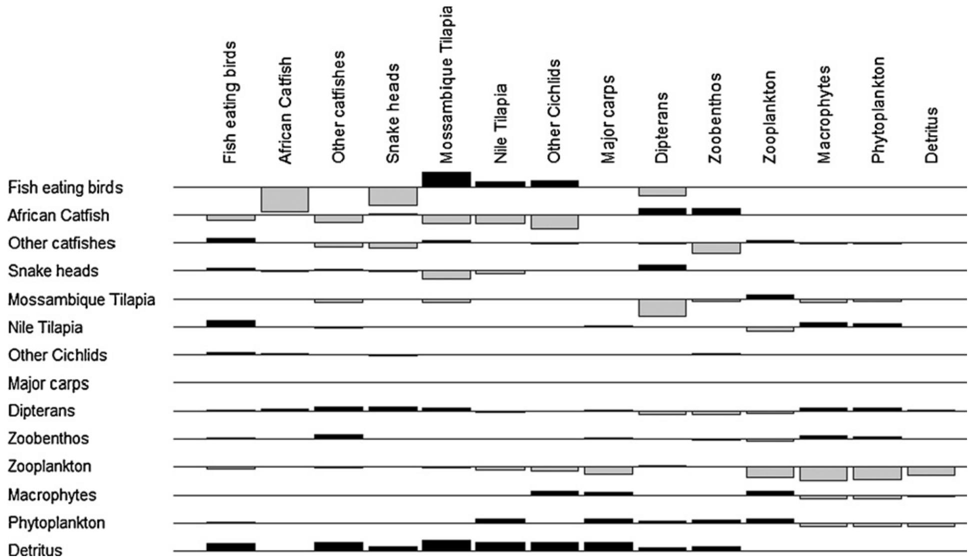

Fig. 4. Mixed trophic impacts in Kelavarapalli reservoir. The bars pointing upwards indicate positive impacts, while the bars pointing downwards show negative impacts. The impacts are relative and comparable between groups. The impacts refer to a postulated change of biomass.

were partly involved at TL III, IV and V. Flows above TL IV were primarily involved by snake heads, African catfish and fish eating birds. Although there were six trophic levels, flows at TL V and VI were so small in relation to the flows in lower trophic levels (Fig. 5) and could be neglected. The trophic flows primarily occurred in the first four TLs and the food web structure in this reservoir ecosystem was characterized by the dominance of low trophic level organisms, with the highest trophic level (TL) of only 3.57 for the top predator, fish eating birds, and a TL of 3.47 for another top predator, African catfish. The commercial catch trophic level was 2.21 since the most important fishery in the reservoir is Nile Tilapia.

3.6. Flow indices

The high values of ascendancy (35.9%) in this reservoir seem related to low levels of maturity in the system and vice versa: this was demonstrated by comparison of a high number of models (Christensen, 1995). Finn's cycling index was 3.04% of TST and mean path length was 2.312 which also indicate that the system has not attained maturity.

3.7. System summary statistics

The system statistics for Kelavarapalli reservoir is summarized in Table 4. This is the ratio between in a system. Odum (1969) demonstrated that total primary production and total respiration ratio

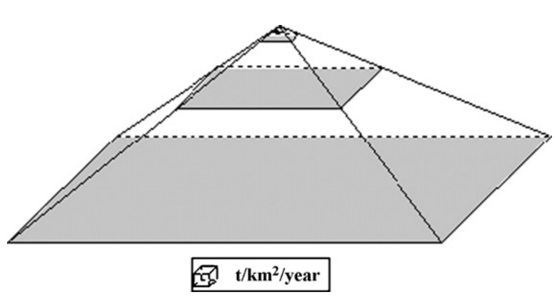

Fig. 5. Flow pyramid showing the flux in Kelavarapalli reservoir. The volume of each trophic level is proportional to the total throughput at this level whereas the angle on the summit is inversely proportional to the mean efficiency of the system. The lower compartment represents the consumers of the primary production. Proportion of total flow originating from detritus: 0.47. Transfer efficiencies (%) from primary producers: 3.0.

(TPP/TR) describes the maturity of an ecosystem. The rate of primary production exceeds the rate of community respiration during early stages of ecosystem development, and hence TPP/TR is greater than one. However in mature system the ratio approaches one in that energy fixed tends to be balanced by the energy cost of maintenance. Within this context, TPP/TR ratio of Kelavarappalli reservoir is 7.780, which is much larger than 1, leading to a conclusion that this reservoir is relatively at developmental stage or a young ecosystem. Net system production is the difference between total primary production and total respiration. The net system production will be large in immature systems and close to zero in mature ones. The high net system production (10,655.07 t km^{-2} year^{-1}) in this reservoir shows this is an immature system. Total primary production/total biomass ratio is also expected to be a function of its maturity. The value for Kelavarappalli reservoir is very high (76.07) (Table 4) indicating the immaturity of this system. Total biomass/total throughput can be expected to increase to a maximum for the most mature stages of a system. This value (0.006) also shows that this system is in development stage (Table 4).

