



Research article

Trophic interactions and energy flows in ponds used for culture-based fisheries, with emphasis on giant freshwater prawn

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Abstract

A culture-based fishery (CBF) is a simple technology with a low capital cost to enhance fisheries production by stocking fish in small water bodies. A mass-balance Ecopath model was constructed in two CBF ponds in Nonghai and Nongtubkwai, Northeastern Thailand. A steady-state trophic model was constructed and used to examine the roles in ecological processes of each component in the CBF ponds with an emphasis on the stocked giant freshwater prawn *Macrobrachium rosenbergii* De Man, 1879. There were 12 and 7 fish components in the Nonghai and Nongtubkwai models, respectively. The trophic levels (TL) of the components ranged from 1 (for plant, phytoplankton and detritus) to over 3 for carnivorous fish. The TLs of the stocked components were between 2 and 3. The ecotrophic efficiency (EE) values of all components were less than 1 ranging from 0.13 to 0.89. The EE value of *M. rosenbergii* was about 0.8 and higher than for the other stocked fish species. The results also revealed that the grazing food chain was prominent in the CBF ecosystem. However, it was the detrital food chain that *M. rosenbergii* depended on, which made the prawn less competitive with other fish components in the ecosystem. The mixed trophic impact showed that the TL = 1 components had positive impacts on all the higher TL components, indicating bottom-up control.

Introduction

Freshwater aquatic animals are regarded as the most common animal protein source for the people of the Lower Mekong Basin (LMB) countries. Each year, 14 kg of freshwater fish are consumed per person in the LMB countries compared to the annual global average of about 2 kg per person (International Center for Environmental Management, 2010). Even though demand is high for freshwater aquatic animals, supply is often unstable and decreases due to over-exploitation and other human pressures such as infrastructure development, so there is an urgent need to improve freshwater fish production to reduce the gap

between supply and demand (Phomsouvanh et al., 2015). Many inland fishery enhancement programs have been applied to meet this demand in the LMB countries, in which culture-based fisheries (CBF) is one of the success programs (De Silva, 2003; Phomsouvanh et al., 2015). The CBF program is commonly conducted in small water bodies in rural areas and aims to raise the production and supply of food as well as to generate income by stocking fish fingerlings and letting them grow naturally to become adults (De Silva, 2003)

The CBF program is always conducted with less intensive resource and less technical expertise than conventional aquaculture (De Silva et al., 2006). In Thailand, the CBF in pond is controlled

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by the village fishery committee, which assumes responsibility for pond management including controlling bank erosion, eliminating predators, liming and fertilization (Jutagate and Rattanachai, 2010). Harvesting in a CBF pond is allowed once a year, generally at 9–11 mth post-stocking. The average yield from a CBF pond in Thailand fluctuates and can vary from less than 50 kg/ha/yr to in excess of 2,000 kg/ha/yr, depending on the trophic status of the water body and the stocking density (Lorenzen et al., 1998). Similar to CBF practices elsewhere, the fish species used in CBF in Thailand are always species that are available from fish farms and have rapid growth.

Other than finfish, an uncommon species in CBF is the giant freshwater prawn, *Macrobrachium rosenbergii* De Man, 1879 (New and Kutty, 2010; Jutagate and Kwangkhang, 2015). The advantage, other than food security, of stocking this non-fish species, is its high price. For example, in Thailand, the price can be as high as USD 15/kg compared to about USD 3–5/kg of other stocked finfish species (Jutagate and Kwangkhang, 2015; Likittrakulwong et al., 2017). Thus, there is now an attempt to promote *M. rosenbergii* in CBF practice in Thailand.

The questions that always arise in a stocking program, from a pond ecology point of view, concern competition of the stocked species with the native residents, disrupting the food chain as well as overcrowding that could lead to an imbalance in the ecosystem, which then causes failure of the program. Much evidence has been provided showing that the food web structure and food web dynamics are susceptible to human activities, including fish stocking programs

(Khan et al., 2015). The impacts of stocking large inland water bodies, such as lakes and reservoirs, have been studied in detail, and the results have shown both the potential of negative and positive impacts, depending on the stocked species and ecosystems (Khan et al., 2015). However, few studies have looked at small water bodies under the CBF program. Thus, the objectives of this study were to construct a steady-state trophic model for CBF examples and to examine the roles in the ecological processes of each component, with emphasis on *M. rosenbergii*, using the mass balance Ecopath model (Christensen et al., 2005). This model is considered one of the most effective and straightforward methods for quantifying the food web interactions and fisheries ecosystem dynamics (Christensen et al., 2005; Khan et al., 2015).

