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Toward an ecological understanding of a flood-pulse system lake in a tropical ecosystem: Food web structure and ecosystem health

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ABSTRACT

Tonle Sap Great Lake (TSL) is the largest freshwater lake ecosystem in Southeast Asia and receptacle of impressive biodiversity. However, there is surprisingly little knowledge of its ecosystem structure and functioning. The main objective of the current work was to quantify the food web structure and assess the ecosystem health status of the TSL system by constructing the first holistic food web model using Ecopath with Ecosim (EwE). The results indicate that the ecotrophic efficiency (EE) values were very high for most of functional groups (EE > 0.5) except molluscs (0.146) and macrophytes (0.102). The high EE values together with the MTI (Mixed Trophic Impact) analysis indicated the overexploitation and degradation of fishery resources in the TSL system. The discrete trophic levels varied from 1 (phytoplankton, macrophytes and detritus) to 3.17 (snakehead). The energy transfer in the TSL food web was based mostly on the detrital food chain (77.9%) rather than the grazing food chain (22.1%), with an average transfer efficiency of 8.27%. The ratios of total primary production to respiration (TPP/TR) and to biomass (TPP/TB) were 1.23 and 2.04, respectively, while the Ascendency and Finn cycling index (FCI) of the system were estimated at 27.4% and 23.62%. Nevertheless, the connectance index (CI: 0.253) and system omnivory index (SOI: 0.075) were in-between compared to other lake ecosystems, which indicated that the food web structure was characterized by linear, rather than web-like features. Systematic analysis and indicators suggested that the ecosystem was a relatively healthy ecosystem achieving a certain stage of maturity, albeit with a vulnerable food web structure. Accordingly, some ecosystem-based strategies are presented for the improvement of fishery management and ecosystem conservation in TSL.

1. Introduction

There is ample evidence that freshwater ecosystems globally suffer from overexploitation, environmental pollution, biodiversity decrease and habitat loss and/or degradation (De Kerckhove et al., 2015; Fang et al., 2006). Natural resource management and aquatic ecosystem assessment currently challenge both scientific communities and environmental managers. In view of these facts, it is widely recognized that an ecosystem-based approach is important for managing sustainable natural resources and maintaining ecosystem health in freshwater systems (FAO, 1995; Li et al., 2009).

Tonle Sap Lake (TSL) is acknowledged as being the largest freshwater ecosystem in Southeast Asia and is an ecological hotspot zoned as biosphere reserve in 1997 by UNESCO (United Nations Educational, Scientific and Cultural Organization) (Lamberts, 2006; UNESCO, 1997). The lake is characterized by the flood-pulse system, interconnected with the Great Mekong River through the Tonle Sap River (120 km long), creating hydrological processes unique worldwide with the reversed flow from the lake into the Mekong in the dry season when water in the Mekong starts to recede (Arias et al., 2013). Moreover, Tonle Sap Lake is one of the largest contributors to freshwater fish which include more than 296 species ranking the 3rd in the world just after 2 African Great Lakes: Malawi (433 species) and Tanganyika (309 species) (Baran et al., 2007). Fishes are the main sources of nutrition representing 80% of Cambodians dietary proteins (Hortle, 2007). Therefore, TSL is not only important due to its large area but it has also played a crucial role in ecological, economic and socio-cultural values to sustain the livelihoods of millions of people for centuries (Lamberts, 2006). Indeed, Tonle Sap fisheries represent more than 60% of Cambodia's inland fisheries captures – estimated between 289,000 and 431,000 tons of catch annually (Van Zalinge et al., 2001). The average annual catch

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from TSL was reported to be between 179,500 and 246,000 tons (Baran and Myschowoda, 2008).

In contrast to its importance, little effort has been focused on understanding its aquatic communities, fishes and fisheries, biological status and primary production, let alone holistic studies as such as that investigating food web and ecosystem properties in TSL system (Lamberts, 2006). It was shown that among the world's largest tropical lakes and floodplains, TSL is the one where hydrology and ecology has been studied the least (Junk et al., 2006a). So far, most of the previous studies in TSL have focused mainly on fishery production and its relationship with hydrological and environmental factors (Baran and Myschowoda, 2008; Baran et al., 2001). For instance, Lake George in Uganda which is 60 times smaller than TSL and supports the livelihood of about 1700 households, has probably received 100 times more research attention (Keizire and Muhwezi, 2006).

Due to the limited studies and related ecosystem approaches, up until now, little is known about the ecosystem status and food web structure of TSL, since the interactions of biodiversity within an ecosystem are very complex (Baran and Myschowoda, 2008; Baran et al., 2007; Van Zalinge et al., 2001). Recent studies have shown that TSL fisheries exert over exploitation. Subsequently, multiple significant indicators have shown that the system, previously home to many giant catfishes, giant barbs and stingrays, is now dominated by small and low value species (Cooperman et al., 2012; Enomoto et al., 2011), questioning the sustainability of the fisheries in the lake. As a matter of fact, overfishing can impact the food web structure and change the abundance of predators that can alter the prey abundance leading to a cascade of trophic effects (Sala et al., 1998). It is believed that the more an ecosystem is large and complex, the greater its vulnerability (MacDougall et al., 2013).

Nevertheless, what do we know about the ecological interactions of the TSL ecosystem, how can we optimise management of the natural resources and maintain a healthy ecosystem? To address these issues, a holistic ecological understanding is fundamental contributing to balancing productivity and maintaining the health of ecosystems in response to present needs. The food web is one of the key components in an ecosystem and ecologists have been struggling for centuries to understand the real trophic interactions among its living organisms (Ings et al., 2009). Food web structure and interactions play a decisive role in determining the dynamics of an ecosystem, and are of interest in many ecological studies (Kitchell et al., 2000). This knowledge contributes not only to maintaining the stability and sustainability of ecosystem functioning, but also to the conservation and management of the ecosystem to mitigate the present and future needs for feeding (Van Worm and Duffy, 2003).

In recent years, Ecopath with Ecosim (EwE) has been widely used all over the world to describe the trophic relationship and the quantitative ecosystem properties (Christensen et al., 2005). Many applications have been constructed on the largest and most productive aquatic, terrestrial and coastal ecosystems (i.e., Lake Malawi, lake Tanganyika, Gironde estuary, Mediterranean Sea) (http://www.ecopath.org/models). Moreover, EwE is a very suitable approach to study the ecological functioning of the large ecosystem with limited availability of information and data, such as Tonle Sap Lake (Coll et al., 2009).

This study aims to establish the first systematic model of trophic interactions and ecosystem properties for the important, yet poorly studied TSL ecosystem. Our main objectives are to (1) quantify the food web structure and trophic interactions in TSL; (2) assess the TSL ecosystem properties and health status based on the ecological indicators attributed by the model; and (3) propose ecosystem-based strategies for the improvement of fisheries management in TSL. The results are critically important for effective decision making and policy development in terms of conservation and sustainability of fishery resources and ecosystem health in large freshwater lakes worldwide.

