

Food web structure and trophic interactions of the tropical highland lake Hayq, Ethiopia

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ABSTRACT

We generated a mass-balance model to figure out the food web structure and trophic interactions of the major functional groups of the Ethiopian highland Lake Hayq. Moreover, the study lay down a baseline data for future ecosystem-based investigations and management activities. Extensive data collection has been taken place between October 2007 and May 2009. Ecotrophic efficiency (*EE*) of several functional groups including phytoplankton (0.8) and detritus (0.85) was high indicating the utilization of the groups within the system. However, the *EE* of *Mesocyclops* (0.03) and *Thermocyclops* (0.30) was very low implying these resources were rather a 'sink' in the trophic hierarchy. Flows based on aggregated trophic level *sensu* Lindeman revealed the importance of both phytoplankton and detritus to higher trophic levels. The computed average transfer efficiency of 11.5% for the first four trophic levels was within the range for highly efficient African lakes. The primary production to respiration (*P/R*) ratio (1.05) of Lake Hayq indicates the maturity of the ecosystem. We also modeled the food-web by excluding *Tilapia* and reduced phytoplankton biomass to get insight into the mass balance before *Tilapia* was introduced. The analysis resulted in a lower system omnivory index (*SOI*=0.016) and a reduced *P/R* ratio (0.13) that described the lake as immature ecosystem, suggesting the introduction of *Tilapia* might have contributed to the maturity of the lake. *Tilapia* in Lake Hayq filled an ecological empty niche of pelagic planktivores, and contributed for the better transfer efficiency observed from primary production to fish yield.

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1. Introduction

Food webs provide a framework for integrating population dynamics, community structure and ecosystems processes (Kaunzinger and Morin, 1998), and are a central idea in ecology (Wilbur, 1997). Predator–prey interactions provide a means to examine the species' roles in ecological processes, and to understand community and ecosystem functioning (Thapanand et al., 2009). Furthermore, food-web structure also affects primary production through its influence on grazing (Carpenter et al., 1998). For instance, in a three trophic-level food chain, predators can reduce herbivore zooplankton indirectly benefiting the primary producer phytoplankton, which partly explains the variation that otherwise would remain unexplained by the effect of nutrient input experiments (Carpenter et al., 1985; Carpenter and Kitchell, 1993; Bronmark and Hansson, 2005). Moreover, it gives a clue whether the basal trophic groups such as phytoplankton are ade-

quate to sustain the whole ecosystem through estimates of primary production required (Christensen et al., 2005). Experiments and modeling approaches are two ways to study structure and function of an ecosystem, the former being more informative in a whole-lake experiment (Carpenter and Kitchell, 1992). Ecosystem-level experiments, however, are few due to methodological problems, large economic costs and time requirements (Wetzel and Likens, 1991). Among the different hypothesis, trophic cascades are typically strong in aquatic ecosystems particularly in whole-lake experiments (Carpenter and Kitchell, 1992). Nevertheless, trophic interactions in aquatic ecosystems are much more complex and dynamical than thought before (Paine, 1980; Wetzel and Likens, 1991). In biomanipulation research, for example, juvenile predator fish, which are expected to be piscivore, are zooplanktivore and are able to reverse the effect of biomanipulation (Hansson et al., 1998). An alternative to experimental approaches is ecosystem modeling that can be used to describe pathways of organic matter, to predict ecosystem responses of perturbations and to identify higher-level properties of the ecosystem that are not readily measurable, such as the goal functions (Muller and Leupelt, 1998). We used the modeling software Ecopath, which offers a network analysis and provides insights into the structure and dynamics of aquatic ecosystems

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(Wulff and Ulanowicz, 1989; Christensen et al., 2005). In Ecopath, the trophic levels are represented both as fractions (Christensen et al., 2005) and as integers *sensu* Lindeman (1942) offering more opportunity to describe the trophic interactions. Ecopath has been used to address trophic interactions and flows on both freshwater and marine environments (Christensen and Pauly, 1993; Mavuti et al., 1996; Christensen et al., 2005; Thapanand et al., 2009). The structure of food webs has important implications for ecosystem stability (De Ruiter et al., 1995; McCann et al., 1998), biogeochemical cycling (Berg et al., 2001), and fishery harvest (Ryther, 1969). Furthermore, food-web interactions may play a key role for understanding the effects of climate change on lakes (Straile, 2005). For instance, the impact of global warming on the food web structure of Lake Tanganyika has been demonstrated accompanied with fishery reduction (O'Reilly et al., 2003; Verburg et al., 2003; Verschuren, 2003). Nonetheless, though ecological management based on food web studies is common practice in temperate lakes, it is generally meager in tropical-African water bodies.

In Ethiopia, food web studies are an emerging field of interest (Fetahi and Mengistou, 2007). Food web studies will increase the optimum utilization of the inland water bodies by pointing out mis-utilization and/or overexploited resources in an ecosystem context. The present study focuses on Lake Hayq, which is located in the highlands of Ethiopia. The lake provides different purposes for the local inhabitants: fishing, drinking water and source of income via tourism. The lake switched to a eutrophic status some 25 years ago, caused most probably by the introduction of planktivorous Tilapia fish (Kebede et al., 1992; Fetahi et al., submitted for publication-a) but the stocking effect was not addressed until now. It is a deep lake having functional groups at different trophic levels, and thus amenable to trophic analysis even though it has never been attempted before. We applied the software ecological tool Ecopath with Ecosim (EwE version 5.0 beta; Christensen et al., 2005) to describe the trophic structures, their linkage and mass balance flows of Lake Hayq. The paper also attempts to explain the trophic interactions before and after Tilapia introduction in the ecosystem.

2. Materials and methods

2.1. Study site

Lake Hayq (11°15'N, 39°57'E; Fig. 1) is located some 440 km north of Addis Ababa, the capital of Ethiopia, at an altitude of 2030 m a.s.l. (Baxter and Golobitsch, 1970). The study area is categorized as sub-humid tropical with an annual rainfall of 1173 mm and a mean air temperature of 18.2 °C (National Meteorological Service Agency). The lake has a surface area of 23.2 km², a maximum depth of 88 m and a mean depth of 37.37 m (Baxter and Golobitsch, 1970). Previously, Lake Hayq was connected to the nearby Lake Hardibo (11°14'N, 39°46'E; altitude 2150 m a.s.l.) through Ankwarka River. However, at present these lakes are terminal and there is no known surface outlet due to the irrigation scheme upstream. Lake Hayq is a deep, steeply shelving lake, with a maximum depth of 88 m recorded in 1938 (Baxter and Golobitsch, 1970). The lake is fresh water, with a salinity of 0.83 g L⁻¹ (Zinabu et al., 2002) and has never been saline (Lamb et al., 2007). Predominant cations and anions are magnesium and carbonate/ bicarbonate, respectively (Fetahi et al., submitted for publication-a).

