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Trophic niche differences between coexisting omnivores silver carp and bighead carp in a pelagic food web

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Abstract Understanding how omnivorous consumers are affected by their resources and how this is expressed through the food chain is a fundamental issue in ecology. We used stable isotope analysis of archived scales of two pelagic single-chain omnivorous fish species, bighead carp (*Hypophthalmichthys nobilis*) and silver carp (*H. molitrix*), to reconstruct historical trophic interactions patterns along a gradient of resources. We found that, although bighead carp and silver carp utilize the similar resources from the pelagic food chain, they can coexist and persist not only by regulating their trophic position and trophic dissimilarity, but also by regulating trophic niche width. Omnivorous fish often exhibit flexible foraging strategies, which is closely related to the availability of ecologic context. We found a positive relationship between trophic dissimilarity and zooplankton density, which may indicate that the competitive interactions induce strong top-down effects on zooplankton, and/or that high zooplankton availability release the between-population trophic interaction through bottom-up effect. The trophic niche width of bighead carp was positively related with zooplankton availability, probably reflecting that the niche of an omnivore at a higher trophic position is more sensitive to high quality resources. Our results indicate how different aspects of the trophic partitioning of coexisting omnivores may be regulated by different ecological contexts. These alternatives are not mutually exclusive and further theoretical work should include both these mechanisms to re-evaluate the effects of omnivory on food web properties.

Keywords Fish scales · Historical food web · Niche width · Stable isotopes · Trophic niche

Introduction

Understanding and predicting the factors regulating food web structure has long been an active area of ecological research (Paine 1980). In aquatic ecosystems, fisheries production, biogeochemical cycling, and ecosystem responses to anthropogenic activities were strongly influenced by food web interactions (Brett and Goldman 1997). Omnivory, a common feature of food webs that reflects the flexibility of consumers in energy acquisition, was traditionally defined as feeding at more than one trophic level within a single food chain (Pimm and Lawton 1978; Yodzis 1984; Vadeboncoeur et al. 2005). The important role the trophic omnivory play in the structure and dynamics of food webs causing a long-term controversy in ecology (Holt and Polis 1997; Vandermeera 2006). An analysis of natural food webs suggests that, above the herbivore trophic level, food webs of omnivores were more tangled and complexed (Thompson et al. 2007). For example, in lake ecosystems, piscivorous and benthivorous fishes can derive energy from both benthic- and pelagic-based food chains, while planktivorous fishes show a consistent energetic link to pelagic-based food chain (Vadeboncoeur et al. 2005; Zhang et al. 2013a, b; Xu et al. 2014).

Omnivorous fish often exhibit flexible foraging strategies, which is closely related to the availability of food resources (Gregersen and Aass 2006; Corrigan et al. 2011; Xu et al. 2016). Omnivory has been suggested to stabilize consumer-resource interactions, diffuse top-down influences through food webs and alter the expression of top-down control (McCann and Hastings 1997; Loeuille and Loreau 2004). Pelagic ecosystems are often considered as linear food chains with distinct trophic levels, which is why trophic cascades are more commonly identified in aquatic than in terrestrial ecosystems (Carpenter and Kitchell 1996; Carpenter

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et al. 1996; Pace et al. 1999). However, strong top-down control is actually likely to lead to reduced consumer-resource stability, especially as ecosystem productivity increases (Rosenzweig 1971; Strong 1992), and because of omnivory, top-down regulation is not expressed similarly in all ecosystems (Pace et al. 1999; Vadeboncoeur et al. 2005; Xu et al. 2012). Therefore, it is crucial to understand how omnivorous consumers partition their trophic niches in time, as well as how their trophic niches are regulated by resource availability and competition when coexisting in a single food chain.

Stable isotope ratios can be used in measuring trophic patterns as the values measured in consumer tissues are tightly related to those in their diet (Minagawa and Wada 1984; Vander Zanden et al. 1997; Post 2002). For example, the $\delta^{15}\text{N}$ is analogous to a trophic position axis, because ^{15}N increases in a stepwise fashion with each trophic level; the $\delta^{13}\text{C}$ is analogous to an axis of primary carbon source origins, because ^{13}C alter slightly with trophic level transfer. Thus, isotopic data of animal tissues essentially delineates an animal's isotopic niche (Newsome et al. 2007), which is tightly correlated to the trophic niche (Hutchinson 1957). The isotopic niche of consumers provide ecologically relevant information about the individual, population or community they represent as it is predominantly ecological in origin (Jackson et al. 2011). Additionally, stable isotope compositions offer time-integrated trophic information of consumers, which is an integrated measure of niche width as the selection of tissues with appropriate turnover rates in consumers can be linked qualitatively to the variance among individuals in isotope space (Bearhop et al. 2004).

