

Primary Research Paper

## Food web of macroinvertebrate community in a Yangtze shallow lake: trophic basis and pathways

Xue-Qin Liu<sup>1,2</sup>, Hong-Zhu Wang<sup>1,\*</sup> & Xiao-Min Liang<sup>1</sup>

<sup>1</sup>State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, 430072, China

<sup>2</sup>Graduate School of the Chinese Academy of Sciences, Beijing, China

(\*Author for correspondence: E-mail: wanghz@ihb.ac.cn)

Received 11 August 2005; in revised form 27 March 2006; accepted 26 April 2006; published online 29 July 2006

**Key words:** Yangtze shallow lake, macroinvertebrates, trophic basis, food web quantification

### Abstract

No detailed food web research on macroinvertebrate community of lacustrine ecosystem was reported in China. The present study is the first attempt on the subject in Lake Biandantang, a macrophytic lake in Hubei Province. Food webs of the macroinvertebrate community were compiled bimonthly from March, 2002 to March, 2003. Dietary information was obtained from gut analysis. Linkage strength was quantified by combining estimates of energy flow (secondary production) with data of gut analysis. The macroinvertebrate community of Lake Biandantang was based heavily on detritus. Quantitative food webs showed the total ingestion ranged from 6930 to 36,340 mg dry mass m<sup>-2</sup> bimonthly. The ingestion of macroinvertebrate community was higher in the months with optimum temperature than that in other periods with higher or lower temperature. Through comparison, many patterns in benthic food web of Lake Biandantang are consistent with other detritus-based webs, such as stream webs, but different greatly from those based on autochthonous primary production (e.g. pelagic systems). It suggests that the trophic basis of the web is essential in shaping food web structure.

### Introduction

Food webs hold a central place in ecology (Cohen et al., 1990) and the study of their structures is considered to be important to the understanding of ecosystem function (Pimm, 1982). Analyses of food web data from past decades have revealed certain constant patterns (Cohen, 1977; Briand & Cohen, 1984; Sugihara et al., 1989; Cohen et al., 1990), but doubts have also existed in the patterns on account of the insufficient data and variable methodology (Pimm et al., 1991; Polis, 1991). Neglect of some trophic interactions in a web might have arisen from the limitations of data collection. Comparisons of webs were also confounded by the difference of data gathering. To

improve food web studies, analytical methods should be standardized so as to yield results of “more explicitness and more exhaustiveness” (Cohen et al., 1993). However, food webs are not only complex (Hall & Raffaelli, 1991; Williams & Martinez, 2000; Jones & Waldron, 2003), but hardly a static entity. Previous studies have shown that the temporal variations of webs are considerable (Warren, 1989; Closs & Lake, 1994; Tavares-Cromar & Williams, 1996; Schmid-Araya et al., 2002; Froneman, 2004). A good understanding of web patterns requires integrating most dynamics into food web studies.

Standard binary food webs which only show the presence or absence of feeding links dominate the published literatures. Such qualitative analysis is

problematic because all species and links are given equal weighting (Benke & Wallace, 1997). It has also resulted in a bias focusing on patterns (e.g. connectance) rather than processes (e.g. energy flow, population dynamics) (Hall & Raffaelli, 1993; Woodward & Hildrew, 2002). Polis (1994) pointed out that it is difficult or impossible to understand the dynamics and structure of food webs and interacting populations without incorporating energy flow. However, such attempts at detailed feeding pathways in aquatic webs were rare and mainly concentrated on streams (e.g. Benke & Wallace, 1997; Benke et al., 2001) and estuarine/marine systems (e.g. Raffaelli & Hall, 1996). Similar work has not been done in lakes so far.

Lakes are ideal ecosystems for food web studies because they have clearly defined boundaries with adjacent ecosystems. For many years, limnologists have focused mainly on pelagic pathways and ignored benthic processes. However, a conservative estimate showed that the benthic invertebrates contributed about 42% of whole lake secondary productivity (Vadeboncoeur et al., 2002). Thus, the research of benthic food web is essential to enhance our understanding of lake functions (Jeppesen et al., 1997; Vadeboncoeur & Lodge, 2000; Vander Zanden & Vadeboncoeur, 2002).

There are hundreds of shallow lakes along the Yangtze River in China, but to date no food web study was conducted on benthic invertebrate there. To determine the trophic basis and pathways of macroinvertebrate food webs in these lakes, a macrophytic lake, Lake Biandantang, was chosen for the purpose.

## Methods

### *Study site*

Lake Biandantang (30° 17' N, 114° 43' E) is located in the south of middle reach of Yangtze River (Fig. 1). This lake (333 ha) was formerly a part of Lake Baoan, Daye City, Hubei Province, but has been separated from the latter by a stony dike. Around the lake there are ponds and farmlands. The climate is warm, with an average annual rainfall of 1283 mm (Deng & Jin, 1991). Lake sediment consists of mud and plant material. During the research period, water temperature was  $17.9 \pm 2.5$  °C (mean  $\pm$  SE, the same below). Water depth and transparency were  $2.17 \pm 0.09$  m and  $133.0 \pm 3.7$  cm, respectively. Total organic matter in sediment was  $7.1 \pm 1.3\%$ . Total nitrogen