Fishes that inhabit Lake Hayq are *Oreochromis niloticus* Linnaeus (Nile Tilapia), *Clarias garapienus* Burchell (African catfish), *Cyprinus carpio* Linnaeus (common carp) and *Garra dembecha* Getahun and Stiassny. The latter two species were introduced in Lake Hardibo most likely in 1980 and eventually reached Lake Hayq due to the connecting river (Tizazu, personal communication). Tilapia was



Fig. 1. The map of Lake Hayq together with sampling stations (dots: SS – Shore Station and OS – Open Station) (redrawn from Demlie et al., 2007).

also introduced in 1978 (Kebede et al., 1992) putting catfish as the only indigenous fish species (Baxter and Golobitsch, 1970). Phytoplankton biomass is dominated by the diatoms in particular by *Fragilaria*, *Navicula* and *Synedra*, and several green algae (Fetahi et al., submitted for publication-a). The dominant zooplankton species are *Mesocyclops aequatorialis* Van de Velde, *Thermocyclops ethiopianus* Kiefer, *Ceriodaphnia reticulata* Jurine, *Daphnia magna* Straus, *Diaphanosoma excisum* Sars and rotifers (Fetahi et al., submitted for publication-b). The benthos in the littoral, sublittoral and profundal is dominated by mollusks (Assefa, 2010).

2.2. Ecopath with Ecosim model

A mass-balanced model was constructed using EwE software (Christensen et al., 2005; freely available at www.ecopath.org); basic input parameters were mostly obtained from studies done since October 2007. Growth parameters like asymptotic length (L_{inf}), asymptotic weight (W_{inf}) and other parameters are presented in Table 1. The model comprised of 15 functional groups including detritus, bacteria and fish-eating birds so as to assess a holistic picture of the lake. The model comprises a set of simultaneous linear equations, one for each group under consideration, and assumes a mass balance where the production of the group is equal to the sum of all predation, non-predatory losses and export integrated in the

Table 1

Fish asymptotic length (L_{inf}), weight (W_{inf}), mean temperature (T) and the von Bertalanffy growth function (K). A aspect ratio, h a dummy variable expressing food type (1 for herbivores, and 0 for detritivores and carnivores), d a dummy variable also expressing food type (1 for detritivores and 0 for herbivores and carnivores).

Growth parameters	Tilapia	Catfish	Carp	Garra
L_{inf} (cm) ^a	42	66	55	15.4
W_{inf} (g) ^a	1440	1947	2500	44
T (°C) ^a	22	22	22	22
K (y ⁻¹) ^a	0.4	0.18	0.13	1.5
A ^b	1.8	1.5	2.8	1.4
h	1 ^c	0 ^d	1 ^c	1 ^d
d	0	0	0	0

^a The present study.

^b Fetahi and Mengistou (2007).

^c Worie (2009).

^d Alemayehu (2009).

Table 2
Conversion factors and formula used to derive input parameters.

Items	Conversion factor/formula	References
Phytoplankton	Carbon to chlorophyll a 40:1 ratio Wet weight (WW) = 10 × carbon	Jones (1979)
Zooplankton	WW = 5 × dry weight	Hall et al. (1976) and Burgis (1974)
Zooplankton	$\log(P/B) = -0.73 - 0.23 \times \log(w)$; CF = 1.12, where P/B is production to biomass ratio per day, w is body mass (mg dry weight), and CF is a correction factor for the back-transformation from logarithmic units.	Kuns and Sprules (2000)
Detritus (D , g C m ⁻²)	$\log D = 0.954 \times \log PP + 0.863 \times \log E - 2.41$; where PP – primary production; E – euphotic depth (m)	Christensen and Pauly (1993)
Ciliate	WW = dry weight/0.59	
Bacteria	Carbon weight = 0.5 × dry weight WW = dry weight/0.4	Bratbak and Dundas (1984)
Consumption/biomass ratio	$\log(Q/B) = 7.964 - 0.204 \log W_{inf} - 1.965T + 0.083A + 0.532h + 0.398d$; where Q/B is consumption to biomass ratio; W_{inf} is the asymptotic weight (g); T an expression for the mean annual temperature of the water body, expressed using $T = 1000/K$ ($K = ^\circ C + 273.15$); A aspect ratio ($Ar = h^2/s$ —of the caudal fin of fish, given height (h) and surface area (s); h a dummy variable expressing food type (1 for herbivores, and 0 for detritivores and carnivores) and; d a dummy variable also expressing food type (1 for detritivores and 0 for herbivores and carnivores).	Palomares and Pauly (1998)

master equation of Ecopath (Christensen et al., 2005)

$$B_i \times \left(\frac{P}{B_i} \right) \times EE_i = Y_i + \sum B_j \times \left(\frac{Q}{B_j} \right) \times DC_{ij} \quad (1)$$

where B_i = the biomass of prey group i ; P/B_i = production/biomass ratio of group i ; EE_i = ecotrophic efficiency, i.e. the fraction of production consumed within the system by predation or fishing exploitation; Y_i = its yield (=fishery catch); B_j = the biomass of predator group j , the consumer of i ; Q/B_j = the food consumption per unit biomass of j ; and DC_{ij} = the fraction of i in the diet of j . Each compartment requires estimates of B , P/B , Q/B , DC and EE . However, one out of the parameters B , P/B , Q/B , EE can remain unknown for each functional group as it can be estimated by the model. Input data were standardized, B as wet weight (t km⁻²) and P/B and Q/B as annual rates. EE has no unit and is usually estimated by the model.