Materials and Methods

Study sites and CBF practice

The CBF in the two communal ponds in the LMB (Fig. 1) were located in Ubon Ratchathani, Northeastern Thailand, in Nonghai (1.14 ha; 14°46.944'N, 105°5.862'E) and Nongtubkwai (2.07 ha; 14°54.170'N, 104°55.783'E). The main difference between the two case study ponds was that the one in Nonghai had more carnivorous fish. Both ponds were within the range of appropriate pond sizes for CBF of 0.8–2.4 ha (De Silva et al., 2006) and had operated as a CBF for more than 5 yr and had similar pond characteristics.

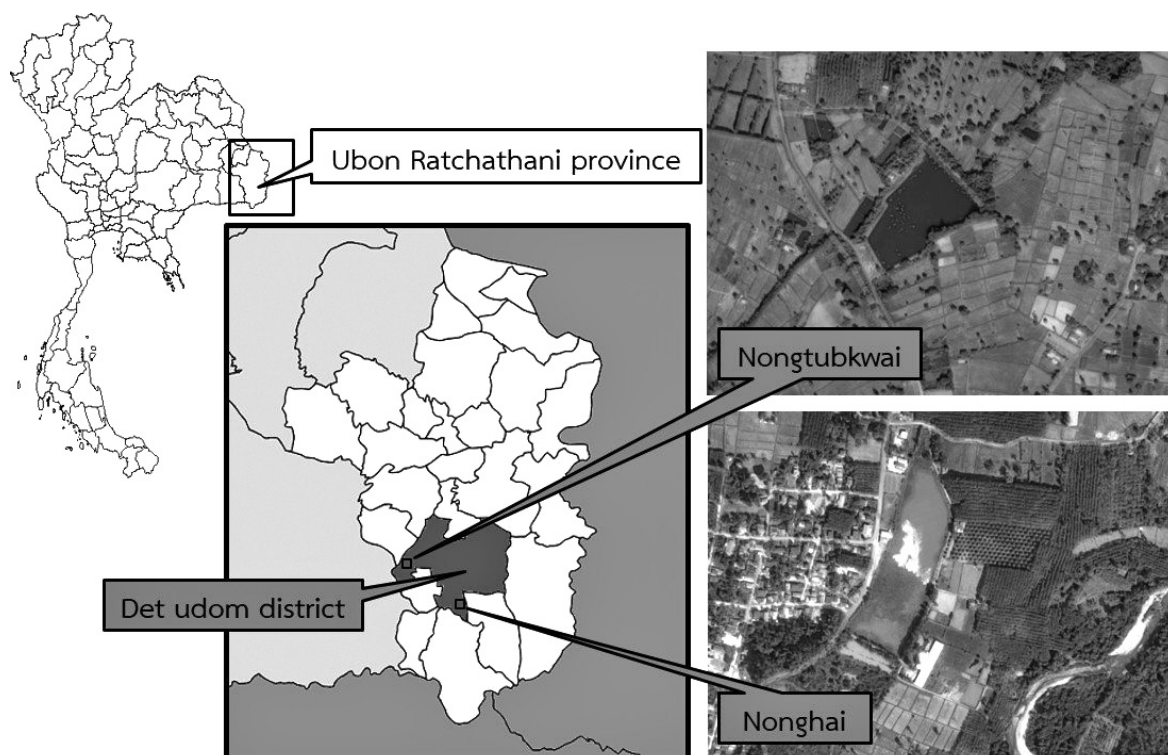


Fig. 1 Locations and aerial views of the culture-based fishery ponds in this study

About a week prior to stocking, lime (about 40 kg/ha) was added to improve the water and soil quality. Rice bran, dried manure and hay were also added to create natural food sources (plankton). Artificial habitat was constructed using tree branches and bamboo as shade for the stocked fish fingerlings and *M. rosenbergii* post larvae (PL), before being moved out after 3 mth of stocking.

