Resources utilization and trophic niche between silver carp and bighead carp in two mesotrophic deep reservoirs

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ABSTRACT

Resources utilization and trophic structure in aquatic food webs play important roles in the ecosystem stability and functioning. Silver carp (SC, \textit{Hypophthalmichthys molitrix}) and bighead carp (BC, \textit{Hypophthalmichthys nobilis}) are intensively stocked in lakes and reservoirs in China and share similar food resources and trophic positions in water bodies. To better understand the ecological roles of SC and BC in natural freshwater, two mesotrophic reservoirs (Nanwan and Nianyushan) were selected to compare resource utilization and the trophic niche of these two fish species. Data analysis using Bayesian mixing model showed that SC was more like a fine particulate organic matter (fPOM) feeder, while BC consumed more coarse particulate organic matter (cPOM) and displayed a higher trophic position in both reservoirs. In contrast, niche breadths represented by the corrected standard ellipse area (SEAC) were essentially the same for SC and BC in Nanwan (SEAC\textsubscript{SC} = 6.1 for SC and BC), but much larger for silver carp in Nianyushan (SEAC\textsubscript{Sc} for SC: 11.6, SEAC\textsubscript{BC} for BC: 4.2). The high stocking ratio of SC/BC in Nianyushan was the probable reason for the large SEAC of silver carp, which suggested that silver carp could use more food resources and become more competitive with a higher stocking biomass ratio. The results indicated that the trophic partitioning of filter feeders might be regulated by the stocking biomass ratio of the fish to some extent.

Introduction

Understanding the ecological mechanisms of the resources utilization and trophic niche of two or more species is an important objective of ecological studies. Niche breadth is a fundamental parameter for the evaluation of the level of dietary specialization. Species with narrow niches are always more specialized than typical generalists with larger trophic
niches (Newsome et al. 2007). These generalists could coexist despite occupying similar niches when differences in relative competitive ability are minor. Furthermore, researchers usually use trophic niche overlap to predict the intensity of resource competition (Chase and Leibold 2003; Corrêa et al. 2011). For two species with minor differences in competitive ability, higher niche overlap is always due to more source utilization but may not cause competitive exclusion (Bulleri et al. 2016).

The trophic filter feeders play important roles in the structure and dynamics of food webs (Thompson et al. 2007; Yao et al. 2016). Filter-feeding fish is defined as feeding suspended food, mostly phytoplankton, detritus and small zooplankton (Vadeboncoeur et al. 2005). To some extent, filter-feeding fish could stabilize consumer-resource interactions, alter the strength of top-down regulation, and play different ecological roles in water bodies (McCann and Hastings 1997; Loeuille and Loreau 2004). However, ecological role is not always expressed similarly in aquatic ecosystems because different filter feeders partition various trophic niches according to their species, densities and stocking ratios in a water body, and competition with other species (Vadeboncoeur et al. 2005; Xu et al. 2012; Yao et al. 2016). Therefore, it is important to understand how filter-feeding consumers partition their trophic niches in a single food chain.

In tropic and subtropic regions of China, silver carp (SC, Hypophthalmichthys molitrix) and bighead carp (BC, Hypophthalmichthys nobilis) are the most dominant species and are of economic importance. Both SC and BC have been intensively stocked in lakes and reservoirs in China since the 1970s (Han 2010). By 2010, these two species accounted for more than 6.5 million tons and over 19.3% of the total freshwater fish production all over the world (Fisheries and Aquaculture Department (US) 2012). They are also stocked together into lakes and reservoirs to utilize food sources and are used as a tool to control cyanobacteria in many highly eutrophic lakes (Ke et al. 2008; Xu et al. 2012; Guo et al. 2015). However, these carp species are considered invasive species that could compete with native species sharing similar trophic positions for natural resources in the United States (Irons et al. 2007). Whatever their ecological roles, they always coexist in a single water body and use similar food resources. Previous findings have suggested that SC and BC share a similar trophic niche for natural resources (Gu et al. 1996a; Zhou et al. 2009; Chen et al. 2011). They also share a similar diet, but a different food composition because of different meshes of their gill rakers (Li et al. 2013). Jayasinghe et al. (2015) indicated that SC is more considered as a phytoplankton feeder, while BC is more likely a zooplankton feeder.

