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Growth and food availability of silver and bighead carps: evidence from stable isotope and gut content analysis

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Abstract

A 2-year investigation of growth and food availability of silver carp and bighead was carried out using stable isotope and gut content analysis in a large pen in Meiliang Bay of Lake Taihu, China. Both silver carp and bighead exhibited significantly higher $\delta^{13}C$ in 2005 than in 2004, which can probably be attributed to two factors: (i) the difference between isotopic compositions at the base of the pelagic food web and (ii) the difference between the compositions of prey items and stable isotopes. The significantly positive correlations between body length, body weight and stable isotope ratios indicated that isotopic changes in silver carp and bighead resulted from the accumulation of biomass concomitant with rapid growth. Because of the drastic decrease in zooplankton in the diet in 2005, silver carp and bighead grew faster in 2004 than in 2005. Bighead carp showed a lower trophic level than silver carp in 2005 as indicated by stable nitrogen isotope ratios, which was possibly explained by the interspecific difference between the prey species and the food quality of silver carp and bighead.

Keywords: silver carp, bighead carp, stable isotope, gut content, growth, food availability

Introduction

Understanding trophic relationships is fundamental to investigations of ecosystem processes. However, it is difficult to determine such relationships in the natural environment (Polis & Winemiller 1996). A case in point is the aquatic environment, which limits the number of techniques available to aquatic ecologists and makes accurate evaluations on predator–prey relationships difficulty (Hobson & Welch 1995). Traditionally, investigations of predator–prey relationships have relied on gut content analysis (Hysop 1980). Gut content analysis allows the gut contents of a predator to be quantified in terms of specific taxa ingested, but not necessarily assimilated (Grey, Thackeray, Jones & Shine 2002). Stable isotope analysis is another technique to study the trophic relationships in aquatic food webs, which can provide a reflection of an organism's assimilated feeding history integrated over time rather than a snapshot of recently ingested material (Michener & Schell 1994; Richoux & Froneman 2007). Stable nitrogen isotopes ($\delta^{15}N$) usually generate a progressive enrichment of approximately 3–4‰ from prey to predator (Minagawa & Wada 1984; Fry 1988; Post 2002), and hence $\delta^{15}N$ has been used to define the trophic levels in food webs (Fry 1991). Stable carbon isotope ($\delta^{13}C$) also produces a trophic enrichment (0–1‰) for clarifying carbon sources in aquatic ecosystems and tracing carbon flow from primary producers to top consumers (Vizzini, Sara, Michener & Mazzola 2002; Persic, Roche & Ramade 2004). The two techniques are interdependent, each providing a level of resolution that cannot be easily achieved by the other.

All living organisms in an ecosystem occupy their specific levels of stable isotope ratios because a consu-

mer's tissue reflects the composition of its diet (DeNiro & Epstein 1978; Watanabe, Seikai & Tominaga 2005). When a consumer modifies its feeding habit and utilizes food sources with different isotopic compositions from previous intake, it progressively equilibrates with new isotopic signatures being integrated into its tissues (Riera, Montagna, Kalke & Richard 2000). Such modification results from two simultaneous processes: (i) a progressive dilution of the 'older' isotopic signature due to the growth of new tissue and (ii) a loss of an 'older' isotopic signature due to the metabolic turnover of the tissues (Anderson, Parker & Lawrence 1987). Tissue turnover in juvenile and adult animals is primarily a function of weight gain and time respectively (Fry & Arnold 1982). Watanabe *et al.* (2005) have indicated the dependence of $\delta^{13}C$ change on the growth rate [for total length (TL) and body weight (BW)]. Layman, Winemiller, Arrington and Jepsen (2005) have also shown that body size is necessarily correlated with trophic position for any given food chain within a complex web where predators are larger than their prey.

Silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*) are planktivorous fish. They have been cultured worldwide because of their excellent biological characteristics (Dong, Li, Bing, Shi & Wang 1992). In recent decades, silver carp and bighead have received considerable attention to deal with nuisance phytoplankton blooms (Xie 1996; Fukushima, Takamura, Sun, Nakagawa, Matsushige & Xie 1999; Turker, Eversole & Brune 2003). Their feeding habits have been the focus of numerous studies, primarily using gut content analysis (Nie & Chiang 1954), with silver carp mainly feeding on phytoplankton and bighead carp on zooplankton (Nie & Chiang 1954; Cremer & Smitherman 1980). Only a few studies on silver carp and bighead have relied on the utilization of stable isotope analyses, including short-term investigations of stable isotopes on dietary overlap in ponds (Gu, Schell, Huang & Yie 1996) and carbon sources and trophic relationships in lake (Xu & Xie 2004). However, under field conditions, plankton biomass and community may vary due to grazing by filter-feeding fish (Domaizon & Devaux 1999; Fukushima *et al.* 1999). Temporal variations may occur in the prey composition of silver carp and bighead, which can progressively influence the isotopic composition of silver carp and bighead. Hence, temporal-scale dynamics based on both stable isotope and gut content analysis is necessary to evaluate the growth and food utilization of silver carp and bighead that are cultured in the pen.

The main objectives of the present study were to: (i) determine the potential relationship between growth (TL and BW) and isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of silver carp and bighead; and (ii) discuss the mechanism of isotopic changes underlying food availability; (iii) assess the interspecific differences between silver carp and bighead in feeding strategy and trophic level.

Materials and methods

Study area and sampling

The fish pen (surface area 1.035 km^2) was located near the bank of Meiliang Bay, Lake Taihu, where heavy cyanobacterial blooms (mainly Microsystis, Spirulina, Oscillatoria in 2004 and Microsystis in 2005 respectively) occurred in the warm seasons. This bay had a mean water depth of 2.1 m and an average water temperature of 21.3 °C during the experimental study. Fingerlings of similar sizes and weights were stocked into the pen, in order to control heavy cyanobacterial surface blooms. The first batch fingerlings (with an average of 18.4 ± 2.8 cm, 133.3 ± 55.2 g for silver carp and 21.4 ± 1.3 cm, 242.1 ± 44.4 g for bighead carp respectively) were stocked in March 2004 and harvested in December 2004. The second batch fingerlings (with an average of 19.8 ± 3.3 cm, 160 ± 81.3 g for silver carp and 18.5 ± 1.9 cm, 139 ± 43.8 g for bighead carp respectively) were also stocked into the same pen in January 2005 and captured in December 2005. The stocking densities of silver carp and bighead were 0.27 and 0.2 g m^{-3} in 2004 and 7.91 and 3.44 g m^{-3} in 2005 respectively. Fish samples for gut content and stable isotope analysis were collected monthly from April to December in 2004 and 2005. About 30 silver carp and 30 bighead carp were randomly captured from the pen by seine ormulti-mesh gillnets to examine individual growth (BW and TL) on each sampling date. Generally, three to five individuals of each carp were utilized monthly. Stable isotope analysis included the same fish as gut content analysis.

Stable isotope analysis

Dorsal muscle tissues were anatomized from carps. Muscle tissues were roasted at 60 °C to a constant weight and ground to a fine powder using a mortar and pestle. Muscle samples were analysed using a Carlo Erba EA-1110 elemental analyzer (Farmitalia Carlo Erba, Milan, Italy) along with a Delta Plus Finni-

gan isotope ratio mass spectrometer (Thermo-Finnigan, Bremen, Germany) via a continuous flow II interface. Isotopic ratios were expressed relative to international standards (Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen). Delta values were defined as: $\delta R = [(X_{sample} - X_{standard})/X_{standard}] \times 10^3$ (‰), where $R = {}^{13}C$ or ^{15}N, and X is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Analytical deviations for replicates were less than 0.2‰ and 0.3‰ for carbon and nitrogen respectively.

Gut content analysis

To examine food items, both carps were killed and the guts were removed immediately by dissection monthly. Fore-gut contents were collected from the proximate end of the intestine to the middle of the first loop. Food in this part of the intestine was considered to be little digested because this part usually comprises $< 1/12$ of the total intestine length (Xie 1999). Individual samples of gut contents were fixed in Lugol's iodine for a few minutes, and then preserved in 10% formaldehyde solution. In the laboratory, the gut contents were homogenized in cool distilled water with an electronic stirrer for 3–5 min, and then examined under a microscope.

Statistical analysis

The correlations between isotopic compositions ($\delta^{13}C$ and $\delta^{15}N$) and growth coefficients (BW and TL) of silver carp and bighead were determined using SPSS 11.5 version. Pearson's *t*-test was performed to determine whether there were significant differences between the isotopic compositions of silver carp and bighead in 2004 and those in 2005 as well as between the percentage compositions of phytoplankton and zooplankton in the gut of both carps in 2004 and 2005. Moreover, TL and BW of silver carp and bighead in 2004 were compared correspondingly with those in 2005 using Pearson's *t*-test statistical analysis. The correlation was expressed by a *P*-value and an *r*-value, and the difference test by the *P*-value only.

