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PRIMARY RESEARCH PAPER

Role of body size and temporal hydrology in the dietary shifts of shortjaw tapertail anchovy *Coilia brachygnathus* (Actinopterygii, Engraulidae) in a large floodplain lake

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Abstract Seasonal water-level changes in floodplain lakes can induce variations in primary and secondary production, thus affecting trophic interactions. In this study, we tested the latter by studying size- and temporal hydrology-related shifts in the diet of shortjaw tapertail anchovy *Coilia brachygnathus* (Actinopterygii, Engraulidae) from Lake Poyang. During the wet season, $\delta^{13}C$ values ranged from −28.2‰ for small anchovies to −24.6‰ for larger individuals, but $\delta^{15}N$ ranged from 18.9‰ for smaller fish to 12.4‰ for larger fish. Significant ^{13}C-enrichment and ^{15}N-depletion occurred with increasing size, revealing that different carbon sources were used as the fish grew. Given the high hydrologic fluctuation levels, significant differences in $\delta^{13}C$ values were observed among larger anchovies between seasons, indicating a temporal dietary shift. Anchovies fed primarily on shrimp and fish during the low-water season despite the predominance of zooplankton during the two seasons studied, which indicated increased piscivorous reliance. *C. brachygnathus* exhibited higher $\delta^{15}N$ values during the wet season because the food items were ^{15}N-enriched. Human waste brought by floods could be another possible interpretation. Considering *C. brachygnathus* is an important link between plankton production and higher piscivorous trophic levels, changes in the species are expected to affect the functioning of lake food webs along the trophic pathway.

Keywords *Coilia brachygnathus* · Dietary shifts · Lake Poyang · Stable isotope analysis · Trophic interaction

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Introduction

Dietary shifts are a common feature of the early life of many fish (MacNeil et al., 2005; Eloranta et al., 2010). These phenomena are usually caused by migration, size-related morphologic constraints, habitat use, and other reasons (Grey, 2001; Barbini et al., 2010; Ginter et al. 2011) Thus, these behaviors affect species interaction and community structure (Werner & Gilliam, 1984). Dietary shifts can also be expressed as changes in the trophic levels of fish (Xu et al., 2007;

Wang et al., 2011a) that integrate changes in population dynamics, prey availability, and predator–prey interactions (Vögler et al., 2009).

Anchovies are a geographically widespread pelagic fish species in marine and freshwater ecosystems. They are of great economic and ecological importance because of their significant biomass. As essential intermediate-level components in aquatic food webs, anchovies play an important ecological link between plankton and higher piscivorous trophic levels. Most marine anchovy species that undergo dietary shifts in their early life stage, such as the European (*Engraulis encrasicolus*) and Japanese (*E. japonicus*) anchovies (Bacha & Amara, 2009; Islam & Tanaka, 2009; Yasue et al., 2010), have been widely studied. However, few studies are available on freshwater anchovy species (Tang, 1987; Xu et al., 2005, 2007).

According to the Food and Agriculture Organization (FAO) Fisheries Synopsis, *C. brachygnathus* is the only anchovy species that exclusively lives in freshwater environments (Whitehead et al., 1988). It is one of the dominant fish species in important fisheries in Lake Poyang, a large freshwater floodplain lake connected to the Yangtze River. Spawning once a year from April to July, anchovies reach maturity within 5–6 months (Liu, 2008). Anchovy stocks have been greatly reduced because of the deterioration of lake environments and overfishing (Zhang & Li, 2007). Thus far, most studies on *C. brachygnathus* have concentrated on its taxonomy and nomenclature. However, information regarding the feeding strategies of the species, particularly in the Yangtze-connected lake, is rare. Therefore, research on the dietary shifts of C. *brachygnathus* is important to improve current understanding of its trophic ecology, thereby facilitating its management and conservation.

Seasonal water-level changes in floodplain lakes could induce variations in the primary and secondary production, thus affecting trophic interactions. Trophic patterns of *C. brachygnathus* may also be affected by seasonal hydrological changes. A previous study on the diet of *C. brachygnathus* was based on stomach content analysis (Institute of Hydrobiology of Hubei Province, 1976). However, this technique is often biased because the diet is only assessed over small temporal scales, and they exclude information regarding assimilation (Hyslop, 1980). In the current study, the stable isotope technique was used to distinguish size-related changes in the diet of *C. brachygnathus* in Lake Poyang. Variations in the $\delta^{13}C$ and $\delta^{15}N$ values of the particulate organic matter (POM) and primary consumers were determined during the dry and wet seasons. We also compared the variations between seasons in the carbon and nitrogen isotope signatures among large anchovies and their dominant food items to examine whether a temporal dietary shift occurred. Using the stable isotope analysis in R (SIAR), a recently published Bayesian mixing model (Parnell et al., 2010), we estimated the feasible contributions of dominant food sources assimilated by *C. brachygnathus* and further addressed the possible dietary shift mechanisms associated with seasonal hydrologic changes.