Stocking always done during the onset of the rainy season (May or June) and the culture cycle lasts for 9–10 mth. The fingerlings of various species are released every year, with the stocking density in the range 500–1,500 fingerlings/rai regardless of the species, but never for *M. rosenbergii*. In the cycle of 2015–2016, at 20 d PL, the *M. rosenbergii* (Jutagate et al., 2017) were stocked at a rate of 5,000 prawns/ha and 10,000 prawns/ha for Nonghai and Nongtubkwai, respectively. Stocking was conducted on 30 April 2015 and 29 May 2015 in the respective ponds, and the cycle of CBF was about 10 mth. The form of CBF management for both ponds was in Category 3 as described by Phomsouvanh et al. (2015), in which the community committee takes care of any poaching and harvesting is allowed once a year. On the harvest day (22 March 2016 and 6 April 2016 in Nonghai and Nongtubkwai, respectively), tickets were sold to whoever wanted to catch fishes and prawns.

The Ecopath model

Ecopath is a user friendly software program developed to construct a model of the trophic flows in an ecosystem based on mass-balanced models (Christensen et al., 2005). The software partitions the living organisms in the ecosystem into components (species or groups), according to physical habitat, similar diets and life-history characteristics.

To construct the Ecopath, the model is expressed in terms of utilization of production of each component in the ecosystem at an arbitrary time period, and expressed using Equation 1:

$$B_i \times (P/B)_i \times EE_i = \sum_{j=1}^n B_j \times (Q/B)_j \times DC_{ij} + EX_i \quad (1)$$

where, subscripts *i* and *j* refers to the prey and predator groups, respectively; B_i is the biomass; $(P/B)_i$ is the production/biomass ratio; EE_i is the ecotrophic efficiency (the fraction of the production that is utilized within the ecosystem by predators or exported to a fishery); B_j is the biomass of predator *j*; $(Q/B)_j$ is the relative food consumption of *j*; DC_{ij} is the fraction of prey *i* in the diet of predator *j*; EX_i is an export from the ecosystem, mostly through fisheries.

From Equation 1, the four parameters, B_i , $(P/B)_i$, EE_i and $(Q/B)_j$, as well as the diet composition of each component are required as inputs to construct the Ecopath model. At least three out of the four parameters have to be input to the model for each component and then *n* linear equations for *n* components are solved for the remaining parameter (Christensen et al., 2005; Khan et al., 2015).

Inputs and parameters estimation

There were 12 and 7 fish/group defined to establish Ecopath in Nonghai and Nongtubkwai, respectively. The components, defined as

a group were species having similar diets and life-history characteristics (Christensen et al., 2005), which were obtained from FishBase (Froese and Pauly, 2017). Other than the fish species, *M. rosenbergii*, zooplankton, zoobenthos (annelids, isopods and mollusks), plants and phytoplankton were in the ecosystem of both ponds. The biomass amounts of the finfish and prawns were based on measurements from the harvest. In addition, a supplement beach sein was dragged through the ponds the following day to add to the actual biomass of each component.

The biomass amounts of the zooplankton, zoobenthos and phytoplankton were adopted from data from the Sirindhorn Reservoir, 40 km distant from the two study sites (Jutagate et al., 2002). Littoral vegetation (plants) was collected from three randomly selected sites in each pond using a 1 m² × 1 m² quadrat, weighed and then used to estimate the total biomass according to the plant-covered area around the pond. Standing stock of detritus (D, measured in grams per square meter) was estimated using Equation 2 according to Pauly et al. (1993):

$$\log_{10}D = -24 + 0.954\log_{10}PP + 0.863\log_{10}E \quad (2)$$

where, PP is the primary productivity (measured in grams per square centimeter per cycle) and E is the eutrophic depth (measured in meters). PP was set as a pond having added natural fertilizer at 9.8 g/cm² /day or about 2,940 g cm⁻² cycle⁻¹ (Olah et al., 1987), so that one cycle took about 10 mth or 300 d, while the water level of the pond was maintained at about 2.5 m throughout the cycle. The biomass amounts of all components were converted into tonnes per square kilometer per cycle as input to the model.