In general, both silver and bighead carps consume particulate foods of many types in the 10–1000 micrometer-range particles, including phytoplankton, zooplankton, plant pollen, detritus and incidental sediment (Cremer and Smitherman 1980; Kolar et al. 2005; Li et al. 2013). Lazzeri (1987) pointed out that they are particulate feeders in larval and pre-juvenile stages, with a body length smaller than 30 mm, while adult fish are omnivorous filter feeders (Spataru and Gophen 1985; Vörös et al. 1997). Past dietary studies of the two species were mostly based on analysis of gut contents, which may not represent the growth of the fishes and did not provide insight into the magnitude of stocking ratio between the two species.

Stable isotopes of carbon (δ¹³C) and nitrogen (δ¹⁵N) can be used in measuring trophic niche since the stable isotope values in consumer tissues are closely related to their food resources (Gu et al. 1996a; 1996b; 1997; Jayasinghe et al. 2015). Hence, the SI technique has been used to analyze the trophic dynamics of SC and BC (Gu et al. 1996b, Li et al. 2013), as well as the dietary overlap between both species (Gu et al. 1996a; Li et al. 2013; Jayasinghe et al. 2015; Yao et al. 2016). Most researches indicated that food resources
were responsible to the trophic niche and overlap. For example, Jayasinghe et al. (2015) pointed out that niche overlap was variable with food resources but in general clear size-based resource partitioning was observed, with bighead carp preying more on zooplankton and occupying a higher trophic position. However, except food resources, their trophic niche and overlap may be affected by fish stocking ratio either. To elucidate whether the trophic niche width and overlap of the two carps affected by fish stocking ratio, seasonal samples (including four food sources and fish muscle tissue) were taken over two full annual cycles in two deep and meso-eutrophic reservoirs in China. Selecting two reservoirs with similar habitats provides different fish stocking ratio, which in turn allows for the observation of their trophic niche in the food web. The main objectives of the present study are to: (i) examine the degree of trophic niche and dietary overlap between the two species in the two reservoirs, and (ii) check whether the fish stocking ratio has effect on trophic niche of the two carps.

**Materials and methods**

**Study sites**

The Nanwan (32°4’N, 113°57’E) and Nianyushan (31°47’N 115°20’ E) Reservoirs are monomictic meso-eutrophic reservoirs, with a 130 km distance from each other. The basic features and trophic states of the two reservoirs are shown in Table 1. Private business for fishery were prohibited from 2004 instead of governments management, leading to fish density increasing in the two reservoirs. Fish feeding on natural food and resources because bait is also forbidden in the reservoirs. SC and BC have been intensively stocked by governments in the past 15 years, so that they are the dominant fishes (more than 85% of the fish yield) in the two reservoirs. But the specific fish densities and yields are unknown. The dry season runs from October to May; about 60% of annual precipitation occurs in the wet season, from June to September. In addition, the watersheds of the two reservoirs are covered with pine forest (mainly Pinus massoniana). In spring, when pine forests blossom, the surface water is covered with pine pollen. All water samples were collected in the lacustrine zone, including three sampling sites in each of the reservoirs shown in Figure 1.

**Sample collection and plankton analysis**

Sampling was carried out seasonally (four times in one year) at three sites in both reservoirs from 21 August 2014 to 31 June 2016. Water samples for nutrients were collected with a 5 L sampler from the 0.5 m below the surface. Total phosphorus (TP), total nitrogen (TN), and chlorophyll-a (Chl-a) concentrations in the water samples were determined according to the Chinese National Standards for water quality and the USA Environmental Protection Agency standards (APHA 1989). Fish density and stocking ratio between the two fishes were estimated from fish yield information (Dick and MacCall 2011) provided by the reservoirs’ administration in Xinyang, China.

