

Trophic fingerprint of fish communities in subtropical floodplain lakes

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Abstract – Stable nitrogen isotope ratios ($\delta^{15}N$) and gut content analysis are commonly used to detect trophic relationships in aquatic systems. Nonetheless, the use of $\delta^{15}N$ in determining the suitability of quantitative and qualitative dietary data as representations of trophic relationships in lake ecosystems remains unverified. Quantitative and qualitative dietary data on 46 fish species were obtained from field surveys in the floodplain lakes of the Yangtze Plain to calculate trophic position and benthivory. Dietary measures using the stable isotope approach were validated. The dietary approach yields comparable results in detecting trophic relationships in lake ecosystems. Our estimation of the benthivory of the 46 fish species ranged from 1.5% to 100%, with an average of 60.3%. These figures support the assumption that benthic energy pathways account for more than half of total fish consumption. Our feeding guild data confirm that more than 50% (including 25 species) of the studied fish species in the floodplain lakes of the Yangtze Plain are omnivorous, suggesting that omnivory is prevalent among subtropical floodplain lakes.

Key words: trophic position; stable isotope; dietary; fish; benthic; omnivory; habitat coupling; feeding guild; trophic relationship

Introduction

The complex and intense trophic interactions between organisms are critical characteristics of food webs, which influence community structure, species, and stability (Carpenter et al. 1987; Sabo & Power 2002). Food webs and food chains are two of the most useful approaches for studying trophic interactions. Food webs depict the complex trophic interactions inherent among organisms within ecosystems (Post 2002a; Sabo et al. 2009), and food chains are caricatures of communities, tracing either the linear energy or strength pathways from primary producers to apex predators embedded within more complex food webs (Lindeman 1942; Sabo et al. 2009). Food web and food chain approaches represent the extreme end-points of the models used to depict trophic relationships. Both approaches, however, may yield incorrect energy flow and mass transfer data. The accurate

representation and description of the trophic relationships of fishes in aquatic ecosystems are essential. Moreover, understanding trophic relationships is significant in restoring, conserving and managing lake ecosystems.

Organisms are traditionally classified by trophic level, which depicts the relative position of an organism within a food web, but does not account for complex trophic interactions. One example is omnivory (Kling et al. 1992), which is defined as feeding on more than one trophic level (Fagan 1997). Trophic position (TP) is a continuous variable that accounts for omnivory and tracks matter transfer and energy flow within a food web (Kling et al. 1992; Vander Zanden & Rasmussen 1996; Post 2002b). The TP of fishes can be obtained in two ways. One is through TP estimation from gut content analysis (GCA), which can also provide diet information on species. This approach explains only the instantaneous tempo-

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ral measure of an organism's diet and not long-term mass transfer (Vander Zanden et al. 1997). The other approach is stable isotope analysis (SIA; Post 2002b; Rybczynski et al. 2008; Vander Zanden et al. 1997). The SIA approach relies on the consistent enrichment of nitrogen isotope ratio ($\delta^{15}N$); that is, the $\delta^{15}N$ of consumers is enriched by approximately 3‰ to 4‰ relative to food sources during trophic transfer (Post 2002a,b; McCutchan et al. 2003).

GCA and SIA have unique advantages. Unlike GCA, SIA measures the TP of an organism, which accounts for omnivory and long-term patterns of mass transfer. SIA cannot provide taxonomic information on the prey of organisms (Vander Zanden et al. 1997; Rybczynski et al. 2008). Vander Zanden et al. (1997) found that GCA and SIA can provide comparable results for fish TP in the lake ecosystems of North American temperate lakes. Few researchers have calculated the TP of fishes in floodplain lakes, which are rich in omnivorous Cyprinidae fish. Moreover, direct comparisons between the two methods for application in floodplain lakes are limited.

A lake consists of discontinuous habitats and is linked by a series of important ecological processes (Schindler & Scheuerell 2002). Recent limnological research has reflected increasing interest in the interactions between pelagic and benthic habitats. (Schindler & Scheuerell 2002; Lamberti et al. 2010). Fishes play a key role in habitat coupling because of their high mobility and flexible foraging tactics, thereby linking benthic and pelagic ecological systems through inter-habitat omnivory (Schindler & Scheuerell 2002). Studies that have effectively linked benthic and pelagic habitats within a food web perspective of lakes are rare (Lodge et al. 1988; Vadeboncoeur et al. 2001; Schindler & Scheuerell 2002). Investigations that incorporated benthic–pelagic links through fishes in models of lake food webs have repeatedly demonstrated the importance of benthic subsidies to the effects of fishes on pelagic habitats. Two approaches can be used to examine the contribution of benthic production to fishes in lake ecosystems. The first is dietary data analysis, which reflects direct consumption, and the second is the use of stable isotopes, which reflects prey assimilation. Only a few studies have directly resulted from these two analyses (Vander Zanden and Vadeboncoeur, 2002). Potentially serious limitations exist when using nonintegrated approaches in aquatic ecology. Stable isotope and GCA data have been extensively compared and integrated in previous studies (Vander Zanden et al. 1997; Rybczynski et al. 2008; Zhou et al. 2009). The integration of benthic and pelagic resources in lake food webs has also been comprehensively demonstrated. To our knowledge, few researchers have used dietary observations (i.e., gut

content data) to calculate trophic characteristics (i.e., TP and benthivory) or have compared these values with stable isotope data.