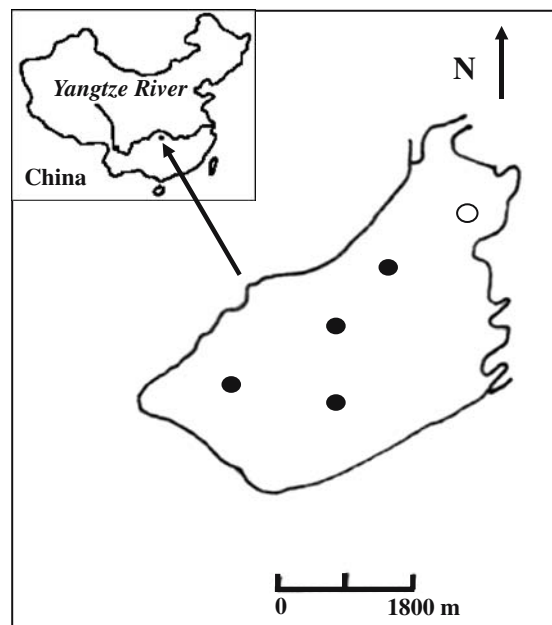


Figure 1. Location of study sites in Lake Biandantang, Hubei, China. White dot is the additional site.

and phosphorus in water were  $0.58 \pm 0.37 \text{ mg L}^{-1}$  and  $0.57 \pm 0.54 \text{ mg L}^{-1}$ , respectively. Chlorophyll *a* in lake water was  $5.81 \pm 2.61 \mu\text{g L}^{-1}$ . Biomass of macrophytes was  $279.2 \pm 121.3 \text{ g m}^{-2}$  by wet weight, comprising mainly *Ceratophyllum demersum* L. and *Myriophyllum spicatum* L. The standing crop of zooplankton was  $576.7 \text{ ind L}^{-1}$  in density and  $0.65 \text{ mg L}^{-1}$  in wet weight biomass (Liu, 2003). Aquaculture has flourished in this lake for decades and Chinese mitten crab is heavily stocked. Altogether forty-five fish species were recorded in the lake, and 70% were minnows (Zhang, 2004). Fishes of high commercial value include *Siniperca chuatsi* (Basilewsky), *Pseudobagrus fulvidraco* (Richardson), *Culter* spp., etc.

#### *Sampling and food analysis*

Quantitative samples were collected monthly from March, 2002 to March, 2003 from four stations within the lake. An additional sampling site was set up in a weedy bay northeast in the lake from July, 2002 for supplement purpose (see Fig. 1). About 10–12 samples were collected per month. Plankton, periphyton, macrophytes and sediment were collected extensively for potential food analysis. In the field, bottom samples were collected with a modified Peterson sampler ( $1/16 \text{ m}^2$ ) and cleaned gently with a  $425 \mu\text{m}$  sieve. Animals were sorted in the laboratory and cleaned with distilled water prior to preservation in 10% formalin. All specimens were identified to species, or to genus whenever the species was undeterminable.

Over 10 individuals of each taxon in monthly samples were taken randomly for gut analysis. Once the specimens were less than 10, all were used. Animals were measured and weighed. Biomass of small worms was calculated by length-weight relationships (Yan, 1998). Animals were cleaned thoroughly in distilled water before dissection. Stomach and foreguts of gastropods were separated from the shell and placed on slides, and all the food contents were scraped or squeezed out under a dissecting microscope. Chironomid larvae and oligochaetes were directly placed on slides and squeezed out food remains from gut along the body under a dissecting microscope. Gut contents were then dispersed gently using a dissecting needle with care to avoid damaging food items.

All stomachal or foregut contents were carefully transferred onto a slide and stained with Lugol's iodine solution for microscopic determination. Large food items were identified and enumerated from whole slide under  $10 \times 10$  magnification. Algae and other small items were identified and counted under  $10 \times 40$  magnification, using a method after Huang (1999). All food items were measured using an eyepiece micrometer and computed their volumetric contribution to the total contents.

Based on Tavares & Williams (1990) with some modification, food types were classified as follows: detritus, cyanobacteria, green algae, diatoms, other algae, fresh macrophytes, protozoans, rotifers, crustaceans, oligochaetes, chironomids, chitin fragments and other material (mainly unidentified and inorganic material).

#### *Food web quantification*

All taxa used for web analysis were common in Lake Biandantang (Wu, 1991; Liang et al., 1995; Yan, 1998; Gong, 2002), and those having their frequency of occurrence less than 10% in the samples were excluded. For the sake of authenticity, macroinvertebrates were treated on the basis of taxonomic names (species or genera).

In order to quantify the linkage strength, we combined the data of gut analysis with the measures of energy flow (secondary production). Both production and ingestion of macroinvertebrates attributed to various food types were estimated, following the procedure applied to an assemblage of caddisflies in a mountain stream (Benke & Wallace, 1980) (Table 1). The same assumption of assimilation efficiencies (AE) of aquatic insects were used as that of Benke & Wallace (1980): 10% for vascular plant and amorphous detritus, 30% for algae, and 70% for animal food. One kind of food type named "other material" was classified in our study. Since it mainly comprised unidentified material, the AE was assumed to be 10%, the same value as detritus. With regard to aquatic oligochaetes, little information about their AE values was available from literatures, and we assumed the same AE values as that of aquatic insects for different food types. For gastropods, we used an AE of 15% for algae based on Calow (1975), and 60% for animal

Table 1. Procedure of calculating production and ingestion attributed to each food type