4. Discussion

A mass balance model using EwE was created for Kelavarappalli reservoir to assess the impact of invasive fishes in the reservoir. The

Table 4
Summary statistics of Kelavarapalli reservoir.

Parameter	Value	Units
Sum of all consumption	4133.080	t km^{-2} year^{-1}
Sum of all exports	10655.070	t km^{-2} year^{-1}
Sum of all respiratory flows	1571.600	t km^{-2} year^{-1}
Sum of all flows into detritus	11903.870	t km^{-2} year^{-1}
Total system throughput (TST)	28264.000	t km^{-2} year^{-1}
Sum of all production	13961.000	t km^{-2} year^{-1}
Calculated total net primary production	12226.660	t km^{-2} year^{-1}
Total primary production/total respiration	7.780	
Net system production	10655.070	t km^{-2} year^{-1}
Total primary production/total biomass	76.070	
Total biomass/total throughput	0.006	
Total biomass (excluding detritus)	160.715	t km^{-2}
Connectance index	0.296	
System omnivory index	0.156	
Ascendancy (% of capacity)	35.92	
Finn's mean path length	2.312	
Finn's cycling index	3.04	% of TST

low EE of phytoplankton indicates that a major part of the production dies off perhaps due to reduced predation pressure from the herbivore zooplankton, Tilapia and major carps. That means supply exceeds demand, much of this excess production goes to detritus. Lower utilization of macrophytes may be due to lack of grass carp *Ctenopharyndedon idella* in this reservoir. The positive effect of detritus on all consumer groups may be seen as a manifestation of the 'indirect dependencies' of these groups from detritus (Carrer and Opitz, 1999). Zooplankton had a negative impact on most of the groups, may be because it consumes directly the main indirect resource of the other groups. The negative effect is strengthened by the fact that low predation on this group (EE = 0.146), so that an eventual increase in biomass production is not transferred to higher trophic levels. This holds true for the scarcely predated planktivores, the major carps (EE = 0.005) which did not have visible impact on any other groups. Primary production can support much more than the present herbivorous animals. In contrast the consumers are highly exploited by the system indigenous catfishes with EE = 0.903, for example, is overexploited.

The African catfish had a high TL (3.42) which can be explained by the higher predation on fish by this group, compared to the other groups of fish. This fish also had a low omnivory index as this is highly specialized in the food habit, feeding almost exclusively on fishes. This is in conjunction with the findings of Gamito and Erzini (2005) in a water reservoir of Ria Formosa. The mean TL of the commercial fishery is 2.21 (Table 3) as it targets mostly Nile Tilapia.

Acclimatization of stocked species has been observed in some African lakes such as Kariba (Karenge and Kolding, 1995), Navaisha (Muchiri et al., 1995; Moreau et al., 2001) as well as in other ecosystems in the world (Vitousek et al., 1997; Wilcove et al., 1998; Latini and Petrere, 2004). Environmental condition modifications have already been cited as a major factor in enhancing long-term success and dominance of exotics species in several ecosystems (Muchiri et al., 1995; Smith et al., 2000; Dudgeon et al., 2006). Nile Tilapia, most abundant in the commercial catch still remains at limited levels without major impacts on the indigenous major carps in Kelavarapalli reservoir. This fish did not negatively impact the other fish groups and has no detrimental effect on other groups. Similar results have been obtained in Lake Kivu where fish introductions showed no detrimental changes at both the biodiversity and ecological levels of the fish community (Marshall, 1995; Ogutu-Ohwayo et al., 1997; Villanueva et al., 2008). Similarly, Harvey and Kareiva (2005) reported that predation on *Oncorhynchus tshawytscha* and *Oncorhynchus mykiss* juveniles were affected very little by non-indigenous species reduction in a Columbia River reservoir. Every introduction likely has some influence on the host ecosystem, but most influences are thought to be benign, or their impacts are undetectable, especially at early stages of establishment. Initially the decline of haplochromine cichlid populations in Lake Victoria was attributed almost completely to predation by Nile perch. Later, it was discovered that increased eutrophication through pollution and over-exploitation may have also played a role in the decline of haplochromine cichlids (Pitcher and Hart, 1995).