To fill these gaps, we established two objectives for the current study. The first is to build a continuous measure of TP for freshwater fish species on the basis of quantitative and qualitative datasets. We designed dietary data expressed as the percentage of weight and the percentage of the total number or volume of prey organisms, which is also reported as the per cent frequency of occurrence as quantitative dietary data. We defined dietary data using descriptive words to express the abundance of prey items without using numerical value as qualitative data. The other objective is to verify the dietary approach using SIA. The TP and benthic-versus-pelagic subsidies of 46 fish species of the flood plain metacommunity were determined and compared using dietary data and SIA. The means for TP and benthivory were calculated using both approaches.

Materials and Methods

Sampling and sample treatment

From 2002 to 2010, 46 fish species were collected from Lake Poyang, Lake Dongting, Lake Taihu, and Lake Chaohu, located at 110°40' to 120°36' and 28°22' to 31°43'N (Appendix 1). *Bellamyia aeruginosa* and *Corbicula fluminea* were collected from the four lakes. Adult fishes were collected from fishermen or by casting nets from both littoral and open water areas. A filet of dorsal muscle (white muscle) was removed from each fish. These tissues represent the overall stable isotope signature in a fish (Hesslein et al. 1993). After collection and transport to the laboratory, the samples were either immediately processed or kept frozen for later processing. Before analysis, the samples were sorted, rinsed with distilled water and oven dried at 60 °C to a constant weight. The samples were then ground into fine powder using a mortar and pestle. The mortar and pestle was acid washed and dried to prevent cross-contamination between the samples. Subsequently, all the samples were analysed with a Carlo Erba NC-2500 elemental analyzer coupled with a Delta Plus (Finnigan) isotope ratio mass spectrometer via a continuous flow II interface. The results are presented in Appendix S1.

Estimation of benthivory and TP

The fundamental aim of the current study was to determine the relative contribution of different primary producers to the diets of consumers. An isotopic mixing model was therefore necessary, although

mathematical and biological limitations constrain the application of such a model (Ben-David & Schell 2001; Phillips & Gregg 2001, 2003). Early approaches based on Euclidean distance do not provide a mathematically correct solution. Overemphasis of the contribution to diet is possible if one source has a signal similar to that of a sink, and precise solutions cannot be obtained unless all end-members are included. These problems are compounded by variations in absorption and fractionation between different food sources (Adams & Sterner 2000; Ben-David & Schell 2001; Phillips & Gregg 2001, 2003; McCutchan et al. 2003) and variations in source signal, which depends on the relative supply and demand placed upon the element in question. Nevertheless, we followed the method used by Vander Zanden et al. (Vander Zanden et al. 1999; Vander Zanden & Vadeboncoeur 2002; Vander Zanden & Fetzer 2007) and (Post et al. 2000; Post 2002a). We used these simple models as heuristic tools in investigating the patterns within our isotopic data; we did not expect the models to yield exact solutions.

Long-lived macroinvertebrates, the grazing snail *B. aeruginosa*, and the filter-feeding *C. fluminea* are less sensitive to the seasonal fluctuations in the isotopic compositions of primary producers. These organisms reflect the baseline of benthic and pelagic food webs. They also provide an isotopic baseline for estimating the TP of higher trophic level consumers in lake ecosystems (Vander Zanden et al. 1999; Post 2002a). Thus, we used these species as benthic and pelagic end-members for each sampling period. Freshwater snail *B. aeruginosa* grazes mainly on epiphytic algae (Xu et al. 2003), whereas the Asiatic clam *C. fluminea* filters phytoplankton from the water column (Havens et al. 2003). To compare the variations in reliance of the benthic-versus-pelagic prey of the fishes, we used the mass balance mixing model to estimate the contribution of benthic secondary production to fishes with the following formula:

$$\text{Benthivory} = \frac{\delta^{13}\text{C}_{\text{fish}} - \delta^{13}\text{C}_{\text{pelagic}}}{\delta^{13}\text{C}_{\text{benthic}} - \delta^{13}\text{C}_{\text{pelagic}}} \quad (1)$$

where $\delta^{13}\text{C}_{\text{fish}}$, $\delta^{13}\text{C}_{\text{pelagic}}$, and $\delta^{13}\text{C}_{\text{benthic}}$ are the mean $\delta^{13}\text{C}$ of fish species, pelagic baseline (mean $\delta^{13}\text{C}$ of *C. fluminea*) and benthic baseline (mean $\delta^{13}\text{C}$ of *B. aeruginosa*), respectively. To capture the potential spatial heterogeneity in the $\delta^{15}\text{N}$ baseline of fishes that feed on both pelagic and benthic food webs, we calculated TP as follows:

$$\text{TP} = \delta^{15}\text{N}_{\text{fish}} - [\delta^{15}\text{N}_{\text{pelagic}} \times (1 - \alpha) + \delta^{15}\text{N}_{\text{benthic}} \times \alpha] / 3.4 + \lambda, \quad (2)$$