Silver carp (*Hypophthalmichthys nobilis* [Richardson, 1845]) and bighead carp (*H. molitrix* [Valenciennes, 1844]), collectively known as Asian carps, are important cultivated and invasive fishes in many parts of the world. These carps are omnivorous filter-feeding fish, i.e. feeding from different trophic levels (phytoplankton and zooplankton). Silver carp feeds mainly on phytoplankton, whereas bighead carp feeds mainly on zooplankton; these two species also exhibit flexible foraging strategies, i.e. change of the diet proportions of planktonic resources, depending on the status of food sources (Gu et al. 1996; Xu and Xie 2004; Zhou et al. 2009a; Xu et al. 2016). High biomass of these filter feeders can substantially reduce phytoplankton and zooplankton biomass, which caused competition for available feeding source with larval fishes and other planktivores (Xie 2001; Kolar et al. 2005; Cooke et al. 2009). These carps are invasive species and have become an ecological threat to numerous lake and river ecosystems in United States (Garcia-Berthou et al. 2005) and in China (Xu et al. 2015). These species are also the main focus of a non-traditional biomanipulation technique which has been applied to control cyanobacteria in many highly eutrophic lakes (Xie and Liu 2001; Zhang et al. 2008; Zhou et al. 2009a, b; Xu et al. 2014). Therefore, determinations of trophic

interaction of Asian carps across a productivity gradient is essential to understand the prevalence and impact of Asian carp as both invasive and biomanipulative species throughout the world.

Here we used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signals of nonlethally sampled, fish scales, as an archived integrated trophic niche indicator in stable isotopic space. Fish scales provided reliable indications of potential food sources or trophic relationships in the food web in consumers' ontogeny, as there are intrinsic relationships between scales and the muscle tissue (Estep and Vigg 1985; Wainright et al. 1993; Pruell et al. 2003; Kelly et al. 2006). We hypothesized that variable contributions of phytoplankton and zooplankton to the diet of those omnivores would regulate their trophic niche partitioning to facilitate their coexistence. Figure 1 presents a schematic illustration of trophic interaction in a pelagic food web dominated by bighead and silver carps. The figure illustrates that these coexisting omnivores in the pelagic food chain regulate their trophic dissimilarity (from A to B), or niche width (from B to C) to adapt to accommodate inter-specific resource sharing (i.e. zooplankton and phytoplankton), which may not be mutually exclusive (from A to C). These possible mechanisms suggests that variable dietary contributions of phytoplankton and zooplankton would regulate their trophic niche partitioning to facilitate the coexistence of both omnivorous fish. We used stable isotope analyses of fish scales from an eleven-year-long survey to construct the historical trophic niches dynamics of two planktivorous fish, which are dominant in a pelagic food chain. Specifically, we first used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signals of the fish scales as an archived integrated trophic niche indicator in stable isotopic space. Secondly, we used stable isotopes ratios of both populations to calculate two stable isotope population metrics, trophic dissimilarity between the two populations and the trophic niche width of each population. Finally, we related these trophic indices to the resource availability and competition to determine how the trophic niches are regulated in this ecological context.

Materials and methods

Field collection and lab processing

Lake Donghu (30°33'E, 114°23'N) located in middle reaches of Yangzi River in China with a surface area 32 km² and the maximum depth 4.5 m (Liu 1984). The lake is eutrophic, and total phosphorus and nitrogen concentrations varied between 0.1–0.3 and 1.2–2.5⁻¹ mg L⁻¹ during studied years. Silver carp and bighead carp are the native species and the main commercial fish in this lake. Scales of bighead and silver carps were obtained from an archived collection maintained by the Donghu Experimental Station of Lake Ecosystems, Chinese Ecosystem Research Network (DESLE, CERN) from 1994 to 2004. More than 85 % of the fish