Food type	Food type in gut (% by volume)	Assimilation efficiency (AE)	Net production efficiency (NPE)	Relative amount to production	Production attributed to food type (%)	Production attributed to food type ( $\text{mg m}^{-2}$ bimonthly)	Gross production efficiency (GPE) ( $\text{AE} \times \text{NPE}$ )	Amount of food ingested ( $\text{mg m}^{-2}$ bimonthly)
Detritus	50	$\times$ 0.10	$\times$ 0.20	= 1.0	16.7	8.3	+ 0.02	= 417
Algae	10	$\times$ 0.30	$\times$ 0.20	= 0.6	10.0	5.0	+ 0.06	= 83
Animal material	30	$\times$ 0.70	$\times$ 0.20	= 4.2	70.0	35.0	+ 0.14	= 250
Others	10	$\times$ 0.10	$\times$ 0.20	= 0.2	3.3	1.7	+ 0.02	= 83
Total	100			6.0	100	50		833

We assume that the production of a speices is  $50 \text{ mg dry mass m}^{-2}$  bimonthly.

material according to Palmer (1992) and Wang et al. (2000). The same AE values for other food types were estimated as that of aquatic insects. Net production efficiency (NPE, production/assimilation) values for macroinvertebrates (Yan, 1998) were listed in (see Electronic supplementary material<sup>1</sup>).

Production of macroinvertebrates in each bimonthly interval was estimated by multiplying bimonthly  $P/B$  and mean biomass. The bimonthly  $P/B$  was simply estimated to be one sixth of the annual value (Yan, 2000; Yan et al., 1999a–c; Yan et al., 2001; Yan & Wang, 1999) (see Electronic supplementary material). Although  $P/B$  varies with time, it seems that there is little effect on our results because production is more heavily dependent on biomass values than the variation in  $P/B$  (Benke & Wallace, 1997). Wet biomass was transferred to dry mass using a dry/wet ratio (Yan & Liang, 1999) (see Electronic supplementary material).

Based on the estimation of production attributed to various food types, we calculated dietary overlap among taxa using Pianka's Niche Overlap Index:

$$O_{jk} = O_{kj} = \frac{\sum_i^n P_{ij}P_{ik}}{\sqrt{\sum_i^n P_{ij}^2 \sum_i^n P_{ik}^2}}$$

where  $P_{ij}$  and  $P_{ik}$  are the proportions of the  $i$ th resource used by the  $j$ th and the  $k$ th species, respectively (Pianka, 1973). This equation generates a single overlap value between zero (no overlap) and one (complete overlap) for each pairwise comparison.

Based on estimation of ingestion, quantitative food webs were constructed bimonthly except that of March, 2002, since the guts were not always enough for monthly analysis. For comparison, the web of March, 2002 was compiled in the same way as the others. Food web diagrams were compiled bimonthly. We did not calculate food web statistics because our web was a sub-web of the lake.

<sup>1</sup> Electronic supplementary material is available for this article at <http://dx.doi.org/10.1007/s10750-006-0248-3> and accessible for authorised users.

## Results

### Community structure

The common species of benthic macroinvertebrates in Lake Biandantang included 1 oligochaete, 5 gastropods and 15 chironomids (see Electronic supplementary material). The standing crop of zoobenthos in this lake was  $262.2 \pm 85.7$  ind  $m^{-2}$  (mean  $\pm$  SE) in density and  $10.5 \pm 4.2$  g  $m^{-2}$  in wet biomass. Insects and molluscs were the most abundant groups, comprising 68.9% in density and 88.0% in biomass (Fig. 2). Generally, higher density and greater biomass were observed in spring and winter. The predominant species were one oligochaete (*B. sowerbyi*), three molluscs (*P. striatulus*, *A. longicornis* and *Hippeutis* sp.) and five chironomids (*E. nachitochaeae*, *Polypedilum* sp., *Chironomus* sp., *P. akamusi* and *Cladopelma* sp.).

### Trophic basis of macroinvertebrates production

Totally 600 guts were analyzed. The number of guts with food seemed small in several species (e.g. *Bellamya* sp., *Cryptotendipes* sp. and *Tanytus* sp.) mainly due to the occurrence of empty guts and the difficulty of collection. This may not be a serious problem because most species were detritivores in our study and no significant difference of diets was detected among individuals within a species. Five functional feeding groups were observed in Lake Biandantang based on dietary analysis (see Electronic supplementary material). Among them, chironomid collectors and gastropod scrapers were dominant groups and made up 55% of total density and 84.7% of total wet

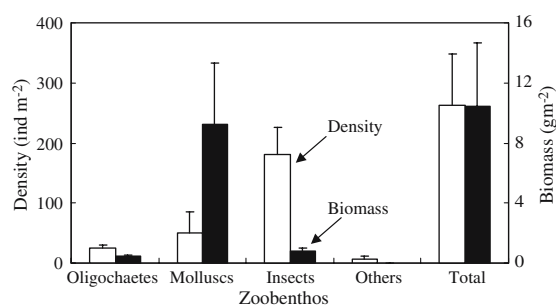


Figure 2. Density and wet biomass (mean  $\pm$  SE) of zoobenthos in Lake Biandantang.





overlaps among species of collectors + scrapers were very high, with 77% of  $O_{jk}$  values reaching 0.90–1.0, meaning that there was heavy utilization of detritus in the group. The oligochaete *B. sowerbyi* and a chironomid *P. akamusi*, however, had relative lower  $O_{jk}$  values than other collectors, because a large amount of dead crustaceans and green algae were respectively found in their guts. Among the three predators, the overlap between *Clinotanypus* sp. and *Procladius* sp. was much higher than other pairwises.