where 3.4 is the generally assumed per trophic level enrichment of $\delta^{15}\text{N}$ (Post 2002a); α is the proportion of nitrogen in the consumer derived from the baseline of the benthic food web, and was estimated using carbon isotopes by the formula mentioned above (Post 2002a,b a); $\lambda = 1$ denotes primary producers and $\lambda = 2$ represents primary consumers. The values of $\delta^{15}\text{N}_{\text{fish}}$, $\delta^{15}\text{N}_{\text{pelagic}}$, and $\delta^{15}\text{N}_{\text{benthic}}$ represent the mean $\delta^{15}\text{N}$ of fishes, pelagic baseline (mean $\delta^{15}\text{N}$ of *C. fluminea*), and benthic baseline (mean $\delta^{15}\text{N}$ of *B. aeruginosa*), respectively. Several recent studies have synthesised trophic level fractionation values from literature. We used a universal trophic fractionation value of 3.4‰ to ensure the consistency of methods across studies (Vander Zanden & Rasmussen 2001; Post 2002a) and assumptions in previous comparative food web research (Vander Zanden et al. 1999; Post et al. 2000; Vander Zanden & Fetzer 2007). These models use primary consumers (rather than primary producers) as isotopic endpoints; thus, the contributions of pelagic and benthic secondary production are estimated, assuming that trophic enrichment does not exist in $\delta^{13}\text{C}$ (trophic fractionation = 0‰) and mixing is linear (Vander Zanden et al. 1999; Post et al. 2000; Post 2002a). We used this method to estimate the TP and benthivory of the 46 fish species (see Appendix S1 in Supplement).

Dietary data collection and analysis

Dietary data were collected by conducting an exhaustive literature search from books, several databases, and ichthyographies. We then examined the citations included in the original studies. All data were on Chinese ecosystems, and more than 95% of the populations are located in the middle and lower areas of the Yangtze River.

Some published studies divided dietary data into groups based on year, season, month, and fish size. We used only the diet data on adult fishes to avoid potential errors caused by diet shifting during ontogeny. The average of different dietary data was obtained for each lake. Dietary data for most fish species were collected from different ecosystems and subsequently averaged. To avoid bias in favour of better sample components in the population, averages were not weighted based on sample size. Data from multiple studies on the same ecosystem were also averaged in this study, but data from studies with only one sample collection were not used in the current work because of potential bias. We retained only the dietary data on adult fishes for analysis when adult and juvenile fishes were discretely reported. The dietary data on the 46 fish species were collected from 24 literature sources. In addition, the fish dietary dataset contains 83 populations for a total of 9752

individual fishes. The average diet for each fish species (the per cent volumetric contribution of each prey item) was calculated (see Appendix S2 in Supplement).

The continuous measurement of fish TP is possible by GCA, which necessitates estimating the TP of prey organisms and the per cent volumetric contribution of each prey item, preferably for large numbers of fishes. We used this method to estimate the TP of the 46 fish species (see Appendix S2 in Supplement) found in floodplain lakes. Thus, before final TP calculation, substantial data were collected and classified into two types: qualitative and quantitative. The dietary data on 28 species of fish in our dataset are quantitative, those on 12 fish species are qualitative, and those on the remaining 6 species are both qualitative and quantitative (see Appendix S2 in Supplement).

Using quantitative dietary data to calculate fish TP

The quantitative data were collected from previous studies, and are expressed in several ways. In this study, we used diet data expressed as the percentage of weight and the percentage of the total number of prey organisms, which is also reported as per cent frequency of occurrence. The dietary data expressed as frequency of occurrence were converted into the percentage of weight before use in fish TP estimation. The formula used for conversion was

$$W_i = C_i / \Sigma C_i \quad (3)$$

where W_i is the weight contribution of the i th food item, and C_i is the frequency of occurrence of the i th food item. Using dietary data to calculate the TP of a fish population necessitates employing the TPs of prey organisms. Therefore, appropriately determining the TPs of prey items is crucial (details of the TP determination of prey items are provided in the Supplement). The TPs of prey items vary within systems and across time. Fortunately, our large sample size would render any errors associated with these assumptions, which are constant among fish species included in this study. We followed the method of Winemiller (1990) and Vander Zanden et al. (1997) for the dietary data and TP estimation of prey items. The following equation was used to calculate the TPs of fishes in this study:

$$TP_a = \Sigma(W_i * TP_i) + 1 \quad (4)$$

where TP_a is the mean TP of the α th kind of fish, W_i denotes the weight contribution of the i th food item, and TP_i represents the TP of the i th prey organism. Although most prey organisms were designated to discrete trophic levels, omnivory among fishes resulted in the fractional measurement of the TP of each species.

Using qualitative dietary data to calculate fish TP

Some species (see Appendix S2 in Supplement) in our study are not economic fishes. Only a few researchers have paid close attention to the diet of such fishes; thus, detailed quantitative dietary data are lacking. In several ichthyographies, brief qualitative dietary descriptions of these fishes based on field observations are available. We collected qualitative data mainly from books (see Appendix S2 in Supplement) because species biodiversity can be represented by the amount or relative abundance of species in an area (Major, 1962). Although the qualitative description of prey items in these ichthyographies is highly variable, classifying the qualitative data into five grades is possible. Following Major (1962), we classified the description data into five levels: very abundant, abundant, common, occasional, and rare (Supplement). The following scores were then assigned to the levels: 100 for very abundant, 75 for abundant, 40 for common, 5 for occasional and 1 for rare. The score assigned to each prey item was used to calculate their per cent weight contribution to total diet (Supplement). With the scores, we calculated the weight contribution of each prey item using

$$W_i = 1 / \sum_{i=1}^n S \quad (5)$$

where W_i is the weight contribution of the i th food item, S is the score of the prey organism and n denotes the total number of prey items of fish species. We then used the same standard as that employed for the quantitative data to calculate the TP of each fish species.