Materials and methods

Study area

Lake Poyang (N 28°22′–29°45′, E 115°47′–116°45′), located in the northern part of Jiangxi Province, is the largest freshwater lake in China, covering an area of 3,283 km^2. The lake receives runoff water from five tributaries, namely Ganjiang, Fuhe, Xiushui, Raohe, and Xinjiang. Lake Poyang is pivotal to the biodiversity conservation of Yangtze floodplain ecosystems, being one of the two largest freshwater lakes that are still naturally connected to the Yangtze River. The lake serves as an important nursery and feeding ground for numerous fish species, including some endangered anadromous species, such as *Acipenser sinensis*, *C. nasus*, and *Tenualosa reevesii*. However, fish biodiversity is seriously threatened by increasing anthropogenic activity in Lake Poyang (Zhang & Li, 2007). The lake undergoes considerable seasonal hydrologic changes, with the high-water period occurring from June to September and the low-water period from October to March. In one hydrologic cycle, the area of the lake fluctuates from less than 1,000 km^2 during the dry season to more than 4,000 km^2 during the flood period (Yin & Zhang, 1987; Min, 1995). The lake is comparable to a river during the dry season but becomes a lake during the flood season. Our study was conducted in Hukou (Fig. 1), the only outlet connecting Lake Poyang to the Yangtze River. This site has the greatest seasonal water-level fluctuation, averaging more than 10 m (Yin & Zhang, 1987; Min, 1995). Aquatic macrophytes are rare in this region because of

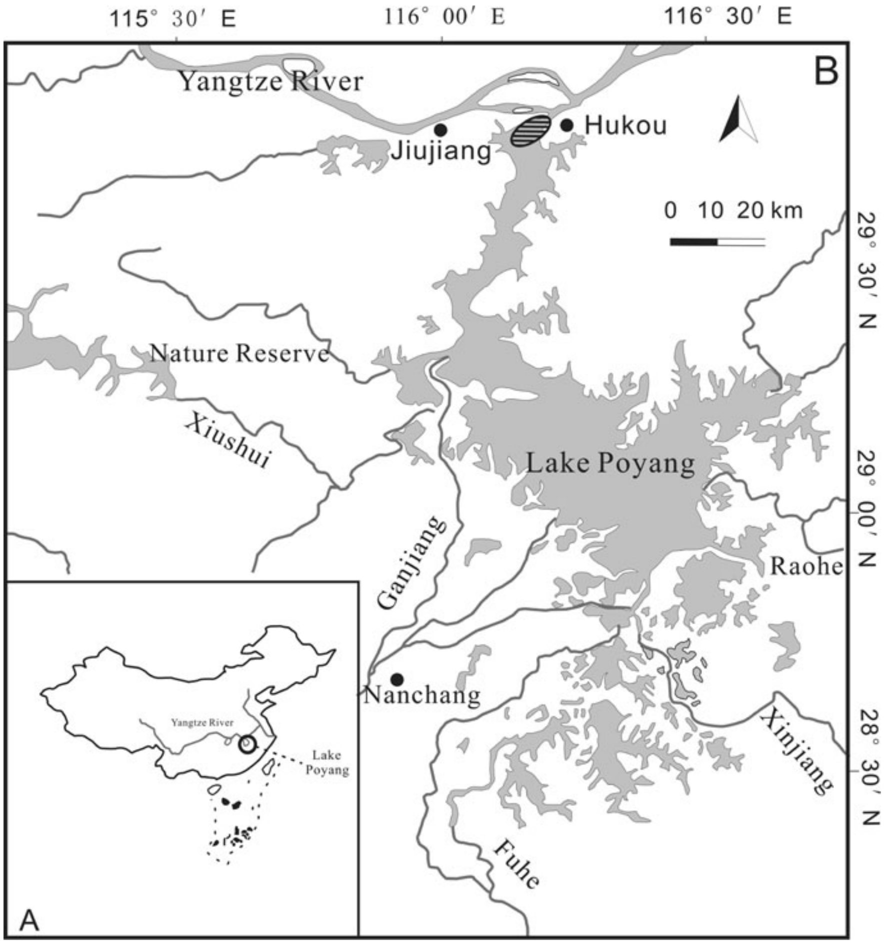

Fig. 1 **A** Location of Lake Poyang in the mid-lower Yangtze River Basin, China. **B** Lake Poyang area with main towns. The *shaded area* denotes the approximate location where the samples were collected

the rapid water flow and sandy sediment (Guan et al., 1987). Anchovies prefer the habitat in the northern part of Lake Poyang because of the specific environmental conditions, consequently becoming the most important fish resource harvested on an annual season in Hukou (Liu, 2008).

