Fundamental and Applied Limnology
Archiv für Hydrobiologie
Vol. 171/4: 297–309, May 2008

Food web of benthic macroinvertebrates in a large Yangtze River-connected lake: the role of flood disturbance

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With 6 figures, 1 table and 1 appendix

Abstract: This study was conducted in Lake Dongtinghu, a large river-connected lake on the Yangtze River floodplain, China. Our goal was to determine trophic relationships among benthic macroinvertebrates, as well as the effects of flood disturbance on the benthic food web of a river-connected lake. Macroinvertebrates in the lake fed mainly on detritus and plankton (both zooplankton and phytoplankton). Food web structure in Lake Dongtinghu was characterized by molluscs as the dominant group, low connectance, high level of omnivory, based on detritus and primary production, and most ingestion concentrating on a few links. Our analyses showed that flood disturbance is an important factor affecting the benthic food web in Lake Dongtinghu. The numbers of species and functional feeding groups (FFGs), and the density and biomass of macroinvertebrates decreased significantly during flooding. Connectance was higher during the flood season than in other seasons, indicating that floods have a strong effect on connectance in this Yangtze River-connected lake. Flood effects on the benthic web were also evident in the decrease of niche overlaps within and among FFGs. Our results provide useful information regarding biodiversity conservation on the Yangtze floodplain. Reconstructing and maintaining natural and regular flow regimes between Yangtze lakes and the river is essential for restoration of macroinvertebrates on the floodplain.

Key words: macroinvertebrates, food web, flood disturbance, floodplain, Lake Dongtinghu.

Introduction

Disturbance is important in structuring ecological communities. A disturbance occurs when damaging forces are applied to habitat space occupied by a population, community, or ecosystem (Lake 2000). In freshwater lotic ecosystems, flood disturbances are regarded as one of the most important perturbation factors that stimulate productivity and link river channels to floodplains (Junk et al. 1989, Lake 2000, Lake et al. 2006). Recent studies have demonstrated that flooding effects vary substantially according to location within a riverine network, i.e. they act as damaging forces in upland streams but as replenishing forces in lowland floodplains (Lake et al. 2006). Although a large number of studies deal with the effects of floods, most are concentrated on streams and rivers. A relatively small number of studies have examined riverine wetlands such as river-connected lakes on floodplains (Kingsford et al. 2004). However, species richness and abundance are often higher in floodplains than in river channels (Ward et al. 1999). Hence, considering spe-

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DOI: 10.1127/1863-9135/2008/0171-0297
1863-9135/08/0171-0297 $ 3.25

cies biodiversity conservation, it is necessary to understand how flood disturbances affect the communities in river-connected wetlands.

Macroinvertebrates are important groups of benthic communities in the riverine network. They are more vulnerable to bed movement during flooding than more mobile animals such as fish. During flooding, macroinvertebrates are affected by a combination of water velocity and scouring (Holomuzki & Biggs 2000) and by physical bed movement of the stream bottom (Biggs et al. 2001). A large number of studies have dealt with the effects of floods on macroinvertebrates (e.g. Sagar 1986, Parker & Huryn 2006, Suren & Jowett 2006), most showing that flood disturbances result in a reduction of species richness and abundance, but that recovery was rapid (e.g. Lake 2000, Gjerlov et al. 2003). Moreover, they also showed a shift in community composition to one dominated by opportunistic taxa tolerant of unstable conditions (e.g. Townsend et al. 1997). Other studies indicate that floods could alter interspecific interactions such as competition and predation (Thomson 2002). However, only a small number of studies actually deal with the influences of floods on benthic webs. It has been long known that food webs are important in understanding flows of material and energy in ecosystems (Hardy 1924, Odum 1971). Studies on the effects of floods on macroinvertebrate food webs might provide useful information for ecosystem management of floodplain ecosystems.

As one of the largest floodplains in the world, the Yangtze River floodplain is characterized by many shallow lakes interlacing with the river network. From the 1950s to 1970s, most lakes were isolated from the main channel by dams and levees, and only three currently retain natural connection with the river. The destruction of hydrological connectivity between the river and lakes resulted in a loss of habitat heterogeneity and species biodiversity, as well as other environmental problems such as lake eutrophication (Cai & Zhou 1996, Wang et al. 2005). When considering restoration of the Yangtze floodplain, it is important to have an understanding of the floodplain ecosystem. However, most studies have concentrated on lakes that had been isolated from the Yangtze River (e.g. Liang & Liu 1995, Li & Cui 2005), while little has been done on Yangtze River-connected lakes.

This study focuses on research conducted on a large Yangtze River-connected lake, Lake Dongtinghu, in the middle reaches of the Yangtze River. Our goal is to determine trophic relationships among benthic macroinvertebrates and the effects of flood disturbance on the benthic food web of a river-connected lake.