Gross primary production (mean = 162.42 mg O₂ m⁻³ h⁻¹) and biomass (as Chlorophyll a = Chl a , 13 mg m⁻³) were measured from October 2007 to October 2008 on a monthly basis (Fetahi et al., submitted for publication-a) and the values were converted into wet weight (Table 2). The biomass of detritus was calculated using the empirical formula given in Table 2, which is a function of primary production (PP, g C m⁻² y⁻¹) and euphotic layer depth (E , in meter), obtained from Fetahi et al. (submitted for publication-a). Five major functional zooplankton groups were considered in the model: *Mesocyclops*, *Thermocyclops*, Nauplii, cladocerans and rotifers. Zooplankton abundance and biomass was determined weekly to biweekly from October 2007 to January 2009 (Fetahi et al., submitted for publication-b). To determine numerical abundance, samples were vertically hauled from 10 m to the surface at both stations with a 30 μ m mesh tow net. The samples were immediately preserved with sugar-formalin to a final concentration of approximately 4%. The concentrated original sample of 250 mL was mixed homogeneously and a 25 mL subsample was taken with a wide mouth pipette (Wetzel and Likens, 1991), then poured into a gridded glass chamber, settled overnight and counted. Zooplankton biomass was measured on a dry weight basis for Lake Hayq and then converted into wet weight (Table 2). Zooplankton production to biomass ratio (P/B) was calculated after Kuns and Sprules (2000) (Table 2). Diet composition for zooplankton groups was obtained from literature (Dussart and Defaye, 2001; Benzie, 2005; Mengistou, 1989). Bacteria biomass was calculated assuming a cell volume of 0.04 μ m³ and a density of 1, and ciliate biomass with an average dry weight of 0.04 μ g (Wetzel and Likens, 1991); conversion factors to wet weight are given in Table 2.

The abundance value was obtained from Fetahi et al. (submitted for publication-a,b) and Kebede et al. (1992), respectively. Production/consumption (P/Q) ratio of 0.3 was used to estimate food consumption per unit of biomass (Q/B). Zoobenthos biomass was calculated based on abundances values (Assefa, 2010) and their weight are adopted from Fetahi (2005) for Lake Awasa, Ethiopia. P/B and Q/B ratios of zoobenthos for Lake Hayq were computed using Ecoempire (which is an interactive routine included in EwE containing several empirical relationships to facilitate parameterization) for benthic invertebrate populations (Christensen et al., 2005). Each fish species that inhabit the lake was considered as a functional group: Tilapia, Catfish, Carp and Garra. Catch statistics collected at 4 landing sites 3 times per week for 7 months were used for the model (Tables 2 and 3). Furthermore, catch data from Amhara Regional Agricultural Research Institute (ARARI) were also included. Length-frequency data were analyzed using the ELEFAN procedure available in FiSAT II to estimate asymptotic length (L_{inf}), weight (W_{inf}) and the von Bertalanffy growth function (K). Total mortality (Z), under the condition assumed for the construction of mass-balance models, equals to production over biomass ratio (P/B) (Allen, 1971; Christensen et al., 2005) and Z was estimated from length-converted catch curves using FiSAT II software (Gayaniilo et al., 2002). Natural mortality (M) for unexploited fish species (catfish, Carp and Garra) was estimated using FiSAT II software and considered as P/B since they do not suffer from fishing mortality. Annual stock biomass (B) was estimated using length-structured virtual population analysis (VPA), and yield Y was estimated assuming equilibrium conditions: $Y = B \times F$, where F is the fishing mortality coefficient. Food consumption per unit of biomass (Q/B) was calculated using the multiple regression formula of Palomares and Pauly (1998) (Table 2). Diet composition for *O. niloticus* was obtained from Worie (2009) that analyzed 326 gut content sampled between August 2008 and March 2009. The feeding habits of *G. dembecha* ($n = 580$) and *Clarias gariepinus* ($n = 121$) were studied between January 2009 and June 2009 (Alemayehu, 2009). Diet matrix of common Carp was obtained from Workiye Worie sampled between January 2009 and June 2009 (personal communication).

Fish-eating birds in Lake Hayq include Great Cormorants, White Pelicans, Sacred Ibis and the scavenger Marabou Stork (Mengistu Wondafraash, personal communication). As no data regarding actual abundance, biomass, consumption and mortality are available; we adopted data of Moreau et al. (1993) for Lake George, Uganda since the birds are assumed to be similar to Lake Hayq. Tilapia fish was introduced in the late 1970s (Kebede et al., 1992) and we have