**Table 1. Basic features and trophic states (mean values during 2014–2016) of the two reservoirs.**

| Reservoir   | Total volume $(\times 10^8 \text{ m}^3)$ | Surface area (km²) | Mean depth (m) | TN (µg/L) | TP (µg/L) | SD (m) | Chl-a (µg/L) |
|-------------|------------------------------------------|-------------------|----------------|-----------|-----------|--------|---------------|
| Nanwan      | 16.33                                    | 1100              | 13.5           | 822.9     | 22.1      | 2.53   | 5.57          |
| Nianyushan  | 8.51                                     | 963               | 18             | 627.6     | 19.5      | 2.50   | 6.00          |

TN: total nitrogen; TP: total phosphorus; SD: Secchi depth; Chl-a: chlorophyll-a.
Fish samples for isotope analysis were collected by fishermen by net casting (with same pore size) from the three sites at each reservoir. Individuals of each species from ages 4 to 5 were selected from each site to reduce the age variance. We collect samples from full annual cycles because they could better represent trophic niche of fish. Of the eight sampling occasions, 24 SCs and 24 BCs (every sampling occasion has three samples) were chosen from each reservoir. Body length was measured with a ruler with an accuracy of 1 mm. Body weight was measured with a balance with an accuracy of 1 g. After measuring the body length and weighing each fish, white dorsal muscle tissue was collected. The muscle tissue samples were freeze-dried, ground to a fine homogeneous powder and encapsulated into tin capsules for isotope analysis.

Previous research showed SC and BC are filter feeders based on the structure of gill rakers and the size of suspending food particles (Zhou et al. 2009). Therefore, we categorized potential food particles as follows: suspending particles of >64 μm as coarse particulate organic matter (cPOM, mainly consisting of phytoplankton), suspending particles of 0.45–64 μm as fine particulate organic matter (fPOM), zooplankton (Zoopl) and pollen of *Pinus massoniana*. We collected cPOM from 5 L of 0.5 m underwater filtered with a 64-μm nylon mesh and concentrated to 10–20 ml. This procedure can guarantee what we collecting was particles >64-μm. Then we filtered the concentrated liquor on Whatman GF/F filters (pore size = 0.45 μm) and dried at 60 °C in an oven. For fPOM of
0.45–64 μm, we collected 3–5 L of water from the surface and passed it through a 64-μm nylon net to remove plankton and greater debris; the filtered water was then filtered on Whatman GF/F filters (pore size = 0.45 μm) and were also dried at 60°C in an oven. Both cPOM and fPOM samples were scraped from the filters and loaded into tin capsules for mass spectrometer analysis. Zooplanktons were sampled with a 120 μm mesh net in vertical tows through the whole water column. The mixed zooplankton was kept alive about 6–8 hours for gut clearance and was then picked out one by one under a microscope. Zooplankton samples were then put into tin capsules and oven dried at 60°C to a constant weight for stable isotope analysis. In spring, we collected pollen for stable isotope analysis from Pinus massoniana trees on the islands inlayed in the reservoirs.

**Stable-isotope analysis**

All isotope samples were analyzed with a Carlo Erba EA-1110 elemental analyzer accompanied by a Delta Plus Finnigan Mat isotope ratio mass spectrometer via continuous flow II interface by Zhengzhou Customs of the People’s Republic of China. Isotopic ratios were expressed relative to international standards. Stable isotope values were defined as:

\[ \delta R (\text{‰}) = \left( \frac{X_{\text{sample}}}{X_{\text{standard}}} - 1 \right) \times 10^3 \]

where \( R = ^{13}\text{C} \) or \( ^{15}\text{N} \), and \( X \) is the corresponding ratio \( ^{13}\text{C}/^{12}\text{C} \) or \( ^{15}\text{N}/^{14}\text{N} \). The precision of measurements was ±0.1 ‰ for \( ^{13}\text{C} \) and ±0.2 ‰ for \( ^{15}\text{N} \).