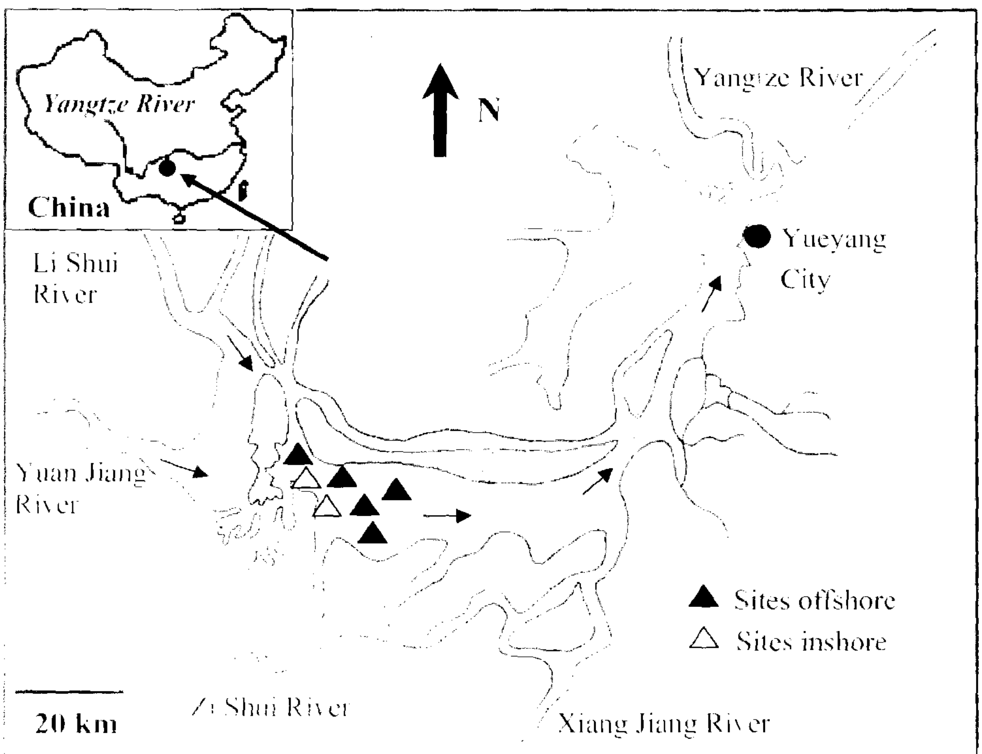

Fig. 1. Sampling sites on Lake Dongtinghu, Hunan, China. Shaded areas are seasonally flooded areas. Arrows show the direction of water flow.

Material and methods

Study site

Lake Dongtinghu (N 28°44′ – 29°35′; E 111°53′ - 113°05′) is located in northeastern Hunan Province. It is a large river-connected lake in the middle reaches of the Yangtze River (Fig. 1). Its area is ca. 2,625 km^2 when water level is at 33.5 m (above sea level, Yueyang station, Huang Hai mean sea level). The annual air temperature is 16.4–17.0 °C and annual rainfall is 1,200–1,400 mm. Most rainfall is in spring and summer. The mean water depth is 6.4 m with the maximum at 23.5 m (Dou & Jiang 2000). The mean annual water input is 3,126 × 10^8 m^3, and the retention time is 18.2 days (Dou & Jiang 2000). The lake has both lotic and lentic environments. Most of the lake has flowing water with a mean water velocity of 0.23 m s^{-1}, while other regions are relatively lentic. Flood pulses are regular and seasonal. The highest water level usually occurs in July–September and the lowest in January–March (Li & Zhang 2003).

During the sampling period, the water temperature was 22.5 ± 1.0 °C (mean ± SE, the same below) and Secchi depth was 75 ± 6 cm. The concentration of total suspended matter in the water was 30 ± 4 g L^{-1}. Total nitrogen and phosphorus in the water were 1.40 ± 0.10 mg L^{-1} and 0.132 ± 0.008 mg L^{-1}, respectively. Chlorophyll-*a* in lake water was 3.03 ± 0.43 μg L^{-1}. The lake sediment comprises mainly hard soil and sand grains. Most aquatic plants were present near shore regions. The dominant species of aquatic plants included *Miscanthus sacchariflorus* (Maxim), *Phragmitas communis* Trin, *Artemisia selengensis* Turez et Bess and *Scirpus triqueter* L.

Sampling and dietary analysis

We separated the lake into approximately two regions: near shore (water depth < 2 m) and offshore (water depth > 2 m). A total of seven sampling sites were set up in the southern part of the lake where water flows slowly and thus makes it relatively easy to get samples (Fig. 1). Five sites were set up offshore while the other two were in the near shore region. Samples were collected in May, July, September and November, 2004.

To determine the potential food species of macroinvertebrates, plankton, periphyton and sediment were collected qualitatively each month. Plankton was sampled with a plankton net (64 μm). Periphyton was brushed from surfaces of stones and aquatic plants, and subsequently collected with a 64 μm mesh. Sediment was taken using a modified Peterson sampler (area 0.06 m^2; Liu & Wang 2007). To quantify benthic community structure, seven quantitative samples were taken on each occasion. Benthic macroinvertebrates were collected using a modified Peterson sampler in offshore waters. Since molluscs are relatively large in body size and burrow into sediments, the Peterson sampler was not adequate. We used a net (mesh size, 1.0 cm) attached on a D-shape harrow (length, 0.6 m) to collect molluscs along a 10–15 m transect (2–3 transects on each sampling occasion). Qualitative samples were taken in a variety of ways to supplement specimens for gut content analysis. A modified long line fishing gear (length, 50 m) with blunt hooks was used to collect bivalves in fast-flow waters. The gear was attached on two boats and drawn by natural flow force. In natural conditions, bivalves open their shells to filter food and obtain oxygen; when disturbed by such an event as inserting a [illegible] they close their shells around the hook.

Animals were collected along a 500 m transect on each occasion. Benthic macroinvertebrates were also collected by hand in shallow near shore waters. Zebra mussels attached on hard substrata were collected by net. In low-flow regions with aquatic plants, zoobenthos were collected by a hand net. Macroinvertebrate specimens were also collected from fishing trawls. Samples were taken to the laboratory and preserved in 10 % formalin prior to sorting. All specimens were identified to species level when possible, based on the keys in Sperber (1948), Liu et al. (1979), Morse et al. (1994) and Epler (2001). Animals in quantitative samples were counted and weighed. The wet weight mass was subsequently transferred to dry weight mass using a dry/wet ratio (Yan & Liang 1999). Temporal changes in density and biomass of macroinvertebrates were assessed by one-way ANOVA.

Ten individuals from each species from each month were taken randomly for gut content analysis. If there were less than 10 specimens, all were used. Woodward & Hildrew (2001) found that large numbers of individual guts (> 100) are necessary to detect all trophic links, however, such an effort was not feasible especially in the large Yangtze River-connected lake due to logistic reasons. Moreover, ten guts were used commonly in food web studies and confirmed to be enough for most macroinvertebrates (e.g. Tavares-Cromar & Williams 1996, Thompson & Townsend 2003, Liu et al. 2006).

Stomachs and foreguts of animals were removed and placed on slides and all food contents were scraped or squeezed out under a dissecting microscope. Food contents of bivalves were removed from stomachs using a pipette. Very small worms were mounted whole. Stomach and gut contents were processed and examined according to methods in Liu et al. (2006) and Liu & Wang (2007). Food contents were stained with Lugol's iodine solution and mounted for microscopic determination. Large food items (> 50 μm) were examined under 100× magnification. Algae and other small items (< 50 μm) were examined under 400× magnification and identified to the lowest taxonomic level possible, according to Chinese Water Analysis Methods Standards (Huang et al. 1999). All food items were measured using an eyepiece micrometer, and their volumetric contributions were computed with common formulae, by length (L) - volume (V) relationships (e.g. $\log_{10}V = \log_{10}a + b \log_{10}L$; see Zhang & Huang 1991), or using mean volumes of food species in the environment.