2. Materials and methods

2.1. Tonle Sap Lake

Tonle Sap Great Lake (Fig. 1) is the most important wetland within the Lower Mekong Basin and characterized by tropical monsoon climate (Arias et al., 2013). The water level in the lake varies from 0.8 m in the dry season to 9 m in the rainy season causing an expansion of the lake's area from 2500 km^2–3000 km^2 to reach 10,000 km^2–16,000 km^2 when full (Matsui et al., 2005). More than 60% of the lake's water originally comes from the Mekong River through the Tonle Sap River (120 km) with just 40% being drained within the TSL lake basin and its tributaries (Matsui et al., 2005). Since the area of the lake varies greatly between the dry and rainy seasons, only 10,500 km^2 were taken in account for our study area by assuming 2500 km^2 of permanent water and 8000 km^2 for the average productive area of the floodplains within 3 months of flooding periods (Koponen et al., 2010). Under the tropical wet and dry monsoon regime, the annual rainfall within the lake area is between 1300 mm and 1900 mm, with the mean water temperature about 30 °C (MRC, 2010). The TSL has been described as a meso to eutrophic lake (Junk et al., 2006a) the average nutrient concentrations of 0.17 mg L^{-1} for total nitrogen, and 0.06 mg L^{-1} for total phosphorus, with pH remaining almost neutral (Table 1).

2.2. Modelling approach

Ecopath with Ecosim (EwE) is free ecological modelling software developed by Christensen and Pauly (1993), which creates a static mass-balanced snapshot of the resources in an ecosystem and their interactions, represented by trophically linked biomass "pools" or ecological guilds (Christensen et al., 2005). In recent years, EwE has been widely used to address ecological questions, evaluate ecosystem properties, study trophic relationships, explore the fisheries management and restoration policies; and evaluate the effect of environmental changes in continental and coastal ecosystems (Coll and Libralato, 2012; Kao et al., 2014; Rogers and Allen, 2012). The algorithm of EwE is based on parameterization of the two master equations known as: (1) Production = catch + predation + net migration + biomass accumulation + other mortality; (2) Consumption = production + respiration + unassimilated food, can be simplified and expressed as follows (Christensen et al., 2005):

$$B_i \cdot \left(\frac{P}{B}\right)_i \cdot EE_i - \sum_{j=1}^{i} B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ji} - EX_i = 0 \quad (1)$$

where B_i is the biomass of group i; $(P/B)_i$ the production biomass ratio of group i, which is equal to the coefficient of total mortality (Z) under the steady state condition; EE_i is the ecotrophic efficiency of group i; B_j is the biomass of predator group j; $(Q/B)_j$ is the con-

Table 1
Physicochemical parameters of water quality in Tonle Sap Lake during 1995–2010.

Parameters	Unit	Mean ± SD
Water temperature	°C	30 ± 0.45
pH	–	7 ± 0.07
Dissolved oxygen	mg L^{-1}	6 ± 0.89
Specific conductivity	$\mu S\ cm^{-1}$	68 ± 39
Total suspended solids	mg L^{-1}	109 ± 62
Total phosphorus	mg L^{-1}	0.06 ± 0.09
Total nitrogen	mg L^{-1}	0.17 ± 0.04
Secchi depth	m	1.07 ± 0.26

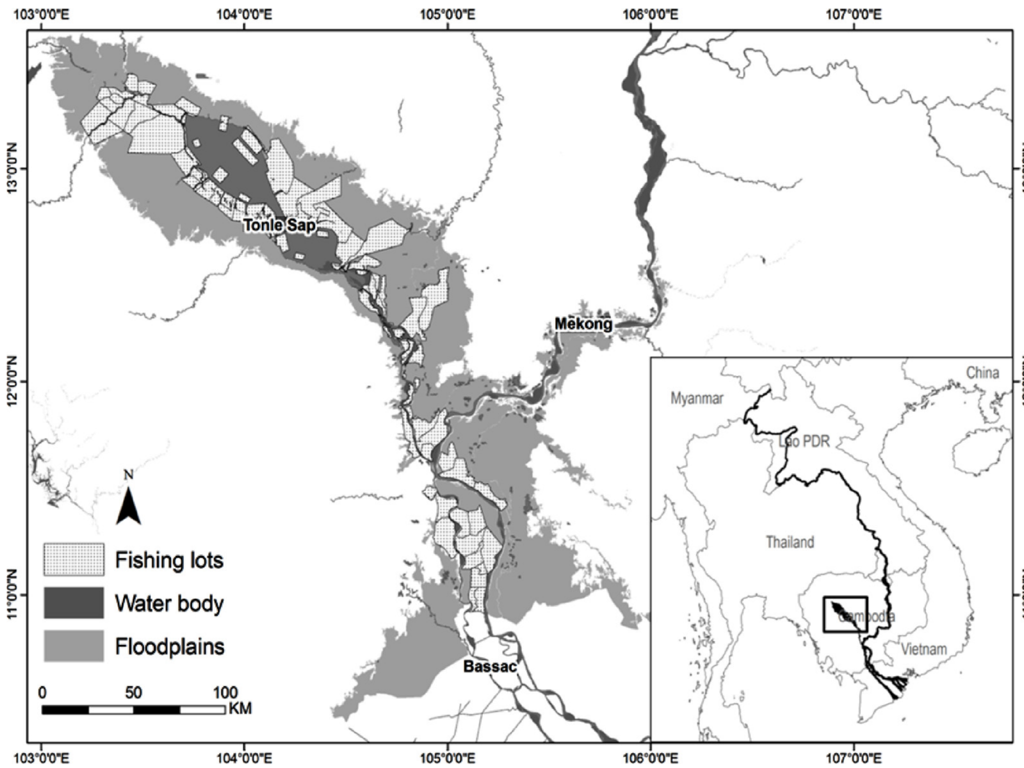

Fig. 1. Geographic location of Tonle Sap Great Lake.

sumption biomass ratio of the predators j; EX_i is the export of group i; i and j are respectively numbers of prey and predator groups.

Biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B), ecotrophic efficiency (EE) and diet composition (DC) are the main parameters of the Ecopath model. To construct the model, the composition of the diet and at least three of the four parameters (B, P/B, EE, and Q/B) are needed for the basic input of the model for each functional group (detailed in Section 2.2.1). Additionally, the one unknown parameter can be estimated by the model through the Ecopath parameterization algorithm.

2.2.1. Functional groups

EwE model provides a quantitative representation of the energy flows in the food web of the ecosystem studied. This ecosystem is represented by different categories, defined by the functional properties of taxa included in each category and considered as functional groups, which can be composed of one or many ecologically similar species (Coll et al., 2009). In TSL, 21 functional groups have been defined to construct the mass balance model in order to study the trophic relationship of this ecosystem (Table 2). There were 12 fish functional groups, crabs, shrimps, molluscs, other zoobenthos, macrozooplankton, microzooplankton, phytoplankton, macrophytes and detritus. The aggregation of the fish functional groups was based mostly on the composition of diet, traits (size), ecological guilds and commercial landing statistics (Poulsen et al., 2004).

2.2.2. Data collection and preparation

2.2.2.1. Fish. Seventy common fish species with an important economic value were selected for the study and were aggregated into 12 functional groups according to their ecological similarity. The biomass (B) and production/biomass ratio (P/B) of each fish functional group were calculated by the empirical relationship of Pauly (1980) and Beverton and Holt (1957) as follows (Christensen et al., 2005):

$$B = \frac{Y}{F}; \quad F = Z - M; \quad Z = \frac{P}{B} = K.\frac{L_\infty - \bar{L}}{\bar{L} - L'} \tag{2}$$

where B, Y, F, Z and M represent the biomass ($\mathrm{t\,km^{-2}}$), the annual catch yield ($\mathrm{t\,km^{-2}\ year^{-1}}$), the fishing mortality ($\mathrm{year^{-1}}$), total mortality ($\mathrm{year^{-1}}$), and natural mortality ($\mathrm{year^{-1}}$); K, L_∞, $\bar{L}$, L' represent the growth rate of VBFV, asymptotic length of fish (cm), mean length of fish (cm), cut off length of fish (cm). K, L_∞, $\bar{L}$, L' were derived from the FishBase website (www.fishbase.org) and previously published studies.