**Zooplankton biomass analysis**

A total of 30 L of water was collected by a 5 L iron sampler for a zooplankton sample from the surface to a 15 m depth at 3 m intervals at the sampling sites (Zhang et al. 2015). For rotifers and protozoa were present but in low biomass in the reservoirs (Zhang et al. 2015), we can almost ignore their ecological roles in our experiment. Therefore, the water was filtered into a net with a 120 μm mesh, and then concentrated to 10–20 ml and preserved with 4% formaldehyde. Counts were made under a microscope at magnification of 5× (Nikon Corp SMZ645). The biomass of each species was estimated by measuring the length of at least 20 specimens whenever a sufficient number of animals were available. Individual body wet weight (μg) was estimated following the equations from Dumont et al. (1975) and Zhang and Huang (1991).

**Data analysis**

We carried out statistical analyses of stable-isotope data using the ‘SIAR’ package (Parnell et al. 2010; Parnell and Jackson 2013) in the R language environment. The Bayesian mixing model uses standard Markov Chain Monte Carlo fitting algorithms and Dirichlet prior distributions to estimate the posterior distribution of proportional dietary intake for consumers (Parnell et al. 2010). For the SIAR mixing model, we produced a source table of \( \delta^{13}\text{C} \) and \( \delta^{15}\text{N} \) in cPOM, fPOM, zooplankton and pollen (mean and standard deviation). The consumer table included all sampled individuals of \( \delta^{13}\text{C} \) and \( \delta^{15}\text{N} \) in SC and BC, using Group 1 and Group 2 as replacements. Trophic enrichment factors of 0.8 ± 0.5% for carbon and 3.4 ± 1% were used for nitrogen as correlations for both carp species (Post 2002). Consequently, we launched two ‘SIAR’ models using SIAR matrix plots and correlation values to identify the contributions from four food sources separately for the two
reservoirs. We assessed the percentage contribution from each food source of both carps by running the model.

To quantify the extent of isotope niche overlap between the two fish, we used the SIBER approach available in SIAR, which is built on Layman metrics and computes the standard ellipse area (SEA). The SEA, reflecting the mean core population isotope niche, was used to evaluate the isotope niche breadth of SC and BC. The SEA is calculated based on the δ¹³C and δ¹⁵N values and contains about 40% of the data, which reveals the core niche area (Jackson et al. 2011). Moreover, the corrected standard ellipse area (SEAC) was used to estimate the fish niche overlap, following a Bayesian approach to estimate a 95% confidence interval (Jackson et al. 2011). Explicitly, SEAC = SEA × (n − 1)/(n − 2).

The differences in the nutrient concentrations, Chl-a concentration, zooplankton biomass and SI values between the two reservoirs were tested by one-way non-parametric analyses of variance (NPANOVA). The assumed significance level was α = 0.05. The statistical analyses were run with SPSS (SPSS for Windows, version 24.0).

Results

Both reservoirs were meso-eutrophic according to the TN, TP, SD and Chl-a concentrations (Table 1). Our results showed that no significant differences were observed in TN, TP, SD and Chla (NPANOVA, p > 0.05), compared to those in the Nianyushan Reservoir.

No differences in the body length of the SC and BC samples between the two reservoirs were found (Table 2, NPANOVA, p > 0.05). In the Nanwan Reservoir, the biomass ratio between SC and BC was 1:3, and the total fish density was 5.7 g/m³, estimated from reservoir volume and fish harvests during 2011–2015. The biomass ratio between SC and BC was 1:2, and total fish density was 6.2 g/m³ in the Nianyushan Reservoir. The actual isotope values of the four food sources are shown in Table 3. The δ¹³C and δ¹⁵N of each food source and two carp species were presented separately on isotopic biplots from the two reservoirs (Figure 2(a,b)). When comparing the same species in the different reservoirs, the SC in the Nanwan Reservoir showed significantly lower δ¹³C values than those in the Nianyushan Reservoir (NPANOVA, SC: p = 0.003; BC: p = 0.115).

