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A preliminary snapshot of the trophic model and ecosystem attributes of Kaptai reservoir ecosystem, Bangladesh*

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Abstract A mass-balanced Ecopath model presents a quantitative description of the trophic structure, flow of energy and trophic interaction among ecological groups of an ecosystem. The Ecopath with Ecosim (EwE) modeling program (Version 6.5) was used to develop a preliminary trophic model for a tropical freshwater reservoir. The total fish biomass was 6.245 t/km^2 and the highest trophic level of the reservoir was 3.362 (for snakehead). The ecosystem is phytoplankton based because primary producers originated 68% and detritus originated 32% of the total flow from lower trophic level. The gross efficiency of the fishery was 0.004, suggesting the inefficiency of the system. The positive effect of phytoplankton and detritus on most of the other groups were evident from mixed trophic analysis while moderately higher ecotrophic efficiency (EE) of phytoplankton shows the ecosystem's potential bottom-up control. The competition for the same resources among different groups was also obvious. The ratio of primary production/respiration (1.969) suggests that the ecosystem is at the developing stage and utmost contemplation should be given to concerned human activities. The low value of relative ascendancy (30.13) and overhead (69.87) reveals the stability of the ecosystem and some degrees of maturity. It also predicts the presence of significant strength in reserve of the system to withstand or overcome any perturbation. However, ecologically sustainable resource management plans should be implemented to ensure the sustainability of this reservoir resources.

Keyword: Ecopath; Kaptai reservoir; trophic interaction; transfer efficiency; energy flow

1 INTRODUCTION

The management of exploited fish species requires an ecosystem-based approach for their future sustainability (Garcia and Cochrane, 2005). In recent years, it has been recognized that the ecosystem approach provides an important insight in supporting fish stock assessment and management strategies (Christensen and Pauly, 1993; Walters et al., 1997; Hilborn et al., 2003). The Ecosystem-Based Fishery Management (EBFM) method aims at maintaining the health of both the aquatic system and its fisheries (Pikitch et al., 2004). The maintenance of sustainable fisheries and a sound ecosystem has been at the forefront of ecosystem-based fisheries management (EBFM) (NRC, 1999; Hollingworth, 2000; Bodal, 2003), which considers both the inevitable impacts of an ecosystem and its existing fishery resources on each other through fishing. Factors such as interspecies interactions, climatic and environmental changes along with fishing that affect the sustainability could be integrated into this EBFM strategy (Browman and Stergiou, 2004). In an ecosystem, species interact through food webs (Pascual and Dunne, 2006). Therefore, trophic structures and biodynamic interrelations of living individuals play a role in maintaining the sustainability of an aquatic ecosystem. The transferred energy, as well as nutrients among

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functional groups, seems to be a matter of contention for grasping the functions and food network of an ecosystem (Odum, 1969; Gislason et al., 2000). Hence, knowledge of species interrelationships within an ecosystem, the structure of the ecosystem, and governing linkages of the system are a primary requirement for proper sustainable ecosystem management. Moreover, trophic network analysis can also be used to quantify the ecosystem health, integrity, and maturity (Christensen and Pauly, 1998), which provides better information for sustainable management.

The biodynamic trophic modeling approach Ecopath with Ecosim (EwE), a user-friendly ecosystem-based software model has been used universally for structural assessment and effects of fishing on the ecosystem (Christensen and Walters, 2004). It is designed for straightforward construction, parameterization, and analysis of mass balance trophic models of an ecosystem (Christensen et al., 2002). The Ecopath model can effectively integrate complex trophic interactions of an ecosystem (Christensen et al., 2008). This model also can determine the food web network of an ecosystem (Vidal and Pauly, 2004; Sandberg, 2007; Villanueva et al., 2008). Trophic links of fisheries resources in an ecosystem could be figured out with ease using this modeling approach (Christensen and Pauly, 1995). In addition, the inclusion of this steady-state trophic model in fisheries management policy (Zetina-Rejón et al., 2004; Tsehaye and Nagelkerke, 2008; Araújo et al., 2008) and its meaningful prediction about fishing effects on the ecosystem has set a remarkable benchmark for this model.

Since the very beginning of the Ecopath development, most studies on EBFM has been done with the marine ecosystem however it is also an important approach for freshwater. Inland fisheries are more susceptible to environmental changes (FAO, 2002). Besides, reservoirs are characterized as an "unstable ecosystem" because it changes its status from riverine condition to lacustrine. Eutrophication, changes in diet composition, increasing fishing pressure, and multiple uses of reservoir resources could be the potential reasons behind this instability. Angelini and Petrere (2000) stated that modeling of reservoirs might be more complicated as these resources are used by several stakeholders and mostly with contradictory needs.

Kaptai reservoir is one of the most important sources of capture fisheries of Bangladesh. Since this reservoir has a significant fishery potential, it has been overexploited and the situation has worsened by the motorization of boats and use of small-meshed nets in recent years. Recent study by Khatun et al. (2019) showed a remarkable declining trend in the productivity of high value-fishes. At this point, traditional approaches do not contend well with proper fisheries management protocols. In spite of the importance of Kaptai reservoir, detailed ecosystem studies significantly lack on the structural functioning of this system. To date, no attempt has been made to understand the population dynamics of this reservoir at ecosystem level through trophic interactions. The lack of study on ecosystem functioning unifying the required data has interrupted the assessment of ecosystem dynamic. Hence, an analysis was attempted to determine the existing functional integrity, trophic structure, and the trophodynamics using trophic interactions and quantifying the flow of energy. Thus, construction of a preliminary model would be helpful to identify the existing data gap and create a benchmark for future research directions.

2 METHOD

2.1 Study area

Kaptai reservoir, a man-made reservoir, is the largest synthetic freshwater reservoir resource of South-East Asia. It is located between 22°22′N and 23°18′N latitude, and 92°00′E and 92°26′E longitude (Fernando, 1980) (Fig.1). In 1961, this reservoir was constructed for hydro-electrical power generation damming the river Karnafuli. It receives nutrient-rich discharges from Karnafuli River and occupies an area of 688 km^2 encompassing an average depth of 9 m. The average temperature of this ecosystem is 27°C. Ahmed et al. (2001) reported that Kaptai fishery includes 74 freshwater fish species and 2 prawn species (Chakma, 2007) contributing about 6 000 mt annually in their study. Fisheries resources are exploited by artisanal fishers and they supply a major portion to the total fish production of Bangladesh. Multi species gears specially seine net, gill net, cast net, hooks and lines and Fish Aggregating Device (FAD) are used with mechanical and non-mechanical vessels to catch fishes here. The reservoir fish production is dominated mainly by carp (*Labeo rohita*, *L. gonius*, *L. bata*, *Catla catla*, *Cirrhinus cirrhosis*, *Cyprinus carpio*), tiliapia (*Oreochromis niloticus*, *O. mossumbicus*), *Anabas testudineus*, snakehead (*Channa striatus*, *C. punctatus*, *C. marulius*), catfish (*Sperata aor*, *S. seenghala*, *H. fossilis*, *Clarias*