yield was from silver and bighead carp in the sampling years. The fish were caught using a commercial trolling net (mesh size $2 \times 2 \text{ cm}^2$ with a trawling speed ~ 3 miles per hour) in December each year. At capture, the scales used for age determination were removed from the body side above the lateral line, and then dry-preserved and archived with entire scale. Seven to eight scales were removed from each fish to determine fish age. Eight to thirteen individuals of each species at age three were selected per year to reduce the age effect on further analysis. The average body length of the bighead and silver carp was 46.6 ± 1.2 and 41.7 ± 2.3 cm, respectively. After age determination for each individual, one entire scale per fish were used for stable isotope analysis. The isotopic ratio of whole fish scales reflects the entire life span of the fish, but because fish scales grow exponentially, the final year of scale material contributed a larger weight to the total of the 3 years growth. Scales were soaked in deionised water and any connective tissue removed with an abrasive pad (Pruell et al. 2003). For stable nitrogen isotope analysis, scales were not decalcified because acid washing may alter the $\delta^{15}\text{N}$ values of natural materials and increase isotopic variability (Bunn et al. 1995). For stable carbon isotope analysis, scales were decalcified because fish scales are a mixed-origin tissue, with organic and inorganic fractions (Fincel et al. 2012). For an accurate measurement of the $\delta^{13}\text{C}$ of the proteins, the scales were decalcified for 2 min in 1 mol L^{-1} HCl and rinsed in deionised water before analysis according to previously established protocols (Perga and Gerdeaux 2003; Pruell et al. 2003; Gerdeaux and Perga 2006).

Sampling for phytoplankton and zooplankton community was carried out at monthly intervals between January 1994 and December 2004 by DESLE, CERN. Each sample was a mixture of several subsamples collected from the surface to the bottom at 0.5 m intervals. The quantitative samples (1 L) for phytoplankton were fixed with Lugol's solution and sedimented for 24 h, then concentrated to 50 mL. Samples were observed and identified under a compound microscope under $400\times$ magnification and algal species were identified and counted on a cell-by-cell basis. Biomass of the dominant species were calculated using the formulae for solid geometric shapes most closely matching the cell shape under the assumption that 1 mm^3 weight is 1 g based on the measurement of 30 individual cells. The zooplankton samples were obtained by filtering the lake water through a zooplankton net (mesh size $120 \mu\text{m}$) and preserved with 5 % formalin. Zooplankton, i.e. copepods and cladoceran, was identified and the volumes were estimated by using geometric figures of their approximate shape and well established weight—body size regression (Lu et al. 2002). We used data for the densities of zooplankton, phytoplankton and the stocked fingerlings to further analysis the trophic patterns of carps under this ecological context. Methods for sample counts for plankton, and estimation of stocked fingerlings were described in previous publications

(Yang et al. 1998; Xie and Liu 2001; Xie and Xie 2002; Lei et al. 2005). We used triennial averages of monthly monitoring data to test our hypothesis because isotopic compositions of fish scales reflects the entire life span of the fish. In our study, it represents a trophic integrator of 3 years. All samples were oven-dried at $60 \text{ }^\circ\text{C}$ for at least 48 h to constant weight and ground to homogeneous powder using mortar and pestle (Xu et al. 2012).

Stable isotopic analysis

The carbon and nitrogen stable isotope compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were determined with a Delta Plus (Finnigan, Bremen, Germany) continuous-flow isotope ratio mass spectrometer coupled to a Carlo Erba NA2500 elemental analyzer (Carlo Erba Reagenti, Milan, Italy) in the Institute of Hydrobiology, Chinese Academy of Sciences. Stable isotope ratios were expressed as parts per thousand (‰) deviation from the international standards according to the equation: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is ^{15}N or ^{13}C and R is the corresponding ratio $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$. δ is the measure of heavy to light isotope in the sample, whereby higher δ values denote a greater proportion of the heavy isotope. The standards for nitrogen and carbon are atmospheric nitrogen and Vienna Pee Dee belemnite, respectively. The reference materials for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were ammonium sulphate (IAEA-USGS25), and carbonate (IAEA-NBS18), respectively, supplied by the U.S. Geological Survey (Denver, Colombia, USA) and certified by International Atomic Energy Agency (Vienna, Austria). On a daily basis, an internal urea working standard ($\delta^{15}\text{N} = -1.53 \text{ }‰$; $\delta^{13}\text{C} = -49.44 \text{ }‰$) was employed. Twenty percent of the samples were run in duplicate; the average standard errors of replicate measurements for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were both less than $0.3 \text{ }‰$.