Sample collection

Coilia brachygnathus (Actinopterygii, Engraulidae) was collected from a fisherman's catch in Hukou during two hydrologic seasons. Sampling during the low-water period was performed on March 5, 2010, and on August 3, 2010 during the high-water period. A total of 76 and 15 *C. brachygnathus* individuals were collected during the wet and dry seasons, respectively. After body weight (0.1 g) and length (mm) were measured, anchovies were subsequently divided into small (<500 mm) and large size (>500 mm). In the wet season, 57 individuals were large size, and all in the dry season.

Potential food items of anchovy were also collected from the fishing region during the same period. Water samples were filtered using precombusted glass microfiber filters (Whatman GF/F) and then analyzed as POM. Zooplankton (mostly copepods, *Mesocyclops*) was collected using a plankton net (mesh size, 112 μm) and then transferred into distilled water by hand under a microscope to allow gut evacuation. The samples were then filtered through precombusted glass microfiber filters (Whatman GF/F). We also collected the benthic-grazing freshwater snail, *Bellamya aeruginosa*, and the filter-feeding mussel, *Corbicula fluminea*. Two dominant shrimp species (*Macrobrachium nipponense* and *Exopalaemon modestus*) and three fish species (*Saurogobio dabry*, *Carassias auratus*, and *Parabotia fasciata*) were also sampled during the dry and wet seasons. All samples were stored at −20°C until use in the laboratory. A sample of muscle tissue was taken from each mollusk, small fish, shrimp, and anchovies for stable isotope analysis. All samples were dried at 60°C for at least 48 h to a constant weight and then ground into fine power using a mortar and pestle.

Analysis of stable isotopes

The stable carbon and nitrogen isotope ratios were measured using an EA 1110 elemental analyzer (Carlo Erba, Italy) with a Finnigan Delta Plus continuous flow isotope ratio mass spectrometer (Thermo Scientific, USA). The isotopic values were expressed in delta (δ) notation per thousand (‰) according to the following equation: δX (‰) = $[(R_{sample}/R_{standard}) - 1] \times 1000$, where $R = {}^{13}C$ or ${}^{15}N$, and X is the corresponding ratio ${}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The standards used for $\delta^{13}C$ and $\delta^{15}N$ were the Vienna Pee Dee Belemnite and atmospheric N_2, respectively. Approximately, 20% of the samples were analyzed using two or more replicates. Two standards were also run after every 10 samples to compensate for the drift over time. The deviations in the analysis of $\delta^{13}C$ and $\delta^{15}N$ replicates were both within 0.3‰.

Data analysis

According to a previous analysis of the gut content of *C. brachygnathus* (Anonymous 1976), the dominant food items among anchovies were classified into three groups (i.e., zooplankton, shrimp, and fish) to estimate effectively the proportional contribution of each group to anchovies. Two zooplankton samples collected in July 2009 were provided by Dr. Wang (unpublished data). No significant interannual differences were found among the $\delta^{13}C$ and $\delta^{15}N$ values during the wet season ($P = 0.837$, $\delta^{13}C$; $P = 0.927$, $\delta^{15}N$). Thus, the zooplankton samples were pooled. *M. nipponense* and *E. modestus* exhibited low variations among the $\delta^{13}C$ and $\delta^{15}N$ values, respectively ($P < 0.01$, $\delta^{13}C$; $P = 0.640$, $\delta^{15}N$, Supplementary Table 1 in Appendix). Similarly, we pooled *S. dabry*, *C. auratus*, and *P. fasciata* into a single sample because no size-related shift (Pearson correlation, $n = 7$, $r = 0.616$, $P = 0.141$, $\delta^{13}C$; $n = 7$, $r = -0.220$, $P = 0.635$, $\delta^{15}N$, for *S. dabry*; Pearson correlation, $n = 7$, $r = 0.616$, $P = 0.141$, $\delta^{13}C$; $n = 7$, $r = -0.220$, $P = 0.635$, $\delta^{15}N$, for *C. auratus*) and no significant differences ($P = 0.795$, $\delta^{13}C$; $P = 0.515$, $\delta^{15}N$) were observed in our study, although the sizes of the fish prey collected in our study were slightly larger than those consumed by *C. brachygnathus*. The seasonal contributions of the dominant food sources to the 72 large individuals from both seasons were determined using the SIAR software (Version 2.13.1). Based on the Bayesian approach, SIAR estimates the possible distributions of resource contributions to a consumer diet by considering all uncertainties in the input data (Parnell et al. 2010). We used the fractionation factors and uncertainties published in the Post (2002), 0.4 ± 1.3‰ for $\delta^{13}C$ and 3.4 ± 1.0‰ for $\delta^{15}N$, to account for trophic fractionation. In running the mixing models, the appropriate number of iterations (up to 5×10^5) was chosen according to the convergence diagnostic of SIAR. The procedure then provided information on the range and distribution of possible source contributions. Based on the resulting 30,000 dietary proportions, we selected the maximum feasible contribution of food sources to each individual from the highest distribution options indicated in the histograms. The sum of the combinations of each source contribution was 100%. We defined the benthic carbon sources assimilated by anchovy as shrimp and fish prey, given that these preys are traditional benthic dwellers and mainly consume benthic basal sources (Xu et al., 2008).