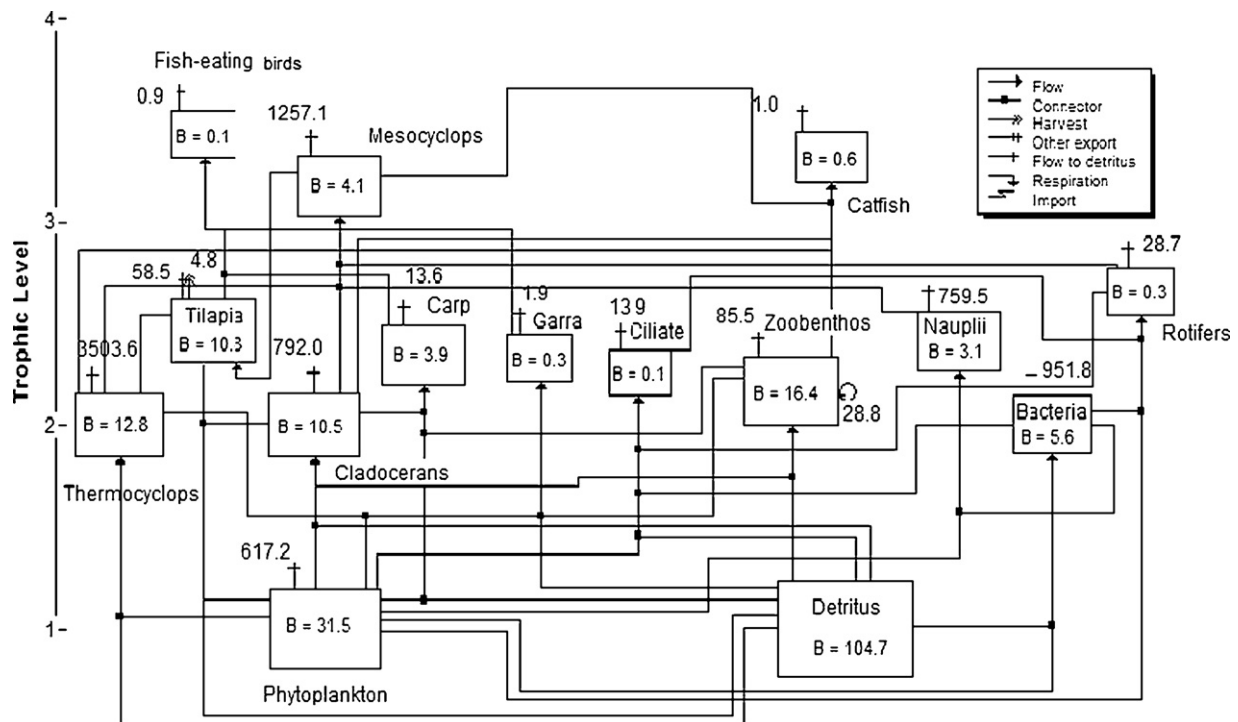


Fig. 2. Flow diagram showing trophic flows in Lake Hayq, Ethiopia. Flows are expressed in $\text{t km}^{-2} \text{y}^{-1}$.

attempted to assess the impact of the fish on the lake ecosystem by analyzing before and after stocking.

The model was balanced by checking the values of EE and gross efficiency of food conversion (GE), a fraction between 0–1 and 0.1–0.3, respectively, and input data (B , P/B , and particularly DC since it is the most uncertain parameter), were modified until we obtained acceptable runs (Christensen et al., 2005). The pedigrees were coded to quantify the uncertainty associated with input data (Pauly et al., 2000) and to validate the overall quality of the model (Thapanand et al., 2009; Villanueva et al., 2006). Trophic levels (TL) are outputs of Ecopath; TL = 1 (first TL) by definition is assigned to primary producers and detritus; for consumers TL are estimated as $1 +$ (the weighted average of the TLs of the preys in the stomach content of the predators). The estimated flows were aggregated into integer trophic levels that yield a simplified representation of the food web called Lindeman Spine. Such aggregation provides useful insights on flow transfers (Baird and Ulanowicz, 1989) and allows for estimating the transfer efficiency (TE) as the ratio between productions at two consecutive integer trophic levels ($TE = PTL/PTL.1$) (Lindeman, 1942). In the present work, a modified Lindeman Spine was used to demonstrate the contribution of detritus-based and grazing food chains separately. The Modified Lindeman Spine uses the outputs of Ecopath in terms of estimated flows by integer trophic level (called “trophic level decomposition”). EwE provides a mixed trophic impact routine that quantifies all direct and indirect trophic effects by summing the negative and positive impacts for each group (Christensen et al., 2005). In ecological succession, a system will have some indices of maturity (Christensen et al., 2005): total primary production to total respiration (P/R) is an important ratio for description of the maturity of an ecosystem (Odum, 1971) and the ratio should approach 1 in matured ecosystem. Total primary production to total biomass (P/B) is also a function of maturity: in immature systems production exceeds respiration and the biomass could accumulate over time that results the ratio to be less than 1. System Omnivory Index (SOI) is defined as the average Omnivory Index of all consumers weighted by the logarithm of each consumer’s food intake. It is a measure of how the feeding

interactions are distributed between trophic levels. Finn’s Cycling Index (FSC) is a fraction of an ecosystem’s throughput that is recycled and quantifies one of Odum’s (1969) 24 properties of system maturity (Christensen, 1995). The ratio of fishery catch to Primary Production (catch/PP) is computed as the sum of all realized fisheries catches relative to the total primary production (Christensen et al., 2005).

3. Results

The basic input values accompanied with computed parameters estimated by EwE (in bracket) for Lake Hayq is given in Table 3, and the diet matrix presented in Table 4. Flows and biomass for the balanced lake ecosystem along with fractionated trophic levels are shown in Fig. 2. Most functional groups were between TL2 and TL3 since they feed on first trophic levels. The highest TL (>3) was estimated for fish-eating birds, catfish and Mesocyclops, which are carnivore (Table 4). The mean TL of catches is 2.46, which corresponds well to TL of Tilapia and also shows a strong trophic link of Tilapia with plankton. Biomass and flows were aggregated into integer trophic levels *sensu* Lindeman (Fig. 3) using the modified Lindeman Spine, which indicated the importance of both phytoplankton and detritus in the food web of the lake. Furthermore, the modified Lindeman Spine demonstrated that flows at lower TLs in the grazing food chain (from I to II = $8868 \text{ t km}^{-2} \text{y}^{-1}$ and from II to III = $1765 \text{ t km}^{-2} \text{y}^{-1}$) are slightly larger than to the detritus food chain (8110 and $1419 \text{ t km}^{-2} \text{y}^{-1}$, respectively). Total fish biomass of Lake Hayq is about 15.16 t km^{-2} and its yield was $4.8 \text{ t km}^{-2} \text{y}^{-1}$, basically caught from Tilapia.

Ecotrophic efficiency (EE) is the fraction of production consumed within the system and ranges between 0 and 1, where 1 indicates total exploitation in a system. EE of both phytoplankton (0.8) and detritus (0.85) were high (Table 3). However, the EE values estimated for Mesocyclops (0.03) and Thermocyclops (0.30) were very low because these groups were mildly consumed by their predator, i.e. catfish. EE were high for catfish, Garra and common