Annual fish yields of TSL were derived from the fish catch statistic survey 1994–1997 of the fishing lots and fishermen in the fishing lot zones around the lakes (Fig. 1) conducted by Mekong River Commission (MRC) under the support of DANIDA (Danish International Development Agency) in collaboration with Fisheries Administration of Cambodia (Ly and van Zalinge, 1998). Fishing lots (Fig. 1) are the commercial fishing zones around the lakes auctioned by Cambodian government to the highest bidder for exclusive exploration, so it is one of the government's main instruments for extracting fisheries resources from the lake (Van Zalinge et al., 1998). There were about 125 fishing lots located around the TSL, its floodplains, and Tonle Sap River. After the fisheries reform in 2012, the fishing lots were completely removed from the lake leaving 65% of the lake open to family fishing activities under the management of community fisheries (CFi) and 35% for conservation purposes (CDRI, 2013). In our study, the average catch of the TSL was assumed to be 235,000 tons per year, and the total fish yield/landing was computed at 22.38 $\mathrm{t\,km^{-2}}$ by Van Zalinge et al. (2001) and Ly and van Zalinge (1998).

The consumption biomass ratio (Q/B) was estimated from FishBase website (www.fishbase.org). The diet composition of each fish functional group was based on the literature reviews and report from the previous studies Guo et al. (2013), Jia et al. (2012) and Lim et al. (1999).

Table 2
Main species composition of each category for the Tonle Sap lake ecosystem.

No	Category name	Main species composition
1	Snakehead	*Channa micropeltes*, *Channa striata*, *Channa gachua*, *Channa lucius*
2	Catfish	*Pangasius* sp. *(hypophthalmus*, *conchophilus)*, *Pangasius larnaudii*
3	Soldier river barb	*Cyclocheilichthys enoplos*
4	Perch	*Anabas testudineus*, *Pristolepis fasciata*, *Parambassis wolffii*
5	Other carnivores	*Hampala* sp., *Boesemania microlepis*, *Oxyeleotris marmorata*, *Wallago attu*, *Lycothrissa crocodilus*, *Notopterus notopterus*, *Chitala ornata*, *Kryptopterus cheveyi*, *Ompok siluroides*, *Cephalocassis borneensis*, *Mastacembelus armatus*, *Phalacronotus apagon*, *Belodontichthys truncatus*, *Colia lindmani*
6	Large herbivores	*Labeo chrysophekadion*, *Cirrhinus microlepis*, *Osteochilus melanopleara*, *Catlocarpio siamensis*, *Cosmochilus harmandi*, *Tenualosa thibaudeaui*, *Barbichtys laevis*
7	Small herbivores	*Thynnichthys hynnoides*, *Labiobarbus leptocheilus*, *Amblyrhynchichthys micracanthus*, *Gyrinocheilus pennocki*, *Labiobarbus siamensis*
8	Omnivorous fish	*Hypsibarbus malcolmi*, *Osteochilus vittatus*, *Puntioplites proctozysron*, *Barbonymus altus*, *Puntioplites bulu*, *Systomus orphoides*, *Albulichthys albuloides*
9	Benthivorous fish	*Hemibagrus spilopterus*, *Leptobarbus rubripinna*, *Clarias* sp., *Hemibagrus filamentus*, *Macrognathus siamensis*, *Cynoglossus cynoglossus*, *Yasuhikotakia modesta*, *Cyclocheilichthys apogon*, *Pangasius macronema*, *Toxotes* sp., *Hyporhamphus limbatus*, *Thryssocypris tonlesapensis*, *Macrochirichthy smacrochirus*, *Bagarius bagarius*, *Probarbus labeamajor*
10	Gourami fish	*Trichopodus* sp., *Trichopodas pectoralis*
11	Mud carp	*Henicorhynchus* sp.
12	Small fish	*Paralaubuca typus*, *Rasbora tornieri*, *Rasbora dusonensis*, *Parambassis apogonoides*, *Corica laciniata*, *Puntius brevis*, *Parachela siamensis*, *Mystus* sp. *(atrifasciatus*, *albolineatus)*
13	Crabs	*Sommanniathelaphusa lacuvita*
14	Shrimps	*Macrobrachium lanchesteri*
15	Molluscs	*Corbicula* sp., *limnoperna* sp.
16	Other zoobenthos	Oligochaeta, Insecta (chironomidae), others
17	Macrozoopankton	Copedoda, Cladocera
18	Microzooplankton	Protozoa, Rotifera
19	Phytoplankton	Chlorophyta, Cyanobacteria, Bacillariophyta, Euglenophyta
20	Macrophytes	*Barringtonia acutangula*, *Eichhornia crassipes*
21	Detritus	-

2.2.2.2. Crabs and shrimps. The biomass of crabs and shrimps was estimated from the field survey conducted by MRC in 2008 in the northern part of Tonle Sap (Battambang province). MRC reported that other aquatic animals (OAAs) including crabs, shrimps, snakes, frogs and others represented approximately 24% of the total catch (Hortle et al., 2008). Crabs and shrimps composed of 35.5% and 22.5% of total OAAs' biomass, respectively. The estimated biomass of crabs and shrimps were 3.76 t km^{-2} and 2.36 t km^{-2} respectively. The value of *P*/*B* and *Q*/*B* were modified from Guo et al. (2013) and Jia et al. (2012).

2.2.2.3. Zooplankton and zoobenthos. The biomass of zooplankton and zoobenthos were estimated from the field survey in TSL (Ohtaka et al., 2010). In our study, the zooplankton communities were divided into 2 functional groups: macrozooplankton (copepoda and cladocera) and microzooplankton (protozoa and rotifers). The mean densities of zooplankton communities were: copepods (347 ind. L^{-1}), cladocera (87 ind. L^{-1}), protozoa (1040 ind. L^{-1}) and rotifers (260 ind. L^{-1}). It was noted that more than 70% of zooplankton in TSL were microzooplankton, particularly protozoa.

Zoobenthos communities were categorized into 2 different functional groups: molluscs and other zoobenthos (i.e., oligochaeta, insects including chironomidae). The estimated biomass of molluscs was exceptionally high compared to other zoobenthos, with an average biomass of 143.14 g m^{-2} and 1.19 g m^{-2}, respectively. The *P*/*B* and the production to consumption ratio (*P*/*Q*) of zooplankton and zoobenthos communities were modified from Guénette et al. (2008) and Guo et al. (2013).

2.2.2.4. Primary producers. The primary producers were characterized by 2 functional groups: phytoplankton and macrophytes. The biomass of phytoplankton and macrophytes were computed as 5.48 t km^{-2} and 1489 t km^{-2}, respectively, from the previous primary production model of the lake (Junk, 2006; Koponen et al., 2010). In the TSL system, the phytoplankton was constituted mainly by algal production (i.e., chlorophyta, cyanobacteria, bacillariophyta, euglenophyta) while the rooted and floating macrophytes typed as terrestrial vegetation were dominated by *Barringtonia acutangula*, *Eichhornia crassipes* (Campbell et al., 2006). Furthermore, the *P*/*B* values of phytoplankton and macrophytes were estimated at 185 year^{-1} and 1.67 year^{-1}, respectively, similar to many Chinese and tropical lakes.

2.2.2.5. Detritus. The biomass of detritus was calculated using the empirical equation from the primary production and euphotic depth suggested by Christensen and Pauly (1993):

$$\log\ D = 0.954\ \log\ PP + 0.863\ \log\ E - 2.41 \tag{3}$$

where *D* is the detrital biomass in (g C m^{-2}), *PP* is the primary production in (g C m^{-2}); E is the euphotic depth in meters. The depth of the euphotic zone was calculated as follows: $E = 2.5 \times \mathrm{SD}$ (Secchi depth in meters), the average SD of TSL is 1.07 m and therefore $E = 2.68$ m.