The size-related effect on the C and N isotope signatures of anchovy collected from both seasons was investigated using Pearson's correlations and one-way ANOVA. Pearson's correlations were also used to determine the correlation between $\delta^{13}C$ and $\delta^{15}N$ for all individuals. ANOVA was used to determine the isotopic signatures of the large-sized *C. brachygnathus* individuals, as well as the isotopic signatures and feasible contributions of their prey items during the dry and wet seasons. All statistical analyses were performed using SPSS 16.0 (SPSS Inc., Chicago, USA).

Results

During the wet season, the $\delta^{13}C$ values for *C. brachygnathus* ranged from −28.2 to −24.6‰, and showed a significant positive relationship with increasing fish body length ($n = 76$, $r = 0.533$, $P < 0.001$, Fig. 2a). Large individuals caught during the dry season also tended to have higher ${}^{13}C$ with increasing

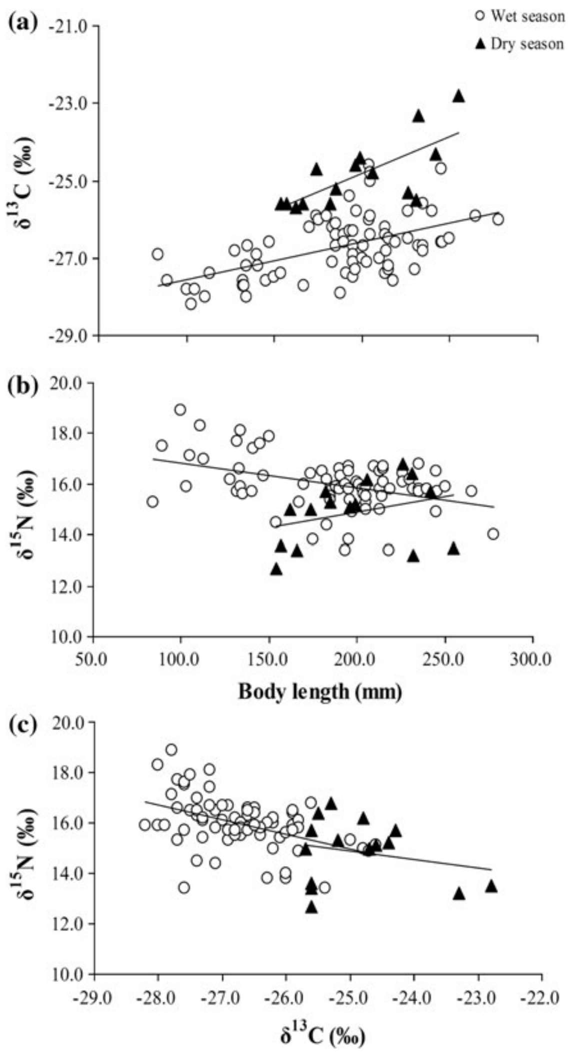

Fig. 2 Variations in **a** δ^{13}C and **b** δ^{15}N signatures among individual *C. brachygnathus* ($n = 76$, wet season; $n = 15$, dry season) with increasing body length. **c** Stable isotopic carbon δ^{13}C and nitrogen δ^{15}N plots of anchovies during both seasons. The *solid circle* represents the dry season, and the *empty triangle* represents the wet season. The *lines* represent relationships among the δ^{13}C and δ^{15}N values (‰) of *C. brachygnathus*, the isotope values (δ^{13}C, δ^{15}N), and fish length (mm)

size ($n = 15$, $r = 0.715$, $P < 0.01$, Fig. 2a). The δ^{15}N values varied from 18.9 to 12.4‰, showing significant ^{15}N depletion as the fish grew ($n = 76$, $r = -0.449$, $P < 0.001$, Fig. 2b). In addition, a strong negative relationship was observed between the δ^{13}C and δ^{15}N values ($n = 76$, $r = -0.412$, $P < 0.001$, Fig. 2c) obtained during the high-water period, whereas no significant relationship was observed ($n = 15$, $r = -0.236$, $P = 0.397$, Fig. 2c) during the dry season.