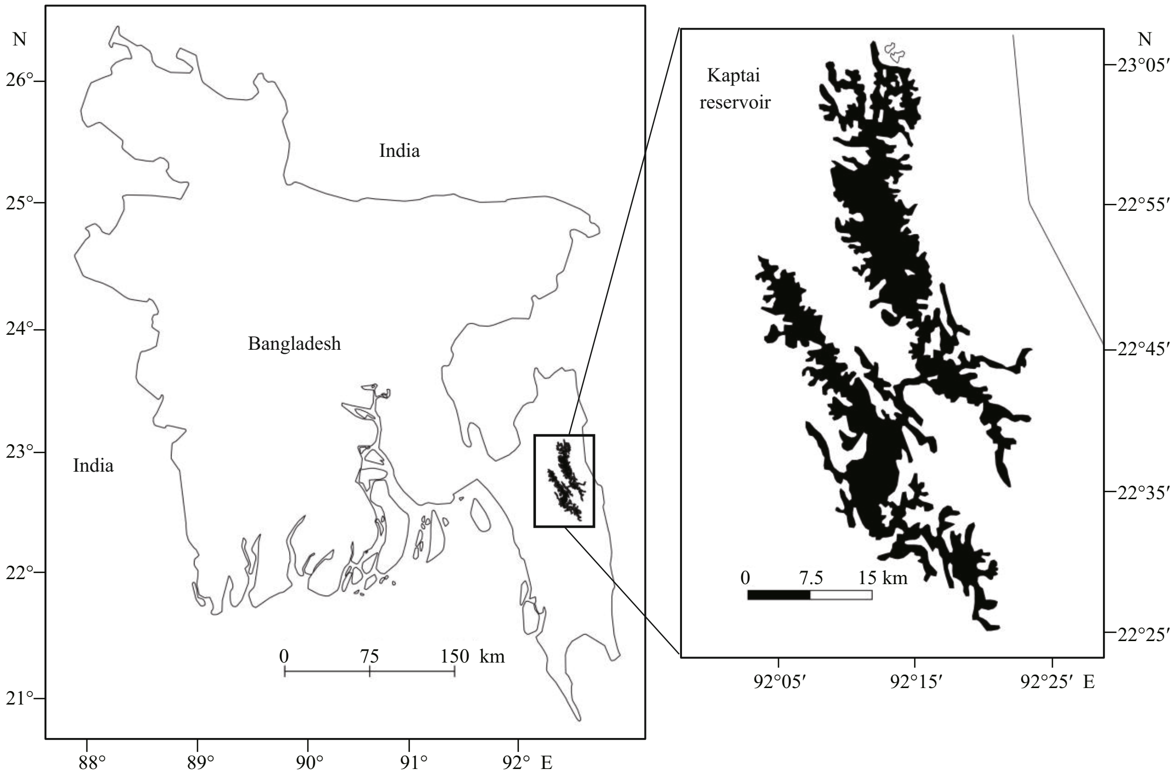

Fig.1 Geographical location of Kaptai reservoir

Solid black portion represents the study area.

batrachus), sheatfish (*Wallago attu*, *Ompok pabda*), clupeid (*Corica* spp., *Gudusia chapra*), minnows (*Puntius sarana*, *Amblypharyngodon mola*) and so on.

2.2 Modeling approach

Polovina (1984) first developed the Ecopath software for energy flow analysis between species or groups of species in an aquatic ecosystem. Primarily, the biomass estimates and food consumption relationships were the basis of this software. Later on, it went through several subsequent modifications (Christensen and Pauly, 1993; Pauly et al., 2000; Christensen et al., 2002) using some of the analytical methods of Ulanowicz (1986). Furthermore, the Ecopath model conceptualizes the ecological relationships among different groups at equilibrium state assuming the production of any given prey equal to the biomass consumed by predators plus the biomass caught plus any exports from the system:

$$B_i \times (P/B)_i \times \mathrm{EE}_i = Y_i + \Sigma(B_j) \times (Q/B)_j \times \mathrm{DC}_{ji} + \mathrm{EX}_i,$$

where B_i defines the biomass of prey group i; $(P/B)_i$ is the production/biomass ratio of group i; EE_i represents the ecotrophic efficiency; Y_i is its yield (fishery catch); B_j defines the biomass of predator group j; $(Q/B)_j$ is the food consumption per unit biomass of j; DC_{ji} is the fraction of i in the diet of j and EX_i is the export of i.

The energy balance of each component in the system is given by consumption (Q_i)=production (P_i)+respiration (R_i)+unassimilated food (U_i), which means the energy input and output of all living groups in the model must be balanced. The Ecopath model constructs a mass-balanced snapshot of an ecosystem presenting the interspecies interaction. Network analysis in EwE provides a linear food chain and predicts energy transfer efficiency at different trophic levels. Moreover, Ecopath also supports Odum's theory of ecosystem development (Odum, 1969) in terms of ecosystem state, maturity, efficiency, health and development. In our study, we used Ecopath with Ecosim suite version 6.5 (Christensen et al., 2008).

2.3 Model construction

2.3.1 Fishery catch data

The actual catches were based on landing statistics. Catch data provided by Bangladesh Fisheries Development Corporation (BFDC) and compiled by Fisheries Resource Survey System (FRSS) was considered for the functional groups. The annual catch of the considered functional groups/species for the year of 2016 is presented in Table 1.

Table 1 Population parameters of the representative species of different functional groups in Kaptai reservoir system along with their annual catch

Group/species	Annual catch	L_∞	K (/a)	M (/a)	F (/a)	Z (/a)	E	Reference
Carp	98.26							
Labeo rohita	8.160	93.28	0.920	1.220	1.310	2.53	0.500	Ahmed et al., 2005
Catla catla	8.160	94.30	0.959	0.629	2.600	3.23	0.805	Palaniswamy et al., 2011
Cirrhinus cirrhosus	16.42	71.00	0.845	0.627	1.470	2.1	0.701	Palaniswamy et al., 2011
Labeo calbasu	3.650	69.00	1.100	1.480	4.230	5.71	0.740	Haroon et al., 2001
Labeo bata	15.77	32.10	1.500	2.285	1.400	2.80	0.500	Azadi et al., 1996
Labeo gonius	43.76	53.00	0.890	1.390	1.390	2.78	0.500	Haroon et al., 2001
Cyprinus carpio	2.340	58.66	0.958	0.708	1.412	2.12	0.663	Palaniswamy et al., 2011
Catfish	426.0	53.00	0.280	0.450	0.450	0.90	0.500	Villanueva et al., 2006
Sheatfish	80.00							
Wallago attu	22.00	99.75	1.300	1.470	1.900	3.37	0.560	Thella et al., 2018
Ompok pabda	58.00	21.00	1.000	1.920	0.290	2.22	0.130	Gupta et al., 2015
Tilapia	159.77							
Oreochromis niloticus		55.59	0.390	0.800	0.590	1.39	0.420	Ahmed et al., 2003
Anabas testudineus	48.44	17.10	1.400	2.520	1.895	3.79	0.500	Mustafa and De Graaf, 2008
Knife fish	74.00							
Notopteurs notopterus		34.91	0.380	0.910	0.280	1.19	0.240	Mustafa et al., 2014
Snakehead	247.81							
Channa punctatus		24.00	0.900	2.160	1.565	3.13	0.500	Mustafa and Da Graaf, 2008
Minnow	550.70							
Puntius sarana	70.700	26.00	0.400	0.930	1.640	2.57	0.640	FishBase
Amblypharyngodon mola	480.00	10.46	0.950	1.220	2.040	3.26	0.630	Azadi and Mamun, 2009
Clupeid	5 285.0							
Corica soborna	2 558.0	5.700	2.620	5.110	3.400	8.51	0.400	FishBase
Gudusia chapra	2 727.0	19.40	1.230	2.450	4.180	6.63	0.630	Kumari et al., 2018

2.3.2 Functional group

Several important characteristics including population parameters, similarities in ecological habitat (water column/sediment), feeding habits (filter feeders, mixed feeders, predators), types of food (herbivorous, carnivorous, detrivorous, omnivorous), physiological behavior, taxonomy, distribution and maximum obtained body size (micro-, meso- and macro-) have been taken into account for plotting the functional groups. Fourteen functional groups were recorded considering their important roles in the ecosystem including nine fish groups (carp, catfish, sheatfish, tilapia, *Anabas testudineus*, knife fish, snakehead, minnow, and clupeid), one group of prawn, insects/larvae, zooplankton, phytoplankton, and detritus. Each group consists of one or more representative species as per their contribution to fisheries, similar biology, and accessibility of information. Although macrophytes act as the grazing ground for some minor carps and minnows as well but considering its low presence in diet and very minor ecotrophic efficiency (0.008) in the similar reservoir ecosystem in same geographical location (Panikkar et al., 2015) we excluded this group from out study. In addition, we used data from existing pieces of literature and FishBase (www.fishbase.org; Froese and Pauly, 2019) to adjust the information gaps whenever needed. However, data from local and regional origin was at first priority, while data from similar ecosystems were also adopted in the absence of local information.