Trophic dissimilarity and trophic niche width

To evaluate the extent to which bighead carp and silver carp utilize planktonic resources differently, trophic dissimilarity between silver carp and bighead carp was estimated as the Euclidean distance between the centroids of silver carp and bighead carp populations in stable isotopic space for each year. The centroid is the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value for all individuals of each population in each year. Thus, trophic dissimilarity was calculated to determine the difference feeding strategies between these coexisting omnivores. To make comparison between species populations with varying sample sizes, trophic dissimilarity was derived from bootstrapped (999 times) isotopic data (Layman et al. 2007).

Considering the variation in sample size, the standard ellipse area (SEA), which reflects the mean core population isotopic niche, was used to evaluate the isotopic niche width of bighead carp and silver carp. The standard ellipse

Table 1 Two-factors analysis of variance for stable isotope comparisons

Factors	d.f.	Sum square	Mean square	<i>F</i>	<i>P</i>
$\delta^{13}\text{C}$ (‰)					
Year	10	20.61	2.061	6.291	< 0.001
Species	1	5.11	5.111	15.599	< 0.001
$\delta^{15}\text{N}$ (‰)					
Year	10	88.33	8.83	18.9	< 0.001
Species	1	150.09	150.09	321.1	< 0.001

Statistically significant differences at $P < 0.05$ are indicated by bold letters

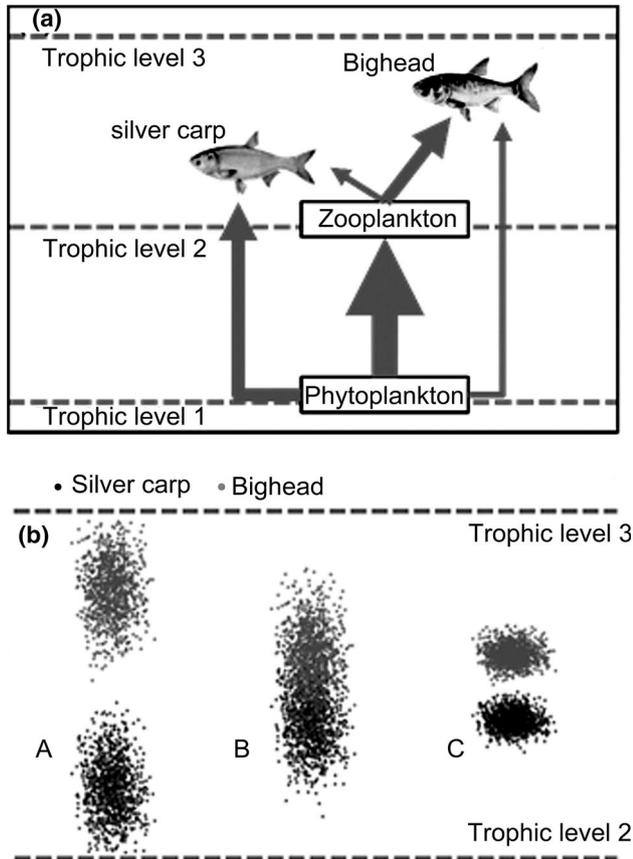


Fig. 1 Schematic illustration of trophic interaction in a pelagic food web dominated by bighead and silver carps. In this diagram, phytoplankton represent trophic level 1 and zooplankton trophic level 2, which pass to bighead carp and silver carp through two distinct trophic transfers. We hypothesized that these coexisting omnivores in the pelagic food chain regulate their trophic dissimilarity (from A to B), or trophic niche width (from B to C) to accommodate inter-specific resource sharing (i.e. zooplankton and phytoplankton), but these two regulatory mechanisms may not be mutually exclusive (from A to C). The dots represent the isotope position of the fish

is calculated based on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value and contains about 40 % of the data, which reveals the core niche area (Jackson et al. 2011). We used corrected standard ellipse area (SEAc), a sample size corrected version of the standard ellipse area, as a measure of the mean core population isotopic niche (hereafter “trophic niche