### Table 2. Biomass density and total body length of two carp species (Silver carp: SC, Bighead carp: BC) sampled from two reservoirs.

| Reservoir     | SC:BC stocking ratio | Total density (g/m³) | Fish species | Sample amount (ind.) | Total length range (cm) | Mean length (cm) |
|---------------|-----------------------|----------------------|--------------|----------------------|-------------------------|------------------|
| Nanwan        | 1:3                   | 5.7                  | SC           | 24                   | 52.1–68.5               | 61.9             |
|               |                       |                      | BC           | 24                   | 50.8–74.6               | 67.0             |
| Nianyushan    | 1:2                   | 6.2                  | SC           | 24                   | 42.4–63.6               | 55.7             |
|               |                       |                      | BC           | 24                   | 40.1–61.7               | 58.4             |

### Table 3. Mean and standard deviation of stable isotopes of four food sources. cPOM: coarse particulate organic matter, fPOM: fine particulate organic matter, Zoopl: zooplankton, and pollen: pollen of *Pinus massoniana*.

| Stable isotope | Nanwan δ¹³C (%) | Nanwan δ¹⁵N (%) | Nianyushan δ¹³C (%) | Nianyushan δ¹⁵N (%) |
|---------------|----------------|----------------|---------------------|---------------------|
| fPOM          | −26.00 ± 2.12  | 6.76 ± 0.97    | −24.17 ± 0.62       | 6.73 ± 1.00         |
| cPOM          | −26.21 ± 1.68  | 8.48 ± 0.45    | −25.46 ± 1.02       | 7.93 ± 1.27         |
| Zoopl         | −29.75 ± 0.87  | 10.73 ± 1.22   | −27.96 ± 0.78       | 10.67 ± 0.91        |
| pollen        | −25.40 ± 0.44  | 12.24 ± 0.63   | −25.09 ± 0.84       | 12.36 ± 0.63        |
comparing the different species in a single reservoir, the $\delta^{15}$N in the BC showed significantly higher than those in the SC in both of the reservoirs (NPANOVA, Nanwan: $p = 0.003$, Nianyushan: $p = 0.005$). Higher $\delta^{15}$N in BC than those of SC, displaying a higher trophic position in the food web. Meantime, the muscle $\delta^{15}$N values of SC and BC
were 2.97‰ and 4.59‰ higher than those in cPOM in the Nanwan Reservoir, and were 2.92‰ and 4.28‰ higher than those in cPOM in the Nianyushan Reservoir.

Box plots based on the Bayesian mixing model showed that fish had similar diet compositions in the two reservoirs (Figure 3). In the Nanwan Reservoir, fPOM, cPOM, zooplankton and pollen constituted 46.7, 24.5, 23.2 and 5.5% for the SC diet, and 49.1, 31.5, 11.6 and 7.7% for the BC diet, respectively (Figure 3(a,b)). In the Nianyushan Reservoir, the four food sources contributed 48.0, 34.8, 11.1 and 6.0% for the SC diet, and 32.9, 47.3, 17.5 and 2.4% for the BC diet, respectively (Figure 3(c,d)). SC showed a higher proportional contribution from fPOM (the lowest δ¹⁵N in the four food sources) than that of BC in both reservoirs, corresponding to the lower trophic position of SC in the food web.