2.3.3 Model parameter

2.3.3.1 Biomass (B)

Biomass (B) depicts the total mass of every functional group per unit area in the habitat area (expressed as t/km^2). We followed $B=Y/F$ (Gulland, 1971) to estimate biomass assuming equilibrium conditions, where Y is the annual average yield of each group and F is the fishing mortality coefficient. Exploitation rate ($E=F/Z$, here Z stands for total mortality) for heavily exploited fish and shrimp species often lies between 0.3 and 0.6 (Dinh et al., 2010) whereas 0.5 is considered as average exploitation rate meaning $F=(P/B)/2$. The population parameter, fishing mortality (F) for some species were absent in the existing literatures without which calculation of total mortality ($Z=F+M$) was impossible. In such cases, we followed Dinh et al. (2010) for the following functional groups: snakehead, catfish, *Labeo bata*, *Anabas testudineus*, and *Macrobrachium lamarrei* (Prawn).

2.3.3.2 Production/biomass ratio

The ratio of production over biomass (P/B) is assumed to be equal to total mortality (Z) following Pauly et al. (2000). Total mortality (Z)=fishing mortality (F)+natural mortality (M) for commercially harvested species. The Ecopath model considers steady-state for every ecotrophic group, where gross production ($P=Z\times B$) is balanced by total mortality (Z) so that the average biomass (B) remains constant. The empirical equation to determine Z for fish species was as follows (Beverton and Holt, 1993):

$$Z=K(L_\infty-L_{avg})/(L_{avg}-L_c),$$

where L_∞ defines the asymptotic length of fishes (in cm), K is the Von Bertalanffy Growth Function (VBGF) (/a) curvature parameter, L_{avg} is the average length (in cm) in the population, L_c represents the mean length at first capture into the fishery (cm). The length-converted catch curve routine of FiSAT package (Gayalino et al., 1996) was used to estimate Z values for all species. Pauly's empirical equation was used to estimate the natural mortality (/a) as follows (Pauly, 1984):

$$\ln(M)=-0.0152-0.279\ln(L_{inf})+0.6543\ln(k)+0.463\ln(T),$$

where, L_{inf} and K are VBGF parameters; and T (27°C) represents the mean water temperature of the ecosystem. The P/B (Z) values for same fish species were adopted either from same or similar system from the available literatures and Fishbase (Table 1).

2.3.3.3 Consumption (Q/B)

The parameter food consumption expresses the volume of ingested food by a certain functional group relative to its biomass in a definite period, where the consumption (Q) is the total production divided by the gross growth efficiency (GE). The empirical equations stated by Palomares and Pauly (1998) along with the user interface database of FishBase were used for each species to calculate the relative food consumption (Q/B) of every group.

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

where, W_∞ defines the asymptotic weight (g) obtained from a VBGF parameter L_∞ (Table 1) and length-weight relationships of the representative species. We used "a" and "b" values of length-weight relationship for each species from FishBase to calculate W_∞. T defines the mean annual habitat temperature (T= 1 000/(T_c+273.15)), in which T_c (27°C) is the average annual water surface temperature; A represents the aspect ratio which is calculated by $A=h^2/s$ equation where h defines the given height and s is the surface area of the caudal fin of fish. The aspect ratio (A) was taken from FishBase for each species of the functional groups; 'h' and 'd' are dummy variables expressing feeding type, for instances, h=1, d=0 for herbivores, h=0, d=1 for detrivores and h=0, d=0 for carnivore fishes. The average Q/B values of selected species were considered as the input Q/B for the functional groups.

2.3.3.4 Diet composition

Food interconnects different functional groups of an ecosystem. Therefore, it is an important prerequisite to know their diet composition to determine the dynamics of the ecosystem. Studies on diet composition of fishes are limited in the Kaptai reservoir (Mamun et al., 2004; Azadi and Mamun, 2009). In this regard, diet composition of study deficient species was taken from the available literatures (Khumar and Siddiqui, 1989; Islam et al., 2006; Weliange and Amarasinghe, 2007; Sarkar and Deepak, 2009; Mondal and Kaviraj, 2010; Srivastava et al., 2012; Roy et al., 2013; Gupta, 2015; Sakhare and Jetithor, 2016). Notably, studying the diet of same species from similar systems was our priority following study of similar species from similar systems. We calculated the average diet composition of fishes in every group as a single diet.

2.3.3.5 Ecotrophic efficiency

Ecotrophic efficiency (EE) defines the fractional production of every consumed group within the system that is transferred through the trophic web or exploited by the fishery. This value should be between 0 and 1. EE greater than 1 implies that the input parameters are not physically possible. According to Christensen and Pauly (1992), EEs could be set as 0.95 for heavily exploited groups. Since there is no measuring procedure or empirical relationship to determine EE, the Ecopath calculated it as output of the model (Christensen et al., 2000). In the absence of reliable biomass data, we used EE as 0.95 for some groups.

2.3.3.6 Other functional group

The zooplankton group includes copepods (such as *Diaptomus*, *Cyclops*, and nauplii), cladocerans (*Daphnia*, *Cheriodaphnia*, *Moina* etc.) and rotifers (*Keratella*, *Filinia*, *Brachionus*, *Asplanhna*). Due to the scarcity of data, zooplankton biomass was taken from a similar ecosystem (Traore et al., 2008). *P*/*B* and *Q*/*B* values were based on the study by Moreau and Villanueva (2002) wherever the diet composition was adopted from Lauzanne (1983). The phytoplankton groups consist of Chlorophyceae (*Spirogyra*, *Volvox*, *Coelastrum*, and so on), Myxophyceae notably *Microcystis*, Bacillariophyceae (*Navicula*, *Gyrosigm*a, *Fragilaria* etc.) and Dinophyceae such as *Ceratium* and *Peridinium*. Biomass' value of phytoplankton was adopted from Traore et al. (2008) and *P*/*B* ratio was used as 203 per year here. Aquatic insects and larvae has important role in the diet of some fishes especially for major and minor carps. Midges, Mayflies, Caddisflies, caddisworms, oligochaetes, insect larvae, bivalves and gastropods constitute this vital group. Biomass, *P*/*B* and *Q*/*B* for insects and larvae were adopted from Villanueva et al. (2006). We used 1 t/km^2 as detritus biomass following Traore et al. (2008) which was calculated by Pauly's empirical equation (Pauly et al., 1993).

2.4 Balancing of model

According to the Ecopath equation, each group must be balanced. It states that catches, consumption, biomass accumulation, and export cannot exceed production for a group. In Ecopath, the degree of energy 'imbalance' of each ecological group could be determined by its ecotrophic efficiency (EE). Therefore, the first step of balancing a model requires the adjustment of input parameters in a way that EE does not exceed 1. In steady-state condition, EE remains less than 1 which makes sense in a realistic model. It indicates that excess biomass may assemble in the ecosystem or be lost by other mortality. EE greater than 1 for any group indicates its demand is too high to be sustainable. In our initial model, EE was greater than 1 for some particular groups. As there was a negligible effect of diet adjustment on balancing therefore, we used EE as 0.95 for those heavily exploited groups. The original inputs were further validated by the consistency of production/consumption (*P*/*Q*) ratio that was between 0.1 and 0.3 supporting the balancing range. During balancing the model, we also checked the Production/Respiration (*P*/*R*) ratio, which was expected to be within the thermodynamic constraints limit (0 to 1). Trophic levels (TLs) are the output in the Ecopath model. The output accuracy of TL depends on the input diet matrix. We did cross check with FishBase with respect for trophic levels and found the range within our output. An estimated pedigree index was 0.533 for this model, which agrees with Christensen et al. (2002). Pedigree values for input data are 0 and 1 for non-locally and locally rooted data respectively.

3 RESULT

3.1 Basic model performance

The relative diet compositions are given in Table 2. The initial input for each of the 14 categorized functional groups along with the estimated output (bold) are shown in Table 3. The total fish biomass was 6.245 t/km^2. EE values for most of the fishes are between 0.744 and 0.982. Ecopath computed low value of EE (0.282) for knife fishes. The computed EE values for zooplankton (0.373) was lower than phytoplankton (0.671). A wide range of gross efficiency (0.052 to 0.348) of fish groups was observed.