Diet composition was examined every 2 mth after stocking. At least 25 samples of each component (about five samples per sampling) were dissected to examine the stomach contents based on the volumetric method and presented as the proportion of total volume of all diets (Hyslops, 1980). Where fish meat was found in the stomach, a proportion was allocated to each fish species/component in the ecosystem according to the relevant literature (Chookajorn et al., 1994; Jutagate et al., 2002; Thapanand et al., 2009). In the Ecopath model, the trophic levels (TL) of producers and detritus are assigned as 1, while the TL of each individual component is estimated as 1 + [the weighted average of the preys' trophic level] (Odum and Heald, 1975).

Because of limited manpower, only the number, length and weight of individuals of *M. rosenbergii* were enumerated during the harvesting day, while the other catches were only identified to the species level and then weighed. It is difficult to estimate P/B through the total mortality coefficient (Z) and the relevant growth parameters. The P/B and Q/B values of the fish were adopted from the FishBase website (www.fishbase.org) and previous published studies (Chookajorn et al., 1994; Jutagate et al., 2002; Thapanand et al., 2009). The Q/B of *M. rosenbergii* was also taken from the literature (Deng et al. 2015), while P/B was estimated using Equation 3:

$$Z = \ln \left(\frac{N_t}{N_0} \right) \quad (3)$$

where, N_t and N_0 are the numbers of *M. rosenbergii* on the harvest day and at stocking, respectively.

In this study, the steady state Ecopath models were constructed using Ecopath with Ecosim version 6.2 (<http://www.ecopath.org>; Christensen and Walters, 2004). The criterion used for balancing the model was that the EE values for each component must be less than 1.0. Moreover, the gross food conversion efficiency (GE) in the system, of each component was required to be in the range 0.1–0.3 (Christensen et al., 2005). Thus, to meet the criteria to balance the model, subtle adjustment was made for diet composition. In Ecopath model, all components were assigned discrete trophic levels according to Lindeman (1942) based on the approach suggested by Ulanowicz (1995). Then, a modified input-output analysis of the mixed trophic impacts was implemented to identify how any group impacted on the other groups in the system (Christensen et al., 2005).

Results

The biomass, P/B and Q/B of each component in the Nonghai and Nongtubkwai CBF systems are shown in Table 1 and Table 2, respectively. The adjusted diet compositions for the Ecopath models of Nonghai and Nongtubkwai are shown in Table 3 and Table 4, respectively. The TLs of the carnivorous fish species were over 3.0, while the TLs of the other fish species in both systems were in the range 2–3. The TL of *M. rosenbergii* was about 2.5, which indicated its feeding plasticity. The calculated EE values varied among components and systems, but all EE values were less than 1 and obeyed the criteria of model balancing. Most of the GE values were in the range 0.1–0.3 except for *Barbonymus* spp. and *M. rosenbergii*, whose GE values were lower than 0.1, which implied a high rate of consumption. The EE values of zooplankton and zoobenthos were

close to 1, indicating that they were the most exploited components in both systems. Considering the autochthonous sources in both ponds, the EE value of the phytoplankton was higher than the EE value of plants, which implied that there was greater consumption of phytoplankton than plants. The detritus (EE values in the range 0.3–0.4) was also regarded as an important food source, which was substantially utilized in both systems.

The EE values of the carnivorous fish species were relatively low, indicating that they were less predated by the other components in the system. In the Nonghai pond, the EE values of the stocked Chinese carp and *Barbonymus* spp. were quite high (greater than 0.6), while in Nongtubkwai, which had an implied less complex system, only *Barbonymus* spp. had a high EE value. For *M. rosenbergii*, the EE value in Nonghai was also higher than in Nongtubkwai, indicating their likelihood of predation on higher TL in the complex system. The proportions of total primary production to total respiration (TPP/TR) were 1.64 and 1.31 in Nonghai and Nongtubkwai, respectively. The connectance index (CI) was quite similar in the two systems (0.39 in Nonghai and 0.38 in Nongtubkwai) but the system omnivory index in Nonghai (0.15) was higher than in Nongtubkwai (0.07). The results of Lindeman's analysis (Lindeman, 1942) showed that the grazing food chain transferred more energy and matter into the system than the detrital-based food chain in both ecosystems by about 1.5 times in Nonghai (1,353 and 932 t/km²/yr) and more than twice in Nongtubkwai (1,069 t/km²/yr and 517 t/km²/yr). The highest transfer efficiency (TE, the ratio between the sum of the exports from a given trophic level, plus the flow that is transferred from trophic level to the next, and the throughput on the trophic level) was observed in TL = 3.