Estimation of fish benthivory on the basis of dietary data

Another aim of this study was to determine the relative contribution of different primary producers to the diets of consumers. To simplify, we also grouped all food sources into two types: benthic and pelagic sources. The sum of the per cent benthic and per cent pelagic sources of each fish species was 100%. Moreover, the conversion of these dietary data into the benthivory of primary producers necessitates assumptions concerning the benthivory of prey organisms. Thus, appropriately assigning the benthivories of prey items is pivotal. The degree of taxonomic detail of prey items in previous studies is highly variable. Fortunately, categorising the prey organisms into the following groups is usually possible: fishes, zooplankton, omnivory insects, predatory insects, crustaceans, molluscs, benthic primary producers and pelagic primary producers. To estimate the benthivory of the fishes in our study, we used the formula

$$B_a = \sum(W_i * B_i) \quad (6)$$

where B_a is the benthivory of the i th fish species, W_i represents the weight contribution of the i th food item, and B_i is the benthivory of the i th prey organism. For the qualitative dietary data, we first converted the data into quantitative data similar to that done for the TP estimation of fish species. We then used the same standard as that employed for the quantitative data to calculate the benthivory of each fish species.

Feeding guilds

The compiled raw dietary data are presented in Appendix 1. We summarised the data by calculating the percentage of the total gut weight of each species. Feeding guilds were determined by adapting the stepwise procedure from de Mérona et al. (2003), who grouped fish species into six feeding guilds. The prey items of fish species differ from those of the species in floodplain lakes. Therefore, the prey items were slightly adjusted according to the prey organisms of the fish species in the current study. The stepwise procedure is presented as follows:

Step 1: More than 70% of plankton in the gut: planktivores.

Step 2: More than 70% of fishes and Crustaceans in the gut: carnivores.

Step 3: More than 70% of insect and mollusc in the gut: invertivores.

Step 4: More than 70% of benthic primary producer in the gut: herbivores.

Step 5: None of the above in the gut: omnivores.

Statistical analysis

Differences in TP_{GCA} , TP_{SIA} , B_{GCA} , B_{GCA} and B_{SIA} among feeding guilds were examined using a one-factor ANOVA, with variance estimated at each feeding

guild. The TP_{GCA} , TP_{SIA} , B_{GCA} , and B_{SIA} data were individually analysed using feeding guilds as the factor and TP_{GCA} , TP_{SIA} , B_{GCA} and B_{SIA} as the dependent variables. When significant differences among treatment and their interactions were found, Tukey's least significant difference test was performed for further comparison. All analyses included an interaction term, with a significance level of $\alpha = 0.05$. The relationship between TP_{GCA} (B_{GCA}) and TP_{SIA} (B_{SIA}) was analysed with a regression linear model. First, a linear regression model was tested separately for each lake. The homogeneity of b (the slopes of the linear regression) was tested when significant regressions ($P < 0.05$) were found among TP_{GCA} (B_{GCA}) and TP_{SIA} (B_{SIA}). In regression relationship analysis, TP_{GCA} (B_{GCA}) was treated as a dependent variable and TP_{SIA} (B_{SIA}) was an independent variable. We used SPSS for Windows (Version 16.0) for statistical analysis.

Results

Dietary, TP_{GCA} and $Benthivory_{GCA}$ as dietary estimates of TP_{GCA} and $Benthivory_{GCA}$

The average percentages of every prey item in the feeding guilds are presented in Table 1. Three species of fish were classified as planktivores with an average of plankton feeding more than 97.3%. Six species were grouped into herbivores and consumed benthic primary producers at an average of 92.4%. Five species were grouped as invertivores, whose average diet consisted of 52% omnivorous insects, 8.8% predatory insects and 23.5% molluscs. More than 50% of the species were omnivorous, including 25 that fed on insects, plankton, crustaceans, benthic primary producers, and molluscs at an average of 31.1%, 25.1%, 13.2%, 10%, and 9.1%, respectively. The remaining 7 species are carnivores, whose average diet consisted of more than 78% of fishes. The TP and benthivory of all the 46 fish species were estimated using these dietary data (see Appendix S1

Table 1. Mean dietary data on different feeding guilds.

FG	NS	Prey category										Average TP	Average B
		Fish	ZP	OMI	PI	Cru	Mol	Bp	Pp	roe			
CAR	7	78.0	0.1	1.3	0.1	19.6	0.3	0.7	0.0	0.1	3.8	73.7	
HER	6	0.0	4.4	0.5	0.0	0.0	0.0	92.4	2.7	0.0	2.1	91.9	
INV	5	0.5	10.4	52.1	7.0	3.4	23.5	3.6	0.1	0.3	3.3	59.4	
PLA	3	0.0	56.9	0.0	0.0	0.0	0.5	1.9	40.6	0.0	2.6	2.4	
OMN	25	8.4	19.4	29.1	2.3	13.2	9.1	10.1	5.7	0.4	3.2	56.1	

FG = feeding guilds, NS = number of species, ZP = zooplankton, OMI = omnivorous insects, PI = predatory insects, Cru = crustaceans, Mol = molluscs, Bp = benthic primary producers, Pp = pelagic primary producers, TP = trophic position, B = benthivory, OMN = omnivores, CAR = carnivores, PLA = planktivores, INV = invertivores, and HER = herbivores.

in Supplement), which exhibited a mean TP_{GCA} calculation ranging from 2 to 4.2 (Fig. 1; Appendix S2). The estimated mean benthivory $_{GCA}$ estimate ranged from 1.5% to 100%.