Food web analysis

All common species were used in the food web analysis while rare species were excluded. Rare species included one oligochaete (*Branchiura sowerbyi* Beddard), five bivalves (*Acuticosta chinensis* (Lea), *Cuneopsis pisciculus* (Heude), *Novaculina chinensis* Liu et Zhang, *Lamprotula fibrosa* (Heude), *Schistodesmus spinosus* Simpson) and one odonate (*Pantala* sp.). They were excluded due to their low frequencies of occurrence in samples (< 5 %). Suctorial animals (mainly leeches) were also excluded from food web analysis because their feeding links could not be determined by gut content analysis. A volumetric percentage was used to quantify the contribution of each food item to the total gut contents.

Connectance food webs were constructed for each sampling date (Cohen et al. 1990). A summary web was also compiled that included all common species. Food web statistics were calculated as follows: total number of species (S), number of zoobenthic species (S'), total number of links (L), connectance

(C, L/S^2, Martinez 1991), linkage density (D, L/S) and omnivory (O, omnivores/ zoobenthos). Trophic basis of the food web was analyzed based on volumetric contributions of food items. Feeding links were also semi-quantified to have a general view of the energy flow pattern.

Niche overlap webs were constructed based on functional feeding groups (FFGs) according to Liu & Wang (2007). Based on dietary information, FFGs were determined according to the feeding method, body size and taxonomic status of species. The feeding method was determined through observation and references (Morse et al. 1994). Insect predators were classified into small groups (body length < 1.0 cm) and large groups (body length > 1.0 cm). Although no small insect predator was included in the present study, we still used the classification for the purpose of comparison with studies in Yangtze River-isolated lakes (Liu et al. 2006, Liu & Wang 2007). Dietary overlap among species was calculated using Pianka's Niche Overlap Index:

$$O_{jk} = O_{kj} = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}}$$

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.

Results

Community structure of macroinvertebrates

The 31 common species of benthic macroinvertebrates in Lake Dongtinghu included one oligochaete, 18 molluscs and 12 insects (Appendix 1). The number of species was much lower during the flood season (July and September) than other periods. The density of zoobenthos in the lake was 70.1 ± 20.7 ind m^{-2} (mean ± SE, the same below) and biomass was 13.3 ± 3.5 g m^{-2} (dry mass). Molluscs were the most abundant group, comprising 61.4 % of the total density and 99.8 % of the biomass. Generally, density and biomass of macroinvertebrates were much lower during the flood season than other periods (Fig. 2) (ANOVA, $p < 0.05$).

Food composition of macroinvertebrates

In total, 839 guts with food from 1,018 dissected individuals were used for dietary analysis. The quantity of gut contents seemed small in several species (e.g. *Chaetogaster limnaei*, *Gomphidia* sp. and *Cryptochi-*

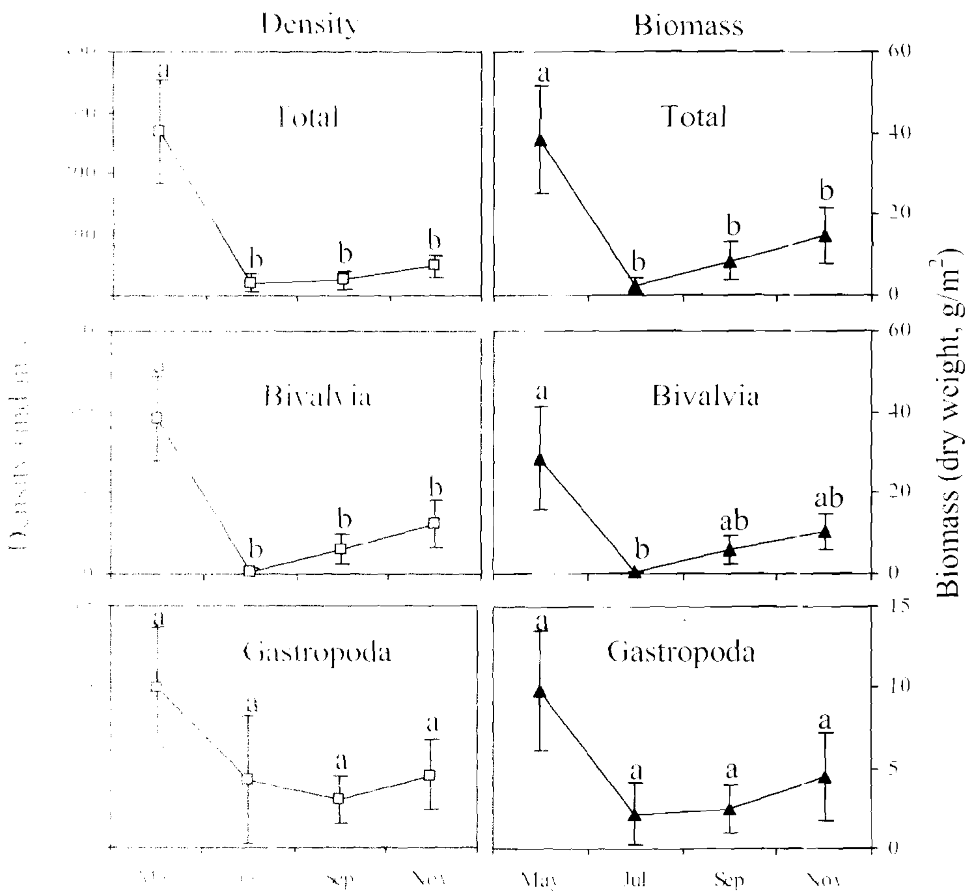

Fig. 2. Density and biomass (dry weight) (mean ± SE) of common macroinvertebrate groups in Lake Dongtinghu during the sampling period (May–November, 2004). Different symbols indicate significantly different groups after a one-way ANOVA, and a Tukey post-hoc test.

ronomus sp.) mainly due to the occurrence of empty guts. Twenty food items were found in the gut contents of all species, including inorganic material, detritus, cyanobacteria (Cyanophyta), diatoms (Bacillariophyta), green algae (Chlorophyta), other algae (mainly dinoflagellates and euglenoids), macrophytes, pollen of conifers, protozoans, hydroids, flatworms, rotifers, nematodes, bryozoan floatoblasts, oligochaetes, crustaceans, water mites, mayfly nymphs, chironomid larvae and miscellaneous material.