2.2.3. Model balancing and uncertainty

The Ecopath model was balanced by launching the first basic estimation in parameterization to get *EE* values ($EE < 1$) and *P*/*Q* values (0.05–0.3) for all functional groups. In practice, a manual modification on the input data was employed to balance the model (Christensen et al., 2005). The new version of the Ecopath model was balanced using ecological knowledge rather than entirely relying on computer algorithms, e.g., the diet compositions of some functional groups were slightly modified in order to get the mass-balance model (the modified diet matrix is shown in Table 4).

Pedigree was used to describe the quality of input data by assigning the confidence interval based on their origins. This can be used to evaluate the certainty of the model. With the individual computation of the pedigree index for each functional group, an overall pedigree index (*P*) for the model was estimated as follows:

$$P = \sum_{i=1}^{n} \sum_{j=1} \frac{l_{ij}}{n},$$

where l_{ij} is the pedigree index for model group *i* and parameter *j*, *n* is the total number of modelled groups (Christensen et al., 2005). The overall model pedigree index (*P*) ranges from 0 (low) to 1 (high)

Table 3
Basic input and estimated parameters (italics) for the 21 functional groups of the Tonle Sap Lake ecosystem.

Group number	Group name	FTL	B (t km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE	P/Q
1	Snakehead	*3.17*	4.48	1.22	6.20	*0.598*	*0.196*
2	Catfish	*2.98*	1.38	0.92	3.70	*0.897*	*0.249*
3	Soldier river barb	*2.77*	3.64	0.94	5.50	*0.936*	*0.171*
4	Perch	*2.74*	1.13	2.85	33.40	*0.565*	*0.085*
5	Other carnivores	*2.96*	5.23	0.96	7.20	*0.898*	*0.134*
6	Large herbivores	*2.00*	7.96	0.38	12.00	*0.600*	*0.031*
7	Small herbivores	*2.00*	13.09	0.68	38.70	*0.952*	*0.018*
8	Omnivorous fish	*2.41*	2.23	2.73	22.90	*0.994*	*0.119*
9	Benthivorous fish	*2.56*	4.89	0.35	5.00	*0.934*	*0.070*
10	Gourami fish	*2.22*	2.26	1.21	10.40	*0.933*	*0.116*
11	Mud carp	*2.00*	5.99	1.53	26.40	*0.938*	*0.058*
12	Small fish	*2.26*	6.07	1.38	18.20	*0.944*	*0.076*
13	Crabs	*2.31*	3.76	2.12	8.48	*0.721*	0.250
14	Shrimps	*2.02*	2.36	4.50	24.40	*0.936*	*0.184*
15	Molluscs	*2.00*	143.10	4.30	*17.20*	*0.146*	0.250
16	Other zoobenthos	*2.00*	1.19	5.00	*25.00*	*0.843*	0.200
17	Macrozooplankton	*2.05*	9.98	*4.29*	*85.87*	0.900	0.050
18	Microzooplankton	*2.00*	3.74	*15.26*	*305.23*	0.950	0.050
19	Phytoplankton	*1.00*	5.48	185.00		*0.936*	
20	Macrophytes	*1.00*	1488.62	1.67		*0.102*	
21	Detritus	*1.00*	24.31			*0.871*	

Notes: FLT stands for fractional trophic level and B, P/B, Q/B, EE, P/Q respectively for Biomass, Production to Biomass ratio, Consumption to Biomass ratio, Ecotrophic Efficiency, Production to Consumption ratio.

quality of the model studied. Indeed, the pedigree values of over 150 Ecopath models published ranged from 0.164 to 0.675 (Morissette et al., 2006).

2.2.4. Network analysis and ecosystem properties

In Ecopath model, all ecological groups were also assigned discrete trophic levels according to Lindeman (1942) with the approach suggested by Ulanowicz (1995). Then, a modified input–output analysis with the procedure "Mixed Trophic Impacts (MTI)" described by Ulanowicz and Puccia (1990) was implemented in the EwE to describe how any group (including fishing fleets) impacts trophically on all the other groups in an ecosystem. It includes both direct and indirect impacts, i.e., both predatory and competitive interactions (Christensen et al., 2005).

Theoretically, in EwE, the ecosystem properties were quantified by implementing the ecosystem theories proposed by Odum and Barrett (1972), Odum (1969) and Ulanowicz (1987). Accordingly, a set of indicators were used to describe and assess the stability and maturity of the ecosystem (Christensen et al., 2005). Indeed, the flow indices, including the connectance index (CI) and system omnivory index (SOI), were used to describe whether the food web is web-like or linear. Whereas, the connectance index (CI) is a measure of the observed number of food links in a system relative to the number of possible links (Gardner and Ashby, 1970). The value of CI depends on both the size of a system and on diet matrices, while the SOI expresses the variance in the TL of the consumer prey groups. Besides, a routine based on the approach suggested by Ulanowicz (1987) was implemented to describe the numerous cycles and pathways implied by the food web representing an ecosystem. Finn's cycling index (FCI) is widely used to calculate the flows with respect to cycled fractions in an ecosystem (Finn, 1976). Moreover, the ecosystem information indices, i.e., ascendancy (A) and system overhead (O), were computed from information theory as a measure of the average mutual information in a system (Ulanowicz and Norden, 1990).

3. Results

3.1. Basic input and output variables

The balanced Ecopath model with the pedigree index (0.511) and the measure of fit (2.523) indicated that the input parameters of the model were based on reliable sources and that the model was robust with a high level of confidence (Table 5).

A set of basic input variables and the estimated parameters from the model are listed in Table 3. Generally, the EE values of all functional groups are less than 1, and most of the P/Q values are between 0.05 and $\sim$ 0.3, meeting the requirements of a balanced model. The EE values of all the commercial fishery objectives (e.g., fishes, shrimps and crabs) were much higher than 0.5. For instance, omnivorous fish suffered the highest EE value of 0.994, followed by small herbivores (0.952), small fish (0.944), mud carp (0.938), shrimps (0.936), soldier river barb (0.936), benthivorous fish (0.934), gourami fish (0.933), other carnivores (0.898), catfish (0.897), crabs (0.721), large herbivores (0.600), snakehead (0.598) and perch (0.565). However, the EE of macrophytes and molluscs were extraordinarily lower than other function groups (i.e., 0.102 and 0.146, respectively) (Table 3).

3.2. Food web structure and trophic analysis

3.2.1. Trophic structure

The fractional trophic levels (FTL) varied from 1 (macrophytes, phytoplankton and detritus) to 3.17 (snakehead) (Table 3). The snakehead group occupied the top trophic level with a biomass of 4.480 t km^{-2} y^{-1}, followed by several carnivorous fish functional groups, such as catfish (2.98), other carnivores (2.96), soldier river barb (2.77) and perch (2.74). All the functional groups consisted of the middle trophic levels of the TSL ecosystem except macrophytes, phytoplankton and detritus. Macrophytes and phytoplankton were the main primary producers in TSL ecosystem. A more concisely web-like figure was also shown in Fig. 2 to indicate the whole interactions and energy flows in the lake food web.

3.2.2. Transfer efficiencies

From the Lindeman spine of the TSL system, two main food chains, a detritus-based food chain and a grazing food chain can be found (Fig. 3). However, around 77.9% of the whole energy and matter (4245 t km^{-2} y^{-1}) flows through the detritus-based food chain, while only 22.1% (1204 t km^{-2} y^{-1}) flows in the grazing food chain, despite the high biomass of the primary producers (1494 t km^{-2} y^{-1}) (Fig. 3).