Results

Interannual variations in stable isotopes of silver carp and bighead

Stable isotope ratios of silver carp from April to December in 2004 and 2005 are shown in Fig. 1. Except for the beginning (April and May), $\delta^{15}N$ of silver carp showed a gradual increase and a linear increase in 2004 and 2005 respectively. The $\delta^{15}N$ values of silver carp varied from 7.50‰ (May) to 16.92‰ (October) in 2004 and from 9.60‰ (May) to 18.71‰ (December) in 2005 respectively. $\delta^{13}C$ of silver carps tended to reach an equilibrium following a short-term drastic fluctuation both in 2004 and in 2005. $\delta^{13}C$ of silver carp ranged from − 31.54‰ (April) to − 25.86‰ (September) in 2004 and from − 27.88‰ (May) to − 21.84‰ (April) in 2005 respectively.

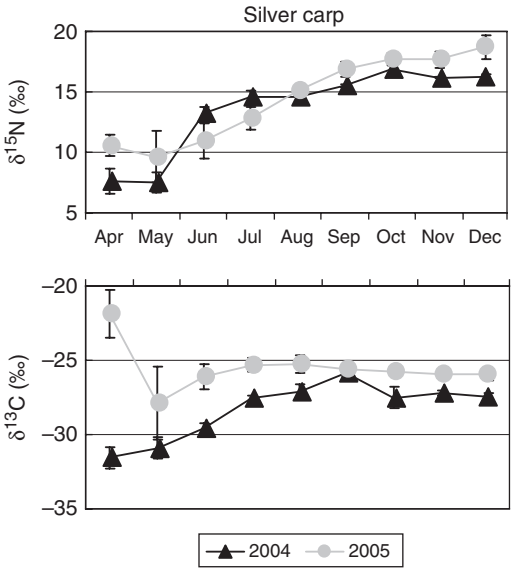

Figure 1 Comparison of stable carbon and nitrogen isotope ratios of silver carp between 2004 and 2005 (means ± 1 SD). Three to five samples were taken monthly for muscle tissue of silver carp from the fish pen. $\delta^{13}C$ of silver carp showed significant difference between 2004 and 2005 ($P < 0.05$). However, there was no significant difference between $\delta^{15}N$ of silver carp in 2004 and 2005 ($P = 0.204$).

For bighead carp, $\delta^{15}N$ ranged between 6.40‰ (April) and 17.91‰ (October) in 2004 and between 7.65‰ (April) and 16.88‰ (December) in 2005 (Fig. 2). $\delta^{13}C$ of bighead carp ranged from − 31.68‰ (April) to − 26.70‰ (October) in 2004 and from − 29.76‰ (May) to − 25.59‰ (September) in 2005. There were more lower values of $\delta^{13}C$ in 2004 than in 2005 during the experimental period.

Growth

The total length and BW of silver carp and bighead in 2004 were compared with those in 2005 (Fig. 3). The total lengths of both carps indicated higher values in

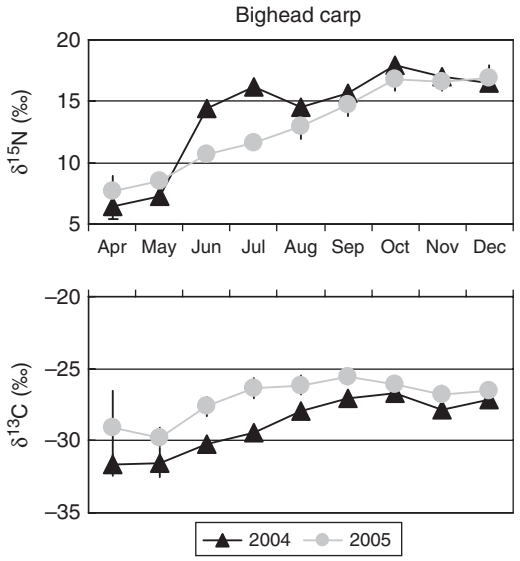

Figure 2 Comparison of stable carbon and nitrogen isotope ratios of bighead carp between 2004 and 2005 (means ± 1 SD). Three to five samples were taken monthly for muscle tissue of silver carp from the fish pen. Significant difference was found between $\delta^{13}C$ of bighead carps in 2004 and 2005 ($P < 0.01$). However, there was no significant difference between $\delta^{15}N$ of bighead carps in 2004 and 2005 ($P = 0.157$).