Detailed information of food composition of macroinvertebrates is given in Appendix 1. In general, most zoobenthos in Lake Dongtinghu consumed a wide range of food items. Detritus, inorganic mate-

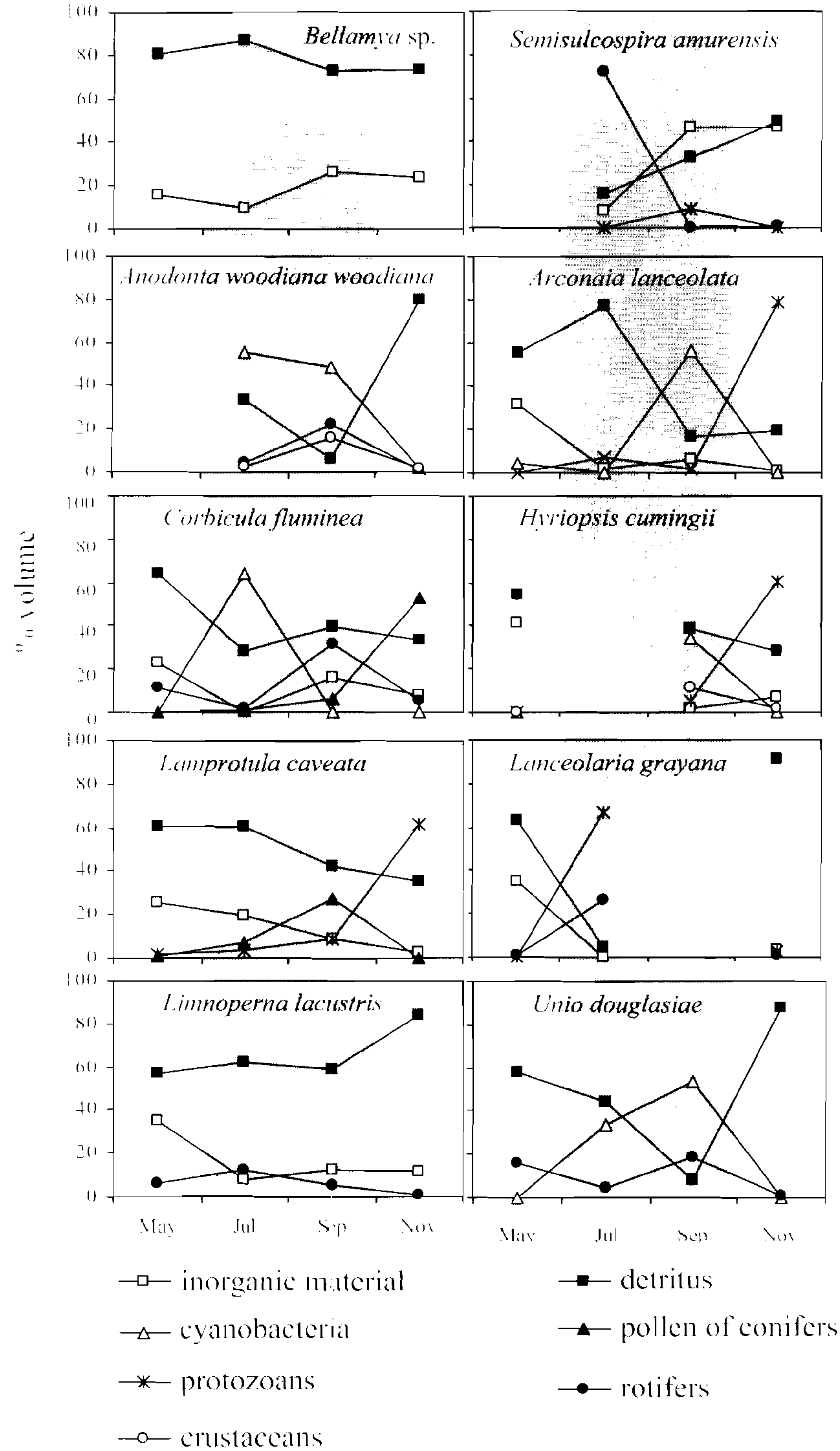

Fig. 3. Variations of major food items of representative mollusc species in Lake Dongtinghu during the sampling period. Shaded areas show data in the flood period. Several data-points are missing because no individuals were collected at that time.

Table 1. Food web statistics for the benthic food web of Lake Dongtinghu during the sampling period. The flood period is from July to September.

Food web statistics	May	Jul	Sep	Nov	Summary
Total number of species (S)	36	29	24	33	51
Number of zoobenthic species (S')	22	12	11	19	31
Total number of links (L)	155	127	108	159	293
Connectance (C, L/S^2)	0.120	0.151	0.188	0.146	0.113
Linkage density (L/S)	4.3	4.4	4.5	4.8	5.7
Omnivory (O, omnivores/zoobenthos)	0.55	0.92	0.91	0.74	0.61

rial, protozoans, rotifers and cyanobacteria dominated gut contents. Animals feeding on higher trophic levels consumed a more limited variety of foods, primarily rotifers, mayfly nymphs and chironomid larvae. With regard to temporal variation of food composition, we considered molluscs because they dominated the zoobenthic community. Generally, food composition of most molluscs changed during the sampling. Molluscs consumed more algae and animal material during the flood season (July and September) than in other months (Fig. 3).

Functional feeding groups (FFGs)

Six FFGs of macroinvertebrates were identified in Lake Dongtinghu as follows: gastropod scrapers (GS), insect collector-gatherers (ICG), bivalve collector-filterers (BCF), insect collector-filterers (ICF), annelid predators (AP) and large insect predators (LIP, odonate nymphs) (Appendix 1). All FFGs were present before the flood (May), while only two FFGs, gastropod scrapers and bivalve collector-filterers, were present during flooding.

With reference to food composition of FFGs, GS consumed mainly detritus and inorganic material.