#### Food web quantification

Supplementary material Table 2 shows the quantities of various food types ingested by macroinvertebrate consumers during sampling period. The total ingestion ranged from 6930 to 36,340 mg dry mass  $m^{-2}$  bimonthly, and the production was 110–690 mg dry mass  $m^{-2}$  bimonthly (Fig. 4.). Both ingestion and production reached maximum in February–March, 2003, mainly due to the fact that a chironomid, *P. akamusi*, emerged in a large number, contributing 35.6% and 64% to the total ingestion and production respectively. On the contrary, this cryophilic species did not occur in March, 2002, probably by reason of the water temperature (21 °C) of that month obviously higher than that in corresponding period of 2003 (12 °C). Generally, the ingestion and production were temperature dependent. The ingestion was higher in the months with optimum temperature (April–July, 2002, February–March, 2003), than

that in other periods with higher (August–September, 2002) or lower (December, 2002–January, 2003) temperature. Differently, the production seemed to have a negative relationship with water temperature, probably animals in hot season should consume more food energy for metabolism than for growth.

The benthic food web of this lake was heavily based on detritus. Among the 13 food types, detritus was most important for macroinvertebrate consumers in all webs. The absolute values of ingestion attributed to detritus ranged from 6280 to 25860 mg dry mass  $m^{-2}$  bimonthly and made up 46.5–96.4% of the total in the system. The food ranked the second was green algae, of which the ingestion varied greatly from 6 to 6700 mg dry mass  $m^{-2}$  bimonthly, and amounted 0.1–42.3% of the total. The third was “other material”, being 20–6340 mg dry mass  $m^{-2}$  bimonthly and 0.1–17.4% of the total. Crustaceans were of some importance, and the ingestion ranged from 10 to 1190 mg dry mass  $m^{-2}$  bimonthly. Other foods were of little amount and the least was “chitin fragments”.

With reference to the temporal pattern, the relative contribution (%) of detritus and protozoans to total ingestion of the community decreased with the course of sampling period, and the coefficient of variability (CV) were 22% and 184% respectively, while that of green algae, diatoms and “other material” increased with the period, and CV ranged from 163% to 221%. The contributions of other food types had no obvious variation.

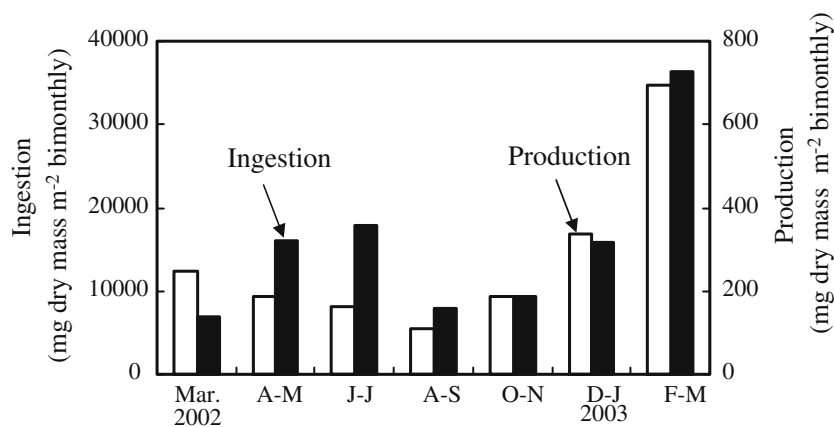


Figure 4. Total ingestion and production estimated for each sampling period in Lake Biandantang.



Quantitative food web diagrams were compiled using the ingestion flows from March, 2002 to March, 2003. These diagrams illustrate intuitively the complexity of the food web and the energy pathways in the system. Two diagrams constructed

for two typical periods (August–September, 2002 and February–March, 2003) are shown in Figures 5 and 6. In the food web of August–September, 2002, all macroinvertebrates analyzed were gastropods, and no predator was present. In

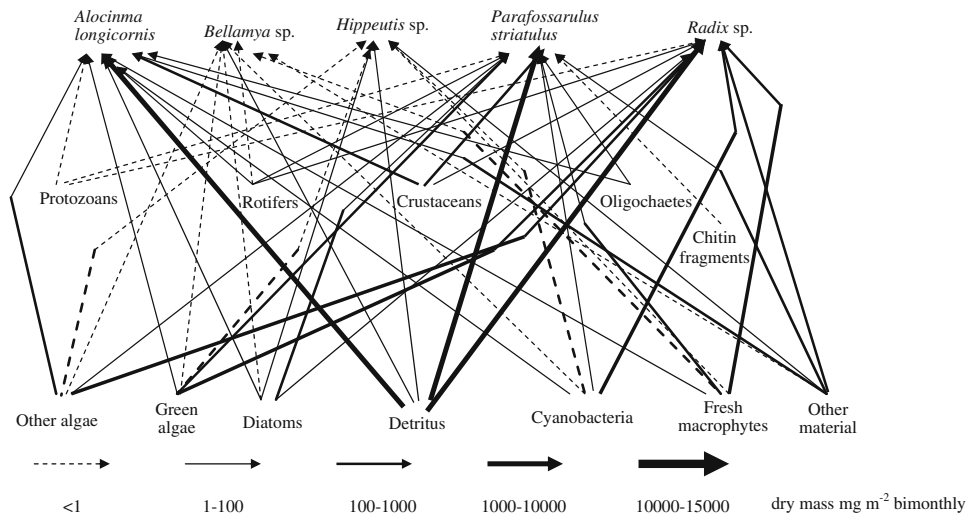


Figure 5. Food web diagram of macroinvertebrate community in August–September, 2002 in Lake Biandantang. Line thickness indicates magnitude of ingestion flows. The total ingestion of macroinvertebrate community was 7840 mg dry mass  $m^{-2}$  bimonthly during this period.