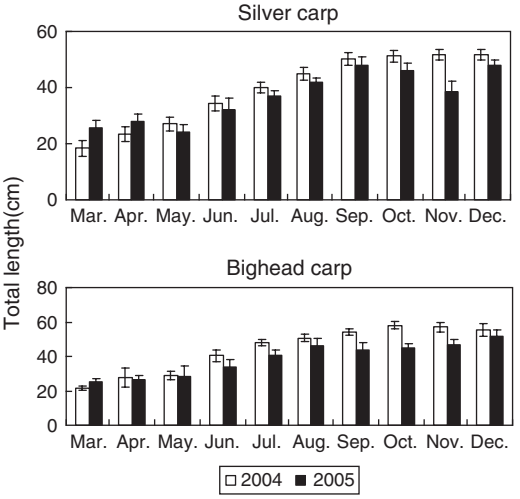

Figure 3 Comparison between the total length of silver carp and bighead in 2004 and that in 2005 ($n = 30$). Total length of silver carp showed no significant difference between 2004 and 2005 ($P = 0.194$). However, significant difference was found between total length of bighead carp in 2004 and 2005 ($P < 0.05$).

2004 than in 2005. Body weights of both carps showed a significant difference between 2004 and 2005 ($P < 0.05$ for both silver carp and bighead).

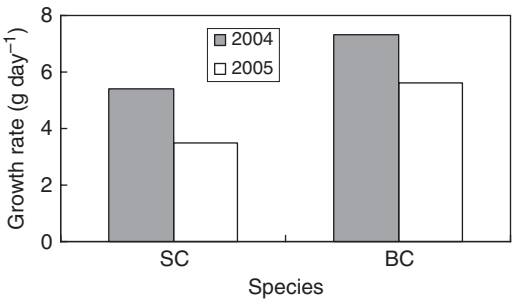

Figure 4 The average growth rates of silver carp and bighead in 2004 and 2005. 'SC' and 'BC' mean 'Silver carp' and 'Bighead carp' respectively.

Table 1 The correlations between growth coefficients (body weight and total length) and stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of filter-feeding fishes with SPSS 11.5 statistical software

	Body weight (g)	Total length (cm)
2004		
SC		
$\delta^{13}C$ (‰)	$R = 0.613$ ($n = 48$)**	$R = 0.724$ ($n = 48$)**
$\delta^{15}N$ (‰)	$R = 0.788$ ($n = 62$)**	$R = 0.903$ ($n = 62$)**
BC		
$\delta^{13}C$ (‰)	$R = 0.689$ ($n = 35$)**	$R = 0.817$ ($n = 35$)**
$\delta^{15}N$ (‰)	$R = 0.692$ ($n = 46$)**	$R = 0.810$ ($n = 46$)**
2005		
SC		
$\delta^{13}C$ (‰)	$P > 0.05$	$P > 0.05$
$\delta^{15}N$ (‰)	$R = 0.911$ ($n = 47$)**	$R = 0.904$ ($n = 47$)**
BC		
$\delta^{13}C$ (‰)	$P > 0.05$	$P > 0.05$
$\delta^{15}N$ (‰)	$R = 0.652$ ($n = 45$)**	$R = 0.664$ ($n = 45$)**

'SC' and 'BC' represent silver carp and bighead carp respectively.
**$P < 0.01$.

Based on the values of BW, the growth rates of both carps were evaluated. The average growth rates of silver carp and bighead were 5.4 and 7.3 g day^{-1} in 2004 and 3.5 and 5.6 g day^{-1} in 2005 respectively. The growth rates of both carps were higher in 2004 than in 2005 ($P < 0.05$ for both carps) (Fig. 4).

The correlations between growth parameters (BW and TL) and stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of silver carp and bighead are shown in Table 1.