The δ^{13}C values of POM increased significantly (ANOVA, $F = 13.885$, df = 8, $P < 0.01$) from the wet season (mean ± SD, -27.1 ± 0.6‰, $n = 6$, Fig. 3) to the dry season (-25.2 ± 1.0‰, $n = 3$). However, no significant difference in zooplankton ^{13}C (ANOVA, $F = 1.343$, df = 4, $P = 0.330$) was found between the wet (-26.9 ± 0.6‰, $n = 3$, Fig. 3) and dry seasons (-27.7 ± 0.8‰, $n = 2$). *C. fluminea* showed a higher ^{13}C depletion during the dry season (ANOVA, $F = 259.798$, df = 4, $P < 0.01$). In the benthic grazers, the δ^{13}C values of *B. aeruginosa* were significantly lower (ANOVA, $F = 41.211$, df = 14, $P < 0.001$) during the wet season (-29.3 ± 1.5‰, $n = 8$, Fig. 3) than during the dry season (-24.5 ± 0.8‰, $n = 7$), thus indicating a marked temporal shift. The δ^{13}C values for the shrimp and fish were also significantly lower (ANOVA, $F = 8.700$, df = 26, $P < 0.01$ for shrimp; $F = 5.951$, df = 21, $P < 0.01$ for fish) during the wet season (-25.6 ± 0.8‰, $n = 17$ for the shrimp; -26.9 ± 1.2‰, $n = 15$ for fish, Fig. 3) than during the dry season (-24.8 ± 0.5‰, $n = 10$ for shrimp; -25.1 ± 0.5‰, $n = 7$ for fish).

For the δ^{15}N signatures, POM showed a significant decrease (ANOVA, $F = 34.722$, df = 8, $P < 0.001$) from the wet season (8.5 ± 0.6‰, $n = 6$, Fig. 3) to the dry season (4.3 ± 0.8‰, $n = 3$). The zooplankton was more ^{15}N-enriched during the wet season (ANOVA, $F = 232.595$, df = 4, $P < 0.01$). The δ^{15}N values of *B. aeruginosa* were significantly lower (ANOVA, $F = 31.319$, df = 13, $P < 0.001$) during the wet season (8.1 ± 0.7‰, $n = 8$) than that during the dry season

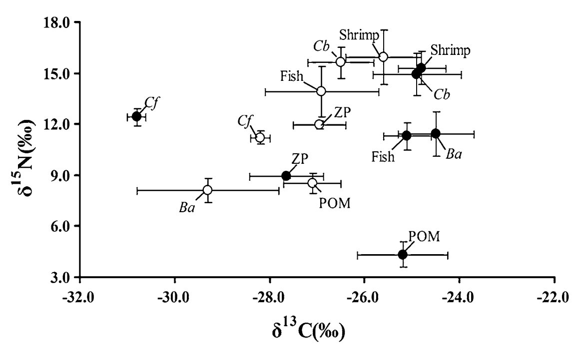

Fig. 3 δ^{13}C and δ^{15}N compositions (mean ± SD) of large anchovies (*Cb*; dry season, 154–255 mm, $n = 15$; wet season, 154–278 mm, $n = 57$), fish, shrimp, zooplankton (*ZP*), primary consumers (*Ba*, *B. aeruginosa*; *Cf*, *C. fluminea*), and producers (*POM*) during the dry and wet seasons in Lake Poyang. The *full circle* represents dry season, and *empty circle* represents wet season

(11.3 ± 1.5‰, $n = 7$). For the filter-feeding mussels, a slight variation in δ^{15}N values was observed between seasons (ANOVA, $F = 9.743$, df = 1, $P = 0.052$). The shrimp had similar δ^{15}N values (ANOVA, $F = 1.107$, df = 25, $P = 0.303$) between the wet (15.9 ± 1.6‰, $n = 17$) and dry seasons (15.3 ± 1.0‰, $n = 10$). The δ^{15}N values for the fish during the wet season (13.9 ± 1.5‰, $n = 15$) were significantly higher (ANOVA, $F = 18.695$, df = 20, $P < 0.001$) than that during the dry season (11.3 ± 0.8‰, $n = 7$).