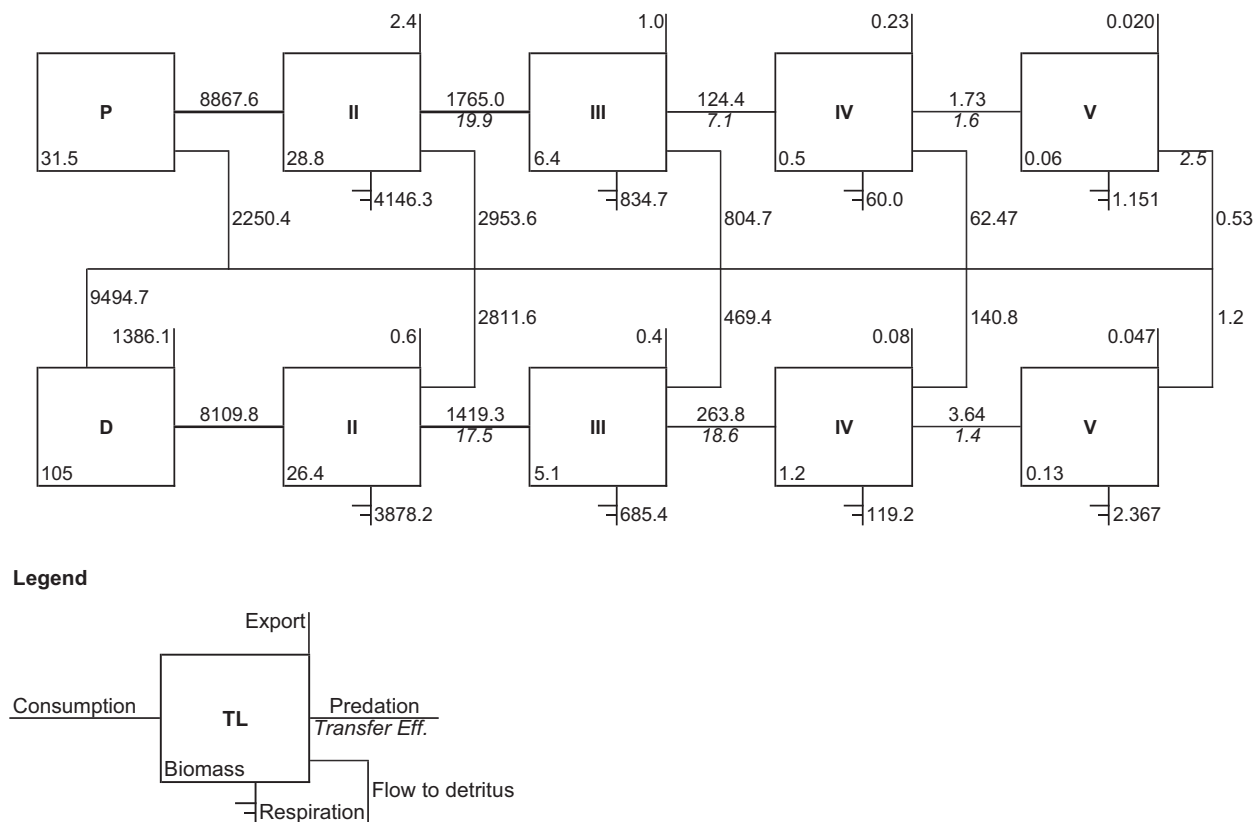


Fig. 3. Biomasses, flows, transfer efficiencies are aggregated into integer trophic levels (TL) in the form of Lindeman spine. P stands for primary producers, D for detritus and TE for trophic efficiencies.

Carp even if they were not currently well-exploited in the commercial fishery, which could be related to the assumption of biomass accumulation of 0.3. However, *EE* for Tilapia fish was relatively low (~ 0.67), and it was calculated zero for fish-eating birds, because it is the top predator in the system.

The result of MTI exhibits both positive and negative effects among each other's (Figs. 4 and 5). Only phytoplankton and detritus have positive impact on most other functional groups, whereas other compartments show direct predator-prey interactions, cascading effects or competition. For instance, Tilapia has a negative effect on Carp and *Garra* which can be seen as a result of competition since the larger portion ($>34\%$) of each of their diet comes from

phytoplankton. The positive impact of *Mesocyclops* on ciliate has a cascading nature, because *Mesocyclops* is consuming rotifers, which otherwise would feed on ciliates. The impact of catfish and ciliates on any other group is negligible, which could be due to their small biomasses—the former being estimated by EwE. Fishery has relatively strong negative impacts to fish-eating birds and Tilapia: the first indicates the result of competition for same resource and the latter indicates the direct impact of this important fishery in the region. Among the negative effects (top-down), fish-eating birds, *Thermocyclops* and rotifers have strong impact from an ecosystem perspective, whereas bottom-up effects are mainly exerted, as expected, by detritus and phytoplankton (Fig. 5).

Table 3

Input parameters and estimated by Ecopath (shown in bracket) for trophic modeling of Lake Hayq, Ethiopia.

Species/group	TL	Yield ($\text{t km}^{-2} \text{y}^{-1}$)	Biomass (t km^{-2})	P/B (y^{-1})	Q/B (y^{-1})	Q ($\text{t km}^{-2} \text{y}^{-1}$)	<i>EE</i>	<i>GE</i>
Water birds ^a	3.43		0.089	0.25	58.00	5.16	0.000	0.04
Catfish	3.32		(0.624)	0.42	5.69	3.55	0.763	0.074
Tilapia	2.46	4.8	12 (10.800)	1.20	21.82	235.66	0.666	0.055
Common Carp	2.34		(3.940)	0.36	20.26	79.82	0.900	0.018
<i>Garra</i>	2.33		(0.280)	2.68 ^b	41.19	11.53	0.856	0.065
Zoobenthos	2.17		16.425 ^d	3.24	36.60	601.16	0.900	0.089
<i>Mesocyclops</i>	3.18		4.092	180.00	506.67	2073.29	0.027	0.355
<i>Thermocyclops</i>	2.00		12.761	200.00	506.67	6465.62	0.272	0.395
Cladocerans	2.00		10.520	76.00	253.33	2665.03	0.808	0.300
Nauplii	2.41		3.067	306.00	972.75	2983.42	0.900	0.315
Rotifers	2.66		0.278	155.00 ^c	516.67	143.63	0.811	0.300
Ciliate	2.26		0.149	200.00	516.00	76.88	0.900	0.388
Bacteria	2.00		5.615	280.00	(933.33)	5240.65	0.819	0.300
Phytoplankton	1.00		26 (31.46)	353.40			0.798	
Detritus	1.00		104.7				0.854	

^a Moreau et al. (1993).

^b Fetahi and Mengistou (2007).

^c Talling and Lemoalle (1998).

^d Assefa (2010).

Table 4
Feeding matrix for Lake Hayq ecosystem, Ethiopia.