3.2 Trophic structure and network analysis

The model output of the food web structure is illustrated in Fig.2. The model identified three trophic levels for Kaptai reservoir and a majority of the trophic flows are found to be occurring in these TLs (Fig.2). Top predators of this ecosystem are snakehead (TL=3.362), catfish (TL=3.266), sheatfish (TL=3.187), knife fish (TL=3.257). On the other hand, secondary consumers of the system are at trophic levels between 2.137 and 2.971. In Ecopath, network analysis epitomizes the complex food web into a simpler one known as "Lindeman spine". It calculates the flow of energy from one trophic level to

Table 2 Input diet matrix of the functional groups for the Ecopath model of Kaptai reservoir

Group No.	Prey/predator	1	2	3	4	5	6	7	8	9	10	11	12
1	Carp	–	0.065	–	–	–	–	–	–	–	–	–	–
2	Catfish	–	0.023	0.150	–	–	–	0.015	–	–	–	–	–
3	Sheatfish	–	0.009	–	–	–	–	0.07	–	–	–	–	–
4	Tilapia	–	0.025	–	–	–	–	–	–	–	–	–	–
5	*Anabas testudineus*	–	0.005	–	–	–	–	–	–	–	–	–	–
6	Knife fish	–	0.003	–	–	–	–	–	–	–	–	–	–
7	Snakehead	–	0.05	–	–	–	–	–	–	–	–	–	–
8	Minnow	–	0.17	0.340	–	0.110	0.100	0.228	–	–	–	–	–
9	Clupeid	–	0.25	0.100	–	0.200	0.200	0.310	–	–	–	–	–
10	Prawn	–	0.08	0.200	–	0.050	0.350	0.180	–	0.050	0.05	–	–
11	Insect/larvae	0.075	0.15	–	0.050	0.160	0.180	0.080	–	0.050	0.2	–	–
12	Zooplankton	0.055	0.07	–	0.246	0.260	0.090	0.060	0.130	0.425	0.2	0.125	0.05
13	Phytoplankton	0.520	0.05	0.080	0.700	0.110	0.050	0.025	0.850	0.375	0.1	0.305	0.8
14	Detritus	0.350	0.05	0.130	0.004	0.110	0.030	0.032	0.020	0.100	0.45	0.570	0.15
	Import	–	–	–	–	–	–	–	–	–	–	–	–
	Total	1	1	1	1	1	1	1	1	1	1	1	1

– indicates no input data was entered or no output value was determined by the software.

Table 3 Basic Ecopath parameters of Kaptai reservoir obtained after mass-balancing

Group No.	Group name	Trophic level	Biomass in habitat area (t/km^2)	P/B (/a)	Q/B (/a)	EE	P/Q	FD (t/(km^2·a))	OI
1	Carp	**2.143**	**0.212**	3.038	18.00	0.950	**0.169**	**0.796**	**0.137**
2	Catfish	**3.266**	1.375	0.900	5.250	**0.982**	**0.171**	**1.466**	**0.296**
3	Sheatfish	**3.187**	**0.141**	2.795	18.40	0.950	**0.152**	**0.539**	**0.508**
4	Tilapia	**2.316**	0.394	1.390	23.80	**0.753**	**0.058**	**3.417**	**0.237**
5	*Anabas testudineus*	**2.971**	0.037	3.790	10.90	**0.757**	**0.348**	**0.115**	**0.305**
6	Knife fish	**3.257**	0.384	1.190	9.800	**0.282**	**0.121**	**1.081**	**0.178**
7	Snakehead	**3.362**	**0.242**	3.130	11.40	0.950	**0.275**	**0.591**	**0.206**
8	Minnow	**2.137**	**1.430**	2.915	56.05	0.950	**0.052**	**28.26**	**0.125**
9	Clupeid	**2.580**	2.03	7.570	46.30	**0.744**	**0.163**	**36.83**	**0.313**
10	Prawn	**2.512**	**3.234**	3.160	12.64	0.950	**0.250**	**8.686**	**0.329**
11	Insects/larvae	**2.132**	**4.125**	4.000	30.00	0.950	**0.133**	**25.58**	**0.121**
12	Zooplankton	**2.053**	12.85	35.00	140.0	**0.373**	**0.250**	**642**	**0.053**
13	Phytoplankton	**1.000**	11.7	203.0	–	**0.671**	–	**781.3**	–
14	Detritus	**1.000**	1	–	–	**0.243**	–	–	–

Output data are presented in boldface. FD means flow to detritus; OI defines omnivory index. – indicates no input data was entered or no output value was determined by the software.

another and transfer efficiencies as well. Ecopath estimated primary production in Kaptai reservoir was around 2 375.3 t/(km^2·a) (Fig.3). Highest fish biomass and catch took place at TLII (Table 4). The system produced 2 312.3 t/(km^2·a) detritus of which the consumed amount was 372.1 t/(km^2·a). The highest trophic flow was 1 966.1 t/(km^2·a) from TL I to TL II. The estimated flow from TL2 to TL3 and TL3 to TL 4 was 100.9 t/(km^2·a) and 7.882 t/(km^2·a) respectively.

Table 4 Distribution of catch and fish biomass among different trophic levels

Trophic level	Catch (t/(km^2·a))	Biomass (t/km^2)
VII	0.000 2	0.000 3
VI	0.002 7	0.003 9
V	0.043 7	0.057
IV	0.539	0.711
III	4.789	4.455
II	4.785	21.23

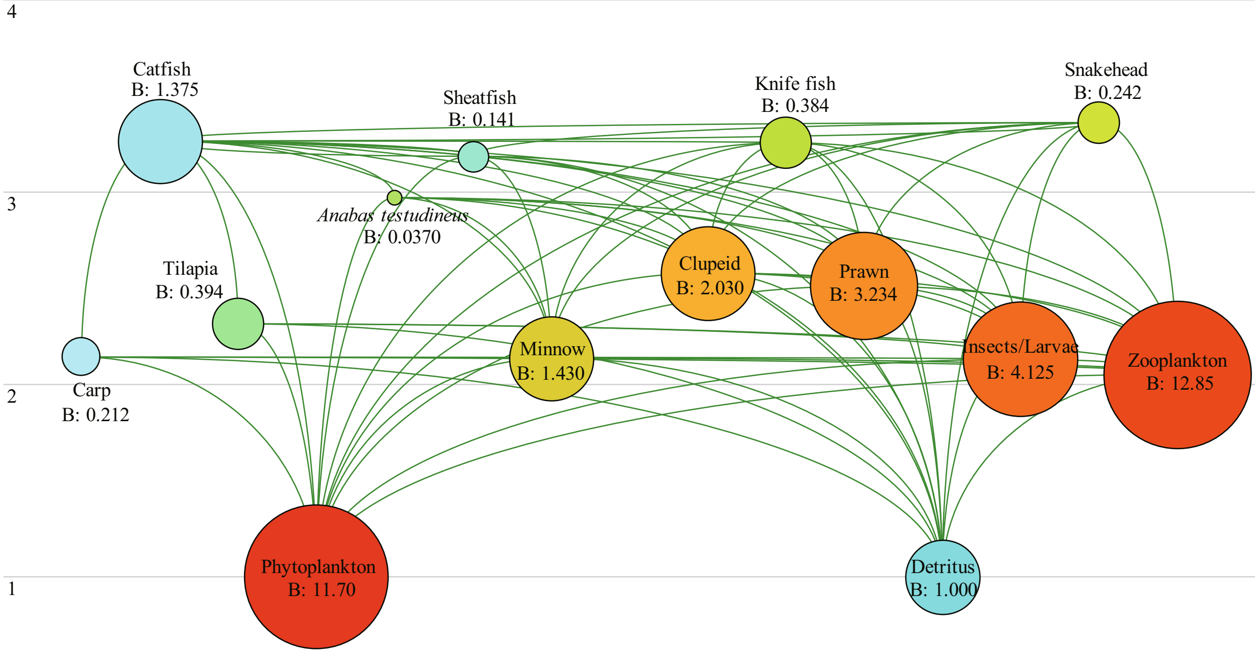

Fig.2 Food web structure of Kaptai reservoir showing relative biomass and flows between functional groups at different trophic levels