TP_{SIA} and Benthivory $_{SIA}$

The TP_{SIA} and B_{SIA} (Benthivory $_{SIA}$) of the 46 species ranged from 1.8 to 3.9 and from 13% to 100%, respectively. The planktivores exhibited the lowest B_{SIA} mean value of 28%, and a variation in B_{SIA} that ranged from 13.6% to 48.1%. Carnivores exhibited the highest TP_{SIA} mean value of 3.7. The mean B_{SIA} value of this guild was 76.8%, and the values of B_{SIA} within the guild varied from 55.4% to 100%. The herbivores showed the lowest mean value of TP_{SIA} , which varied from 1.8 to 2.4. The omnivorous feeding guild showed a moderate TP_{SIA} mean value of 3.1 and B_{SIA} of 59.8%, with considerable variations in TP_{SIA} and B_{SIA} within the omnivorous feeding

guild ranging from 2.7 to 3.5 and from 16.6% to 100%, respectively. The invertivores also showed a moderate TP_{SIA} mean value of 3.2 and B_{SIA} of 65%, with variations ranging from 2.8 to 3.5 and from 52% to 77.3%, respectively.

Relationship between TP_{GCA} (Benthivory $_{GCA}$) and TP_{SIA} (Benthivory $_{SIA}$)

The estimated TP value and benthivory of each species was collected from 2002 to 2010 by analysing $\delta^{15}N$ (Appendix S2). The dietary analysis indicates that *Elopichthys bambusa* had the highest TP, whereas that of *Parabramis pekinensis* had the lowest. The same result for the TP of *P. pekinensis* was determined using $\delta^{15}N$, but *Culterichthys erythropterus* had the highest, as determined by $\delta^{15}N$. However, the TPs of these two species estimated from the dietary data were slightly higher than those estimated from $\delta^{15}N$. Most of the values of these species that were determined using $\delta^{15}N$ data were similar to those calculated using dietary methods. In addition, we directly compared the two pairs of data estimated using dietary and $\delta^{15}N$ methods for each species (Fig. 1). The results of the Pearson correlations showed that the two pairs of data correspond closely ($TP_{SIA} = 0.76 \times TP_{GCA} + 0.72$; $r^2 = 0.794$; Benthivory $_{SIA} = 0.67 \times B_{GCA} + 22.69$; $r^2 = 0.665$). The dietary data on *Aristichthys nobilis* and *Carassius auratus* reveal a TP 0.5 trophic level lower than the value estimated with $\delta^{15}N$. The dietary data on *Ctenogobius giurinus*, *E. bambusa*, and *Pelteobagrus nitidus* indicate a TP 0.5 trophic level higher (Fig. 1(a)).

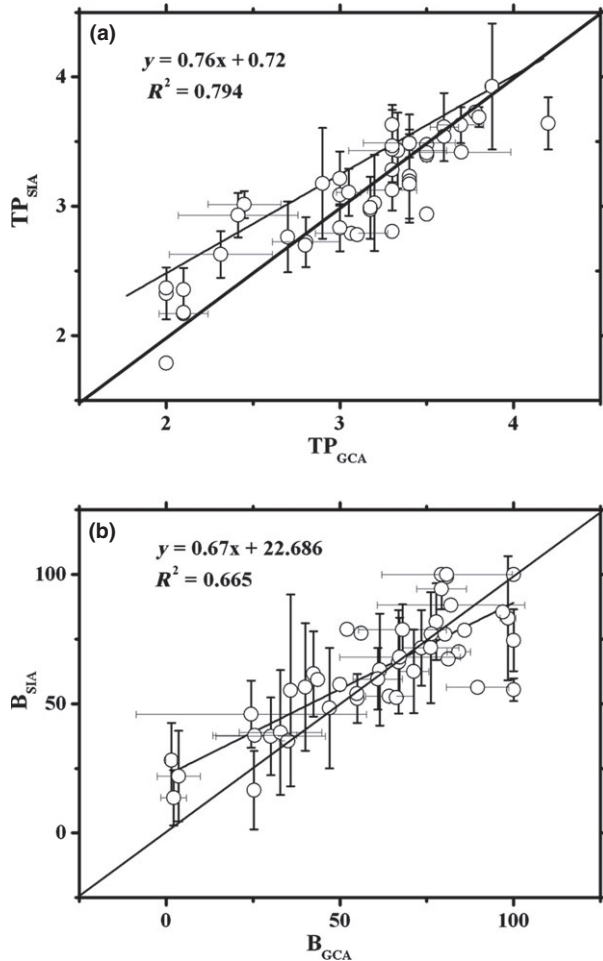


Fig. 1. Comparison of the mean TP and benthic percentage of the food sources of the species included in the study, estimated using dietary and $\delta^{15}N$: (a) comparison of mean trophic position estimated using two methods; (b) comparison of mean benthivory estimated using two methods.

TP_{GCA} and Benthivory $_{GCA}$ of different feeding guilds in fish communities

The carnivores exhibited a higher mean TP_{GCA} than did any other guilds, as indicated by ANOVA ($F_{4,41} = 46.4$, $P < 0.001$, $N = 46$). For the carnivores, the TP_{GCA} ranged from 3.6 to 4.2, with the highest average TP_{GCA} of 3.8; benthivory $_{GCA}$ ranged from 66.9% to 80.8%, with an average of 73.7% (Table 1). The herbivores and carnivores exhibited a higher mean benthivory $_{GCA}$ than did any other guilds, as indicated by ANOVA ($F_{4,41} = 14.5$, $P < 0.001$, $N = 46$) (Fig. 2). The TP_{GCA} of herbivores ranged from 2.0 to 2.1, averaging 2.1; benthivory $_{GCA}$ ranged from 80.8% to 100% (Table 1).