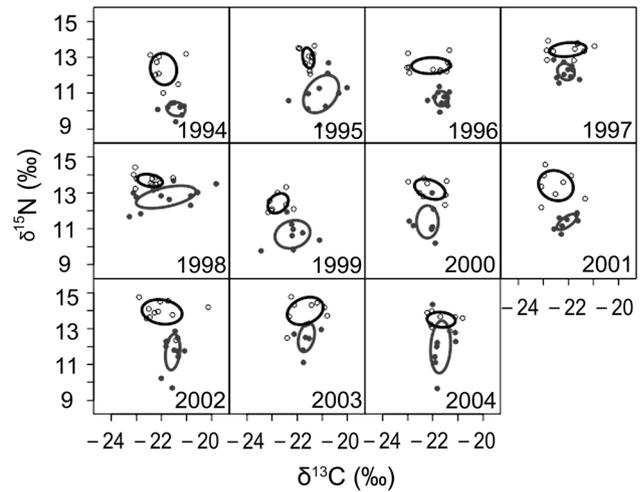


Fig. 2 Isotopic niche widths marked with standard ellipse area corrected for small sample sizes (SEAc) for bighead carp (samples marked with solid circles) and silver carp (samples marked with empty circles) collected between 1994 and 2004

width”), which is expected to be less sensitive to sample size (Jackson et al. 2011, 2012; Syväranta et al. 2013). Explicitly, $SEAc = SEA * (n - 1) / (n - 2)$. This correction leads to a slightly larger ellipse for small sample sizes. Furthermore, SEAc can be used as a quantitative measure of dietary similarity among populations, as it allows the degree of isotopic niche overlap to be calculated. And all metrics were calculated using the R statistical computing package “siar” (Parnell and Jackson 2013).

Statistical analysis

To analyze the differences in stable isotopic values between years and species, multivariate analysis of variance (MANOVA) to compare multivariate ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) means among years and between species was used. To see whether between-population trophic interactions and/or within-population trophic niche widths could be regulated by the resource availability and competition, the relationships between the niche indices (trophic dissimilarity and niche width of carps) and ecological variables (the biomasses of zooplankton and phytoplankton and the densities of stocked fingerlings) were assessed using multiple linear regressions. Statistical analyses provided individual *P* values for each dependent variable for a test of statistical significance at $\alpha = 0.05$. All statistics were conducted using the R statistical computing package (R Development Core Team 2013).

Results

Trophic dissimilarity and trophic niche width

Fish scale isotope ratios of silver carp and bighead carp from 1994 to 2004 reflected long term changes of the

isotopic niches. Isotope values of both species showed significant variation through time (MANOVA, $P < 0.001$, Table 1). Bighead carp had significantly different in stable isotopic values from silver carp ($P < 0.001$). Trophic dissimilarity ranged from 1.12 to 2.28 (Fig. 3a). Annually, scale $\delta^{13}\text{C}$ of silver carp ranged from -22.2 to -21.0 ‰ and scale $\delta^{15}\text{N}$ from 10.1 to 12.8 ‰; scale $\delta^{13}\text{C}$ of bighead carp ranged from -22.8 to -21.6 ‰ and scale $\delta^{15}\text{N}$ from 12.3 to 14.0 ‰ (Fig. 2). Standard ellipse areas (SEA_C) based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bighead carp and silver carp showed clear resource partitioning during 1994 to 2002 but some iso-

topic niche overlap in 2003 and 2004 (Fig. 2). Trophic niche width (SEA_C) ranged from 0.36 to 2.19 for silver carp (Fig. 3b) and from 0.39 to 1.82 for bighead carp (Fig. 3c). Niche widths represented by SEA_C were generally larger for silver carp.

Trophic niche regulation factors

Trend of triennial averages of monthly monitoring data of plankton biomass indicated that both biomass of zooplankton and phytoplankton varied remarkably