Considering that small-sized anchovies are lacking during the dry season, we selected similar-sized anchovies to compare the temporal variations in isotopic values. The isotopic compositions of the larger *C. brachygnathus* individuals between the hydrologic seasons were markedly different (Fig. 3). The δ^{13}C values of *C. brachygnathus* (−26.5 ± 0.7‰, $n = 57$, Fig. 3) during the wet season were significantly lower (ANOVA, $F = 51.169$, df = 70, $P < 0.001$) than those during the dry season (−24.9 ± 0.9‰, $n = 15$), indicating anchovies consumed more δ^{13}C-enriched food sources during the low-water period. However, the δ^{15}N values of the anchovies significantly decreased (ANOVA, $F = 7.600$, df = 70, $P < 0.01$) from the wet season (15.6 ± 0.9‰, $n = 57$, Fig. 3) to the dry season (14.9 ± 1.3‰, $n = 15$), showing a significant temporal dietary shift.

Zooplankton, an important carbon source for anchovy, accounted for a significantly larger (ANOVA, $F = 17.514$, df = 70, $P < 0.001$) contribution to the *C. brachygnathus* diet during the wet season (50.2 ± 14.8%, $n = 57$, Fig. 4) than during the dry season (33.1 ± 10.6‰, $n = 15$). However, the proportional contributions of shrimp and fish were significantly lower (ANOVA, $F = 18.302$, df = 70, $P < 0.001$ for shrimp; $F = 1.699$, df = 70, $P = 0.197$ for fish) during the wet season (15.4 ± 9.1‰, $n = 57$ for shrimp; 34.4 ± 11.7‰, $n = 57$ for fish) than during the dry season (28.3 ± 14.6%, $n = 15$ for shrimp; 38.5 ± 6.8‰, $n = 15$ for fish). Hence, they appeared to be the more important contributors to anchovies during the low-water period, reflecting an increase in piscivorous reliance.

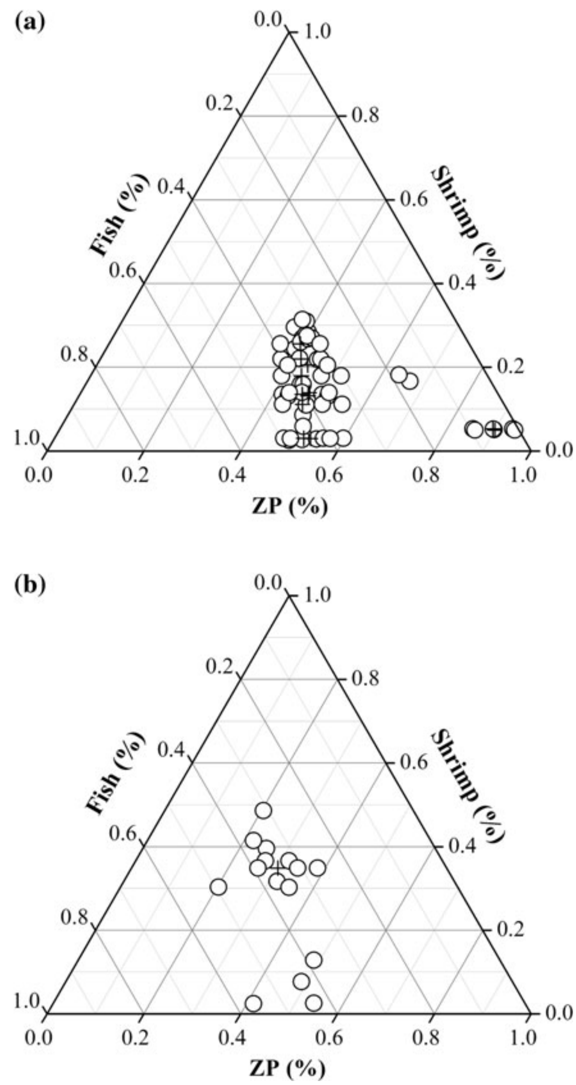

Fig. 4 Estimated proportion of the feasible contributions of the dominant prey items, including fish, shrimp, and zooplankton (*ZP*), for *C. brachygnathus* between the wet (**a** 154–278 mm, $n = 57$) and the dry season (**b** 154–255 mm, $n = 15$). Overlapping points are represented by the *plus* (+) sign. Each point shows the feasible contributions of the three food sources to the large anchovies. For example, the summit of the *triangle* shows that the fish and zooplankton both have maximum contributions of 0% to the diet, whereas shrimp has a maximum contribution of 100%, and that their sum is 100%

Discussion

Coilia brachygnathus exhibited significantly increased δ^{13}C values with increasing body length, indicating a size-related shift in diet. This result is consistent with a previous study, in which the *C. brachygnathus* were shown to ingest different food items during the growth stage (Anonymous, 1976). Zooplankton, particularly copepods, is a major component of the diet of small anchovy, whereas larger anchovy individuals fed more on shrimp and fish larvae (Anonymous, 1976; Tang, 1987). Tang (1987) and Xu et al. (2007) found that larger prey items were an important part of the *C. ectenes taihuensis* diet, and were positively selected with size. This change involved an increase in the quality of the diet, wherein small crustaceans were replaced with larger prey. In addition, the increased proportion of larger prey in the diet probably reflected the enhancing effect of optimal foraging behavior on rapid growth (Wanink & Joordens, 2007). The main characteristics of anchovy include high growth rates and early maturity (Liu, 2008; Bacha & Amara, 2009). Thus, the high energy required for anchovy growth and reproduction likely accounts for the size-related dietary shift.