Five discrete trophic levels (TL from I to V) including all the functional groups of the TSL ecosystem were also pictured according

Table 4
Diet composition matrix of the 21 function groups of the Tonle Sap lake system.

Group	Prey\predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	Snakehead																		
2	Catfish	0.005																	
3	Soldier river barb	0.030																	
4	Perch	0.040																	
5	Other carnivores	0.070																	
6	Large herbivores																		
7	Small herbivores	0.060	0.030		0.080	0.050													
8	Omnivorous fish	0.060	0.110			0.050													
9	Benthivorous fish	0.005																	
10	Gourami fish	0.005	0.001		0.030	0.015													
11	Mud carp	0.040	0.150		0.030	0.050													
12	Small fish	0.080	0.050		0.100	0.010								0.005					
13	Crabs	0.130	0.050																
14	Shrimps	0.015	0.050		0.160	0.025							0.010						
15	Molluscs	0.260	0.415	0.400	0.100	0.565			0.250	0.350			0.150	0.300					
16	Other zoobenthos			0.050	0.050	0.010				0.050	0.020				0.001				
17	Macrozooplankton	0.150	0.045	0.300	0.150	0.150			0.150	0.150			0.050						
18	Microzooplankton										0.200		0.050		0.020			0.050	
19	Phytoplankton		0.049	0.150	0.150		0.200	0.600	0.050		0.100	0.600	0.040	0.090	0.279	0.030	0.200	0.350	0.100
20	Macrophytes				0.050		0.800	0.200	0.350	0.100	0.080	0.200	0.050	0.400	0.050				
21	Detritus	0.050	0.050	0.100	0.100	0.075		0.200	0.200	0.350	0.600	0.200	0.650	0.205	0.650	0.970	0.800	0.600	0.900
	Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

to Lindeman (1942) (Fig. 3). The transfer efficiencies (TEs) are the ratios between the sum of exports and flows predated by the next level and the throughput on the trophic level. For the grazing food chain of the TSL ecosystem, the TEs from TL III to TL V were 4.05%, 9.62%, 11.2% respectively, with a mean value of 8.29%. In parallel, for the detrital food chain, TEs were 4.33%, 9.42% and 11% with a mean value of 8.25%. The geometric mean of the trophic transfer efficiency for the TSL Lake ecosystem was 8.27%.

3.2.3. Mixed trophic impacts

The result of MTI exhibited both positive and negative effects among each other's (Fig. 4). Only macrophytes, phytoplankton and detritus had positive impact on most other functional groups, this could explain the bottom-up effects from the ecosystem perspective. The other compartments showed direct predator–prey interactions, cascading effects and competition. For instance, perch showed significantly negative effects on some of the fish diet groups like gourami fish, small fish, shrimps and other zoobenthos mostly because of the predator–prey interactions. A simple example can be also seen from the relationships between macrozooplankton and microzooplankton. The fish groups seemed to have more negative effects on each other mainly due to trophic competition, for instance snakehead showed significant negative effects on catfish, perch and other carnivore groups mostly because they have similar food sources. Fishery had relatively strong negative effects on all the commercial fish and shrimps, but was beneficial for omnivorous fish, crabs and some other forage resources. It was observed that most groups had a negative impact on themselves, interpreted here as reflecting increased within-group competition for resources (Christensen et al., 2005).

Table 5
Ecosystem attributes of Tonle Sap Lake.

Parameters	Value	Units
Ecosystem properties		
Sum of all consumption (TC)	5677.091	$t\,km^{-2}\,y^{-1}$
Sum of all exports (TE)	654.194	$t\,km^{-2}\,y^{-1}$
Sum of all respiratory flows (TR)	2845.601	$t\,km^{-2}\,y^{-1}$
Sum of all flows into detritus (TD)	4873.439	$t\,km^{-2}\,y^{-1}$
Total system throughput (TST)	14050.330	$t\,km^{-2}\,y^{-1}$
Sum of all production (TP)	4297.950	$t\,km^{-2}\,y^{-1}$
Mean trophic level of the catch (TLc)	2.482	–
Gross efficiency (catch/net p.p.)	0.007	–
Calculated total net primary production (TNPP)	3499.795	$t\,km^{-2}\,y^{-1}$
Net system production (NSP)	654.194	$t\,km^{-2}\,y^{-1}$
Total biomass (excluding detritus) (TB)	1716.580	$t\,km^{-2}\,y^{-1}$
Ecosystem maturity		
Total primary production/total respiration (TPP/TR)	1.230	–
Total primary production/total biomass (TPP/TB)	2.039	–
Total biomass/total throughput (TB/TST)	0.122	–
Food web structure		
Connectance Index (CI)	0.253	–
System Omnivory Index (SOI)	0.075	–
Finn's cycling index (FCI)	23.62	% of total throughput
Finn's mean path length (FML)	4.015	–
Ascendancy (A)	0.274	–
System overhead (O)	0.726	–
Model reliability		
Ecopath pedigree index	0.511	–
Measure of fit (t^*)	2.523	–

3.3. Ecosystem properties and indicators

The summary statistics and flow indices of the TSL ecosystem are listed in Table 5. The total system throughput of the lake ecosystem reached 14,050.330 $t\,km^{-2}\,y^{-1}$, of which 40.4% derived from consumption (5677.091 $t\,km^{-2}\,y^{-1}$), 4.65% from exports (654.194 $t\,km^{-2}\,y^{-1}$), 20.3% from respiration (2845.601 $t\,km^{-2}\,y^{-1}$) with 34.68% (4873.439 $t\,km^{-2}\,y^{-1}$) eventually flowing into detritus. The sum of all production (TP) was 4297.950 $t\,km^{-2}\,y^{-1}$, and the calculated total net primary production (TNPP) and the net system production (NSP) were 3499.795 $t\,km^{-2}\,y^{-1}$ and 654.194 $t\,km^{-2}\,y^{-1}$, respectively. Thus, the ratios of total primary production to total respiration (TPP/TR) and total primary production to total biomass (TPP/TB) were 1.230 and 2.039 respectively. The mean trophic level of catch was calculated at 2.482, and the gross efficiency (catch/net primary production) was 0.007 in the TSL ecosystem. Overall, in the TSL ecosystem, the values of flow indices, i.e., CI and SOI, were estimated at 0.253 and 0.075 respectively; while the FCI and Finn's mean path length (FML) calculated by the model were 23.62% and 4.015, respectively (Table 5). Meanwhile, the values of ascendancy and overhead were 27.4% and 72.6% respectively (Table 5).