Gut content analyses

The dietary compositions of silver carp and bighead were analysed monthly with a microscopic observation from April to December in 2004 and 2005 (Figs 5 and 6). The gut contents of silver carp and bighead were composed of phytoplankton and

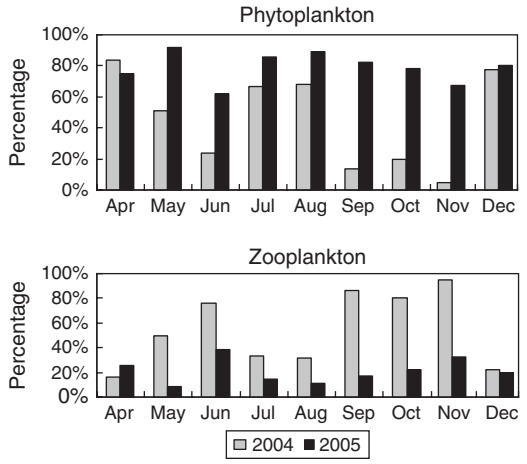

Figure 5 Percentage compositions of phytoplankton and zooplankton in the guts of silver carp from April to December in 2004 and 2005. Data in 2005 was from Ke, Xie, Guo, Liu and Yang (2007).

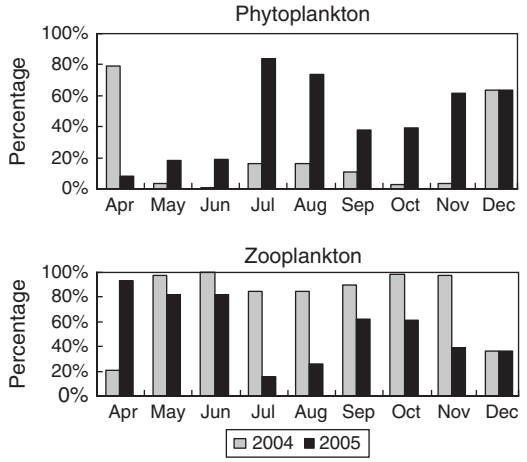

Figure 6 Percentage compositions of phytoplankton and zooplankton in the gut of bighead carp from April to December in 2004 and 2005. Data in 2005 was from Ke *et al.* (2007).

zooplankton, and the percentage compositions of phytoplankton and zooplankton were calculated according to their biomass. The percentage of phytoplankton in the gut contents ranged from 4.8% (November) to 83.9%(April) in 2004 and from 61.6%(June) to 91.6%(May) in 2005 for silver carp, and from 0.7%(June) to 79.6%(April) in 2004 and from 7.9% (April) to 84.6% (July) in 2005 for bighead carp. The average percentages of phytoplankton in the guts of silver carp and bighead were 45.4% ($n = 9$) and 21.8% ($n = 9$), respectively, in 2004 and 79.0% ($n = 9$) and 45.3% ($n = 9$), respectively, in 2005. The gut contents of silver carp showed a higher phytoplankton percentage in 2005 than in 2004, except for the first (April) of the experimental period. Furthermore, there was a significant difference in the phytoplankton percentage in the gut of silver carp between 2004 and 2005 ($P < 0.01$). For bighead carp, there was no significant difference in the phytoplankton percentage in the gut of bighead carp between 2004 and 2005 ($P = 0.134$).

Gut content analysis indicated that the contributions of zooplankton to the diets of silver carp and bighead were 54.6% ($n = 9$) and 78.2% ($n = 9$), respectively, in 2004. However, the contributions of zooplankton to the diets of silver carp and bighead were 21.0% ($n = 9$) and 54.7% ($n = 9$), respectively, in 2005. Consequently, compared with that in 2004, the percentage composition of zooplankton in the diet in 2005 decreased by 33.6% and 23.5% for silver carp and bighead carp respectively.

Table 2 Average $\delta^{13}C$ and $\delta^{15}N$ values of silver carp and bighead in 2004 and 2005 (mean ± 1SD)

	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
2004		
SC	− 28.30 ± 1.89 ($n = 27$)	13.73 ± 3.33 ($n = 40$)
BC	− 28.55 ± 1.85 ($n = 23$)	14.81 ± 3.31 ($n = 32$)
2005		
SC	− 25.55 ± 1.93 ($n = 42$)	14.18 ± 3.55 ($n = 41$)
BC	− 27.01 ± 1.53 ($n = 38$)	13.07 ± 3.42 ($n = 38$)

'SC' and 'BC' mean 'Silver carp' and 'Bighead carp' respectively. '*n*' represents 'number of samples'. $\delta^{15}N$ of both carps indicated no significant difference between 2004 and 2005 ($P = 0.204$ and $P = 0.157$ for silver carp and bighead carp respectively). Contrarily, significant difference was found between $\delta^{13}C$ of both carps in 2004 and 2005 ($P < 0.05$ and $P < 0.01$ for silver carp and bighead carp respectively).