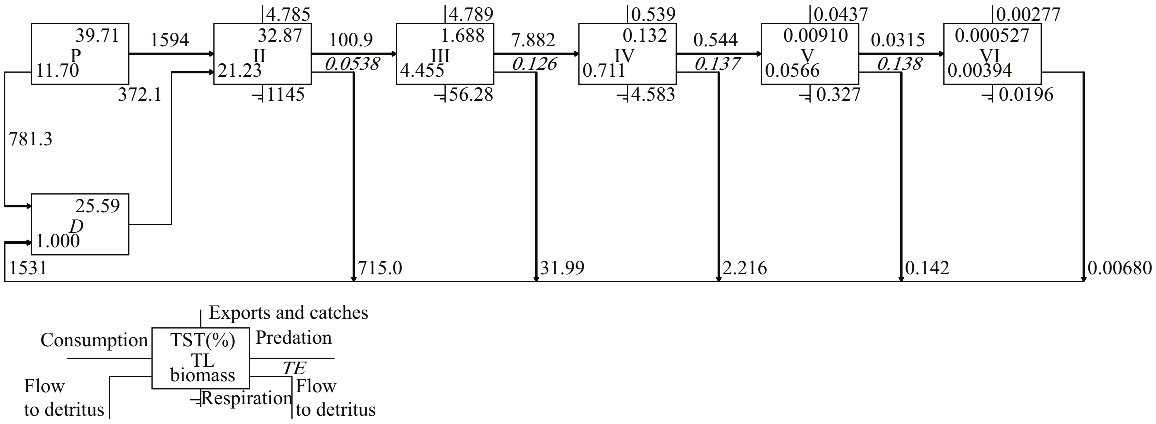

Fig.3 Simpler trophic model of Kaptai reservoir ecosystem representing discrete trophic levels

All flows are expressed as t/(km²·a), P defines primary production and *D* for detritus, both are at TLI.

The calculated mean transfer efficiency from TLII-TLIV was 9.752%, while primary production and detritus originated mean transfer efficiencies were 9.49% and 10.75% in orderly (Table 5).

The trophic network analysis shows that primary producers originated 68% and detritus originated 32% of the total flow from lower trophic level. Computed topmost flow to detritus (FD) in the system accounting for 781.3 t/(km²·a) (Table 3), was observed from the autotrophs, whereas zooplankton incorporated the maximal primary production into the food web. These features reveal the relative importance of riverine zoophagous fish in a newly impounded reservoir. The system omnivory index of Kaptai reservoir was higher (0.198) compared to some other reservoirs. Computed omnivory index for most of the groups is greater than 0.2 (Table 3). The values of respiration/assimilation (*R*/*A*) and production/respiration (*P*/*R*) for all groups were estimated as less than 1. This indicates the developing stage of the ecosystem supporting Odum (1969). The mean trophic level of the catch and gross efficiency (actual catch/primary production) were 2.619 and 0.004 (Table 6) respectively, indicating the predators as the extremely targeted groups in this system. Ecopath computed a few important indices of ecosystem maturity and stability (Table 6) supporting Odum's theory (Odum, 1969).

Table 5 Flows at trophic levels (in t/(km²·a)) and transfer efficiencies (in %) computed by Ecopath in Kaptai reservoir

Trophic level/flow	Predation	Export	Flow to detritus	Respiration	Throughput		
		Flows and biomasses from primary producers					
VII	0	0	0	0.001	0.002		
VI	0.002	0.002	0.005	0.015	0.024		
V	0.024	0.033	0.110	0.247	0.414		
IV	0.414	0.382	1.577	3.322	5.694		
III	5.694	3.581	24.10	42.10	75.48		
II	75.48	3.864	590.2	924.3	1594		
I	1594	0	781.3	0	2375		
Total	1675	7.862	1397	970.0	4051		
		Flows and biomasses from detritus					
VII	0	0	0	0	0		
VI	0	0.001	0.001	0.005	0.008		
V	0.008	0.011	0.032	0.079	0.130		
IV	0.130	0.157	0.639	1.262	2.188		
III	2.188	1.21	7.892	14.18	25.47		
II	25.47	0.921	124.8	220.9	372.1		
I	372.1	1158	0	0	1531		
Total	399.9	1161	133.4	236.4	1930		
Sources/TL	II	III	IV	V	VI	VII	VIII
Producers	4.978	12.29	13.97	13.67	16.20	16.38	
Detritus	7.092	13.33	13.13	14.35	16.10		
Combined	5.378	12.55	13.74	13.83	16.18	16.44	16.15

Total flow proportion from detritus: 0.32; transfer efficiencies (calculated as geometric mean for TLII-TLIV): 9.752%; from primary producers 9.49%; from detritus 10.75%.

Table 6 System statistics of Kaptai reservoir ecosystem

Parameter	Value	Unit	Parameter	Value	Unit
Sum of all consumption	2 167.709	t/(km²·a)	Total biomass/total throughput	0.006	/a
Sum of all exports	1 168.645	t/(km²·a)	Total biomass (excluding detritus)	38.154	t/km²
Sum of all respiratory flows	1 206.455	t/(km²·a)	Total catches	10.16	t/(km²·a)
Sum of all flows into detritus	1 530.586	t/(km²·a)	Connectance Index	0.414	
Total system throughput	6 073.396	t/(km²·a)	System Omnivory Index	0.198	
Sum of all production	2 875.284	t/(km²·a)	Ecopath pedigree index	0.533	
Mean trophic level of the catch	2.619		Measure of fit, t*	2.091	
Gross efficiency (catch/net p.p.)	0.004		Throughput cycled (including detritus)	348.1	t/(km²·a)
Calculated total net primary production	2 375.1	t/(km²·a)	Ascendency	30.13	
Primary production required for catch	699.0	t/(km²·a)	Overhead	69.87	
Total primary production/total respiration	1.969		Finn's cycling index	5.732	% of total throughput
Net system production	1 168.645	t/(km²·a)	Finn's mean path length	2.557	
Total primary production/total biomass	62.250		Loss in production index (L index)	0.145	

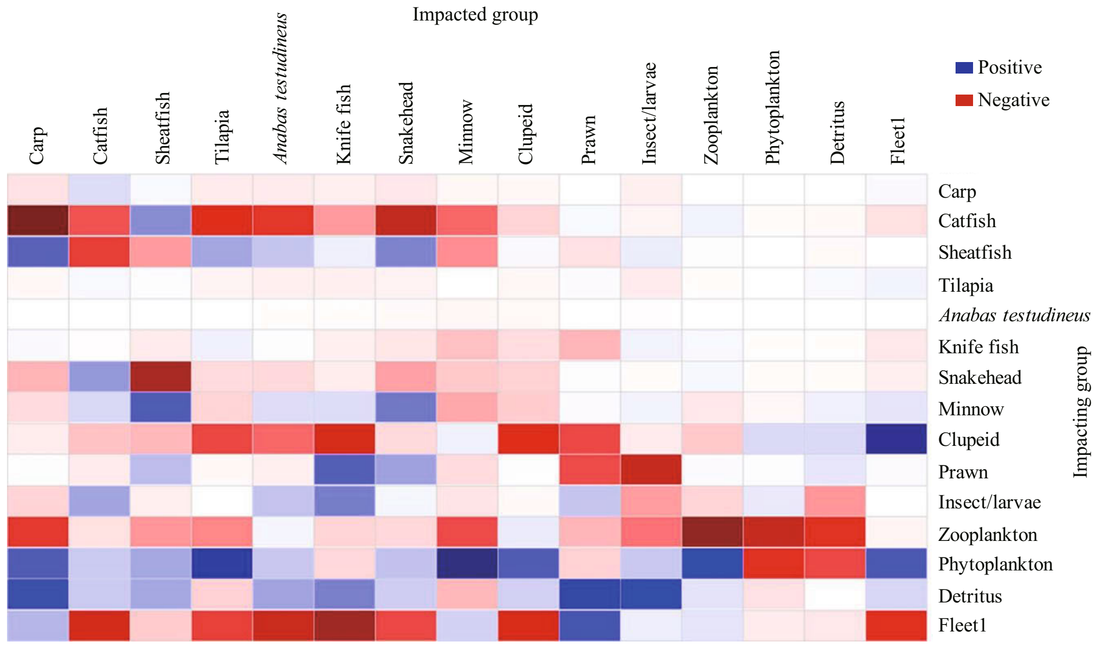

Fig.4 Mixed trophic impact analysis of Kaptai reservoir ecosystem

Blue bars represent a positive impact and red bars define a negative impact; strength of color represents the intensity of impacts.