Table 1 Basic inputs (biomass, production/biomass ratio (P/B) and relative food consumption (Q/B)) and estimated parameters (trophic level, ecotrophic efficiency (EE) and gross food conversion efficiency (GE)) in the Ecopath model of Nonghai ecosystem

Group	Group name	Trophic level (TL)	Biomass (t/km ²)	P/B (per yr)	Q/B (per yr)	EE	GE
1	<i>Channa striata</i>	3.25	0.43	1.00	5.60	0.29	0.18
2	<i>Oxyeleotris marmorata</i>	3.45	0.19	1.50	8.90	0.26	0.17
3	<i>Clarias macrocephalus</i>	3.18	0.71	1.85	9.80	0.16	0.19
4	<i>Ompok bimaculatus</i>	3.20	0.12	1.60	13.40	0.17	0.12
5	<i>Notopterus notopterus</i>	3.00	0.65	1.05	7.70	0.35	0.14
6	Bagrids ^{1/}	3.06	1.92	1.70	14.30	0.23	0.12
7	<i>Mastacembelus armatus</i>	2.98	0.09	3.20	20.61	0.39	0.16
8	<i>Pristolepis fasciata</i>	2.90	0.37	2.10	9.90	0.69	0.21
9	Chinese carps ^{*, 2/}	2.20	1.98	1.10	8.00	0.79	0.14
10	<i>Barbonymus</i> spp. ^{*, 3/}	2.26	3.76	3.30	46.30	0.74	0.07
11	Cyprinids	2.20	13.07	2.50	16.00	0.48	0.16
12	<i>Xenentodon canceloides</i>	3.16	0.06	2.09	16.18	0.13	0.13
13	<i>Macrobrachium rosenbergii</i> *	2.55	4.02	2.30	28.00	0.83	0.08
14	Zooplankton	2.00	2.00	30.00	200.00	0.89	0.15
15	Zoobenthos	2.03	7.80	30.00	200.00	0.63	0.15
16	Plants	1.00	8.56	70.00		0.20	
17	Phytoplankton	1.00	5.80	365.00		0.58	
18	Detritus	1.00	17.50			0.47	

Note: * stocked components; ^{1/} *Hemibagrus nemurus* and *Mystus multiradiatus*; ^{2/} *Hypophthalmichthys nobilis* and *Cyprinus carpio*; ^{3/} *Barbonymus gonionotus*, *Barbonymus schwanenfeldii* and *Puntioplites proctozystron*; ^{4/} *Thynnichthys thynnoides*, *Cyclocheilichthys repasson*, *Labiobarbus siamensis*, *Osteochilus hasseltii*, and *Hemicorhynchus siamensis*

The balanced network analysis (Fig. 2) showed the interaction and energy flows among each component in the system. It was clear that *M. rosenbergii* mostly depended on the detrital-based food chain. The mixed trophic impact (Fig. 3) describes the impact of all components in the system when the abundance of any impacting groups showed an infinitesimal increase, that is 10% in terms of relative but comparable between impacted groups. Increased natural food sources (detritus, zooplankton, zoobenthos, phytoplankton and plants) had a positive impact on most of the remaining components, indicating bottom-up regulation in both the Nonghai and Nongtubkwai ecosystems. Increase in the abundance of carnivorous fish (TL > 3), resulted in a negative impact on most fish groups within this ecosystem. Competition among the stocked fish, such as Chinese carp, *Oreochromis niloticus* and Cyprinids, had negative impacts on each other if their abundance levels increased. An increase in *M. rosenbergii* tended to benefit the higher trophic components and did not impact any natural food resources,

except the zoobenthos. The strong negative impact of an increase in the *M. rosenbergii* population through cannibalism was quite obvious in both ecosystems.