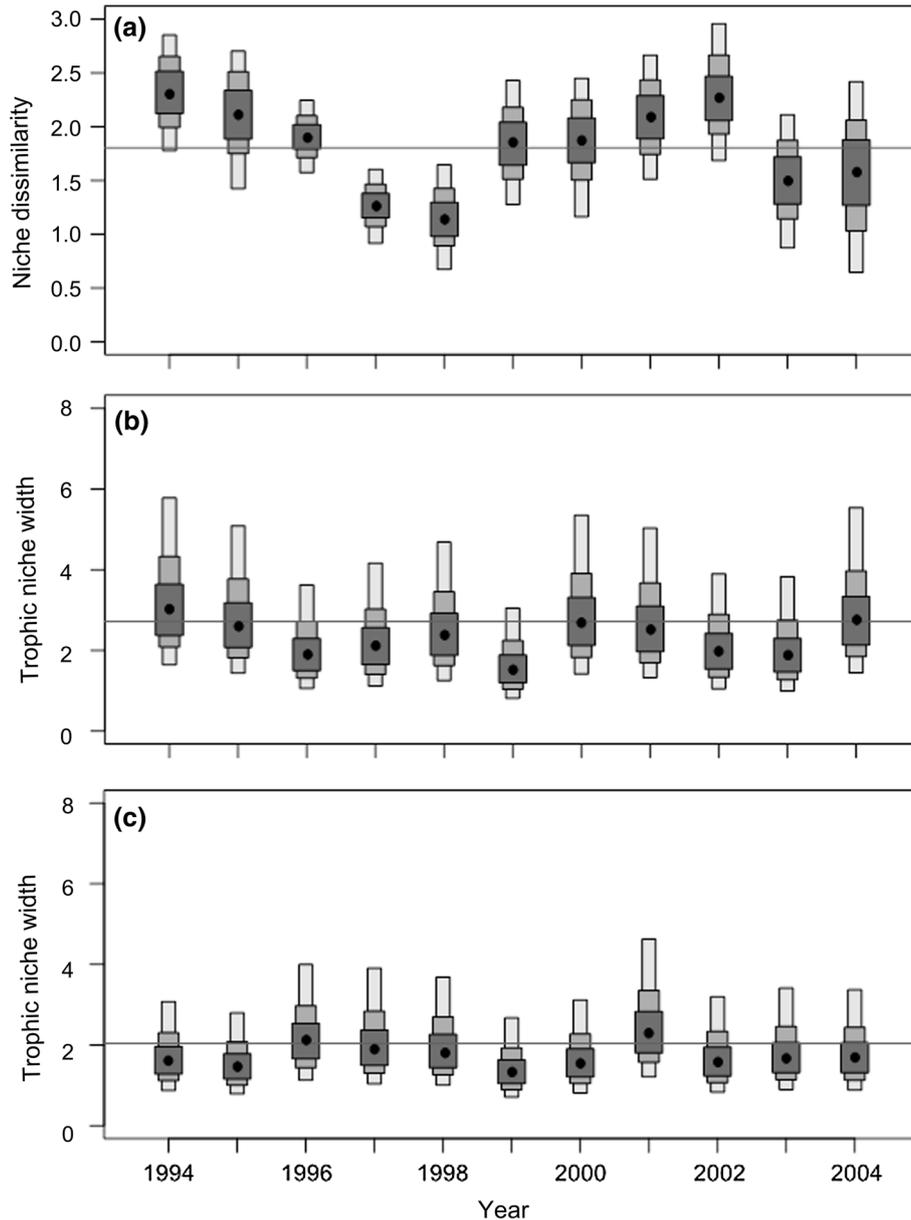


Fig. 3 Corresponding density *box plots* of posterior distributions showing the confidence intervals of trophic dissimilarity and trophic niche width. The *black points* are the mean values while the boxed areas reflect the 95, 75 and 50 % confidence intervals for

each carp. **a** Trophic dissimilarity, **b** trophic niche width of silver carp, and **c** trophic niche width of bighead carp. *Horizontal lines* represent the average value of each trophic index

Table 2 Multiple linear relationships between niche indices and ecological variables

Variables	Coefficients	SE	<i>t</i>	<i>P</i>
Trophic dissimilarity				
Phytoplankton biomass (mg L ⁻¹)	-0.079	0.139	-0.571	0.586
Zooplankton biomass (mg L ⁻¹)	0.897	0.382	2.349	0.050
Stocking biomass (ind. × 10 ⁴)	-0.005	0.003	-1.582	0.158
Trophic niche width (SEAc) of silver carp				
Phytoplankton biomass (mg L ⁻¹)	0.349	0.284	-1.229	0.259
Zooplankton biomass (mg L ⁻¹)	1.125	0.778	-1.446	0.191
Stocking biomass (ind. × 10 ⁴)	0	0	-0.001	0.999
Trophic niche width (SEAc) of bighead carp				
Phytoplankton biomass (mg L ⁻¹)	0.162	0.161	1.004	0.348
Zooplankton biomass (mg L ⁻¹)	1.293	0.443	2.919	0.022
Stocking biomass (ind. × 10 ⁴)	0.004	0.003	1.017	0.305

Statistically significant relationships at $P < 0.05$ are indicated by bold letters