3.3 MTI routine

The mixed trophic impact (MTI) routine assesses the relative impact of biomass change of one functional group over the other groups in the system. The prey affects predators positively, while predators negatively affect prey groups. In the Kaptai reservoir ecosystem, phytoplankton and detritus showed positive effect on other functional groups (Fig.4) and it was found to be greater for its direct predator zooplankton. Furthermore, phytoplankton had significant impacts on minnows, tilapia, and zooplankton in this system. Mixed trophic impact indicated that zooplankton had a significant negative effect on other groups while not on *Anabas testudineus*. A significant impact of detritus group was also obvious on insects and larvae, prawns, and carps. The positive impact of detritus on other groups pinpoints the importance of detritus in the Kaptai reservoir system. Most of the fish groups had a negative impact on themselves. The negative impact of most fish groups on themselves except detritus reveals their competitive nature for the same resources.

4 DISCUSSION

4.1 Model validation

Ecological analysis integrated in Ecopath outlines the state of an Ecosystem and provides a sketch of the existing resources and their interactions through feeding. The total fish biomass (6.245 t/km^2) of Kaptai reservoir was quite low compared to biomasses of Bakreswar reservoir (53.00 t/km^2) by Banerjee et al. (2016), Lake Ayame (8.02 t/km^2) by Traore et al. (2008); Ubolratana reservoir (6.56 t/km^2), Lake Nokoue (132 t/km^2), Ebrie lagoon (9.5 t/km^2), and Bagre reservoir (22.4 t/km^2) studied by Villanueva et al. (2006). On the contrary, the biomass was higher than the recorded biomass of Sri Lanka reservoir: 5.101 t/km^2 (Haputhantri et al., 2008), and Great Bear Lake: 0.89 t/km^2 (Janjua et al., 2015). The biomass of fish in the tropical freshwater Kaptai reservoir is similar to the finding by Christensen and Pauly (1998).

Ecotrophic efficiency is considered as the key evaluating feature of an ecosystem model (Christensen et al., 2000). EE varied considerably ranging from 0.282 to 0.982 in this study ecosystem, while it was more than 0.7 for most groups. A low EE of any group indicates that the group was not exploited either by predators or by fishers. Conversely, an EE close to 1 suggests that the group was highly exploited leaving no individual to die naturally. In an exploited system, most of the fish productions are assumed to be either predated or fished except top predators. The use of multispecies gears in Kaptai reservoir could be a possible reason for greater EE (>0.7) for top predators. In stark contrast, a low EE (0.282) for the top predator knife fish was also realistic as discussed by Christensen et al., 2000. It also suggests that this group had no significant predators in the system. A particularly low value of EE 0.282 was computed for knife fishes resembling a general feature for giant top predators (Christensen et al., 2000). Lower EE for zooplankton compared to phytoplankton might be due to the inadequacy of enough zooplankton eating fish species in the system and thus a major portion of zooplankton remains as residual. Greater EE value for phytoplankton (0.671) was observed in this reservoir system. This may be due to their highest presence in the diet of the lower trophic level fish groups. The estimated EE value (<1) for phytoplankton and detritus agrees with the observation of Christensen and Pauly (1992). The moderately higher EE of primary producer shows the ecosystem's potential bottom-up control (Traore et al., 2008). Furthermore, an EE less than 1 for detritus indicates that more flow was entering into the detritus group than was leaving. The estimated EE value for detritus (0.243) signifies the resource not to be highly exploited. Hypothetically, it supports that the reservoir food web significantly depends on primary producers. It also depicts that the food web was mainly based on primary producers. The computed moderate EE value for detritus could apparently be associated with the inadequacy of typical primary consumers excluding zooplankton. Bagre reservoir has shown a similarity with our result (Villanueva et al., 2006).

In this study, noticeable differences have been found between the primarily estimated and Ecopath computed relative biomass. Different types of traditional gears with different catchabilities are used in this system. Therefore, some species may be under-exploited and some others may be over-caught. Another possible reason contributing to this difference may be the use of catch data to estimate biomass in Ecopath. It means that the greater the catch, the greater the biomass estimates. The production/consumption (*P*/*Q*) is considered as one of the diagnostic features of balancing model, which ranges from 0.05 to 0.3. The present study supports this notion. A low *P*/*Q* ratio computed for tilapia (0.058) and minnows (0.052) suggests their preference for low quality diet, which is mainly composed of Phytoplankton and detritus. This result also agrees with the result of Tilapia from Lake Ayame (Traore et al., 2008). Additionally, the high value of gross efficiency (*P*/*Q*) in some functional groups shows their piscivorous feeding nature.

4.2 Trophic flow

The estimated trophic levels were 1.0 for primary producer and detritus and 3.362 for the top predator (Snakehead). The highest trophic level suggests that Kaptai ecosystem has a relatively longer trophic chain like Lake Ayame (Traore et al., 2008), Bagre reservoir (Villanueva et al., 2006) and Lake Awassa (Fetahi and Mengistou, 2007). The Ecopath usually determines trophic levels higher than 4 (Ulanowicz, 1995). In our study, the trophic aggregation routine determined seven trophic levels aggregating 14 functional groups, which suggests the possible cannibalistic nature of fishes at the upper trophic levels (Table 5). The trophic chain of this reservoir system is based on primary producers and TLII favors most transfer of flow to the upper trophic level. Thus, the governing characteristics of primary producers' abundance over primary consumers that constitute the prey of the highest trophic level support fisheries (Pauly and Christensen, 1995). This sustains the importance of catch, biomass, and ecological production of functional groups at trophic level III along with their influential role for the lake fish production.

The mean transfer efficiency of Kaptai reservoir was comparatively higher (9.752%) than other reservoirs. Excessive utilization (by predation or fishing) of most fish groups might be the cause of high trophic transfer efficiency. Greater flows from detritus (10.75%) than flows from phytoplankton (9.49%) reveal the importance of detrital food chain in this system (Table 5). Furthermore, zooplankton was the major source of flow to detritus next to phytoplankton (Table 3). The low transfer efficiencies for trophic level II (5.378%) might be attributed by the shortage of predators and comparatively higher flow of respiration for the throughput (Table 5). On the contrary, the transfer efficiencies for higher trophic level (>II) were high as the fishery exports were high and fish groups with high EE values dominated those trophic levels. However, the average transfer efficiency of Kaptai reservoir was greater compared to Lake Nakuru (Moreau et al., 2001), Ria Formosa reservoir (Gamito and Erzini, 2005) and Psasak Jolasid reservoir (Thapanand et al., 2007) while it was lower than Lake Ayame (Traore et al., 2008), and Bagre reservoir (Villanueva et al., 2006). The high transfer efficiency in Kaptai reservoir supports the presence of a high diversity of predators in this ecosystem. It is noteworthy to mention that the significance of biodiversity assures the stability of an ecosystem (Naeem and Li, 1997; Loreau et al., 2001). The Kaptai reservoir is a phytoplankton based system as primary producers originated 68% and detritus originated 32% of the total flow from lower trophic level. Recently impounded reservoirs and deep waterbodies retain this remarkable feature (Kapetsky and Petr, 1984; Talling and Lemoalle, 1998).

4.3 Mixed trophic impact

The positive effects of primary producers on other biological groups in the Kaptai system are supported by the finding of Kapetsky and Petr (1984), and Talling and Lamoalle (1998) for the recently impounded reservoir. A significant negative effect of zooplankton on themselves was observed indicating the presence of a huge portion of carnivore zooplankton in the system (Fig.4). Moreover, the life history of some zooplankton such as copepods reveal their herbivorous feeding habit at the juvenile stage while they show omnivorous or carnivorous feeding nature during adult stages (Turner, 1984). The presence of smaller proportion herbivorous of zooplankton was evident by their negative effect on phytoplankton. However, detritus had no effect (positive/negative) on itself in this system. Similar finding were previously reported by Christensen and Pauly (1993) and Fetahi and Mengistou (2007). The MTI routine demonstrates that the functional groups of lower trophic levels dominated the feeding dynamics of Kaptai reservoir system. The direct and indirect negative impact of the biomass of a given group was observed on its prey. Furthermore, negative impact of most of the groups on themselves reveals their competitive nature for same resources. The negative impact of fleet one on most of the groups indicates the possible high fishing pressure. Therefore, increasing fishing activity may have further negative effect on higher predators.