A negative δ^{15}N-size trend among large *C. brachygnathus* occurs during the wet season, which is still commonly observed in other fish (Bunn et al., 2003; Wang et al., 2011a). For example, Wang et al. (2011a) suggested that *Pelteobagrus vachelli* consume more benthic prey with lower δ^{15}N values with increasing body length, thereby decreasing their δ^{15}N signatures. Considering the ^{15}N-rich pelagic zone of lakes, the high δ^{15}N values in small anchovies likely resulted from foraging in the pelagic zone (Vander Zanden & Rasmussen, 1999; Bunn et al., 2003). Copepods have the highest number and biomass among the zooplankton in Hukou (unpublished data) and are therefore the primary carbon source of small anchovies (Anonymous, 1976; Tang, 1987). In this study, a strong negative relationship between the δ^{13}C and δ^{15}N values of *C. brachygnathus*, signifying that ^{13}C-depleted individuals are also ^{15}N-enriched, which is consistent with the ^{15}N-enriched zooplankton endpoint. Similar to *C. ectenes taihuensis* (Xu et al. 2007), the ^{13}C-enriched and ^{15}N-depleted *C. brachygnathus* indicates a size-related dietary shift from zooplankton to benthic sources.

Hydrologic changes are important because they affect the nutrient inputs and isotopic values of carbon sources and consumers (Hein et al., 2003). In this study, we found distinct baseline δ^{13}C and δ^{15}N signatures in the POM and primary consumers for each season. POM was more δ^{13}C-depleted and more δ^{15}N-enriched during the wet season probably because of the reuse of biogenic CO_2 derived from the respiration of phytoplankton (Mook & Tan, 1991), leading to decreased δ^{13}C during the high-water period. Trudeau and Rasmussen (2003) found a strong negative relationship between water velocity and algae δ^{15}N signatures. Compared with the dry season, Lake Poyang had lower water velocity during the wet season (Yin & Zhang, 1987). For primary consumers such as *C. fluminea* and *B. aeruginosa*, significant isotopic shifts were caused by the assimilation of different food sources between seasons, consistent with the study of Wang et al. (2011b). These data suggest that trophic and background changes occur with seasonally varying water levels. Furthermore, the temporal isotopic shift among primary producers and consumers could also influence the stable isotope composition of predators via predator–prey interactions (Wantzen et al., 2002; Wang et al., 2011b).

With respect to δ^{13}C values, *C. brachygnathus* was more ^{13}C-enriched during the dry season than during the wet season. Wantzen et al. (2002) suggested that seasonal isotopic shifts among fish could be elucidated based on the abundant and variable food sources during the wet season and increasing carnivory during the dry season. During the wet season, *C. brachygnathus* derives its biomass significantly from zooplankton carbon sources with ^{13}C-depleted signatures. However, during the low-water period, carnivory increases because of the limited fish movement and the carbon sources available for consumers are diminished (Wantzen et al., 2002; Perga et al., 2005). In Lake Poyang, cladocera and copepod biomass during the dry season was almost three times lower than that during the wet season (Wang et al., 2003), similar to the results obtained by Dr. Zhang in our laboratory (unpublished data). Fish and shrimp also had lower biomass during the dry season (Hu et al., 2011; Hong et al., 2003). However, in the central area of the lake, the prey density and predator–prey interactions increased when the water was limited. The spawning period of *C. brachygnathus* ranged from April to July (Liu et al. 2008). The higher energy demanded for breeding during the dry season could possibly explain the temporal shifts in diet. Our results support that anchovies are largely dependent on shrimp and fish with ^{13}C-enriched signatures during the dry season, which reflects increased piscivory.