Preys		Predators												
		1	2	3	4	5	6	7	8	9	10	11	12	13
1	Fish-eating birds													
2	Catfish ^a													
3	Tilapia ^b	0.73												
4	Carp ^c	0.21												
5	Garra ^a	0.06												
6	Zoobenthos		0.08		0.26	0.17	0.08							
7	Mesocyclops		0.26	0.09										
8	Thermocyclops		0.30	0.09		0.13		0.23						
9	Cladocerans		0.36	0.20	0.09		0.10	0.18						
10	Nauplii							0.29						
11	Rotifers							0.30						
12	Ciliates											0.36		0.04
13	Bacteria										0.41	0.33	0.24	
14	Phytoplankton			0.50	0.36	0.60			0.49	0.8	0.59	0.31	0.11	0.3
15	Detritus			0.13	0.29	0.10	0.82		0.51	0.2			0.61	0.7

^a Alemayehu (2009).

^b Worie (2009).

^c Worie (personal communication).

Table 5 presents the summary statistics and network flow indices. *P/R* approaches unity in matured ecosystem as energy fixed tends to be balanced by the energy cost of maintenance (Odum, 1969), and 1.05 was estimated for Lake Hayq. Finn's cycling index (FCI; Finn, 1976), 15% of total throughput obtained for Lake Hayq, expresses the percentage of the total throughput that is actually

recycled and is a measure of maturity (Odum, 1969; Christensen and Pauly, 1993). Ecopath ran by excluding Tilapia and with lower Chl-a concentration (2 mg m^{-3}) to reconstruct the food web of Lake Hayq before the introduction of Tilapia (Baxter and Golobitsch, 1970; Kebede et al., 1992). The analysis resulted in lower SOI (0.016) and *P/R* ratio (0.13). Keystone index analysis (Libralato

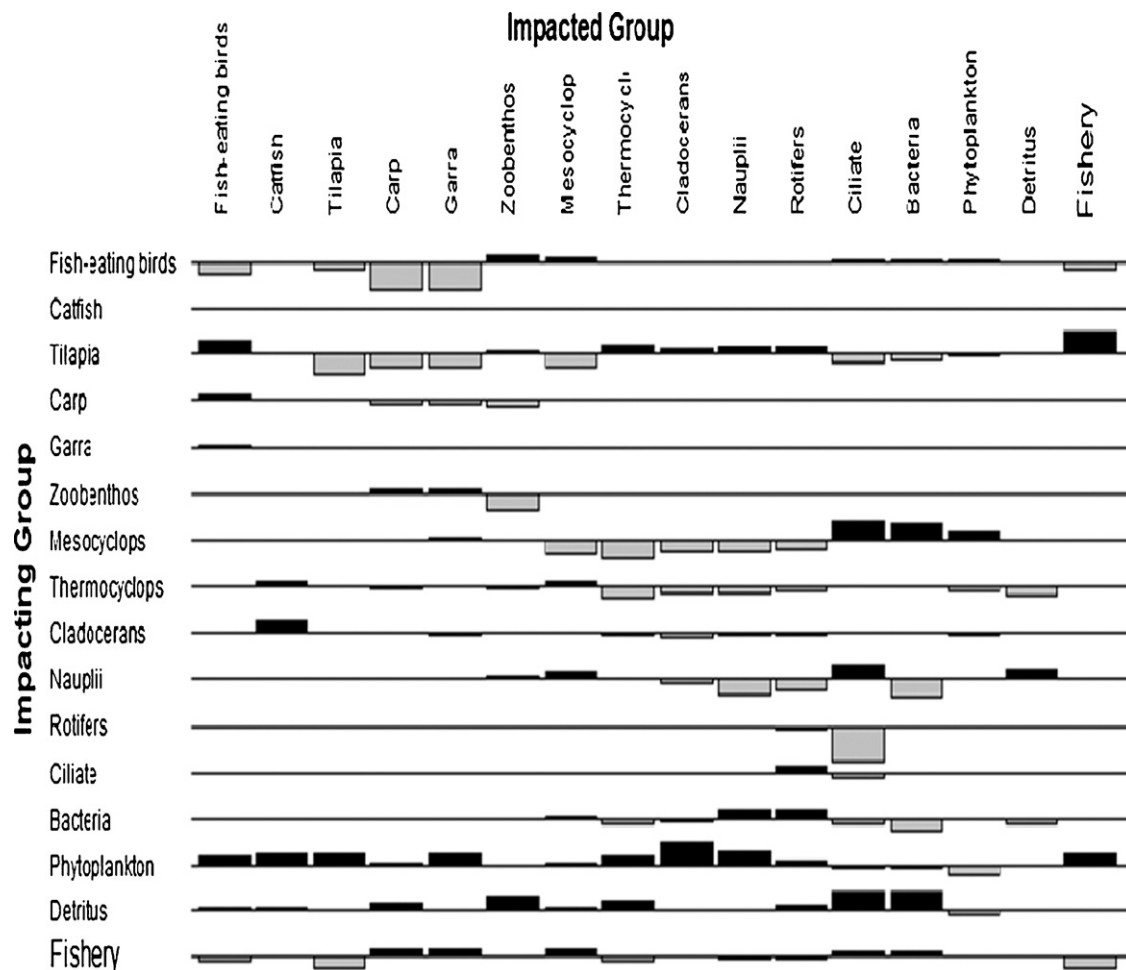


Fig. 4. Mixed trophic impacts (MTI) in Lake Hayq food web showing the combined direct and indirect trophic impacts. Positive impacts are shown above the baseline (black bar) and negative below (grey bar). The impacts are relative and comparable between groups.

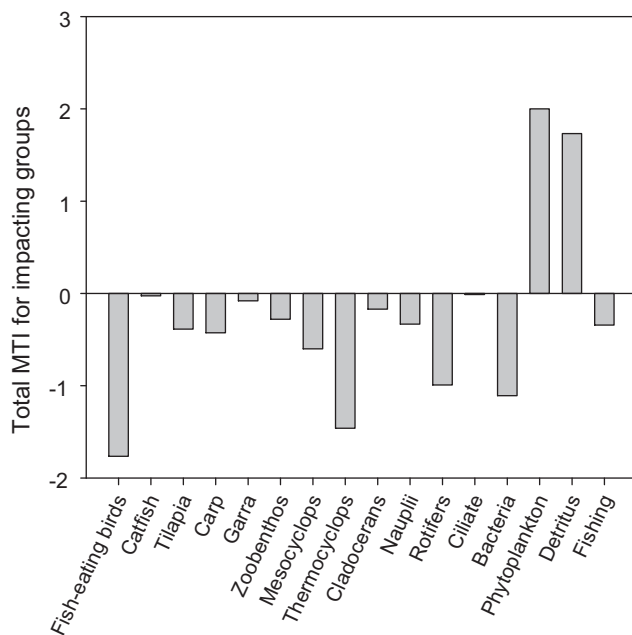


Fig. 5. Total MTI of each impacting groups on the ecosystem.