Discussion

Methodological comparison of SIA and GCA

Two approaches can be applied in estimating continuous TP. The SIA and GCA approaches have

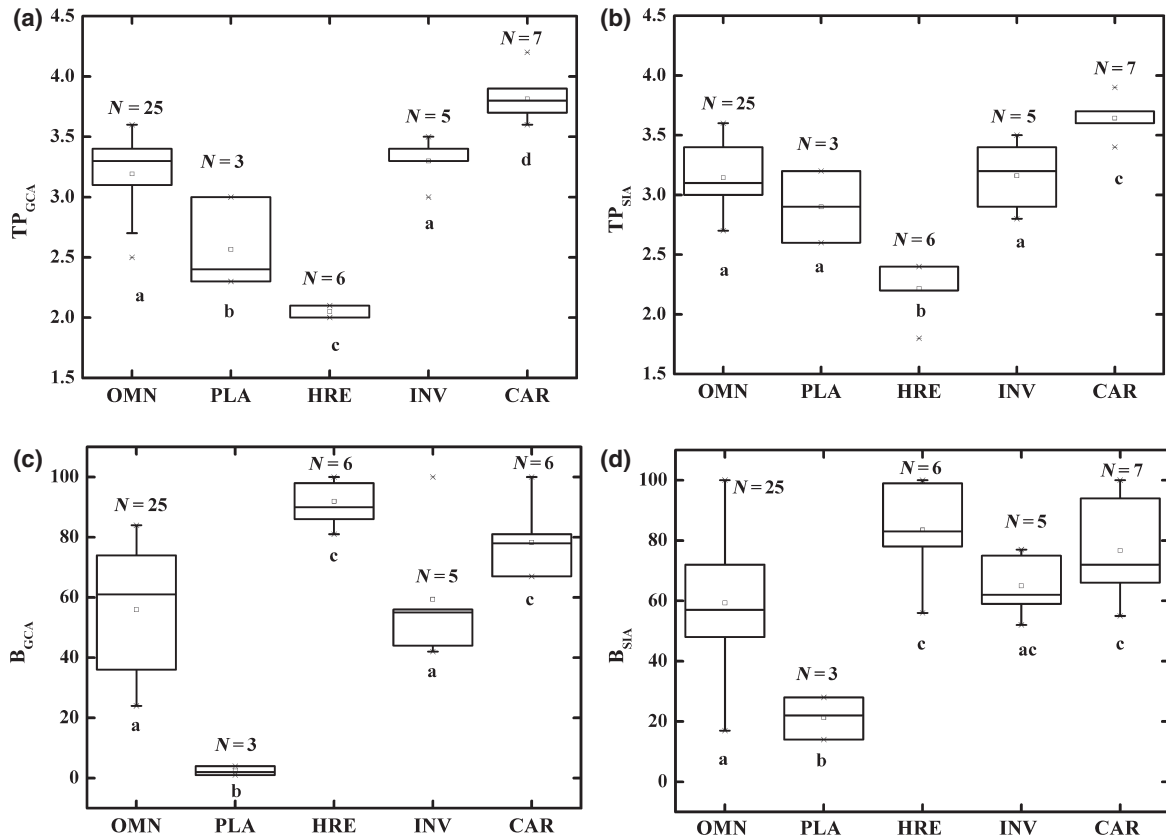


Fig. 2. TP_{GCA}(A), TP_{SIA} (B), B_{GCA}(C), and B_{SIA} (D) of different feeding guilds in floodplain lakes. Similar small letters indicate that no significant differences were found in the TP or benthivory of the feeding guilds at P -level < 0.05. Different letters indicate significant differences. OMN = omnivores, CAR = carnivores, PLA = planktivores, INV = invertivores, and HER = herbivores.

advantages that other approaches cannot offer. SIA provides the distinct isotopic composition of potential sources that are transferred through consumers at high trophic levels (Beaudoin et al. 2001). SIA becomes increasingly limited when multiple sources with high spatial or temporal variability are present, or when stable isotopic signatures overlap in an ecosystem of interest (Beaudoin et al. 2001). The use of GCA in estimating TP, which represents major energy flow pathways, measures fish TP, accounts for omnivory and detects other trophic interactions, as well as provides detailed diet information on species. Although the SIA is commonly used to trace trophic relationships, it is constrained in terms of food webs with history data because of inadequate historical samples. Thus, TP calculation can be used as an alternative method based on dietary data, which are abundant in literature. Our data show that dietary data and SIA can provide comparable results for fish TP in lake ecosystems in a floodplain lake (Table 2 and Fig. 1). The TP of fishes estimated with the two methods were very close, but the potential limitations of the dietary approach should be considered. The limitation lies in using GCA to estimate fish TP; this

approach requires assumptions on the TP of prey organisms, leading to possible fish TP errors. For example, we assigned fishes that cannot be subdivided into a species as TP 3, but our data show that the TP of the fishes in the floodplain lakes ranged from 2.0 to 4.2. These results may cause errors when fishes are classified as TP 3 in calculating the TP of fishes that consume other fishes. Our data also show that the TPs of fishes in the metacommunity are around 3; the mean value may resemble that reported in our study. Our assumption of 2 as the TP of small zooplankton according to diet stems mainly from phytoplankton diet. Vander Zanden et al. (1997) set their TP at 2.5 because omnivory is more important to the diet in boreal lakes than in subtropical lakes. The conclusion is comparable to the result of Vander Zanden et al. (1997).