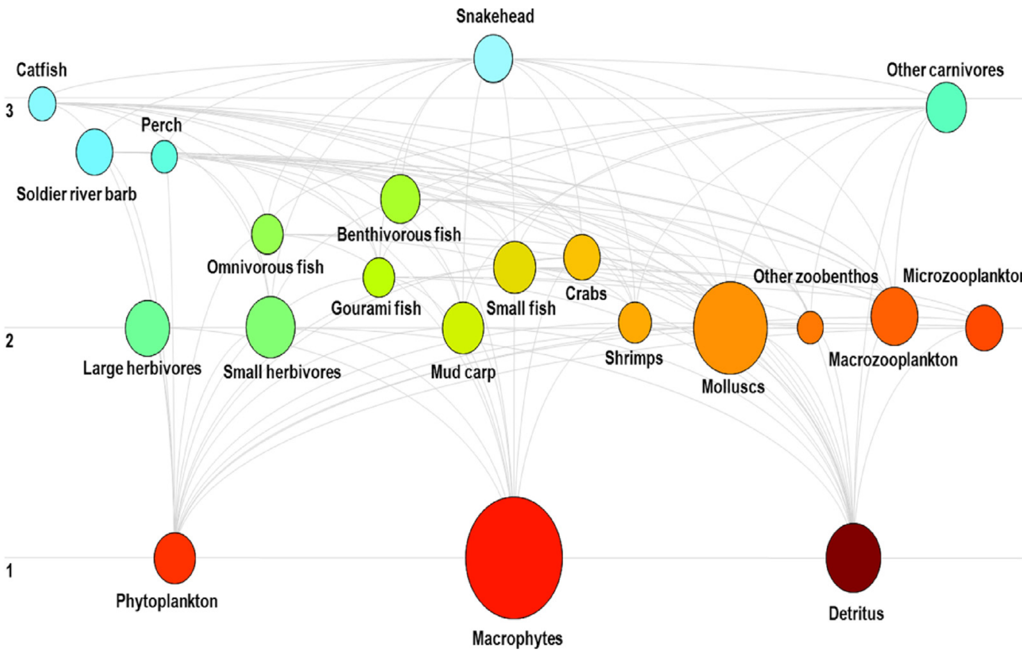

Fig. 2. Schematic diagram of energy flow represented the food web structure of the Tonle Sap ecosystem. The grey lines denote the trophic levels 1, 2 and 3 respectively, while the different sizes of the circles indicate the different biomass ($t\,km^{-2}$) of the function groups.

4. Discussion

4.1. Food web structure in TSL

The current study contributed to constructing the first mass-balance model in the TSL ecosystem where ecological information and understanding were scarce. The model is a useful tool for assessing the ecosystem health and the overall functioning of this large freshwater system. From the basic estimate of the model, the biomass of fish groups in the TSL ecosystem was estimated at $58\,t\,km^{-2}$ higher than the estimated biomass of fish groups in Lake Victoria ($43\,t\,km^{-2}$) and Lake Tanganyika ($35\,t\,km^{-2}$) (Christensen and Pauly, 1993). The relatively high biomass of the top predators in TSL could produce a predation pressure on its forage species through the top-down controls in the food web (Du et al., 2015). The catch statistics from the lake showed that snakehead and catfish were found to be abundant in the TSL system since TSL and its floodplains are suitable feeding and spawning grounds for many carnivore species (Van Zalinge et al., 1998). Indeed, according to their ecological guilds, snakehead and climbing perch (i.e., *Anabas testudineus*) were categorized as "Black fish" or resident fish, they stay permanently in the lake, swamp or pond all year round in contrast to many species of catfish and soldier river barb known as "White fish" that migrate between TSL and the Mekong

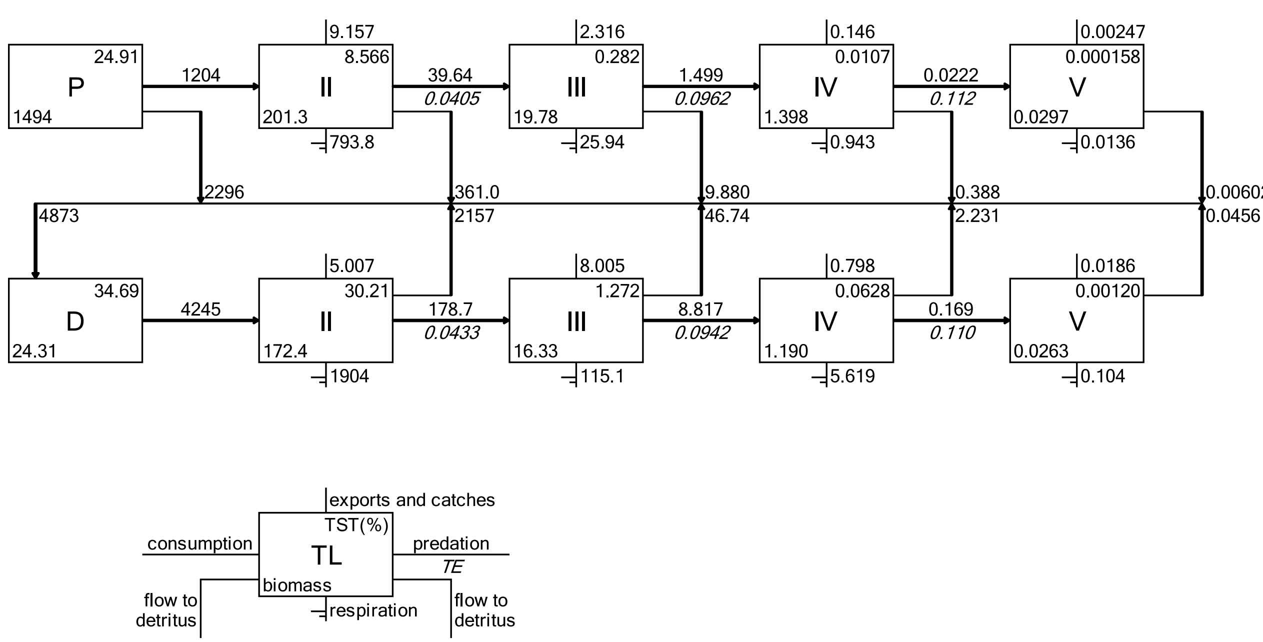

Fig. 3. Lindeman spine of Tonle Sap Lake system. *P* and *D* represent the primary production and detritus respectively, while the values in boxes indicate the biomass and percentage of total system throughput (TST) for each trophic level (TL). The values above and below arrows exhibit the efficiency of energy transfer (TE) through each trophic level.