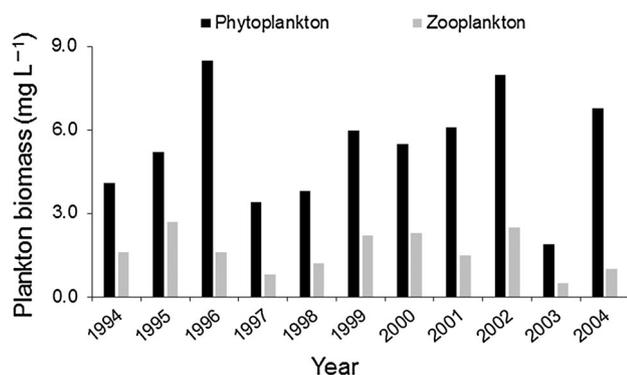


Fig. 4 Trend of triennial averages of monthly monitoring data of zooplankton and phytoplankton biomass

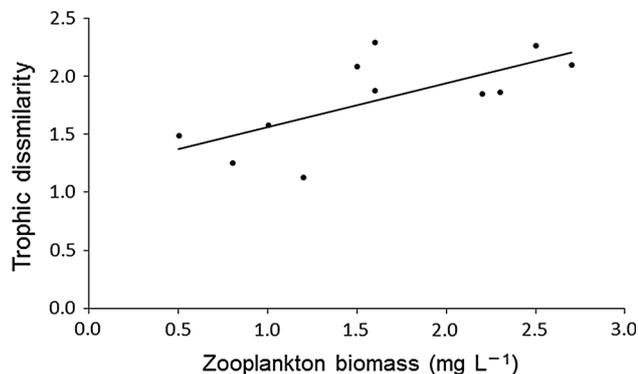


Fig. 5 Linear relationship between trophic dissimilarity and zooplankton biomass. *Solid line* represents the regression line with $R^2 = 0.4831$, $P < 0.01$

(Fig. 4). The multiple linear regression results show that a positive relationship was found between trophic dissimilarity and the zooplankton biomass (Fig. 5) and between niche width of bighead carp and the zooplankton biomass. However, the relationship between the trophic niches of silver carp and the food resource is not notable (Table 2).

Discussion

With the assumption of constant stable isotope fractionation, the differences in isotopic compositions of silver and bighead carp implied utilization of different proportions of phytoplankton and zooplankton. Based on both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, we found that bighead carp and silver carp remained in a constant or similar trophic position through each year relative to each other, between the second and third trophic level with minimal niche overlap, which may be the coexistence mechanism in this fine-scale niche space related to the compositions of their diet (Gu et al. 1996; Xu and Xie 2004; Zhou et al. 2009a). Our results confirm our hypothesis that although bighead carp and silver carp utilize the planktonic resources (zooplankton and phytoplankton), they can coexist and persist by regulating their proportions of assimilated zooplankton and phytoplankton as well as the trophic level they are eating.

Stable isotopic evidence for trophic niche partitioning

We found significant difference in stable isotopes between the species. Several studies using stable isotope analysis on these planktonic omnivores suggested that the $\delta^{13}\text{C}$ of phytoplankton, zooplankton, and muscle tissue and gut contents differed in an arrange about 0.5–2.2 ‰, and the muscle tissue of silver carp and bighead carp ranged only between 0.2 and 1.7 ‰ (Gu et al. 1996; Zhou et al. 2009a, b). Based on gut content analysis, both silver carp and bighead fed on phytoplankton and zooplankton, and their diet shift during the larval stage was accomplished at the very early months during their ontogeny (Zhou et al. 2009a), suggesting that both carp rely steadily on plankton production during the adult stage. Our results also show that, although the difference in $\delta^{13}\text{C}$ between silver carp and bighead carp was significant, the difference is smaller than expected trophic enrichment (1 ‰) between

one trophic level (Post 2002), which indicates that these filter-feeding fishes share similar food resources, i.e. plankton production from the pelagic food web (Kolar et al. 2005; Cooke et al. 2009;). The $\delta^{15}\text{N}$ value of the basal sources (e.g. phytoplankton) was not available in our study and the evaluation the trophic level of each carp was not possible. However, comparison of our $\delta^{15}\text{N}$ values between the carps suggests that bighead carp are less than one trophic level higher than silver carp (Fig. 2), assuming that enrichment factor of $\delta^{15}\text{N}$ per trophic level transfer is 3.4 ‰ (Post 2002). Based on both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, we may conclude that these omnivores coexist in a constant or similar trophic position between the second and third trophic levels with weak niche overlap, which is the coexistence mechanism in this fine-scale niche space related to their energetic uptake.