Discussion

This study was the first attempt to explain the food web structure through a mass balance model of the CBF ecosystem. The Ecopath model was created in two CBF ecosystems to assess the roles and impacts of stocking species, in particular the shellfish *M. rosenbergii*. Although CBF is commonly conducted in village ponds (a lentic ecosystem), most of the CBF water bodies are non-perennial and may only have full storage for 4–6 months of the year. This makes the seasonal variation in nutrient cycling and fish production similar to a riverine system, and for this reason affects the intra- and inter-specific interactions as well as competition for resources (Villanueva et al., 2009; Phomsouvanh et al., 2015).

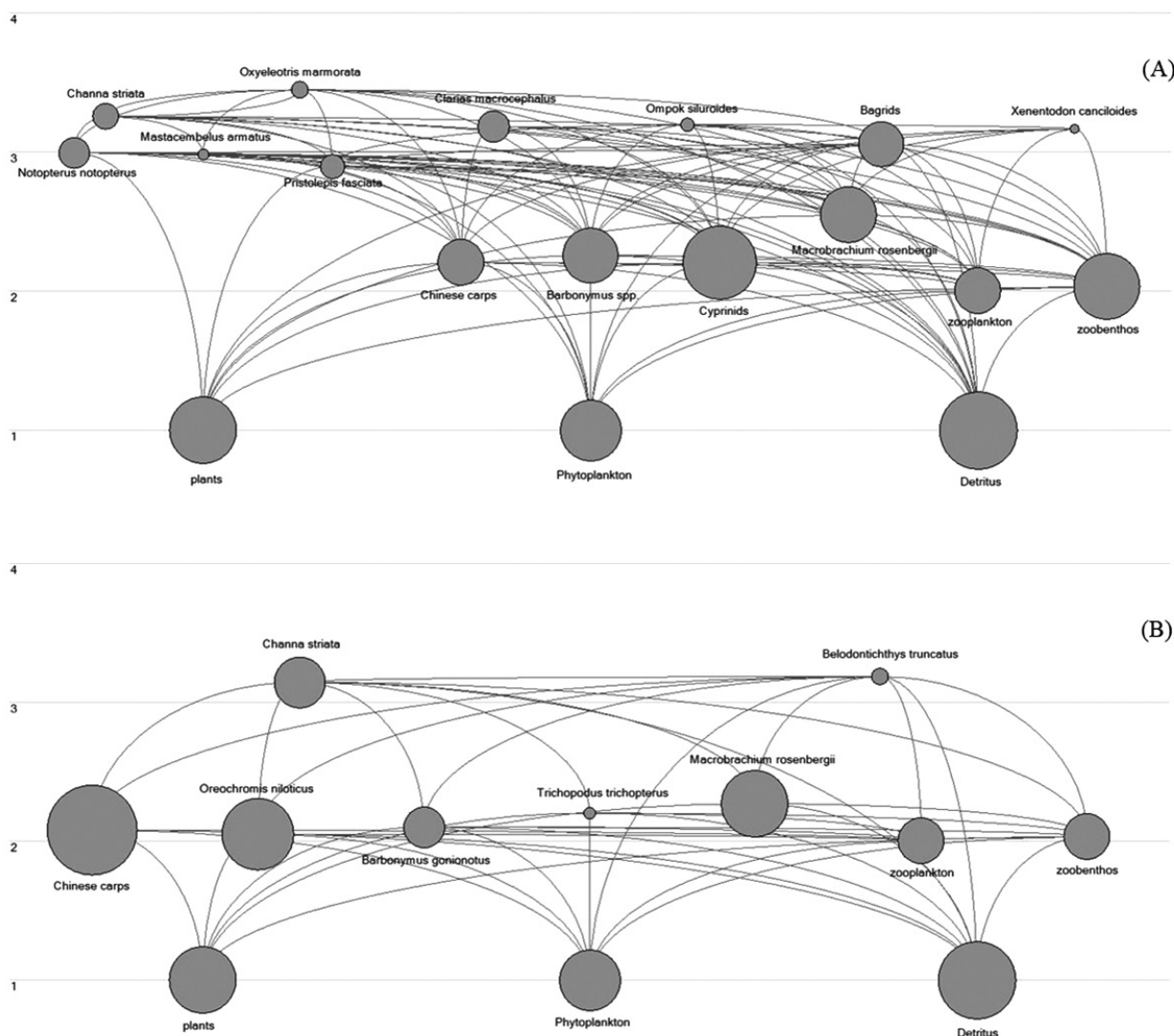


Fig. 2 Schematic diagram of trophic flows and food web structure in the 2 CBF ecosystem (the unit of biomass is t/km²): (A) Nonghai; (B) Nongtubkwai