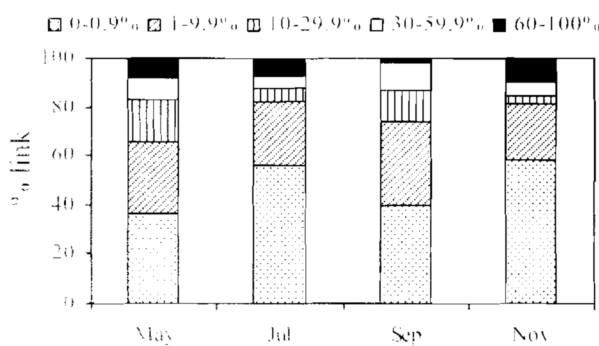

Fig. 4. Temporal variations of proportions of different trophic links in the macroinvertebrate food web of Lake Dongtinghu during the sampling period. Trophic links were quantified by volumetric contribution.

This group also consumed a certain amount of animal material, such as rotifers. ICG primarily fed on detritus (74.2 %), with a certain proportion of inorganic material. With regard to filterers, BCF consumed mainly detritus and protozoans, and they also took a large amount of cyanobacteria and rotifers, while ICF fed primarily on detritus (91.3 %). In the diets of predators, rotifers were the chief food item of AP, while mayfly nymphs (66.2 %) and chironomid larvae (33.7 %) made up almost all gut contents of LIP. With reference to temporal variation, food composition of FFGs varied in the similar way as that of most species, i.e. they ingested more algae and animal material during the flooding.

Food web of macroinvertebrate community

The summary web of Lake Dongtinghu during the sampling contained 51 "species" (including 31 zoobenthos and 20 food items) and 293 links. The linkage density was 5.7 and the directed connectance was 0.113. High levels of omnivory were observed in the benthic community. The ratio of omnivores to zoobenthos was 0.61. There were changes in most food web statistics during the sampling period (Table 1). The total numbers of "species" and links, and the number of zoobenthos were much smaller, while connectance and omnivory were higher during flooding than in other periods.

The benthic food web of Lake Dongtinghu was based on detritus. Among the 20 food items, detritus was most important for macroinvertebrates, accounting for 41.3 % of the total gut contents. Animal material also contributed a certain amount, i.e. protozoans, mayfly nymphs and rotifers comprised 11.4 %, 10.7 % and 9.3 % of the total respectively. Inorganic material and cyanobacteria were of some importance, comprising 9.7 % and 5.3 % of the total, respectively.

The distribution of different kinds of links was analyzed based on the volumetric contribution of each link. Results showed that most links accounted for a

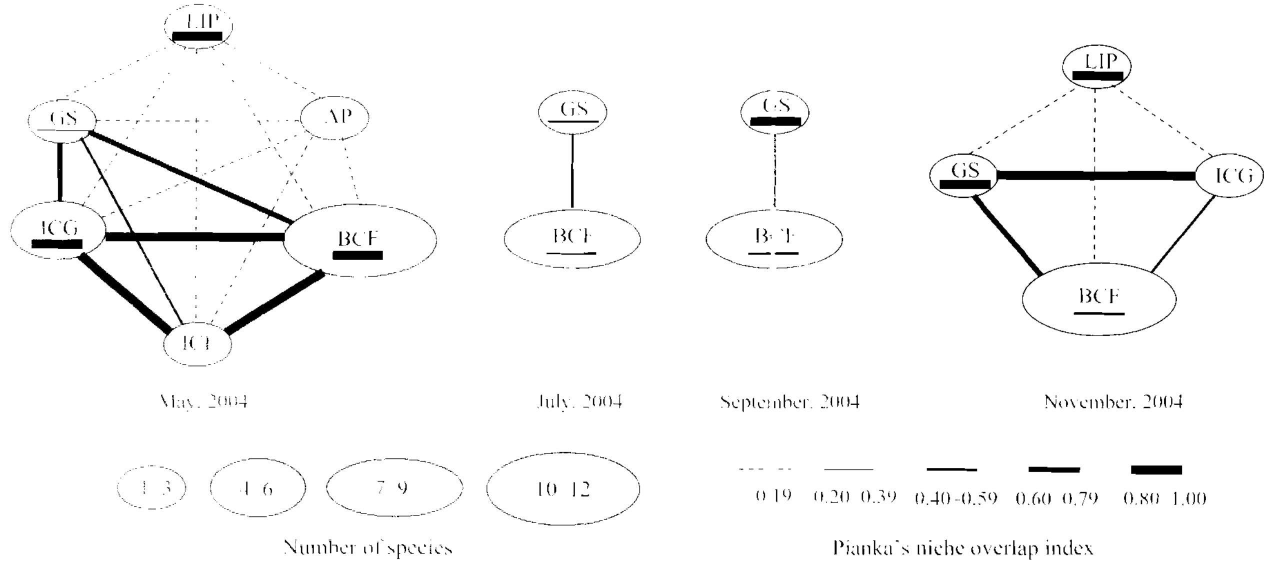

Fig. 5. Dynamics of the niche overlap web of benthic macroinvertebrates in Lake Dongtinghu (May–November, 2004). GS, gastropod scrapers; ICG, insect collector-gatherers; BCF, bivalve collector-filterers; ICF, insect collector-filterers; AP, annelid predators; LIP, large insect predators. The line thickness in each ellipse shows the dietary overlap of species within the functional feeding group.

relatively small proportion of total ingestion. In over 75 % of total links, the volumetric contribution was less than 10 %. A large amount of ingestion occurred in a small number of links (4.6 %), indicating that most energy flows were concentrated in a few feeding pathways. Moreover, this pattern changed little through time and seemed not to be affected by flood disturbance (Fig. 4).

Interaction webs were constructed based on trophic niche overlap among macroinvertebrates. In Lake Dongtinghu, there was moderate dietary overlap among animals with a mean value of Pianka's niche overlap index of 0.40. Generally, dietary overlap among macroinvertebrates decreased slightly during the sampling. The mean value of dietary overlap within each FFG was the highest in ICG (0.96), and the lowest in LIP (0.52). Dietary overlap was much higher among groups of primary consumers than among other groups. The highest overlap occurred between ICG and ICF (0.95), while the lowest was observed between LIP and other groups (less than 0.02). Among groups of primary consumers, dietary overlap between BCF and other FFGs (0.47–0.60) was lower than those among other FFGs (0.66–0.95). With reference to temporal variations, the macroinvertebrate food web in the lake changed greatly during the sampling (Fig. 5). In terms of numbers of species and FFGs, the web structure was much simpler during the flood season than in other months. Dietary overlaps within most FFGs and among FFGs were much lower during the flood season than those in other periods, with the lowest overlap occurring in July.