Table 5
Summary of system statistics.

Parameters	Value
Sum of all consumption ($\text{t km}^{-2} \text{y}^{-1}$)	21492.980
Sum of all exports ($\text{t km}^{-2} \text{y}^{-1}$)	43.539
Sum of all respiratory flows ($\text{t km}^{-2} \text{y}^{-1}$)	10062.830
Sum of all flows into detritus ($\text{t km}^{-2} \text{y}^{-1}$)	8085.361
Total system throughput ($\text{t km}^{-2} \text{y}^{-1}$)	39685.000
Sum of all production ($\text{t km}^{-2} \text{y}^{-1}$)	17857.000
Mean trophic level of the catch	2.46
Gross efficiency (catch/net primary production)	0.000475
Total primary production/total respiration	1.004
Total primary production/total biomass	100.974
Connectance Index	0.214
System Omnivory Index (SOI)	0.220

et al., 2006) resulted in greater than 0.8 relative total impact of Tilapia.

4. Discussion

Lakes are often used as model ecosystems because they have clearly defined boundaries and identifiable connections with adjacent ecosystems (Forbes, 1887; Vadeboncoeur et al., 2002). With 0.64, the pedigree index of the present analysis falls within the range given for overall model quality (Christensen et al., 2005). In point of fact, several functional groups are represented at species level, and most of the input data were system-specific obtained from the present study. The food web of Lake Hayq is characterized by two important pathways: grazing and detritus-based food chains (Fig. 2). Mass flows in the ecosystem based on the aggregated trophic level *sensu* Lindeman (1942) (Fig. 3) reveal the importance of both phytoplankton and detritus to the higher trophic levels. Hence, the food web of Lake Hayq has two energy sources that probably augment the plasticity or resilience of the ecosystem (Dr. Villy Christensen, personal communication).

The main sources for biomass flow to detritus originate from TL1 and TL2 which altogether contribute about 80% of the total biomass flow (Fig. 3) which suggests the microbial loop to be an

essential energy source for the planktonic food chain as pointed out already by Azam et al. (1983) and Suthers and Rissik (2009). Fetahi et al. (submitted for publication-a) have reported high organic matter to Lake Hayq suggesting the presence of adequate substrate to microbes, which also indicates maturity of the ecosystem (Odum, 1969). In the grazer food chain, *Mesocyclops* consumes herbivorous zooplankton, and catfish exclusively feeds on both of them (i.e. catfish is a zooplanktivore). This link shows the transfer of energy from the primary producers to higher trophic levels. Usually, fish is an important component in the diet of catfish (Spataru et al., 1987; Dadebo, 2000), cichlids being the most preferred prey fish in most water bodies (Corbet, 1961; Dadebo, 2000). For instance in Lake Awasa, a freshwater lake in Ethiopian rift-valley, catfish feeds on Tilapia, *Garra* and *Barbus* fishes, the former being the larger (60%) contributor of its diet (Dadebo, 2000; Fetahi and Mengistou, 2007). Interestingly, the catfish of Lake Hayq is still zooplanktivore (Alemayehu, 2009), which can be explained by the feeding habit of long evolution that did not change to any fish diet in the last 30 years, even if the fish prey is available now.

Tilapia consumed about 24% of zooplankton and 68% of phytoplankton, and was assumed as a cause for the trophic status change of the lake (Kebede et al., 1992; Fetahi et al., submitted for publication-a). The question arises how Tilapia could play the key role in changing the trophic status as its impact on zooplankton appears small in comparison to zooplanktivorous catfish. First, based on the summed-MTI analysis, Tilapia has a much stronger impact at the ecosystem level compared to catfish (Fig. 5). Second, the ecological niche of catfish and Tilapia are different; catfish is bottom dweller (Teugels, 1986) but Tilapia is pelagic. Phytoplankton (intuitively zooplankton) remains mostly in the euphotic depth of the upper water column, which is the fundamental niche of Tilapia. And hence, the positive effect of Tilapia by feeding on zooplankton cascade down to primary producers, which eventually resulted into eutrophication. Third, a large Tilapia biomass (10.8 t km^{-2}) in comparison to catfish (0.624 t km^{-2}) specifically feeds on cladocerans (Table 4), which are responsible for high filtering efficiency and clear-water phases (Lampert and Sommer, 1997). In Lake Hayq, there was massive Tilapia fish kill that coincided with mixing, and consequently a large-size *D. magna* appeared indicating the top-down control of Tilapia on large-sized cladocerans.

EE is high to several functional groups including phytoplankton (0.8) and detritus (0.85) which indicates the high utilization of the groups in the system. Contrarily, the *EE* of zooplankton in particular *Mesocyclops* (0.03) and *Thermocyclops* (0.30) was very low implying these huge resources were a 'sink' rather than a 'link' to higher trophic level. The low *EE* of *Thermocyclops* is reasonable as this taxon experienced high abundance and biomass in the lake (Kebede et al., 1992; Fetahi et al., submitted for publication-b) but is only sparsely consumed by catfish due to its low biomass (Table 3). The abundance of cyclopoid copepods in Lake Hayq has reached a maximum of 577 Indl. L^{-1} (Kebede et al., 1992) and a mean of 92 Indl. L^{-1} for *Thermocyclops* alone, signifying the huge resource of this group. Though slightly, MTI indicated that fishery has negative effects on zooplankton, as fisheries can cause depletion of target and non-target species (Coll et al., 2008).

The gross efficiencies (*GE*), which correspond to the production/consumption (*P/Q*) ratio, are generally high for zooplankton (between 0.3 and 0.4), which is in agreement with literature (Christensen et al., 2005; Villanueva et al., 2006). However, *GE* is decreased for Tilapia which may be due to the inclusion of low food quality (detritus) in its diet. Catfish almost entirely consumes zooplankton and has somehow elevated *GE* in comparison to Tilapia, but *GE* still remains low. This can be explained by small-sized prey that requires longer time to satiate the energy demand of large-

Table 6

Comparison of some parameters among different ecosystems. Transfer efficiency data, except Lake Hayq, were obtained from Christensen and Pauly (1993). SOI stands for System Omnivory Index; PP – primary production; R – respiration; TL – trophic level.