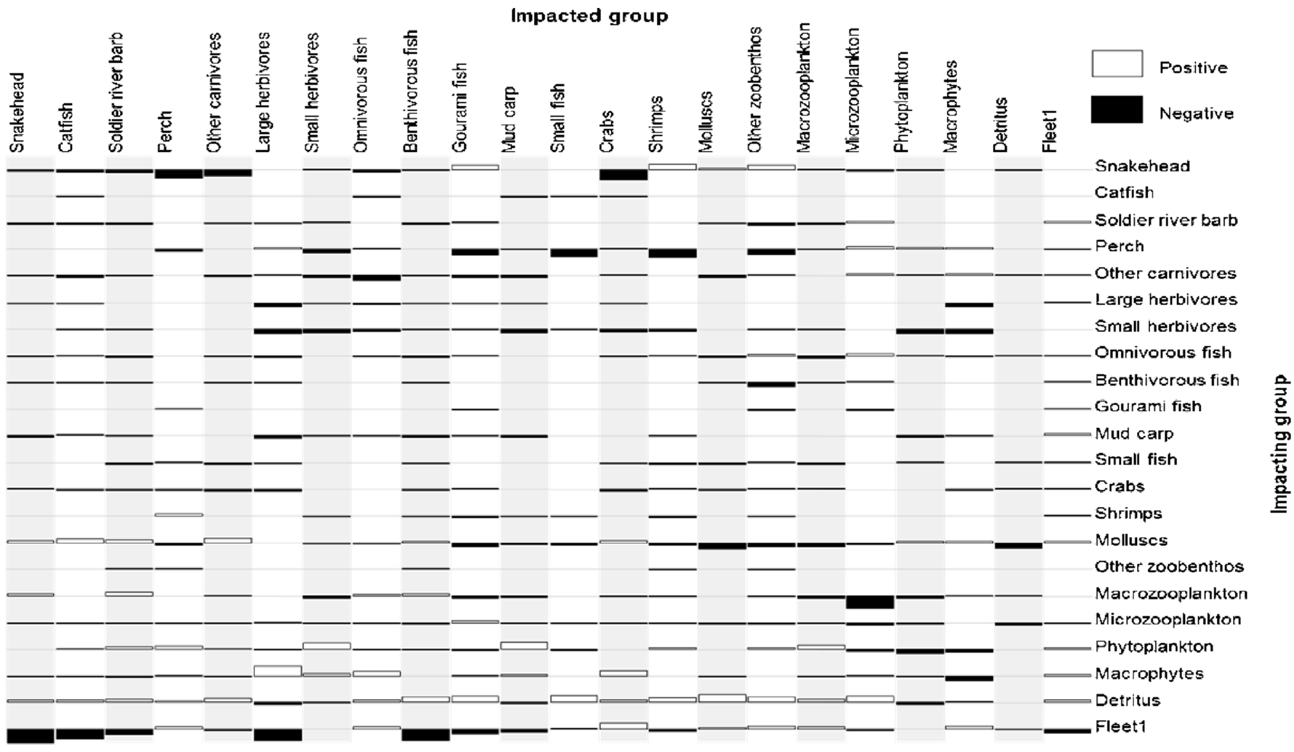

Fig. 4. Mixed trophic impact (MTI) of Tonle Sap lake ecosystem. The black bars pointing downwards show the negative impact on the functional groups, while the white bars pointing upwards indicate the positive impacts. The heights of the bars are proportionate to the degree of the impacts and its values ranges from −1 to +1.

river. Intermittent between black and white fish, many species of other carnivores (i.e., *Wallago attu*, *Hemibargus* sp., *Belodontichthys dinema*, *Colia lindmani*, *Krytopterus cheveyi*) were categorized as "Grey fish"; they do the short distance migration and tend to spend the dry season in the lake rather than migrating to the Mekong river like the white fish (MRC, 2010). This could explain the high proportion of top predators in the TSL food web since TSL is crucial for all fish guilds to complete their life cycles.

One of the most prominent features in the TSL food web could be observed from the variation of the estimated EE values in the constructing functional groups. The EE values are defined as the proportion of production that is exported out of the system through fishing activities or consumed by predators within it (Coll et al., 2009). As a result, the EE values were estimated to be greater than 0.5 for almost all functional groups except molluscs and macrophytes. The high EE values of fish groups illustrated the pressure on the resources suffered from fishing activities as well as predation pressure for the forage fish groups (i.e., mud carp, small herbivores and small fish). This result was consistent with many previous studies on the fishery production of the lake that have drawn their concerns on over exploitation of fisheries resources in the lake (Enomoto et al., 2011). In addition, Enomoto et al. (2011) illustrated the fluctuation of CPUE (catch per unit effort) of snakehead (*Channa* sp.) and catfish (*Pangasius* sp.) which tended to decline compared to those of the opportunist species such as mud carp (*Henicorhynchus* sp.), small herbivores (*Labiobarbus* sp.), and gourami fish (*Trichopodus* sp.). In 2008, the catch statistics from the fishing lots in the East part of TSL (Kampong Thom province) illustrated that the CPUE, i.e., the total catch (t) divided by the total length of bamboo fence systems (km), of snakehead and catfish were about 2 t km^{-1} lower than mud carp (6 t km^{-1}) (Enomoto et al., 2011). Moreover, Lamberts (2001) produced length-weight relationships for soldier river barb (*Cyclocheilichthys enoplos*) and showed that this species, which can reach a total length of 90 cm, was found only at lengths of up to or less than 45 cm, which is the most common in the lake.

In contrast, the estimated EE values of molluscs and macrophytes were very low since molluscs and macrophytes were not well utilized in the TSL ecosystem. Normally, macrophyte communities are not easy to be utilized in the ecosystem when they are alive (Christensen et al., 2005). Campbell (2006) reported more than 200 species of terrestrial vegetation are found in TSL. Moreover, the biomass of macrophytes represented more than 80% of the total biomass in the ecosystem, but from an ecological point of view, there are not many fish species that can consume large portions of macrophytes (e.g., in TSL ecosystem, only large herbivores were able to consume large part of macrophytes). Meanwhile, the underlying reason for the extremely high biomass of molluscs in the lake could be due to their low EE. Lamberts (2001) reported that molluscs made up over 85% of zoobenthos communities by weight. Moreover, Ohtaka et al. (2010) mentioned that molluscs were very abundant compared to the other zoobenthos such as oligochaeta and insects; which were found to be scarce in the lake and which could suffer from predation by benthivorous fish in the system. Indeed, the MTI analysis (Fig. 4) also showed the negative impact of benthivorous fish on other zoobenthos communities; this could confirm its predation pressure on other zoobenthos group. As the energy source of the ecosystem, we found the EE values of phytoplankton and detritus approached 1, which were comparatively high as other African great lakes (i.e., L. Victoria, Tanganyika, Malawi); particularly to Great Lake Chad with similar biomass of phytoplankton, macrophytes and zooplankton communities (Christensen and Pauly, 1993).

Another remarkable feature of the TSL food web is the transfer efficiency (TE) within its food chain. In TSL, the food web was more based on the detrital food chain than on the grazing food chain. By looking at the overall TE within the food web, we found low TE from TL II to TL III and then the TE started to increase significantly from TL III to higher TLs, which is in contrast with the African great lakes (i.e.: L. Victoria, Tanganyika, Malawi), where TEs declined dramatically from TL III to higher TLs (Christensen and Pauly, 1993).

This contrast drives us to point out the good utilization of fisheries resources in TSL for human consumption and predation instead of lacking exploitation as in the African lakes. Nevertheless, overexploitation of the fishery resources in the TSL was notified to fishing down the food chain, consequently dominated by small-sized fish; whereas a large proportion of primary production (macrophytes) was not well utilized in the ecosystem. This conclusion is consistent with the previous study of van Zalinge et al. (1998).

4.2. Ecosystem health assessment

The ecosystem health of TSL was quantitatively assessed using the ecosystem attributes and ecological indicators given by the Ecopath model. Xu et al. (2001) provided some indicators that could be used to assess the lake ecosystem health (i.e., phytoplankton biomass, zooplankton biomass, species diversity, P/R ratio, P/B ratio and buffer capacities). These indicators provided an overall assessment of the lake ecosystem health. Generally, a healthy lake ecosystem is characterized by low biomass of phytoplankton, high zooplankton and macrozooplankton biomass, high species diversity, high P/B ratio and P/R ratio approaching 1 (Xu et al., 2001).

With ecosystem development as stated by Odum (1969), the ratio of total primary production to respiration (TPP/TR) and total primary production to biomass (TPP/B) are two important indicators to measure the maturity of an ecosystem. The mature ecosystem tends to have TPP/TR of nearly 1 and a low TPP/TB value. In the TSL system, the TPP/TR ratio was 1.23, much lower than most the lakes worldwide, as Lake Taihu (3.85), Lake Qiandaohu (3.725), but higher than lake Hayq in Ethiopia (1.05). Therewith, the TPP/TB ratio was 2.482 in between the immature lake ecosystem Taihu (11.6) and mature ecosystem lake Gehu (1.76), much lower than Lake Awassa (5.834) and lake Malawi (66) (Liu et al., 2007; Fetahi and Mengistou, 2007; Darwall et al., 2010; Fetahi et al., 2011; Jia et al., 2012; Li et al., 2010;). According to Ulanowicz and Norden (1990) and Ulanowicz (1987), the ratio of ascendency to system throughput and overhead could also be the measurement of ecosystem growth and development. The high overhead value indicates the stability of the ecosystem; in TSL the ascendency was 27.4%, slightly higher than Taihu lake (25.9%); yet much lower than the mature ecosystem of Bao'an lake (38.7%) and Lake Gehu (33.2%), which suggested that the lake achieved some level of stability close to the mature stage.