Trophic dissimilarity

Our results support our hypothesis that the variation of trophic position and the trophic dissimilarity existed between these species, which is the coexistence mechanism for the omnivores. We found a positive relationship between trophic dissimilarity and zooplankton biomass (Fig. 5), which may indicate that the competitive interactions induce strong top-down effects on zooplankton, and/or the feeding strategies of these omnivores were affected by the zooplankton availability through bottom-up effect. We found that, when zooplankton availability decreases, bighead carp can shift its energy reliance from zooplankton to phytoplankton, which is supported by previous studies (Gu et al. 1996; Xu and Xie 2004; Zhou et al. 2009a). The $\delta^{15}\text{N}$ values, as an indicator of trophic position of these populations, support this view as the change in trophic dissimilarity was coupled with the change in trophic position of bighead carp (Fig. 2). The prediction of the limiting similarity hypothesis (MacArthur and Levins 1967) suggests that there is a limit to the similarity of competing species which can coexist, which is reduced by the limited resource availability in a narrow niche space. In this study, as the level of competition increased as indicated by fish density, the trophic dissimilarity was decreased significantly with the zooplankton availability decreased (Table 2), suggesting that these species the limit of niche similarity is reduced by the limited resource availability.

Trophic niche width

We also found that, although bighead carp and silver carp utilize the planktonic resources (zooplankton and phytoplankton), they can coexist and persist not only by regulating their trophic position, but also by regulating the feeding difference between conspecific individuals. The trophic niche width of bighead carp was positively related with zooplankton availability, probably reflect-

ing that the niche of bighead carp at a higher trophic position is more sensitive to high quality resources. Bigheads prefer to feed on zooplankton, but switch to phytoplankton when zooplankton is sparse (Kolar et al. 2005). A recent study revealed that a decrease in zooplankton in bighead carp diet led to reduced growth rate and a lower trophic level position than silver carp (Zhou et al. 2009a), suggesting a more sensitive response by bighead carp to decreases in zooplankton availability. The lack of relationship between the trophic niche width of silver carp and the food resources may be partially explained by silver carp being less selective on planktonic particles (Kolar et al. 2005; Cooke et al. 2009; Zhou et al. 2009a).

Archived scales for isotope analysis

Stable isotope analysis offers time-integrated information about important energy sources assimilated by consumers. Previous isotope niche studies on fishes were most based on the isotopic signature of muscle tissues, which was found to be less variable in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than all other tissues (Pinnegar and Polunin 1999). However, fish scales provided reliable as an indicator of the potential energetic sources or trophic relationships in the food web, as there are intrinsic relationships between scales and the muscle tissue (Estep and Vigg 1985; Wainright et al. 1993; Pruell et al. 2003; Kelly et al. 2006). For example, Wainright et al. (1993) analyzed scale stable isotopes of archived demersal fishes to study the relationship between long-term changes in trophic structure and a series of environmental and population variables associated with the Georges Bank food web, and indicated that this approach may be useful in discerning alterations to trophic structure in aquatic ecosystems. Here, we used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of fish scales as an archived integrated trophic niche indicator in stable isotopic space, which as we demonstrated, can also reflect the differences in food availability for fish occupying alternate foraging niches. The application of stable isotope analysis to archived fish scales thus has the potential to improve our understanding of alterations in the trophic structure of aquatic ecosystems, which can provide complementary results with other tissues with different turnover rates of stable isotopes.

Concluding remarks

Empirical studies support that omnivory is common in the natural food webs (Polis 1991; Diehl 1993; Wine-miller 1996), and the debate on omnivory and food web properties has persisted for more than 40 years. Pimm and Lawton (1978) simulated simple food webs with multiple trophic levels and omnivory, and demonstrated that food webs with high degree of omnivory are often less stable. However, recent modelling work has suggested that omnivory provides weak interactions in food

webs to facilitate food web properties, such as resilience and persistence (McCann and Hastings 1997; Neutel et al. 2002). An interesting finding arising from our study is that omnivory may contribute to food web dynamics not only through the regulation of trophic dissimilarity in a fine scale niche, but also through the regulation of trophic niche properties, such as niche segregation and niche width. These alternatives are not mutually exclusive and further theoretical work should include both these mechanisms to re-evaluate the effects of omnivory on food web properties.

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