Corrected standard ellipse areas (SEAₜ) for SC and BC showed different isotopic niche overlaps in the two reservoirs (Figure 4). The isotope niche overlaps were 22.8% of SEAₜ for SC and 23.1% for BC in the Nanwan Reservoir, and were 22.3% for SC and 62.2% for BC in the Nianyushan Reservoir. Niche breadths represented by SEAₜ were same in the SC and BC in the Nanwan Reservoir (SEAₜ for SC: 6.1, SEAₜ for BC: 6.1), but were much larger for silver carp in the Nianyushan Reservoir (SEAₜ for SC: 11.6, SEAₜ for BC: 4.2).

Seasonal data showed that no significant difference in the Chl-a concentration between the two reservoirs was found (Figure 5, NPANOVA, $p = 0.483$). However, compared to

Figure 3. Proportional contribution from fine particulate organic matter (fPOM), coarse particulate organic matter (cPOM), zooplankton (Zoopl) and pollen of Pinus massoniana to the diet of silver carp (SC) and bighead carp (BC) in the two reservoirs (Nanwan and Nianyushan). Box levels show 50, 75 and 95% confidence intervals.
Figure 4. Isotope niche breadths marked with corrected standard ellipse areas (SEAC) for the silver carp (SC with black circles) and bighead carp (BC with red circles).

Figure 5. Seasonal data of chla concentration and zooplankton biomass (mean ± SD) in the Nanwan (a) and Nianyushan (b) reservoirs. Zoo:Chla ratio: ratio of zooplankton biomass to chla concentration.
the Nianyushan Reservoir, the zooplankton biomass was significantly higher in the Nanwan Reservoir (NPANOVA, \( p = 0.048 \)), leading to a ratio of zooplankton biomass to Chla concentration (zoo:chla ratio), which were also significantly higher (NPANOVA, \( p = 0.024 \)), especially in the season of spring.

Discussion

Diet of SC and BC

Zhou et al. (2009) observed ontogenetic changes in the isotopic values of SC and BC, which indicates that the changes in SI values stabilized when the fishes grew to >40 cm. All sampled fishes in our study were >40 cm, and no significant changes in SI values were observed for different fish lengths. Hence, for fish >40 cm, muscle tissue SI values can better represent their long dietary periods.

Jayasinghe et al. (2015) indicated that SC is more likely a phytoplankton feeder, while BC is more likely a zooplankton feeder. However, the categories that we used to classify food types would not result in either a phytoplankton-only feeder or zooplankton-only feeder, because both plankton types consisted of species with a wider range in body sizes. Our results showed that SC was more like an fPOM feeder, while BC consumed more cPOM than SC did. In the meso-eutrophic environment, we suggested that fine particles were significant to the diet of SC, while coarse particles were important to the diet of BC. Actually, SC has a more specialized filtering structure, with gill rakers fused, forming a sponge-like filter capable of retaining particles as small as 4.5–10 \( \mu \)m (Xie 1999). In contrast, BC usually filters much larger particles (>10 \( \mu \)m) (Cremer and Smitherman 1980). In fact, most of the previous researches were carried out in eutrophic environments for bio-manipulation (Ke et al. 2008; Chen et al. 2011). Ke et al. (2008) cultured silver and bighead carps in large fish pens to reduce the risks of cyanobacterial bloom outbreaks in Meiliang Bay, Lake Taihu; Both carps fed mainly on zooplankton (>50%) in 2004 when competition was low; they selected more phytoplankton in 2005 when competition was high; silver carp had a broader diet breadth than did bighead carp. Chen et al. (2011) pointed out that the degree of the niche overlap between silver carp and bighead carp varied according to the trophic states; phytoplankton is the dominant dietary component for silver carp in the eutrophic Moyangjiang River. Actually, in oligotrophic or meso-eutrophic environments with fewer amounts of food resources, carps tend to prefer smaller food sizes.