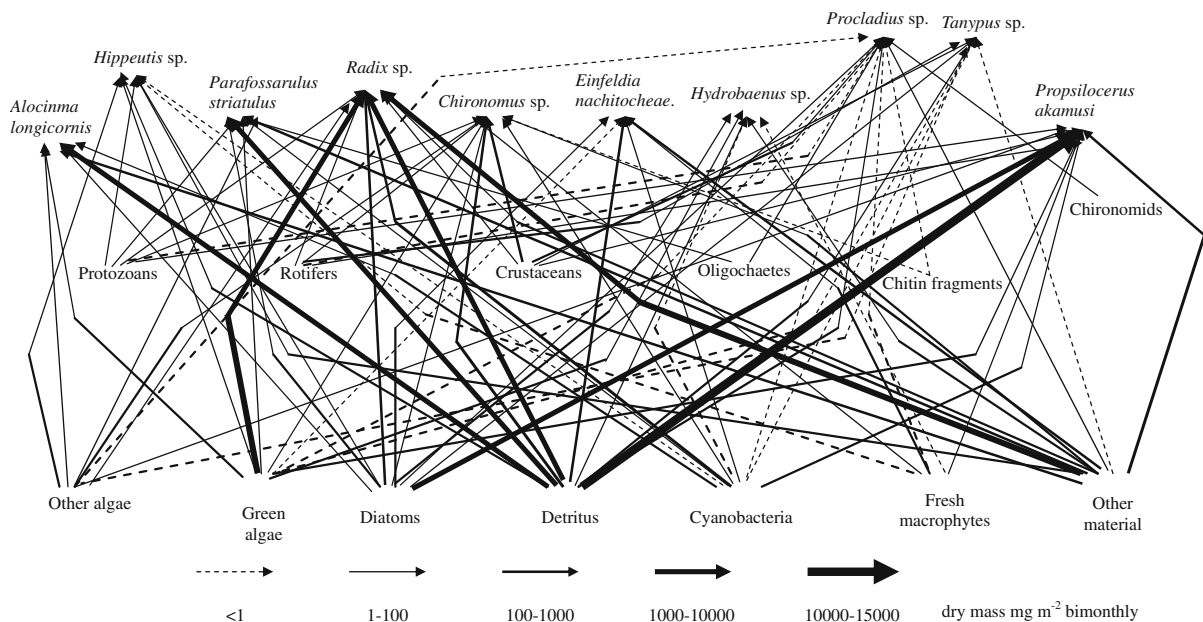


Figure 6. Food web diagram of macroinvertebrate community in February–March, 2003 in Lake Biandantang. Line thickness indicates magnitude of ingestion flows. The total ingestion of macroinvertebrate community was 36340 mg dry mass  $m^{-2}$  bimonthly during this period.

February–March, 2003, the web consisted of gastropods and chironomids, with predators. Summary web was not constructed because the species composition changed considerably over the sampling period, i.e. different species dominated in different seasons. In winter and spring, most species were chironomids (e.g. Fig. 6), while in summer and autumn were gastropods (e.g. Fig. 5). Moreover, both density and biomass of macroinvertebrate consumers in the webs changed obviously during the sampling period (Fig. 7).

### Discussion

Shallow lakes along Yangtze River are generally classified into three types: macrophytic, suburban eutrophic and river-connected lakes. Lake Biandantang is a typical macrophytic lake, through which our study might have shed some light on the trophic puzzle in that kind of lakes. Like other freshwater food web researches (Warren, 1989; Closs & Lake, 1994; Tavares-Cromar & Williams, 1996; Thompson & Townsend, 2003), our results demonstrate that the key basal resource of benthic food web of Lake Biandantang is detritus, and the majority of macroinvertebrates in benthic community of that water are detritivorous species.

The origin and function of detritus are worthy of remark. Contrary to its allochthonous nature in lotic waters, most detritus in lentic waters, such as the shallow lakes, originates from autochthonous

production of aquatic macrophytes and associated attached algae (Wetzel, 2001). This is the case in Lake Biandantang (Su et al., 1995; Yu & Zeng, 1996; Lu & Ni, 1999). Despite the difference in origin, organic detritus invariably acts in water as a generous food donor or, in other words, as the key source of energy and nutrients for macroinvertebrates. Detritus often serves as a habitat, e.g. shelters and refugia, for animals and also modifies the physical structure and conditions of the existing habitat (Moore et al., 2004). Thus it exerts multidimensional effects on the species composition of macroinvertebrates and the benthic community structure, and the detritus-based property further shapes the food web structure in a particular water.

Former freshwater detritus-based food web studies demonstrated that plenty of trophic interactions were weak, so that these webs were donor controlled (DeAngelis, 1975; Pimm, 1982). This character should also exist in Lake Biandantang though we did not demonstrate the effects of consumers on the production of their food supply. However, like other energy flow webs (Raffaelli & Hall, 1996; Benke & Wallace, 1997; Christian & Luczkovich, 1999; Benke et al., 2001), our analysis showed that most energy flows concentrated in a few feeding pathways, and the amount of energy flowing through the rest was less than 1% of the total in Lake Biandantang. We do not think that consumers could have strong effects on the abundant food supply through such weak links in this lake.