4.4 Ecosystem indices and attributes

Ecopath provides important features regarding the maturity and stability of an ecosystem. Some of the theoretical attributes (Odum, 1969) related to the ecosystem's development and maturity have been incorporated in Ecopath models to describe the ecosystem's maturity, stability, and health (Christensen, 1995). The structure of resource biomass shows Kaptai reservoir as a low trophic level driven ecosystem. Total system throughput (TST) represents the sum of all flows within an ecosystem and thus shows the size of the entire system in terms of flow. TST estimated for Kaptai reservoir system was 6 073.396 t/(km^2·a), which is similar to the studies of Darwall et al. (2010). Reversely, it was lower than studies of Fetahi and Mengistou (2007) in Lake Awassa. In Kaptai system, consumptions dominated the TST (36%) followed by flow into detritus (25%) of the total energy flows. The computed low mean trophic level of the fishery (2.619) was due to the absence of specialized top predators. Relatively short food chain may also contribute in this regard. It suggests that the fishermen targeted fishes from higher trophic level. The mean trophic level of the catch is higher than that of Lake Awassa (Fetahi and Mengistou, 2007), and Bagre reservoir (Villanueva et al., 2006). On the other hand, the trophic level of the fishery is lower than Lake Ayame (Traore et al., 2008). The result showed "immaturity" in accordance with the result of Pauly et al., 1998 as this fishery exploits upper tropic levels. The overexploitation of some fishes are already evident (Ahmed et al., 2003, 2005; Khatun et al., 2019 and so on). The gross efficiency (actual catch/primary production) of the fishery of Kaptai reservoir accounts for 0.004, which indicates the inefficiency of the system. Based on the present study, Kaptai reservoir had greater gross efficiency compared to Lake Awassa (Fetahi and Mengistou, 2007), Lake Ilhema and Lake Naivasha (Mavuti et al., 1996) and Lake Ayame (Traore et al., 2008). Conversely, it was lower than those of Lake Victoria (Villanueva and Moreau, 2002) and Lake George (Moreau et al., 1993). Moreover, about 2 375.1 t/(km^2·a) primary production was calculated to sustain the system. Low gross efficiency of the system may be due to the moderate extent of EE values for phytoplankton and lower EE of detritus in Kaptai reservoir.

In accordance with Christensen and Pauly (1992), the linear equation of Ecopath supports Odum's theory of ecosystem maturity (Odum, 1969). Many important ecosystem indices in Ecopath seem to be the indicator of ecosystem's state. The ratio of system primary production to respiration (P_p/R) is one of the principal attributes, which explains system maturity. In the early stage of ecosystem development, primary production exceeds the respiration resulting P_p/R greater than 1. However, with maturity P_p/R ratio decreases until primary production and respiration gets equality and thus approaches 1. The ratio tends to be lower than 1 in a system suffering from pollution or exploitation. Ecosystem maturity decreases if manmade causes and natural disorders disturb the ecosystem. The P_p/R ratio was greater than 1 in Kaptai reservoir (1.969) meaning this system as a developing or young ecosystem when it was much lower than other reservoir such as Ravishankar Sagar (10.36), Ria Formosa (10.52) etc. (Gamito and Erzini, 2005; Panikkar et al., 2015). The P_p/R ratio of Kaptai reservoir is higher than that of Lake Hayq (1.05) and Tonle Sap Lake (1.23), yet comparable to Bakreswar reservoir (1.72) and Lake Gehu (1.76) (Fetahi et al., 2011; Jia et al., 2012; Banarjee et al., 2016; Chea et al., 2016). This result recommends paying proper attention to human actions in the reservoir system including overexploitation of fishes, water pollution, water diversion, etc. as developing ecosystems are sensitive to such ecological disorders. It also predicts if the reservoir is provided a healthy environment then it could gain maturity with time as P_p/R ratio is notably different from 1. Net system production (total primary production-total respiration) is large in immature system while it is close to zero in mature systems. Ecopath estimated net system production for Kaptai reservoir (1 168.645 t/(km^2·a)) also indicates the developing nature of this system. Primary production/total biomass (P_p/B) is another important index of ecosystem maturity. Production exceeds respiration in immature system causing the biomass accumulation over time, which consequently may influence P_p/B ratio. The computed P_p/B ratio for the Kaptai model was 62.25, which reconfirmed the developing feature of the ecosystem discussed earlier. With maturity, P_p/B decreases. The index total system biomass/total system throughput (B/TST) is directly proportional to system maturity. This ratio tends to be low in developing ecosystems while it increases with the maturity and stability of the system (Christensen and Walters, 2004). The Kaptai reservoir had comparatively lower B/TST (0.006) than Ravishankar Sagar reservoir (0.008), Bakreswar reservoir (0.05) Lake Awassa (0.016), and Great Bear Lake (0.07) (Fetahi and Mengistou, 2007; Janjua et al., 2015; Panikkar et al., 2015; Banerjee et al., 2016) while it was greater than Lake Superior (0.004) (Kitchell et al., 2000). Notably, the Indian reservoir Kelavarapalli has the exact B/TST ration (0.006) like Kaptai reservoir (Khan and Panikkar, 2009). The low value of B/TST shows the requirement of high-energy flow comparatively to support the ecosystem biomass. The inverse of P/B ratio of a group represents its size (Christensen and Pauly, 1993). Thus, in ecosystem level, the ratio between total biomass and total production can be used to predict the average size of the system organisms. However, total low biomass excluding detritus might be attributed due to the total low catches of Kaptai reservoir (Table 6).

"Finn's Cycling Index" (FCI) expresses the fraction of an ecosystem's total system throughput that is recycled which was named after Finn (1976). This index was intended to measure maturity, resilience, and stability (Christensen, 1995; Vasconcellos et al., 1997). Detritus had a very important role in all cycles of Kaptai reservoir, where the throughput cycled including detritus was 348.1 t/(km^2·a). Mature ecosystems recycle a greater extent of throughput compared to developing ecosystems and thus they have greater FCIs. Ecosystems with a high capacity to recycle detritus can recover from any external perturbation modulating the ecosystem stable (Vasconcellos et al., 1997). However, the FCI value (5.732%) for Kaptai reservoir was markedly lower than Bakreswar reservoir, Tonle Sap Lake, Lake Gehu, Great Bear Lake while it was higher than the Ravishankar Sagar reservoir, Lake Superior and Lake Chauhu (Kitchell et al., 2000; Jia et al., 2012; Janjua et al., 2015; Panikkar et al., 2015; Banerjee et al., 2016; Chea et al., 2016; Kong et al., 2016). Again, this finding supports our previous statement that Kaptai reservoir is a developing system. The values of ascendancy and overhead have been found to be associated with the ecosystem stability, maturity, eutrophication and human perturbations as well (Aoki, 1995; Christensen, 1995; Ulanowicz, 1997; Nielsen and Ulanowicz, 2000). The relative ascendancy (ascendancy/capacity) is negatively correlated with ecosystem maturity (Christensen, 1995). Ecosystem health can be evaluated using the value of ascendancy (Christensen, 1995; Brando et al., 2004). Low ascendancy value of Kaptai reservoir (30.13) with high overhead value (69.87) showed good stability and an extent of ecosystem maturity. This stability could be due to the greater biodiversity of Kaptai reservoir (Castillo et al., 2000). The lower relative ascendancy value of Kaptai system compared to Lake Gehu, Great Bear Lake, and Lake Superior showed greater maturity and stability among these ecosystems. Overhead indicates the stored energy of an ecosystem to endure disturbances (Christensen, 1995). It can measure ecosystem stability (Christensen, 1995) which reflects the system's potentiality to increase its ascendancy when meet unexpected disturbances. The high overhead showed that Kaptai reservoir had significant strength in reserve to

Table 7 Required primary production in Kaptai reservoir ecosystem to sustain fisheries catches

Group name	TL	PPR	PPR/catch	PPR/Tot.PP (%)	PPR/u.catch
Carp	2.143	2.291	16.02	0.06	0.004
Catfish	3.266	159.4	257.4	4.08	0.066
Sheatfish	3.187	47.15	406.5	1.21	0.104
Tilapia	2.316	16.13	69.54	0.41	0.018
Anabas testudineus	2.971	4.65	66.46	0.12	0.017
Knife fish	3.257	25.28	236.2	0.65	0.060
Snakehead	3.362	84.65	235.1	2.17	0.060
Minnow	2.137	33.78	42.22	0.86	0.011
Clupeid	2.580	324.9	42.31	8.32	0.011
Prawn	2.512	0.79	23.94	0.02	0.006
Total	2.619	699.0	68.80	17.90	0.018

overcome external disturbances to come back quickly to its initial condition. In contrast, Bakreswar reservoir and Lake Ayame has greater maturity than Kaptai ecosystem in accordance with the value of relative ascendancy and overhead. The observed Finn's mean path length (FMPL) (2.557) indicates that detrital pathway cycled a limited portion of matter. MPL was greater in Bakreswar reservoir, Ravishankar Sagar reservoir and Great Bear Lake whereas it was lower in Lake Superior compared to Kaptai reservoir system.