Trophic niche partitioning

Carbon isotopes are typically used to identify the energy flow from resources to consumers (Fry 1991; Gu et al. 1994). Our results showed that the difference in \( \delta^{13}C \) between SC and BC was smaller than expected in the food resource (0.8 ‰) in one trophic level, indicating that these filter-feeding fishes shared similar food sources from the pelagic food web (Post 2002). However, compared to BC, SC was depleted in \( \delta^{13}C \) by 0.69 ‰ in the Nanwan Reservoir, yet it was enriched by 0.5 ‰ in the Nianyushan Reservoir, reflecting the differential fractionation during the uptake of dissolved inorganic carbon between the two reservoirs.

Nitrogen isotopes are useful in defining trophic levels (Montoya et al. 1990; Toda and Wada 1990; Wada et al. 1991; Gu et al. 1994). In our study, the mean value of \( \delta^{15}N \) of BC was 1.63 ‰ higher than of SC in the Nanwan Reservoir and was 1.36 ‰ higher than
that of SC in the Nianyushan Reservoir, which suggests that BC selectively fed on an isotopically heavier portion of the food resources than the SC in the both reservoirs. The evidence from estimated proportional contributions of food sources also supported this conclusion. Relative to SC, BC fed more on cPOM or zooplankton, which was isotopically heavier than that of fPOM.

Resources utilization and coexistence

Trophic niche overlap can be used to predict the pressure of resource utilization (Chase and Leibold 2003; Corrêa et al. 2011). Our results indicated that both carp species remained in similar trophic positions but had different niche overlaps between the two reservoirs. BC occupied a larger isotopic niche overlap (62.2%) in the Nianyushan Reservoir than in the Nanwan Reservoir (23.1%), which indicates that the BC had stronger pressure from resources utilization in the Nianyushan Reservoir. Actually, the low standing stock of zooplankton in the Nianyushan Reservoir inferred that predation pressure from fish to zooplankton was stronger. Under intense resource completion, it is possible that BC shifted its food resources from larger particles like zooplankton to smaller cPOM, leading to a larger niche overlap. Previous literatures also have pointed out that when zooplankton availability decreased, energy reliance could be shifted from zooplankton to phytoplankton or detritus (Gu et al. 1996b; Xu and Xie 2004, Zhou et al. 2009).

Although both species utilize the suspending particle resources, they can coexist by regulating their proportions of these particles and the trophic level. Jayasinghe et al. (2015) pointed out that co-occurring SC and BC showed similar food preference but a different isotopic niche overlap in different lakes with variation of resource availability. In our study, we found that in order to coexist, BC occupied a larger isotopic niche overlap in the Nianyushan Reservoir in our study, possibly because they had to live when differences in relative survival ability were small. Bulleri et al. (2016) also found that for two species with small differences in survival ability, greater niche overlapping due to facilitation (i.e. reduced niche differences) may not cause competitive exclusion.

Trophic niche breadth and fish stocking ratio

Niche breadth is an important concept for understanding adaptation and is relevant to many ecological issues, including niche evolution and ecological specialization (Sexton et al. 2017). Available literatures suggested that the niche breadths of the two carp species were always compared within a single water body (Radke and Kahl 2002; Papoulias et al. 2006; Chen et al. 2007). We compared two deep mesotrophic reservoirs where fish freely foraged within closed geographical regions and in the same time scale. Our results showed that the niche breadth represented by SEA_c for SC became wider in the Nianyushan Reservoir. We hypothesized that the increased biomass stocking of the SC:BC ratio was responsible for this result, suggesting that the silver carp could become more competitive with a higher biomass ratio. Rocha et al. (2018) also found that the local abundance was strongly correlated to niche breadth, and species with high abundance could consume widespread resources and occupy a wide niche breadth. However, little studies using stable isotopes have compared the different responses to stocking fish ratio in freshwater ecosystems. Additional data of trophic niche and overlap under different stocking ratio conditions between the two fish are needed to verify this hypothesis. This study provides important insights into the trophic niches of the two major carps. According to our
results, we propose that SC:BC ratio is meaningful in resource utilization and particle size to some extent.

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