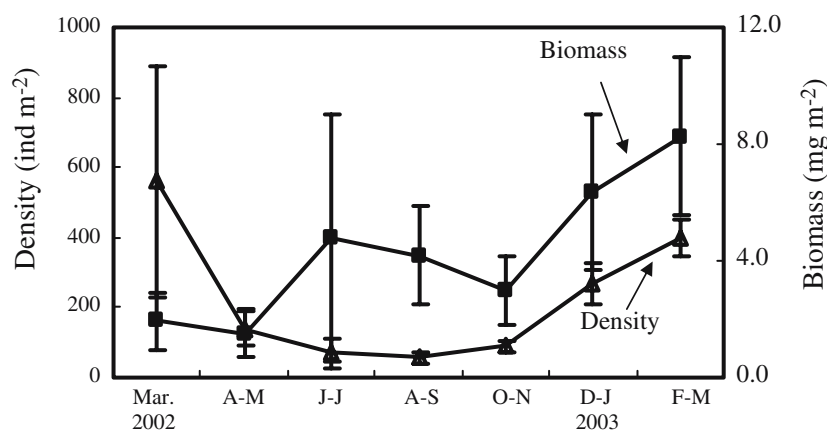


Figure 7. Dynamics of density and wet biomass of macroinvertebrate consumers (mean  $\pm$  SE) in Lake Biandantang during March, 2002–March, 2003.

Strong top-down trophic cascades have been reported from aquatic systems, especially in relatively simple food webs based upon energy from primary production, such as pelagic community in lakes (Strong, 1992). However, such cascades were scarce in those systems heavily based on detritus, such as stream food webs (Hildrew, 1992; Closs & Lake, 1994). The scarcity of strong top-down effects on benthic system is also evident in this lake. Actually, the organic detritus in macrophytic shallow lakes is so abundant (see Study site) that its supply to be strongly affected by macroinvertebrate consumers is unlikely. On the other hand, Hildrew (1992) and Pace et al. (1999) proposed that trophic generalism and omnivory within a food web could potentially weaken the strength of cascades. It is somewhat the fact in Lake Biandantang, where a large number of omnivores (44–64% of the total species) are present in macroinvertebrate community. However, if entire lake system is taken into account, things will be more complicated. The top predators that have not yet been included in our study are surely to have strong effects on their prey, as in the fact that the farming of mitten crabs will always bring forth an obvious reduction of zoobenthos (Xu et al., 2003).

Hunting for web generalities is one of the chief aims of food web ecologists. From our study in Lake Biandantang, some material might be helpful for such an objective. As compared our work with relevant studies in streams (e.g. Closs & Lake, 1994; Tavares-Cromar & Williams, 1996; Benke & Wallace, 1997; Schmid-Araya et al., 2002) and ponds (Warren, 1989), many of the patterns in Lake Biandantang are consistent with that in other freshwater benthic systems. These patterns may be summarized as: great importance of detrital base, obvious seasonal shifts in abundance and biomass of consumers and high levels of omnivory in the webs. Although they may not necessarily represent the “generalities”, they do occur commonly in freshwater benthic systems and differ markedly from those in pelagic systems (e.g. Cohen et al., 2003), where the major energy source relies heavily on autochthonous primary production, and the trophic levels are demarcated more clearly. Furthermore, some patterns, e.g. a relative high level of omnivory, in stream food webs dominated by allochthonous detritus are also present in lake food webs dominated by autochthonous detritus. This

might suggest that the web basis, rather than the ecosystem type per se is of primary importance in structuring a food web. In fact, different ecosystems with same detrital food base may eventually produce approximate food web patterns. Examples are those detritus-based systems like soil food webs (e.g. De Ruiter et al., 1994; Scheu, 2002).

Our lake benthic food web is not a complete one. Microbes and rare macroinvertebrates have not been touched upon. To illustrate a more complete image of benthic food web in Lake Biandantang, top predators such as benthic fish and Chinese mitten crab as well as other elements will be included in our further study.

### Conclusion

As the first attempt on aquatic food web research in China, we have presented a facet of this subject in shallow, macrophytic Lake Biandantang. Conclusively, the food web of macroinvertebrate community in Lake Biandantang is constructed on a detrital base. Generally, the benthic food web in a macrophytic lake is similar to those in streams and other detritus-based webs, but quite different from pelagic systems. It seems that the basis of the web is of primary importance in shaping food web structure.

### Acknowledgements

We thank Messrs. Hai-Jun Wang, Yong-De Cui, and Ms. Jian Wang for fieldwork and environmental data. Special thanks are due to Profs. Yan-Ling Liang and Jian-Kang Liu, and two anonymous reviewers for their invaluable comments on the manuscript. The research was funded by Chinese Academy of Sciences (KSCX2-SW-110) and National Natural Science Foundation of China (30270247).

### References

- Benke, A. C. & J. B. Wallace, 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. *Ecology* 61: 108–118.