The relative total flow from detritus in the Kaptai reservoir was important because of the significant decomposition of organic matters. The importance of detritus as an alternative diet in the food chain of Kaptai ecosystem was evident by its high connectance index (0.414). The decomposition of plant materials improves the nutritive quality of detritus. Furthermore, the higher connectance index (0.414) for Kaptai reservoir over the theoretical value (0.317) supports the diversified diets of some functional groups and certain level of maturity as well (Christensen and Pauly, 1993). High omnivory index (0.198) shows that the diet of several organisms is diversified with greater adaptation to environmental changes. Connectance index along with the omnivory index shows that both the specialized and generalized ecological groups exist in the reservoir in terms of diet. Group diversification supports ecosystem to be stable. Therefore, excessive harvest of fishes influences the diet composition, which may affect the reservoir maturity. Moreover, trophic flexibility of functional groups confers greater possibilities of adaptation. Kaptai reservoir has several fish species, which can adapt to potential environmental changes. Tilapia is recognized worldwide as an example of highly adapted fish in Kaptai reservoir.

Primary Production Required (PPR) is defined as the required energy to support consumption or catches in the ecosystem. It is an important indicator of ecosystem efficiency. The required PPR to support the fish resources in Kaptai reservoir (29.43%) was high when compared with an average value documented for tropical lakes and rivers (23.6%) by Christensen (1995). Primary production required in Kaptai reservoir to sustain fisheries is shown in Table 7. The high utilization of food resources could be the reason behind it. The computed high EE values for most groups also support it. Furthermore, primary production required to sustain fisheries % PPR (PPR as a part of total PP) paired with Trophic Level of Catch (TLc) quantify the effect of fisheries on the ecosystem (Tudela et al., 2005); it is because of the sensitivity of the ecosystem to fisheries depends on both of them. The total primary production required sustaining catches in Kaptai reservoir was 699 t/km^2, of which clupeid, catfish and prawn required 324.9 t/km^2, 159.4 t/km^2, and 0.79 t/km^2 respectively (Table 7). The average fish catch in the system during the modeling period required 17.9% of the available primary productivity (%PPR) while the mean trophic level of fish catch (TLc) was 2.619. Result shows that the fishery was overexploited as per the ecosystem-based pairing of a % PPR-TLc framework (Tudela et al., 2005). Loss in production index (*L* index) is an indicator developed by Libralato et al. (2008) to support the ecosystem-based fisheries management evaluating the fisheries sustainability. *L* index considers both ecosystem properties (primary production and transfer efficiency) and features of fishing activities (TLc and PPR). Ecopath computed *L* index for Kaptai reservoir was 0.145 showing this system as an overfished ecosystem as per the observation of Libralato et al. (2008).

4.5 Model resemblance

In addition, the Kaptai reservoir model is compared with other lake and reservoir ecosystem models in order to know the functioning features of this study reservoir (Table 8). The total throughput of Kaptai reservoir was greater than that of Lake Superior and Great Bear Lake while it was lower than Lake Kariba. Again, similar total system throughput was observed as Lake Malawi and Victoria. According to the ecosystem theory, ecosystems of early developmental stage should have the highest total throughput and

Table 8 Comparison of Kaptai reservoir model with other ecosystem' models

Ecosystem	TST	Catch/P_P	P_P/R	P_P/B	B/T	Net sys prod	Mean TL of catch	OI	Ascendency(%)	Cycling index (%)	Path length
Kaptai[a]	6 073.396	0.004	1.969	62.250	0.006	1 168.645	2.619	0.198	30.13	5.732	2.557
Malawi[b]	6 184	0.000 546	1.588	66.0	0.006	950	2.94	0.148	–	–	–
Kariba[c]	17 475	0.000 487	8.609	45.7	0.017	6.6	2.97	0.129	–	–	–
Victoria[d]	4 947	0.001 751	1.553	22.2	0.017	672	2.99	0.189	–	–	–
Great Bear[e]	118.86	0.000 08	1.44	4.79	0.070	12.26	3.55	0.09	33.02	10.58	2.96
Superior[f]	3 547.7	–	1.60	127.54	0.004	–	–	0.09	50.4	0.39	2.23
Awassa[g, *]	18 217	0.001 44	5.834	28.672	0.016	6 808.069	2.57	–	–	–	–
Ayame[h]	–	0.002 755	–	–	–	–	2.94	0.193	26.40	–	–
Bakreswar[i]	4 435.965	–	1.721 31	9.733 3	0.050	908.222 7	–	0.109	25	8.44	3.08
Ravishankar[j]	38 903	–	10.36	80.33	0.005	15 325.01	–	0.162	46.8	1.99	2.294

* Flows for Lake Awassa are in kg/(m^2·a). a: present study; b: Darwall et al., 2010; c: Machena et al., 1993; d: Moreau and Villanueva, 2002; e: Janjua et al., 2015; f: Kitchell et al., 2000; g: Fetahi and Mengistou, 2007; h: Traore et al., 2008; i: Banerjee et al., 2016; j: Panikkar et al., 2015. – indicates no input data was entered or no output value was determined by the software.

P_p/R is expected to be greater than 1 there. Estimated ratio of P_p/R close to 1.0 for Lake Malawi, Victoria and Great Bear Lake shows comparatively more maturity than other ecosystems. The omnivory index of the Kaptai reservoir could be compared with those of Lake Ayame, which suggests their similar complex trophic interactions. Unlike the Lake Superior ecosystem, the computed ascendency values for the Kaptai reservoir system have not reached its full developmental capacity. The Finn's cycling index reports that the recycling capacity of the system throughput in Kaptai reservoir is higher than Lake Superior but lower than the Great Bear Lake ecosystem. In brief, the mean trophic level of catch (2.619) of this model indicates the predators as target fish. Khatun et al. (2019) reported earlier that harvest of *Labeo calbasu* (carp) in Kaptai reservoir is at risk for further sustainability. However, our finding strongly states to lower the harvest rate in Kaptai reservoir in order to attain a sustainable fishery ecosystem.

5 CONCLUSION

A mass-balanced Ecopath model presents a perceptible description of the trophic structure, energy flow, and interaction through food web among the functional groups of an ecosystem. The Ecopath model of Kaptai reservoir details the fish biomass, rate of consumption, production, trophic structure, and trophic relationships highlighting the observable dynamics of the system. The mean trophic level of catch predicts that top predators are highly targeted species here. Study reports that Kaptai reservoir is an overexploited, developing yet stable ecosystem, which could gradually approach to maturity if it does not get disturbed. This model may function as baseline for the future study to assess the unexpected environmental alterations and identify the effects of excessive fishing activities. Scarcity of relevant data and uncertainties in input parameters especially for lower trophic level could be some feasible limitations of this model. Introducing new model with fresh and reliable data could be a potential improvement to assess the effects of climate change. As synthetic ecosystems usually lack of stability during their developing periods due to potential modification in fishing activities and water quality, environmental issues should be prime concern. Today's better application of management policies and optimal use of resources will sustain tomorrow's ecosystems and economies.

6 DATA AVAILABILITY STATEMENT

All data generated and/or analyzed during this study as well as the data sources are included in this article.

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