Interspecific comparison between $\delta^{15}N$ of silver carp and bighead

The interspecific difference between $\delta^{15}N$ of silver carp and bighead was evaluated monthly in 2004 and 2005 (Fig. 7). In 2004, silver carp showed a higher $\delta^{15}N$ in the initial stages (April and May) and thereafter lower $\delta^{15}N$ than bighead carp. Silver carp showed higher $\delta^{15}N$ than bighead carp throughout the study period in 2005.

Discussion

The $\delta^{13}C$ and $\delta^{15}N$ values of silver carp and bighead exhibited obvious temporal variations in 2004 and

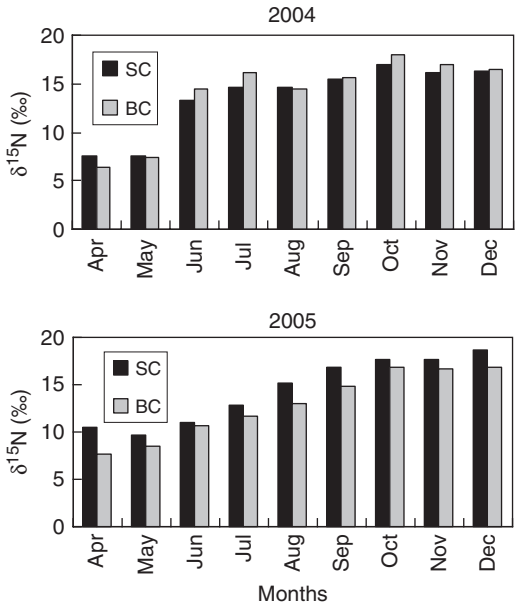

Figure 7 Interspecific comparison of δ^{15}N between silver carp and bighead in 2004 and 2005. No significant difference was found between δ^{15}N of silver carp and bighead in 2004 ($P = 0.213$). However, there was significant difference between δ^{15}N of silver carp and bighead in 2005 ($P < 0.01$).

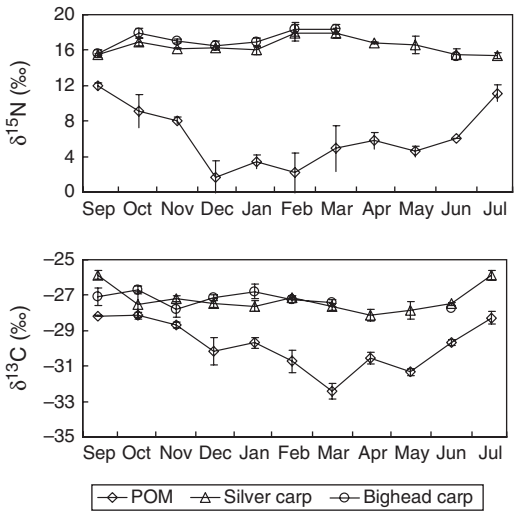

Figure 8 Seasonal variations of δ^{13}C and δ^{15}N in POM and muscle tissues of silver carp and bighead in the fish pen from September 2004 to July 2005 (mean ± 1 SD). Generally, three samples were taken monthly for POM and muscle tissues of silver carp and bighead in the fish pen. Significant correlation was found between δ^{13}C of POM and muscle tissue of silver carp ($P < 0.05$). Data of δ^{13}C and δ^{15}N for POM, silver carp and bighead were cited from Zhou *et al.* 2008.

2005. Stable isotope changes in consumers can result from the trophic level at which they feed, as well as from temporal changes in the isotopic composition at the base of the food web that are transferred through the food web (e.g., Peterson & Fry 1987; Wainright, Fogarty, Greenfield & Fry 1993). Growth and metabolic turnover have been reported to induce changes in stable isotopes in aquatic consumers (e.g., Fry & Arnold 1982; Maruyama, Yamada, Rusuwa & Yuma 2001). Furthermore, stable isotopes of consumers may vary due to an ontogenetic dietary shift (Witting, Chambers, Bosley & Wainright 2004; Xu, Zhang & Xie 2007).