Discussion

A common type of ecosystem on a floodplain, river-connected lakes have properties of both lotic and lentic waters. Our study is the first detailed study on trophic relationships of benthic macroinvertebrates in a Yangtze River-connected lake. Former studies of macroinvertebrate food webs have shown that benthic webs were heavily based on detritus in a wide range of freshwater ecosystems (Warren 1989, Thompson & Towsend 2003, Liu et al. 2006, Liu & Wang 2007). Although detritus made the greatest contribution (about 40 %) of the total ingestion in the food web of Lake Dongtinghu, it contributed much less than those in streams (e.g. Tavares-Cromar & Williams 1996) and river-isolated lakes (most > 80 %) (e.g. Liu et al. 2006). A large amount of energy (about 30 %) in the lake is derived from plankton such as cyanobacteria, protozoans and rotifers.

Many studies on fluvial systems showed that bivalve collector-filterers (BCF) dominate the biomass of benthic communities (e.g. Strayer et al. 1999, Vaughn et al. 2004). Our results demonstrated that BCF were abundant in Lake Dongtinghu in terms of

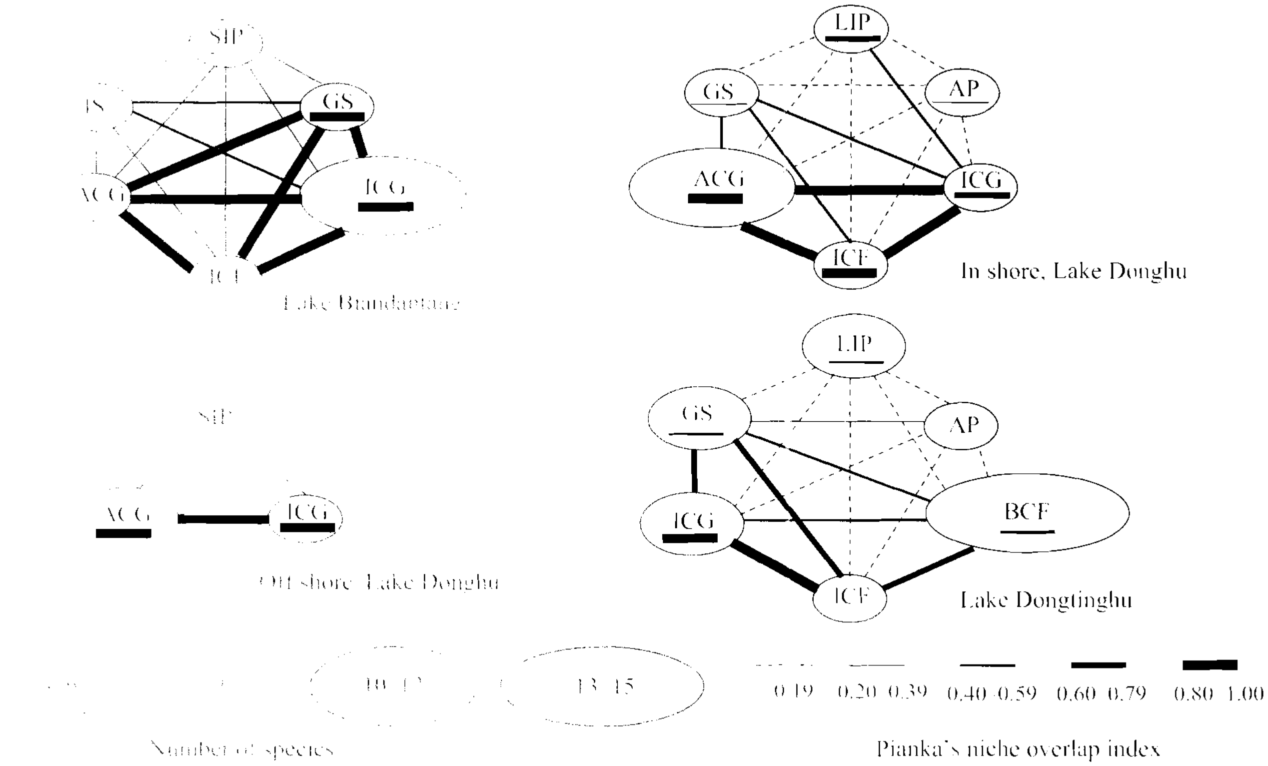

Fig. 6. Comparison of the niche overlap web (summary web) of Lake Dongtinghu with two Yangtze River-isolated lakes. IS, insect shredders; GS, gastropod scrapers; ACG, annelid collector-gatherers; ICG, insect collector-gatherers; BCF, bivalve collector-filterers; ICF, insect collector-filterers; SIP, small insect predators (mainly chironomids); LIP, large insect predators (mainly odonates). The line thickness in each ellipse shows the dietary overlap of species within the functional feeding group. The food web of Lake Bandantang was formed according to Li et al. (2006), and those of Lake Donghu were cited from Liu & Wang (2007).

number of species and biomass. A similar pattern was also found in Lake Poyanghu, another large Yangtze River-connected lake (Wang et al. 2007), but not in Yangtze-isolated lakes (Li & Cui 2005). This suggests that water flow is of importance in structuring benthic communities on floodplain ecosystems. BCF are abundant benthic-pelagic couplers in streams (Vaughn et al. 2004), and play an important role in nutrient recycling of freshwater ecosystems (Howard & Cuffey 2006). BCF can remove large amounts of particles from the water column and transfer these resources to the substrate as biodeposits (faeces and pseudofaeces), thus making suspended material available for other benthic animals such as insect collector-gatherers. Because of their filter feeding mode, BCF are separated from collector-gatherers and scrapers in terms of trophic niches. This explains in part why dietary overlaps between BCF and other primary consumers are lower than those among other primary consumers.

