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

Ratha Chea[a,b], Chuanbo Guo[a,c,*], Gaël Grenouillet[a], Sovan Lek[a]

[a] Université de Toulouse, Labo Evolution & Diversité Biologique, UMR5174 EDB CNRS – Université Paul Sabatier-ENFA, F-31062 Toulouse, France
[b] Faculty of Agriculture and Food Processing, University of Battambang, Raod 5, Battambang city, Cambodia
[c] State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China

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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

* Corresponding author at: State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China. Tel.: +86 27 68 78 07 17.
E-mail address: guochuanbo@gmail.com (C. Guo).

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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):

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

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	μS 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