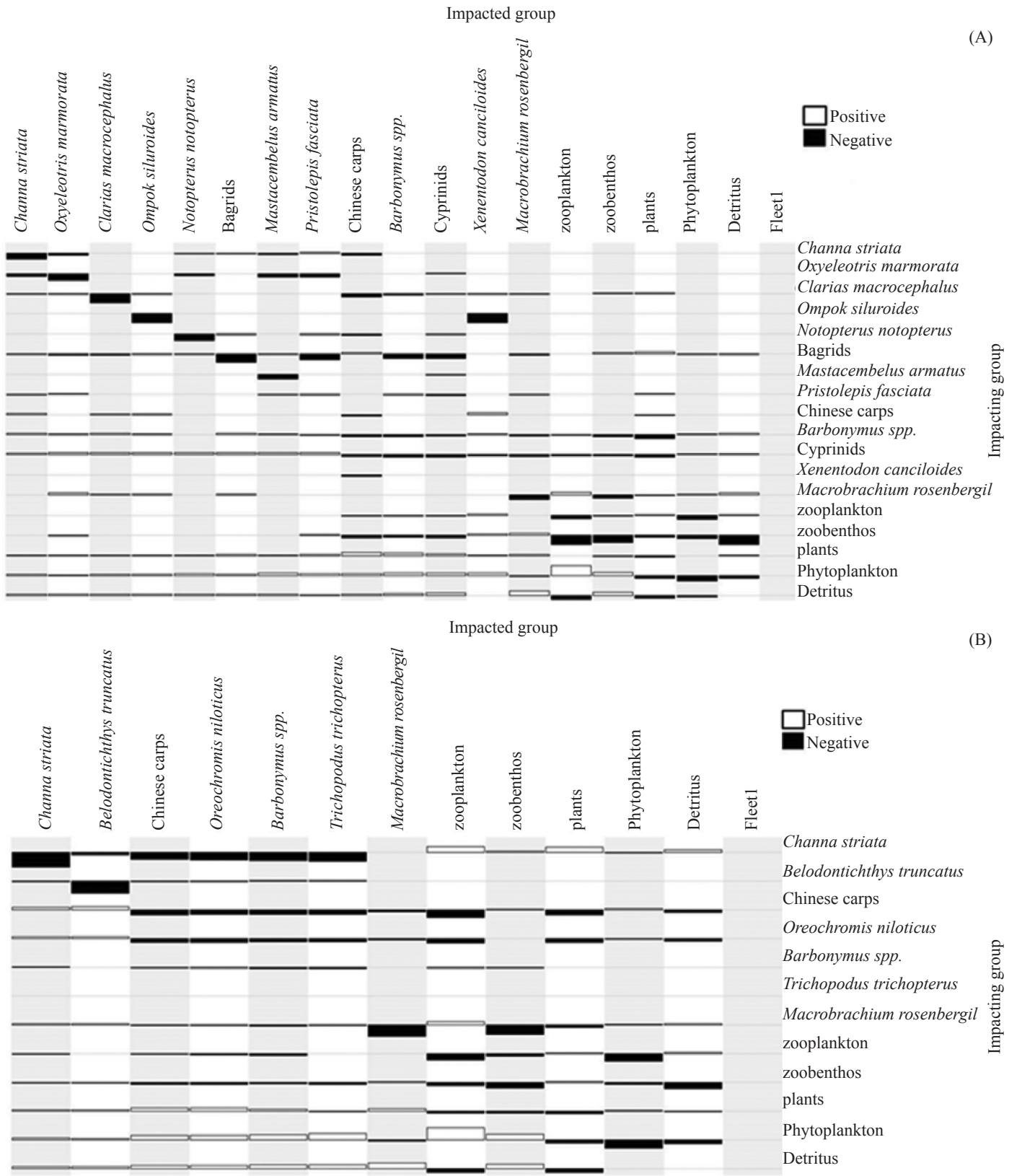


Fig. 3 Mixed trophic impacts in the two culture-based fishery ecosystems, where potentially positive (gray) and negative (black) impacts are, respectively, above and below the baseline