Some patterns in the food web of Lake Dongtinghu are consistent with those in other freshwater benthic webs such as streams (e.g. Benke & Wallace 1997, Benke et al. 2001, Thompson & Townsend 2003), river-isolated lakes (e.g. Liu et al. 2006, Liu & Wang 2007) and ponds (Warren 1989). These include high levels of omnivory and energy concentrated in a small number of links. However, there are some differences in web structure among these ecosystems. First, species composition of Lake Dongtinghu is quite different from that of river-isolated lakes and streams. Bivalve collector-filterers dominate the benthic community in Lake Dongtinghu, but comprise a small proportion of macroinvertebrates in many river-isolated lakes and streams. Second, connectance in the Yangtze River-connected lake is higher than that of streams (Townsend et al. 1998, Thompson & Townsend 2003), while lower than that of Yangtze River-isolated lakes (Liu et al. 2006, Liu & Wang 2007) and ponds (Warren 1989). This suggests that connectance increases as ecosystems change from lotic to lentic waters. Third, with regard to niche overlap webs, the dietary overlaps within and among FFGs are much lower in Lake Dongtinghu than those in Yangtze River-isolated lakes (Fig. 6) and streams (Woodward & Hildrew

2002). Since trophic basis is important in structuring food webs (Rosi-Marshall & Wallace 2002, Liu et al. 2006), it is likely that different trophic bases between the Yangtze River-connected and -isolated lakes shape different webs. The food web of the Yangtze River-connected lake was based on detritus and a large amount of primary production, while those of Yangtze River-isolated lakes and streams heavily relied on detritus (most > 80 %).

Many studies suggest that flood events have a strong modifying influence on the macroinvertebrate community of rivers and streams (e.g. Sagar 1986, Thomson 2002, Suren & Jowett 2006). Our results demonstrate that the benthic community in Lake Dongtinghu changed significantly during the sample period. The numbers of species and FFGs, and the density and biomass of macroinvertebrates decreased during the flood season. However, this study is somewhat confounded by the fact that floods in Lake Dongtinghu were also seasonal. It is difficult to clearly separate the influence of the flood and season in terms of how they influence the benthic community. Studies on benthic communities of Yangtze River-isolated lakes suggest that both density and biomass of zoobenthos changed seasonally, usually with the highest values occurring in summer and autumn (Liang & Liu 1995, Li & Cui 2005, [illegible] et al. 2006). Such a pattern is quite different from that of Lake Dongtinghu. The latter showed the lowest standing crop in summer (July) and autumn (September) when water level was the highest, suggesting that the benthic community in the lake is controlled more by flow related variables than by season. Moreover, the separation of seasonal variation and effects of flooding is supported by the life cycles of mollusc species, which display little or no seasonal pattern. Although little life history information exists for aquatic insects on the Yangtze floodplain, studies in rivers and streams show that many freshwater invertebrates display little seasonal pattern (e.g. Greenwood & McIntosh 2004). Hence floods act as the chief factor affecting the benthic community of Yangtze River-connected lakes.

Strong influences are exerted on benthic communities by floods which can disturb invertebrate populations and physical habitats (e.g. Carling 1992, Nelson & Lieberman 2002). Such influences were also evident in the Yangtze River-connected lake as shown by severely decreased populations of macroinvertebrates. Studies have show that one of the effects of flooding on the benthic community is the reduction of food supply to consumers (e.g. Sagar 1986). However, our [illegible] in the Yangtze River-connected lake suggested [illegible]. Animals in Lake Dongtinghu consumed more planktonic material during the flood season than in other periods. Plankton is abundant in Yangtze lakes during the flood season when water temperature is high (Liang & Liu 1995). It is also likely that the plankton is washed out of lentic and low flowing water by flood waters.

Food web structure also appears to be simplified by flooding. This is shown by a decrease in the number of species and links in the Lake Dongtinghu food web. High connectance values typically occurred in lentic waters compared with lotic habitats. Connectance increased as flooding increased in intensity in Lake Dongtinghu. Since benthic predators decreased in density during the flooding, food webs of those months represent only primary consumers and excluded insect predators. Strong effects exerted by flooding on the benthic food web were also demonstrated by the decrease of niche overlap within and among FFGs during the flood season. This indicates that although species consumed a wide range of food items during the flooding, they seemed not to compete intensely with each other for food. Although floods have strong effects on benthic macroinvertebrates, the benthic community typically recovers quickly after flooding (Lake et al. 2006). This was the case in Lake Dongtinghu, as we saw an increase in macroinvertebrate density and biomass as the flood waters receded. The recovery of the benthic community in the lake may be due to refugia in the floodplain as a result of a regular flood regime in this area.

Our results provide useful information with regard to the restoration of benthic macroinvertebrates in lakes on the Yangtze River floodplain. Connectivity is important in maintaining a high level of habitat heterogeneity and species biodiversity in lakes. Considering conservation of biodiversity in Yangtze River-isolated lakes, it is necessary to increase the connectivity between these lakes and the Yangtze River. Also, natural flood regime plays an important role in structuring the benthic community. Biodiversity conservation should consider reconstructing the natural flow regime in Yangtze River-isolated lakes. With regard to the Yangtze River-connected lakes, the lentic and low-flow regions in Lake Dongtinghu played an important role in supplying foods for animals of fast-flow regions especially during the flood season. Conservation of biodiversity in Yangtze River-connected lakes thus should maintain a certain proportion of lentic or low-flow water area.

This study is the first to show detailed information of trophic relationships among benthic macroinvertebrates in Yangtze River-connected lakes. Animals fed mainly on detritus and also consumed large amounts of plankton. Low food web connectance and high levels of omnivory were found in Lake Dongtinghu. The food web appeared to be based on detritus and primary production, while most ingestion was concentrated in just a few links. Analyses suggest that flood disturbance acts as the chief factor affecting benthic food webs in river-connected lakes. Conservation of biodiversity on the Yangtze River floodplain should consider reconstructing and maintaining the natural flow regime between lakes and the river.

Acknowledgements

We thank Messrs. Xiang Rong Huang and Hui Jun Ru for field work. Special thanks are due to Dr. Daniel H. Shain and two anonymous reviewers for their invaluable comments on the manuscript. This research was funded by 973 Programs of China (2002CB412309 and 2003CB415206).

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Submitted: [illegible] 2007; accepted: 13 January 2008.

Appendix 1. Food composition (% volume) of macroinvertebrates in Lake Dongtinghu. FFG is functional feeding group. GS: gastropod scrapers; ICG: insect collector-gatherers; BCF: bivalve collector-filterers; ICF: insect collector-filterers; AP: annelid predators; LIP: large insect predators. N= guts with food. Ino: inorganic material; Det: detritus; Cya: cyanobacteria; Dia: diatoms; Gre: green algae; Oth: other algae (mainly dinoflagellates and euglenoids); Mac: macrophytes; Pol: pollen of conifers; Pro: protozoans; Hyd: hydroids; Fla: flatworms; Rot: rotifers; Nem: nematodes; Bry: bryozoan floatoblasts; Oli: oligochaetes, Cru: crustaceans; Wat: water mites; May: mayfly nymphs; Chi: chironomid larvae; Mis: miscellaneous material.