Prevalent omnivory in the floodplain fish metacommunity

The evidence provided by the feeding guild data suggests that more than 50% (including 25 species) of the fishes in the floodplain fish metacommunity are

Trophic fingerprint of fish communities

Table 2. Mean trophic position (TP) and benthivory (B) of each species of fish; Standard deviation (SD) of the mean TP and B, as well as the number of fish populations calculated using GCA and SIA.

Species	GCA					SIA					FG
	N	TP _{GCA}	SD	B _{GCA}	SD	N	TP _{SIA}	SD	B _{SIA}	SD	
<i>Channa argus</i>	4	3.6	0.08	79	7.1	2	3.6	0.26	94	7.9	CAR
<i>Culter alburnus</i>	1	3.8		78		3	3.7	0.05	82	14.8	CAR
<i>Siniperca chuatsi</i>	4	3.7	0.13	76	8.1	4	3.6	0.14	72	21.5	CAR
<i>Elopichthys bambusa</i>	1	4.2		67		3	3.6	0.20	66	20.0	CAR
<i>Silurus asotus</i>	1	3.8		100		3	3.7	0.08	55	4.4	CAR
<i>Sinobdella sinensis</i>	2	3.7	0.28	81	18.7	1	3.4		100		CAR
<i>Culterichthys erythropterus</i>	2	3.9	0.04	67	17.4	5	3.9	0.49	68	15.3	CAR
<i>Acheilognathus macropterus</i>	2	2.1	0.14	90	9.0	1	2.2		56		HER
<i>Acheilognathus tonkinensis</i>	1	2.1		86		1	2.2		78		HER
<i>Ctenopharyngodon idellus</i>	2	2.0	0.00	98	2.3	2	2.3	0.20	83	23.9	HER
<i>Megalobrama amblycephala</i>	1	2.0		97		1	2.4		85		HER
<i>Parabramis pekinensis</i>	2	2.0	0.00	100	0.0	1	1.8		100		HER
<i>Rhodeus ocellatus</i>	1	2.1		81		3	2.4	0.17	99	1.6	HRE
<i>Pseudorasbora parva</i>	1	3.3		55		2	3.4	0.34	52	9.4	INV
<i>Abbottina rivularis</i>	1	3.3		42		3	3.5	0.28	62	16.5	INV
<i>Hypseleotris swinhonis</i>	1	3.4		44		1	3.2		59		INV
<i>Mylopharyngodon piceus</i>	1	3.0		100		2	2.8	0.18	75	11.9	INV
<i>Pelteobagrus nitidus</i>	1	3.5		56		1	2.9		77		INV
<i>Salangichthys tankahkeii</i>	6	3.0	0.00	1	1.7	3	3.2	0.21	28	14.4	PLA
<i>Hypophthalmichthys molitrix</i>	3	2.3	0.30	2	3.7	5	2.6	0.18	14	10.8	PLA
<i>Aristichthys nobilis</i>	3	2.4	0.34	4	6.2	6	2.9	0.17	22	17.6	PLA
<i>Hemiculter leucisculus</i>	1	2.7		47		7	2.8	0.27	48	23.3	OMN
<i>Coilia nasus</i>	6	3.3	0.28	24	33.2	6	3.4	0.29	46	13.0	OMN
<i>Protosalanx hyalocranius</i>	1	3.3		25		7	3.3	0.32	17	15.2	OMN
<i>Sarcocheilichthys nigripinnis</i>	1	3.4		61		4	3.2	0.33	63	21.7	OMN
<i>Cyprinus carpio</i>	1	3.2		74		10	3.0	0.37	72	14.7	OMN
<i>Rhinogobius giurinus</i>	1	3.5		40		2	3.4	0.05	56	24.7	OMN
<i>Carassius auratus</i>	2	2.5	0.21	71	4.3	5	3.0	0.11	63	16.2	OMN
<i>Toxabramis swinhonis</i>	2	3.2	0.04	26	12.0	1	3.0		38		OMN
<i>Hemirhamphus intermedius</i>	3	3.4	0.26	30	15.7	7	3.5	0.22	37	15.0	OMN
<i>Ctenogobius giurinus</i>	1	3.3		55		1	2.8		54		OMN
<i>Culter mongolicus</i>	1	3.6		80		1	3.5		77		OMN
<i>Hemibarbus maculatus</i>	2	2.8	0.20	68	12.6	2	2.7	0.19	79	9.8	OMN
<i>Hemiculter bleekeri bleekeri</i>	2	3.2	0.04	33	11.9	4	3.0	0.24	39	24.1	OMN
<i>Misgurnus anguillicaudatus</i>	3	3.1	0.21	35	1.9	1	2.8		36		OMN
<i>Pelteobagrus fulvidraco</i>	1	3.4		36		3	3.2	0.32	55	37.1	OMN
<i>Rhinogobio typus</i>	2	3.0	0.00	82	21.2	1	3.1		88		OMN
<i>Sarcocheilichthys sinensis</i>	1	3.1		76		1	2.8		77		OMN
<i>Saurogobio dabryi</i>	2	3.1	0.07	61	7.1	5	3.1	0.18	60	11.9	OMN
<i>Saurogobio dumerili</i>	2	2.9	0.00	64	6.8	2	3.2	0.43	53	1.9	OMN
<i>Anguilla japonica</i>	2	3.3	0.14	84	3.4	1	3.1		70		OMN
<i>Monopterus albus</i>	1	3.3		52		1	3.6		79		OMN
<i>Leiocassis crassilabris</i> Gunther	1	3.5		79		1	3.5		100		OMN
<i>Pelteobagrus eupogon</i>	1	3.5		81		1	3.4		67		OMN
<i>Coilia brachygnathus</i>	1	3.4		50		2	3.5	0.11	57	2.2	OMN
<i>Botia supercilialis</i> Günther	1	2.8		66		1	2.7		52		OMN