Wang et al. (2011b) also reported a temporal dietary shift in *C. brachygnathus*, but with opposite δ^{13}C values. The ^{13}C-enrichment of anchovies during the wet season were probably due to the consumption and assimilation of ^{13}C-enriched food sources, such as aquatic macrophytes (9–91%), during the high-water period, whereas in the dry season, the fish were strongly dependent on seston (96–100%) during the dry season (Wang et al., 2011b). Considering the rapid flow, high turbidity and sandy sediment conditions in Hukou, aquatic macrophytes are rare in the area (Guan et al., 1987), thus they could not be major carbon sources for *C. brachygnathus* in our study. In addition, the study area and the samples collected in the current study are considerably different from those considered by Wang et al. (2011b). Spatial differences in ecological and geomorphologic characteristics, such as water depth and sediment (Wu et al., 2008), nutrient concentration (Wang et al., 2008), organism assemblage (Guan et al., 1987; Wang et al., 2003), and source availability (Wang et al. 2011a, 2011b), between the two sampling sites were evident. For example, the central area of the lake basin is flat and shallow with well-developed vegetation. However, the northern part is deep and has a high degree of channel incision (Wu et al., 2008). Therefore, *C. brachygnathus* could express different δ^{13}C values between habitats with distinct prey availability.

In terms of δ^{15}N values, however, *C. brachygnathus* showed a significant decrease from the wet season to the dry season. The temporal isotopic shift may have resulted from the different nitrogen sources assimilated by the anchovy. As the δ^{15}N values of prey items during the high-water period increased, the ^{15}N levels in *C. brachygnathus* increased. Flooding provided more allochthonous organic matter, such as urban sewage, to the lake (Bannon & Roman, 2008). Wang et al. (2008) suggested that floods bring water contaminated by agricultural drainage and urban sewage, which contain a high N load, into the tributaries to Lake Poyang, causing an increase in the δ^{15}N signatures of primary sources (Xu & Xie, 2004). These variations are ultimately reflected in the muscles of anchovies.

Given their high growth rates and short life spans, anchovies reach a length of 200 mm within their 6-month lifespan (Tang, 1987; Liu, 2008). The ages of the *C. brachygnathus* in Hukou varied between $0 + y$ and $1 + y$, but 95% of the population is age 0 (Liu, 2008). The anchovy samples collected in our study might contain populations with two age groups, seemingly co-exist during the dry season (Fig. 4b). Notwithstanding, anchovies feed increasingly on shrimp and fish larvae with increasing size (Anonymous, 1976; Tang, 1987; Xu et al., 2007), however, temporal dietary shift of *C. brachygnathus* will not be affected due to similar sizes (>150 mm) collected in both seasons.

Previous studies revealed that the zooplankton biomass is supported by planktonic heterotrophs and detritus via the microbial pathway (Hessen et al., 1990; Hoffman et al., 2008). Lake Poyang has a low phytoplankton biomass because of its high flow (Wang et al., 2004); thus, allochthonous carbon sources are important to consumers (Wang et al., 2011b). Wang et al. (2011a) found that detritus is more ^{13}C-depleted during the dry season in Lake Poyang. We therefore, recognize that the seasonal differences between zooplankton is lacking in our study because of the allochthonous organic matter consumed when the phytoplankton biomass decreased. Considering the mixing model outcomes, the proportion of contributions to the *C. brachygnathus* diet may be biased because of lacking information on the temporal changes in zooplankton δ^{13}C values. No interannual difference in zooplankton samples was found probably because few zooplankton data points were available during data gathering for the wet seasons of 2009 and 2010. The renewal rate of the muscle tissue in fish primarily depends on growth (Perga & Gerdeaux, 2005). Given their high growth rates and low ages, metabolic turnover is rapid in anchovies. Thus, we assumed that zooplankton was the likely carbon source for *C. brachygnathus*, although a variation was not completely captured in our study. The effects will be determined and examined in future studies.

Our findings indicated that the dietary shifts of *C. brachygnathus* were not only related to body size but also associated with temporal hydrological changes. Hydrological fluctuation is considered an important factor influencing primary fish food sources and affecting fish assemblages (Coops et al., 2003). The food web dynamics of Lake Poyang are strongly influenced by changes in the abundance and accessibility of different food sources due to the flood pulse (Wang et al., 2011b). Given the hydrological connectivity, spatio-temporal exchange pathways for water, resources, and organisms along the lateral and longitudinal dimensions frequently occur between Lake Poyang and the connected the Yangtze River. These findings have important implications for conservation and management strategies for fish assemblages in a natural hydrologic floodplain ecosystem.

Conclusion

Stable isotope analysis facilitated the elucidation of the dietary shifts in *C. brachygnathus* and prevented the temporal bias associated with stomach content analysis. Compared with a previous study (Anonymous 1976), we observed that shifts in the diet of *C. brachygnathus* were related to body size and associated with food source changes caused by the flood pulse. Attention should be focused on size-related dietary shifts, as well as on temporal dietary shifts influenced by seasonal hydrological changes, when constructing aquatic food webs. These two shifts are expected to affect the function of the Poyang Lake food web along the trophic pathway.

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