In Kelavarappalli reservoir, these tilapias inhabit essentially the shallow waters (>10 m deep). The *O. niloticus*, however, is abundant in all zones of this reservoir as revealed by experimental fishing conducted by us in this reservoir. Spatial segregation limits competition for food and nursery sites similarly observed in Lakes Victoria and Kyoga (Twongo, 1995). *O. niloticus* and *Oreochromis macrochir* are both microphages which may explain the elevated prey–predator overlap. Resistance of *O. niloticus* may be mediated by its opportunistic behavior despite dietary overlap with Pearl spots. Dietary shifts of *O. niloticus* are similarly observed in Lake Victoria (Njiru et al., 2004). This, however, may not apply to other species of lower environmental tolerance in the reservoir. Low omnivory indices were observed for some groups, indicating a less diversified diet. This is not the case for the sub-littoral inhabiting cichlids which contribute to the efficient utilization of some resources, i.e. here the primary producers. Despite the low contribution of the detritus group, it is still utilized as a buffering agent in case of resource limitation. Similar observations were indicated by in Lake Navaisha (Muchiri et al., 1995; Mavuti et al., 1996) and in some West African lagoons (Villanueva et al., 2006).

According to Odum (1971), the ratio between primary production and total system respiration (PP/R) would decline to 1.0 as an ecosystem develops toward "maturity". A high ratio between production and respiration (7.78) is noted (Table 4) in this reservoir. Most likely, a limited quantity of organic matter is imported by inflowing rivers. An important part of the production of several groups is not utilized (EE is low) and is therefore lost as incorporated into the sediments on the bottom of the reservoir which has a deep anoxic hypolimnion. This might explain this unusually high value of the production/respiration value. Biomass accumulated as the system develops, thus lead to a lower ratio between primary production and biomass (PP/B). PP/B is, also much larger than those for most mature systems such as 10.52 in the Ria Formosa in south Portugal (Gamito and Erzini, 2005), 3.7 of the Broa reservoir (Angelini and Petrere, 1996), 0.239 of Caete Mangrove Estuary (Wolff et al., 2000) in Brazil, 16.24 of Wyra reservoir (Panikkar and Khan, 2008) and even larger than the immature ecosystem, Lake Taihu (11.60), the third largest Chinese lake (Song, 2004). Villanueva et al. (2008), reported a value of 52.22 in Lake Kivu which is lower than the Kelavarapalli reservoir (76.04). All these suggested that the Kelavarappalli reservoir ecosystem was still immature ecosystem and in a developing stage.

Results of mixed trophic impact routine illustrate the importance of lower trophic levels, particularly phytoplankton and detritus in the ecosystem suggesting the existence of 'bottom up' control in the ecosystem. These groups have the most pronounced positive impacts on other groups in the system, providing important food source for the latter groups and hence emphasizing the importance of detritus as the base of the food web in the reservoir. If the biomass of African Catfish (a predator for this particular model) increases the fish exerts a direct negative impact on its prey–indigenous catfishes, Pearl spots and Tilapiines, etc. However, it has a cascading positive impact on dipterans and zoobenthos which is the prey of indigenous catfishes, snakeheads and Mozambique Tilapia. If Mozambique Tilapia is more it exerts a positive impact on zooplankton. The impact of Nile Tilapia is positive, on major carps, macrophytes and phytoplankton. If zoobenthos increase its impact would be positive to indigenous catfishes. However, zooplankton has a negative effect on Nile Tilapia, Pearl spots and indigenous catfishes, not in fact due to direct prey–predator relationship, but may be due to the interaction between zoobenthos and African catfish. *Phytoplankton* has a positive impact on Nile Tilapia and Major carps. All the functional groups except detritus have a negative impact on themselves and this may show within group competition for resources (Christensen et al., 2000).

Given the vulnerability of inland water ecosystems to exotic fish invasions and the projected increases in human population growth, with associated needs for inland water ecological services, action needs to be taken now if we wish to maintain healthy reservoir ecosystems. Practical and sound management is required for sustainable and efficient use of this reservoir. Though the production is high in young ecosystem care should be taken not to exploit it indiscriminately in the name of food self-sufficiency programs.

Acknowledgements

We wish to thank Dr. K.K. Vass, Director, Central Inland Fisheries Research Institute for his support and Dr. V.V. Sugunan, Assistant Director General (Inland Fishery), Indian Council of Agricultural Research, New Delhi for his constant encouragement. We also acknowledge helpful comments from two anonymous referees which improved the manuscript.

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