- Benke, A. C. & J. B. Wallace, 1997. Trophic basis of production among riverine caddisflies: implications for food web analysis. *Ecology* 78: 1132–1145.
- Benke, A. C., J. B. Wallace, J. W. Harrison & J. W. Koebel, 2001. Food web quantification using secondary production analysis: predaceous invertebrates of the snag habitat in a subtropical river. *Freshwater Biology* 46: 329–346.
- Briand, F. & J. E. Cohen, 1984. Community food webs have scale-invariant structure. *Nature* 307: 264–267.
- Calow, P., 1975. The feeding strategies of two freshwater gastropods, *Ancylus fluviatilis* and *Planorbis contortus* L. in terms of ingestion rates and absorption efficiency. *Oecologia* 20: 33–49.
- Christian, R. R. & J. J. Luczkovich, 1999. Organizing and understanding a winter's seagrass foodweb network through effective trophic levels. *Ecological Modelling* 117: 99–124.
- Closs, G. P. & P. S. Lake, 1994. Spatial and temporal variation in the structure of an intermittent-stream food web. *Ecological Monographs* 64: 1–21.
- Cohen, J. E., 1977. Ratio of prey to predators in community food webs. *Nature* 270: 165–167.
- Cohen, J. E., R. A. Beaver, S. H. Cousins, D. L. DeAngelis, L. Goldwasser, K. L. Heong, R. D. Holt, A. J. Kohn, J. H. Lawton, N. Martinez, R. O'Malley, L. M. Page, B. C. Patten, S. L. Pimm, G. A. Polis, M. Rejmanek, T. W. Schoener, K. Schoenly, W. G. Sprules, J. M. Teal, R. E. Ulanowicz, P. H. Warren, H. M. Wilbur & P. Yodzis, 1993. Improving food webs. *Ecology* 74: 2–52–258.
- Cohen, J. E., F. Briand & C. H. Newman, 1990. *Community Food Webs, Data and Theory*. Springer-Verlag, New York, USA.
- Cohen, J. E., T. Jonsson & S. R. Carpenter, 2003. Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences* 100: 1781–1786.
- DeAngelis, D. L., 1975. Stability and connectance in food web models. *Ecology* 56: 238–243.
- Deng, Z. & B. Jin, 1991. The geographical environment and hydrological feature of the Bao'an Lake. In Hu, C. & X. Huang (eds), *Collected Papers on the Fishery Ecology and Exploitation Technology of the Bao'an Lake*. Science Press, China, 16–22 (in Chinese).
- De Ruiter, P. C., J. Bloem, L. A. Bouwman, W. A. M. Didden, G. H. J. Hoenderboom, G. Lebbink, J. C. Y. Marinissen, J. A. De Vos, M. J. Vreeken-Buijs & K. B. Zwart, 1994. Simulation of dynamics in nitrogen mineralization in the belowground food webs of two arable farming systems. *Agriculture, Ecosystem, Environment* 51: 199–208.
- Froneman, P. W., 2004. Food web dynamics in a temperate temporarily open/closed estuary (South Africa). *Estuarine, Coastal and Shelf Science* 59: 87–95.
- Gong, Z., 2002. Studies on ecology of macrozoobenthos in shallow lakes along the middle reaches of the Changjiang River. Ph.D. thesis. Chinese Academy of Sciences, China. (in Chinese).
- Hall, S. J. & D. Raffaelli, 1991. Food web patterns: lessons from a species-rich web. *Journal of Animal Ecology* 60: 823–842.
- Hall, S. J. & D. Raffaelli, 1993. Food webs: theory and reality. *Advances in Ecological Research* 24: 187–239.
- Hildrew, A. G., 1992. Food webs and species interactions. In Calow, P. & G. E. Petts (eds), *The River Handbook*. Blackwell Sciences, Oxford, 309–330.
- Huang, X., 1999. *Survey, Observation and Analysis of Lake Ecology*. Standards Press of China, China (in Chinese).
- Jeppesen, E., J. P. Jensen, M. Sondergaard, T. Lauridsen, L. J. Pedersen & L. Jensen, 1997. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia* 342/343: 151–164.
- Jones, J. I. & S. Waldron, 2003. Combined stable isotope and gut contents analysis of food webs in plant-dominated, shallow lakes. *Freshwater Biology* 48: 1396–1407.
- Liang, Y., T. Wu & Z. Xie, 1995. On the current conditions of zoobenthos in Baoan Lake with an assessment of its potential fishery production capacity. In Liang, Y. & H. Liu (eds), *Resources, Environment and Fishery Ecological Management of Macrophytic Lakes*. Science Press, China, 178–193 (in Chinese).
- Liu, H., 2003. Studies on the impact of water eutrophication and the application of fish medicine on zooplankton. Dsc Thesis. Chinese Academy of Sciences, China (in Chinese).
- Lu, M. & L. Ni, 1999. Ecological studies on the dynamics of submersed vegetation in a small shallow lake, Lake Biandantang. *Acta Hydrobiologica Sinica* 23(suppl.): 47–52.
- Moore, J. C., E. L. Berlow, D. C. Coleman, P. C. De Ruiter, Q. Dong, A. Hasting, N. C. Johnson, K. S. McCann, K. Melville, P. J. Morin, K. Nadelhoffer, A. D. Rosemond, D. M. Post, J. L. Sabo, K. M. Scow, M. J. Vanni & D. H. Wall, 2004. Detritus, trophic dynamics and biodiversity. *Ecology Letters* 7: 584–600.
- Pace, M. L., J. J. Cole, S. R. Carpenter & J. F. Kitchell, 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14: 483–489.
- Palmer, A. R., 1992. Calcification in marine molluscs: how costly is it? *Proceedings of the National Academy of Science* 89: 1379–1382.
- Pianka, E. R., 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4: 53–74.
- Pimm, S. L., 1982. *Food Webs*. Chapman and Hall, London, England.
- Pimm, S. L., J. H. Lawton & J. E. Cohen, 1991. Food web patterns and their consequence. *Nature* 350: 669–674.
- Polis, G. A., 1991. Complex trophic interactions in deserts: an empirical critique of food web theory. *American Naturalist* 138: 123–155.
- Polis, G. A., 1994. Food webs, trophic cascades and community structure. *Australian Journal of Ecology* 19: 121–136.
- Raffaelli, D. & S. J. Hall, 1996. Assessing the relative importance of trophic links in food webs. In Polis, G. A. & K. O. Winemiller (eds), *Food webs: Integration of Patterns and Dynamics*. Chapman and Hall, New York, 185–1991.
- Scheu, S., 2002. The soil food web: structure and perspectives. *European Journal of Soil Biology* 38: 11–20.
- Schmid-Araya, J. M., A. G. Hildrew, A. Robertson, P. E. Schmid & J. Winterbottom, 2002. The importance of meiofuna in food webs: evidence from an acid stream. *Ecology* 83: 1271–1285.