The Finn cycling index (FCI) represents the fraction of an ecosystem's throughput that is recycled compared to total throughput. Finn (1976) stated that this index strongly correlates with ecosystem maturity, resilience and stability. Indeed, cycling index is assumed to increase as systems mature and become more stable (Odum, 1969). This is because low cycling is highly dependent on energy passing rapidly through and is rather unstable and vulnerable to the changes in nutrient input (Christensen and Pauly, 1993). Moreover, a high cycling flow could also actually be a sign of stress, especially if most of the cycling occurs over short periods near the base of the trophic ladder (Christensen et al., 2005). The value of FCI in TSL was 23.62%, slightly lower than in Taihu lake in the 1960s and 1980s (24.2%, 26.56%) and Quiandaoho lake (24.2%), but higher than other Chinese lakes: Gehu lake (14.76%), Bao'an lake (9.25%). Consequently, the higher the cycling index the more the ecosystem is released from stress (Guo et al., 2013; Jia et al., 2012; Li et al., 2010; Liu et al., 2007).

In addition, CI and SOI are the important indices used to describe the food web feature, which could describe the system maturity since the food chain is expected to change from linear to web-like as the mature ecosystem. Ecosystems with higher values of ascendency (%) indeed reflect relatively higher levels of maturity. In TSL system, the value of CI and SOI were 0.253 and 0.075, respectively. Given the fact that the CI value was almost the same as the theoretical value (0.252) calculated using the empirical regression equation (Christensen and Pauly, 1993). Comparatively, the CI and SOI indices were much lower than for Lake Ayame in Ivory Cost (0. 386, 0.193), and Lake Annecy in France (0.258, 0.107) and slightly higher than Chinese lakes: Taihu (0.206, 0.042) and Bao'an (0.205, 0.058) (Janjua and Gerdeaux, 2009; Traore et al., 2008). High values of CI and SOI could reflect the high diversity of diet composition while low values indicate a linear food web pattern rather than a web-like structure.

According to Odum (1969), the high values of TPP/TR and ascendency and the low values of TPP/TB, and the more detritus dominated food chain, we concluded that the TSL ecosystem achieved a certain stage of maturity with a vulnerable food web structure due to the lack of complexity in the food web structure expressed by the low values of CI and SOI. The systematic results globally suggested that TSL could be considered as a healthy ecosystem (i.e., high biomass of macrozooplankton, low biomass of phytoplankton, TPP/TR value near 1), however still suffering from human disturbance (e.g., overfishing) (Odum, 1969; Xu et al., 2001).

4.3. Ecosystem-based fisheries management

The overexploitation of aquatic living resources is common in today's fisheries worldwide, even freshwater ecosystems are heavily influenced by intense fishing activities (Mchich et al., 2006). In view of these facts, it is widely accepted that an ecosystem-based approach to fisheries management is important for maintaining sustainable fisheries and healthy ecosystems (FAO, 1995; NRC, 1999). Ecosystem models are complementary to single-species fisheries models in that they are potentially able to predict otherwise unforeseen effects of trophic interactions; they are now common in stock assessment and fisheries management (Coll et al., 2006; Fletcher et al., 2005). Ecosystem based fishery management has already been widely employed worldwide, as in the Great Lakes in the USA (Kolding et al., 2008), Qiandaohu Lake (Liu et al., 2007), Bao'an Lake (Guo et al., 2013) and Three Gorges Reservoir (Mao et al., 2014) in China.

In the TSL system, MTI analyses have highlighted the fishing pressure on many fish functional groups, especially the top predators (i.e., snakehead, catfish, other carnivores, river barb, large herbivores and benthivorous fish). Many previous studies on fish production of the lake have confirmed this compounded by the over harvesting of the commercial species from the lake (Cooperman et al., 2012; Enomoto et al., 2011). Overfishing could significantly impact the food web structure of the lake causing the shift from *k-selected* species (large long-lived species) to *r-selected* species (small fast growing species) (Travers et al., 2010). Recent statistics of fish catch from the lake showed that the catch composition was dominated by the opportunist species (mud carp, small herbivores) and small size fish even economically important species, that means most of them were caught at the young age or juvenile stage and hadn't reached maturity (Enomoto et al., 2011; Lieng and Van Zalinge, 2003; Van Zalinge et al., 2001). This could introduce the "*fishing down the food web*" concept where large predatory fish at the top of the food web are depleted, increasing the numbers of small fish (Pauly et al., 1998).

Globally, fish and fishery resource management should aim to increase predator diversity since numerous studies showed that predator diversity can strengthen ecosystem function and food web structure, and thus improve the transfer efficiency (Carey and Wahl, 2011; Griffin et al., 2008). As a recent example from the food web model of Lake Hayq, the introduction of African perch (Tilapia) in the lake contributed to improving the transfer efficiency and maturity of the lake (Fetahi et al., 2011).

Based on ecosystem analysis, to improve fishery management and ecosystem health in TSL, ecosystem-oriented strategies are suggested here:

Fish stocking and fry release could be an effective method for compensating the fishery resources degradation. Additionally, the trophic interactions must be considered in the stock assessment and management program since predation could modulate the population dynamics of the most important fishery resources. Specifically in TSL, piscivores and omnivores such as catfish, snakehead, river barb and other omnivorous fish could be advisable for stocking. Since these are the two most important groups to mediate biodiversity–ecosystem functioning relationships in the food web (Bruno and O'Connor, 2005; Petchey et al., 2004).

More efforts should be taken in fish biodiversity conservation, especially for some native species and endangered species. As an example of Giant barb (*Cartlocarpio siamensis*) and Mekong giant catfish (*Pagasianodon gigas*), which are the two giant herbivorous and piscivorous fish in the TSL and Mekong systems. Their populations have decreased dramatically and they are rarely seen in the lake these days due to habitat degradation (i.e., deforestation of flooded forest, which is the key breeding ground for these fish) and pressure from illegal fishing activities. Moreover, restricting the use on fishing gear and the length of the fishing season could be very beneficial to ensure the sustainability of the lake. As a result of the recent stock assessment study in TSL, the reduction of the number of small meshed gill nets (diameter <50 mm) diverting more effort to hook and line has contributed to the improvement of snakehead and river barb production (Yen et al., 2009).

More attention should be also paid to the utilization of primary production and detritus, not only to improve the energy flows in the TSL ecosystem, but also to improve the water quality, especially during the dry season when it shows dramatic degradation due to excess of production algae and submerged terrestrial vegetation. Therefore, stocking with large herbivores and omnivorous fish (e.g., *Labeo chrysophekadion*, *Cirrhinus microlepis*, *Catlocarpio siamensis*, *Hypsibarbus malcolmi*, *Puntioplites proctozysron*) could be very favourable and consistent with the utilization of excess macrophytes.

In combination with the ecological perspective, the construction of hydropower dams along the Mekong mainstream and its tributaries could also be a major challenge leading to the degradation of fisheries resources in the lake since many studies on the impact of dams have concluded that it has a negative impact on the TSL floodplain as well as flood duration, and sediment fluxes, which are the key drivers of the TSL's productivity and sustainability (Arias et al., 2014). Thus, concrete strategic management plans for dam construction are needed to mitigate these issues and ensure fishery resources and the vital roles of this productive ecosystem.

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