Species	FFG	N	Ino.	Det.	Cya.	Dia.	Gre	Oth.	Mac	Pol.	Pro	Hyd.	Fla.	Rot.	Nem.	Bry.	Oli.	Cru.	Wat.	May.	Chi.	Mis.
Oligochaeta																						
Chaetogaster limnaei (von Baer)	AP	2	0	0	0	0.5	0	0	0	0	0	0	0	99.5	0	0	0	0	0	0	0	0
Mollusca																						
Gastropoda																						
Bellamya sp.	GS	49	16.6	80.8	0.9	0.7	0.2	<0.1	0	<0.1	0.5	0	0	0.3	<0.1	0	0	0	0	0	0	<0.1
Parafossarulus eximius (Frauenfeld)	GS	42	11.7	76.3	0	0.2	2.3	0.2	0	<0.1	7.2	0	0	2.0	<0.1	0	0	0	0	0	0	<0.1
Radix swinhoei (H. Adams)	GS	15	14.6	0.5	0	0.2	0.5	0	22.0	0	0	0	0	23.7	0	3.0	0	0	<0.1	0	9.8	25.5
Rivularia auriculata (Martens)	GS	10	43.1	43.7	0	6.0	<0.1	<0.1	0.4	4.0	0.3	0	0	2.4	0	0	0	0	0	0	0	0.1
Semisulcospira amurensis (Gerstfeldt)	GS	38	30.5	29.7	0.3	0.2	0.2	0.1	0.6	3.0	2.8	0	1.7	29.8	0.3	0	0	<0.1	0	0	0	0.7
Bivalvia																						
Anodonta arcaeformis (Heude)	BCF	29	10.1	58.5	1.0	1.2	2.1	2.8	0.8	0.2	5.2	0	0	2.6	0	0	10.1	5.4	0	0	0	<0.1
A. woodiana woodiana (Lea)	BCF	51	1.1	22.1	51.2	1.1	1.5	0.3	<0.1	<0.1	0.7	0	0	12.3	0	0	0	8.6	0	0	0	1.1
Arconaia lanceolata (Lea)	BCF	56	4.3	25.4	18.0	0.6	0.1	0.2	0.4	0.3	43.9	0	0	5.6	0	0	0	1.0	0	0	<0.1	0.2
Corbicula fluminea (Müller)	BCF	79	2.4	30.1	53.4	0.7	0.6	0.2	0	5.3	1.4	0	0	4.1	0	0	0	0.7	0	0	0	1.3
Cuneopsis celtiformis (Heude)	BCF	3	0	89.0	<0.1	0.4	0.8	3.0	0	0	0	0	0	6.8	0	0	0	0	0	0	0	0.1
Hyriopsis cumingii (Lea)	BCF	54	7.7	29.2	2.1	1.2	0.3	0.3	0	<0.1	56.1	0	0	0.7	0	0	0	2.2	0	0	0	0.3
Lamprotula caveata (Heude)	BCF	91	5.2	38.5	0.7	0.3	0.1	0.2	<0.1	3.3	49.7	0	0	1.3	<0.1	0	<0.1	0.2	0	0	0	0.3
L. leai (Gray)	BCF	23	4.6	76.5	<0.1	1.4	0.2	0.2	0	0	8.4	0	0	2.0	0	0	0	0.8	0	0	5.6	0.3
L. rochechouarti (Heude)	BCF	11	0.3	5.5	<0.1	0.2	<0.1	<0.1	0	<0.1	42.6	0	0	51.1	0	0	<0.1	0	0	0	0	0.1

Appendix 1. Continued.

Species	FFG	N	Ino.	Det.	Cya.	Dia.	Gre	Oth.	Mac	Pol	Pro	Hyd.	Hla.	Rot	Nem	Bry.	Oli	Cru.	Wat	May.	Chi.	Mis.
Bivalvia																						
Lanceolaria grayana (Lea)	BCF	9	8.3	37.9	0.4	0.6	0.2	0.3	0	0	37.0	0	0	15.1	0.2	0	0	0	0	0	0	<0.1
Limnoperna lacustris (Martens)	BCF	60	9.8	63.0	0.9	1.5	5.2	0.8	0	2.2	0.1	<0.1	0	11.1	0.1	0.2	0	4.5	0	0	0	0.6
Solenaia oleivora (Heude)	BCF	25	1.9	3.0	<0.1	0.1	<0.1	<0.1	0	0	89.6	0	0	1.5	0	0	0	3.9	0	0	0	<0.1
Unio douglasiae (Gray)	BCF	69	2.0	35.7	36.5	0.8	0.4	1.3	<0.1	0.9	7.9	0	0	9.3	0	0	0	5.1	0	0	0	0.1
Ephemeroptera																						
Ephemera sp.	ICG	10	35.5	60.7	0	0.3	<0.1	0	0	0	0	0	0	3.3	0	0	0	0.2	0	0	0	<0.1
Potamanthus sp.	ICG	10	28.2	59.9	0	1.9	0.3	0	6.5	0	0	0	0	3.2	0	0	0	0	0	0	0	<0.1
Odonata																						
Anotogaster sp.	LIP	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0
Cercion sp.	LIP	22	0	0	0	0	0		0	0	0	0	0	<0.1	0	0	0	<0.1	0	31.6	68.4	<0.1
Gomphidia sp.	LIP	3	0	<0.1	0	<0.1	0	0	0	0	0	0	0	<0.1	0	0	0.7	0	0	99.2	0	0.1
Ischnura sp.	LIP	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<0.1	0	0	99.9	0
Sinictinogomphus sp.	LIP	23	<0.1	<0.1	0	<0.1	0	0	0	0	0	0	0	<0.1	0	0	0	0	0	99.9	0	0
Diptera																						
Crictopus sp.	ICG	5	7.8	85.0	0	5.2	1.3	0	0.7	0	0	0	0	0	0	0	0	0	0	0	0	0
Cryptochironomus sp.	ICG	2	9.0	89.5	0	1.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicrotendipes sp.	ICF	4	3.5	91.3	0	5.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polypedilum braseniae (Leathers)	ICG	10	29.4	68.8	0	1.6	<0.1	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	<0.1
Polypedilum sp.	ICG	14	14.3	81.1	0	4.0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0