- Strong, D., 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73: 747–754.
- Su, Z., T. Zhang & Q. Cai, 1995. On the change of aquatic vegetation in Baoan Lake with remarks on its fishery. In Liang, Y. & H. Liu (eds), *Resources, Environment and Fishery Ecological Management of Macrophytic Lakes*. Science Press, China, 147–159 (in Chinese).
- Sugihara, G., K. Schoenly & A. Trombla, 1989. Scale invariance in food web properties. *Science* 245: 48–52.
- Tavares, A. F. & D. D. Williams, 1990. Life histories, diet, and niche overlap of three sympatric species of Elmidae (Coleoptera) in a temperate stream. *Canadian Entomologist* 122: 563–577.
- Tavares-Cromar, A. F. & D. D. Williams, 1996. The importance of temporal resolution in food web analysis: evidence from a detritus-based stream. *Ecological Monographs* 66: 91–113.
- Thompson, R. M. & C. R. Townsend, 2003. Impacts on stream food webs of native and exotic forest: an intercontinental comparison. *Ecology* 84: 145–161.
- Vadeboncoeur, Y. & D. M. Lodge, 2000. Periphyton production on wood and sediment: substratum-specific response to laboratory and whole-lake nutrient manipulations. *Journal of the North American Benthological Society* 19: 68–81.
- Vadeboncoeur, Y., M. J. Vander Zanden & D. M. Lodge, 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. *Bioscience* 52: 44–54.
- Vander Zanden, M. J. & Y. Vadeboncoeur, 2002. Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology* 83: 2152–2161.
- Wang, W. X., C. Ke, K. N. Yu & P. K. S. Lam, 2000. Modeling radiocesium bioaccumulation in a marine food chain. *Marine Ecology Progress Series* 208: 41–50.
- Warren, P. H., 1989. Spatial and temporal variation in the structure of a freshwater food web. *Oikos* 55: 299–311.
- Wetzel, R. G., 2001. *Limnology, Lake and River Ecosystems* (3rd ed.). Academic Press, USA, pp 731–784.
- Williams, R. J. & N. D. Martinez, 2000. Simple rules yield complex food webs. *Nature* 404: 180–183.
- Woodward, G. & A. G. Hildrew, 2002. Food web structure in riverine landscapes. *Freshwater Biology* 47: 777–798.
- Wu, T., 1991. The standing crop of macro-invertebrates, and its fishery-management in the Bao'an Lake. In Hu, C. & X. Huang (eds), *Collected Papers on the Fishery Ecology and Exploitation Technology of the Bao'an Lake*. Science Press, China, 74–79 (in Chinese).
- Xu, Q., H. Wang & S. Zhang, 2003. The impact of overstocking of mitten crab, *Eriocheir sinensis*, on lacustrine zoobenthic community. *Acta Hydrobiologica Sinica* 27: 41–46 (in Chinese).
- Yan, Y., 1998. Studies on ecological energetics and production of macrozoobenthos in shallow lakes. Dsc Thesis. Chinese Academy of Sciences, China (in Chinese).
- Yan, Y., 2000. Life cycle and production of Chironomidae (Diptera) in Biandantang, a typical macrophytic lake (Hubei, China). *Chinese Journal of Oceanology and Limnology* 18: 221–226.
- Yan, Y. & Y. Liang, 1999. A study of dry- to- wet weight ratio of aquatic macroinvertebrates. *Journal of Huazhong University of Science and Technology* 27: 61–63 (in Chinese).
- Yan, Y., Y. Liang & H. Wang, 1999a. Annual production of five species of Chironomidae (Diptera) in Houhu Lake, a typical algal lake (Wuhan, China). *Chinese Journal of Oceanology and Limnology* 17: 112–118.
- Yan, Y., Y. Liang & H. Wang, 1999b. Energy flow of *Bellamyia aeruginosa* in a shallow macrophyte-dominated lake, Lake Biandantang. *Acta Hydrobiologica Sinica* 23(Suppl.): 115–121.
- Yan, Y., Y. Liang & H. Wang, 1999c. Production of gastropods in Lake Biandantang I. Annual production of *Bellamyia aeruginosa*. *Acta Hydrobiologica Sinica* 23: 346–351 (in Chinese).
- Yan, Y., Y. Liang & H. Wang, 2001. Production of gastropods in Lake Biandantang II. Annual production of *Parafossarulus stritulus*. *Acta Hydrobiologica Sinica* 25: 36–41 (in Chinese).
- Yan, Y. & H. Wang, 1999. Abundance and production of *Branchiura sowerbyi* (Oligochaeta: Tubificidae) in two typical shallow lakes (Hubei, China). *Chinese Journal of Oceanology and Limnology* 17: 79–85.
- Yu, D. & Y. Zeng, 1996. A comparative study on the plant community diversity in two subregions Qiaodunhu and Biandantang, Lake Baoan. *Acta Hydrobiologica Sinica* 20(Suppl.): 156–163 (in Chinese).
- Zhang, T., 2004. Life-history strategies, trophic patterns and community structure in the fishes of Lake Biandantang. Dsc Thesis. Chinese Academy of Sciences, China. (in Chinese).