Systems	Transfer efficiency (%)	SOI	Catch/PP	Total pp/total biomass	Total pp/total R	Mean TL of the catch
L. Hayq	11.5	0.140	0.0004	106	1.05	2.46
L. Awasa			0.0014	28.67	5.83	2.57
L. Kinneret	10.6		0.0015			4.07
L. Chad	11					
L. Kariba	4.6					
L. Malawi	7					
L. Turkana	4.3					
Tanganyika	12.1					
Victoria ^a	11.8					
Victoria ^b	15					
Ubolratana		0.121	0.0012	10.28	4.83	2.6
Pasak Jolasid		0.089	0.0016	19.5	1.21	2.37
Parakrama Samudra		0.031	0.0023	35.58	1.34	2.1
Venice-1998		0.228	0.44483	9.87	2.33	2.31

^a 1971–1972.

^b Represents post-Nile perch (1985–1986).

sized catfish. Generally, large-sized and long lived organisms have low *GE* as they respire most of the assimilated food stuff (Wolff et al., 2000).

Trophic transfer efficiencies of Lake Hayq (Fig. 3) show a similar trend compared to other lakes like Kinneret, Victoria and Malawi: higher efficiencies on lower trophic levels, and decreases in the upper trophic levels (Christensen and Pauly, 1993; Walline et al., 1993). This higher transfer efficiency on lower trophic levels could be related to the higher *GE* of zooplankton and/or fishery activity on the lower TL. Besides, the inclusion of high bacteria numbers could also result in such high efficiency (Walline et al., 1993). The computed average transfer efficiency of 11.5% for the first four trophic levels is within the range (10–15%) reported by Christensen and Pauly (1993) for highly efficient African lakes and also in the range (10–20%) reported in the other literature (Odum, 1971; Le Cren and Lowe-McConnell, 1980) but higher than to some ecosystems (Table 6). This is consistent with the comparison of phytoplankton biomass, primary production and zooplankton biomass with other tropical lakes which places Lake Hayq at an intermediate position (Fetahi et al., submitted for publication-a,b). Even though the transfer efficiency was good, this was not reflected in the overall ecological efficiency of the lake. The gross efficiency of the fishery (catch/PP) of 0.05% is lower than that for Lake Awasa, Ethiopia (0.144%) (Fetahi and Mengistou, 2007), which shows that the high amount of primary production in Lake Hayq (Fetahi et al., submitted for publication-a) is not well-utilized for fishery. However, the efficiency of Lake Hayq is higher than the global average (0.02%) (Christensen et al., 2005).

At the ecosystem level, the top-down control seems weak as several consumers have a 'beneficial predation' on their prey (the direct negative impact on prey is out weighted by positive indirect impacts). The overall impact on the ecosystem (Fig. 5) reveals that only phytoplankton and detritus have positive and strong impacts suggesting the importance of bottom-up control on the lake ecosystem. The keystone species analysis also indicates the importance of phytoplankton in the lake ecosystem. The *P/R* ratio (1.05) of Lake Hayq falls within the acceptable range of Christensen and Pauly (1993) and Lewis (1981), and indicates the maturity of the ecosystem *sensu* Odum (1969). We calculated a high Omnivory Index (OI), which reflects a large feeding spectrum in the diet. An increased OI also indicates the stability of the community (Pimm et al., 1991). Consequently, the SOI for Lake Hayq was relatively high (0.14, Table 6), indicating a high level of ecological maturity (Odum, 1969). Moreover, FCI also indicates the maturity of lake; the value obtained 15% of total throughput lies within the range reported by

Christensen and Pauly (1993) for 41 aquatic ecosystems and it is higher than to several of them.

We also ran Ecopath by excluding Tilapia and with lower Chl-*a* concentration (2 mg m⁻³) to reconstruct the food web of Lake Hayq before the introduction of Tilapia (Baxter and Golobitsch, 1970; Kebede et al., 1992). The analysis resulted in lower SOI (0.016) and *P/R* ratio (0.13), which describes the lake as immature ecosystem in former times. Moreover, the keystone index analysis that resulted in >0.8 of Relative Total Impact of Tilapia signifies the effect of the fish on the ecosystem. The introduction of Tilapia might have contributed to the maturity of the lake as a positive relationship between maturity and diversity in natural communities could be observed (Odum, 1969; Perez-Espan and Arreguin-Sanchez, 2001). Indeed, Tilapia in Lake Hayq filled an ecological empty niche of pelagic planktivores and contributed for the higher transfer efficiency from primary production to fish yield. Additionally, Tilapia is a major success in the economy of the local people (Kebede et al., 1992). The diversity-stability hypothesis is often related to elasticity, the ability to return to the stationary condition particularly following a short disturbance (Lampert and Sommer, 1997). However long-lasting perturbations, such as addition of phosphorus through sewage or introduction of long-lived planktivorous fish species usually result into eutrophication. The latter was the case for Lake Hayq and in the meanwhile, the lake has changed into a new, stable, eutrophic status most probably as a result of food web interactions.

In conclusion, in this analysis we have been able to describe the structure and trophic interactions of the communities from a holistic point of view for the first time. Even though several functional groups were well-utilized in the system, *Mesocyclops* and *Thermocyclops* were under-utilized. The introduction of Tilapia is probably the major cause of the trophic change, and it might also have played a key role for the current maturity and stability. The stocked planktivorous fish occupied an empty niche and is a major success in the economy of the local people (Kebede et al., 1992). In the present analysis, we lumped benthic organisms as a single functional group and future study should investigate them more in detail. Fish-eating birds, though included, are adopted values; we recommend on site estimation as this group may consume large amounts of fish. Cormorants, for example, are usually blamed by feeding high fish biomass greater than or equivalent to fishery catches (Winkler, 1983; Schiemer and Duncan, 1988; Mavuti et al., 1996). This study is an essential step in understanding the ecosystem of this tropical highland lake, and can be seen as a baseline to devise ecosystem-based management in the future.

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