The EE values indicated that most components were substantially utilized within the system. Low EE values of phytoplankton in both ecosystems can be explained by two reasons. First, the supplementary fertilizer into the system caused an oversupply of phytoplankton in the system (Olah et al., 1987). Second, there was lower utilization of phytoplankton by the zoobenthos, zooplankton and herbivorous (TL ~ 2) fish, because they were predated by the higher TL components, in particular the system with an abundance of carnivorous fish (Nongtubkwai). Fluctuation in the EE values of the “TL ~ 2” components from water body to water body was likely caused by predation; Villanueva et al. (2009) reported that the EE values of “TL ~ 2” components could as be high as 0.95 in a system having high abundance of carnivorous fish but, on the other hand, could be less than 0.5 in a system having low abundance of carnivorous fish.

As a consequence of the low EE value of phytoplankton, the excess production then went into detritus, which made the detritus biomass accumulation greater than consumption and hence it was not utilized adequately in the food web (Deng et al., 2015). This highlighted the benefit of stocking bottom feeders such as *M. rosenbergii* to increase the utilization of detritus in the system (Correia et al., 2003). Khan et al. (2015) showed that the EE value of detritus increased from less than 0.1 to 0.25 by stocking with bottom-feeding fish. The high EE values of *M. rosenbergii* in both ecosystems could be explained by cannibalism, in particular during the post larval stage because of frequent molting (New and Kutty, 2010). Lower utilization of plants could be explained by the lack of true plant-eaters such as the stocked Chinese grass carp *Ctenopharyngodon idella* in the ecosystem (Khan et al., 2015). The substantial EE for the top predators (TL ~ 3) was due to cannibalism, which has also been noted in the mixed trophic impacts (Christensen et al., 2005).

Low GE values are common for many tropical herbivorous cyprinids such as *Barbonymus* spp. (Villanueva et al., 2009). This could be explained by their high feeding rate for building mass, growth and gonad development, which occurs all year round (Weliange et al., 2006). According to Odum (1969), TPP/TR in the mature ecosystem should be equal, and the total primary production to biomass should be low. However, the CBF in pond ecosystem is likely to be immature because the total primary production is normally in excess through additional fertilizer. The higher CI (almost 0.4) indicated the high complexity of the food web structure in the CBF pond compared to the CI values in large inland water bodies, which have a CI value of around 2.5 (Thapanand et al., 2009; Villanueva et al., 2009). The higher SOI in Nonghai suggested that the most diverse CBF ecosystem had less dietary specialization (Thapanand et al., 2009).

It was clear that the majority of biomass in both ecosystems came from the TL ~ 2 components, that is the stocking species, such as cyprinids, tilapia and Chinese carps. There was little variation in TL for these fish in both ecosystems compared to other studies, in which the TL was in the range 2.00–2.20 (Jutagate et al., 2002; Villanueva et al., 2009; Thapanand et al., 2009). The TL for *M. rosenbergii* was 2.5, which was reflected in high feeding plasticity, depending on the abundance and availability of food resources around its territory (Nelson and Knight, 1977). This highlighted the potential of this

shellfish as a candidate for CBF activity as it can rely on either the grazing- or detrital-based food chains in the ecosystem.

The mixed trophic impacts demonstrated the characteristics of bottom-up control in the CBF pond ecosystems, in which changes in abundance of the TL = 1 components had positive impacts on most of the other components in the higher trophic level and dominant ecosystem processes (Dyer and Letourneau, 2003; Thapanand et al., 2009). The possible “trophic cascade” in the CBF pond could occur if the pond carnivores are not removed, since they can predate the TL ~ 2 components and consequently produce an increase in phytoplankton abundance (Villanueva et al., 2009). An increased abundance of *M. rosenbergii* showed the negative impact on itself and its major prey (zoobenthos) and the slightly positive impact on the higher TL components. No obvious adverse impacts on any fish living in the same habitat with *M. rosenbergii* have been reported in both native and introduced ranges. Moreover, as *M. rosenbergii* depends on detrital-based food chains, this could minimize trophic competition to other stocking of TL ~ 2 fishes, which depend on the grazing food chain.

Conflict of Interest

The authors declare that there are no conflicts of interest.

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