FG = feeding guilds, TP = trophic position, B = benthivory, OMN = omnivores, CAR= carnivores, PLA =planktivores, INV = invertivores, HER = herbivores, TP = trophic position, GCA = gut content analysis, and SIA = stable isotope analysis.

omnivorous (Fig. 2). Omnivory is common in freshwater food webs, especially among freshwater fish assemblages (Vadas 1990; Diehl 1992; Drenner et al. 1996; Vanni et al. 2005). No discrete food chain or association between food web approaches fully describe the pathways of energy and mass transfer because of the prevalence of omnivory (Vander Zanden & Rasmussen 1996; Vander Zanden et al. 1997). A continuous measurement of TP, which accounts for omnivory rather than the discrete measure

of TP, would be useful in describing trophic relationships.

Our dietary data strongly support this observation for the metacommunity. Our data suggest the prevalence of omnivorous and generalist feeders in floodplain lakes, which support studies concluding that omnivory is more common in aquatic communities (Vadas 1990; Diehl 1992; Drenner et al. 1996; Vanni et al. 2005). The Yangtze floodplain lakes are mostly eutrophic lakes where pelagic habi-

tats provide numerous services to ecosystems, including support for fisheries. The increase in net primary phytoplankton productivity can support more pelagic invertebrates, which are palatable food for several fish species. In addition, as is typical of a piscivorous fish species, *Culter mongolicus* in eutrophic lakes still frequently consume a variety of invertebrates, and are still omnivores according to our data. *H. maculatus* in grass-type lakes are mostly carnivorous, but our data show that these lakes are dominated by pelagic food webs (e.g., Lake Taihu and Lake Chaohu). Our data also support the view that omnivory is common in pelagic and lentic food chains (Sprules & Bowerman 1988).

Fishes as integrators of benthic-pelagic linkage

The benthic percentages estimated from SIA and GCA correspond closely. The results are satisfactory, but certain deficiencies in both approaches must be considered. An apparent limitation is the use of two-source mixing models to estimate benthic percentage values, in which only the benthic and pelagic sources of food are considered. Additionally, riparian sources, which are important food sources for some fish species, are disregarded, thereby causing errors in benthic percentage. Another limitation is the benthic percentage estimation, which necessitates the assignment of benthic food source percentages according to knowledge of food sources. This process is subjective to a certain extent. This subjectivity also introduces errors. Our assumption of 0% as the benthic percentage of the food source according to main prey contrasts with that of Sprules & Bowerman (1988), who reported that North American zooplankton food webs average between three and five trophic levels, with the food source not limited to phytoplankton. To most ecologists, zooplankton mainly preys on phytoplankton. Other sources may be rare, which possibly make our assumption reasonable.

An overlooked feature is that benthic resources provided for fish populations induce pelagic trophic cascades in lakes (Schindler et al. 1996; Vanni 1996). Fishes play an important role in habitat coupling because of their high mobility and flexible foraging tactics that lead to inter-habitat omnivory. Our evidence indicates that benthic matter supports 59.8% of the total consumption of omnivorous fishes (Fig. 2). Our data show that the carnivorous fishes are mostly subsidised by benthic habitats. Even planktivorous fishes are partly subsidised by this habitat. Our dietary data also show that benthic matter supports 73.7% and 2.4% of the total consumption of carnivorous and planktivorous fishes, respectively. This phenomenon results from the opportunistic and flexible nature of fish predation. Piscivorous fishes

consume their preferred prey when available, but they would switch to feeding on benthic invertebrates when their preferred prey is scarce (Hodgson & Kitcheil 1987; Schindler et al. 1997). Fishes are generally effective habitat couplers in lake ecosystems.

Conclusion

In summary, dietary and stable isotope approaches to estimate trophic structure have become powerful tools, facilitating the possibility of gaining objective and repeatable measurements of the TP, omnivory, and benthivory of food resources (Kling et al. 1992; Hobson and Welsh, 1992; Cabana and Rasmussen, 1994). Significant differences were found between temperate lakes in North America and the Yangtze floodplain lakes, which are rich in autochthonal omnivorous Cyprinidae fish. Comparable results can be obtained for temperate lakes (Vander Zanden et al. 1997), indicating that the dietary approach can provide results that are equivalent to those derived by the stable isotope approach in terms of TP measurement. Our data also suggest that dietary data can provide results comparable to those of SIA in terms of benthivory measurements for consumers in floodplain lakes. Regardless of spatio-temporal differences, our results are similar to those of Vander Zanden and Vadeboncoeur (2002). Estimates of zoo-benthivory from the dietary data are closely correlated with the estimates of isotope-based littoral carbon reliance.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Estimation of the trophic position and benthivory of 46 fish species on the basis of stable isotope data.

Appendix S2 Estimation of the trophic position and benthivory of 46 fish species on the basis of dietary data from 83 fish populations.

Table S1. Estimated prey organism trophic position and benthivory values applied in the dietary approach calculation of fish trophic position and benthivory.

Table S2. Estimated prey organism contribution scores applied in the dietary approach calculation of fish trophic position and benthivory.