POM showed seasonal variations in isotopic signatures similar to those of silver carp and bighead, and POM δ^{13}C was positively correlated to that of silver carp (Fig. 8), suggesting that the temporal variation in the stable isotope signatures of POM was transferred to that of silver carp via the food chain (Zhou, Xie, Xu, Ke, Guo & Cao 2008). Based on gut content analysis, both silver carp and bighead fed on phytoplankton and zooplankton. Moreover, fries of silver carp have already finished their diet shift during the larval stage, and have feeding habits similar to those of adult fish (Feng & Zhou 1995), suggesting that both silver carp and bighead rely on plankton production and may not shift their diet from planktivores to other trophic types. Although phytoplankton and zooplankton were the only two prey items in the guts of silver carp and bighead, the percentage compositions of food items showed obvious seasonal variations in 2004 and 2005. Phytoplankton and zooplankton exhibited different stable isotope signatures (Table 3) and fluctuated seasonally in Meiliang Bay, Lake Taihu (Zhou *et al.* 2008), and hence the diet that comprised different percentage compositions of phytoplankton and zooplankton represented distinct isotopic compositions, which can result in changes in the isotopic compositions of silver carp and bighead through diet-tissue fractionation. In addition, the present study showed significant relations between growth parameters and stable isotopes of silver carp and bighead, suggesting that growth could lead to stable isotope changes in silver carp and bighead. Consequently, the δ^{13}C and δ^{15}N changes in silver carp and bighead between the years 2004 and 2005 could probably be attributed to two factors: (i) the difference between isotopic compositions at the base of the pelagic food web (generally speaking, phytoplankton) and (ii) the difference between the compositions of prey items and stable isotopes.

Table 3 Average $\delta^{13}C$ and $\delta^{15}N$ signatures of POM, zooplankton (ZP) and muscle tissues of silver carp (SC) and bighead carp (BH) in the fish pen from July 2004 to December 2005 (mean ± 1SD)

	POM	ZP	SC	BC
$\delta^{13}C$ (‰)	−29.4 ± 1.6 (n = 42)	−27.7 ± 1.1 (n = 3)	−27.9 ± 1.5 (n = 51)	−28.1 ± 1.6 (n = 35)
$\delta^{15}N$ (‰)	7.9 ± 4.5 (n = 42)	14.9 ± 4.2 (n = 3)	16.5 ± 1.3 (n = 54)	16.8 ± 1.3 (n = 38)

'n' represents the number of samples analysed. Data of isotopic compositions for POM, zooplankton and silver and bighead carps were cited from Zhou *et al.* 2008.

Comparison of the TL and the growth rate of both carps in 2 consecutive study years indicated faster growth of silver carp and bighead in 2004 than in 2005. Previous studies reported that silver carp primarily fed on phytoplankton and bighead carp on zooplankton (Nie & Chiang 1954; Cremer & Smitherman 1980). However, algae have a low nutritional benefit and remain undigested during incubation in the gut fluid of stomachless fish like silver carp and bighead (Bitterlich & Gnaiger 1984). Zooplankton is a more valuable nutrient source due to its high protein content and rapid digestibility for silver carp and bighead (Bitterlich 1985). In the present study, gut content analyses indicated that silver carp and bighead fed mainly on zooplankton in 2004. This indicates that nutrition for the growth of silver carp and bighead primarily relied on zooplankton rather than phytoplankton. Furthermore, the percentage composition of zooplankton in the diet of silver carp and bighead decreased by 33.6% and 23.5%, respectively, in 2005 compared with that in 2004, implying a drastic decrease in the protein source from zooplankton, which was in agreement with the fact that silver carp and bighead showed slower growth in 2005 than in 2004. Consequently, the decrease in zooplankton biomass in the guts of silver carp and bighead could be responsible for the slower growth of both carps in 2005.

The significantly positive correlations between growth coefficients (BW and TL) and stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) indicated the close linkage between growth and isotope variations of two filter-feeding fish. Growth is mainly an increase in the protein mass at a given time interval (Conceicao, Houlihan & Verreth 1997). Peragon, Barroso, Higuera and Lupianez (1998) also suggested that liver growth was characterized by a linear increase in protein. In addition, the enrichment between the consumer and the diet resulted typically from the preferential excretion of the lighter ^{14}N as a by-product of protein synthesis and the relative enrichment of consumer's ^{15}N compared with the diet (Richoux & Froneman 2007). Consequently, variations in $\delta^{13}C$ and $\delta^{15}N$ could be attributed to the accumulation of biomass concomitant with the rapid growth of silver carp and bighead in the juvenile stage.

Both silver carp and bighead showed enriched ^{13}C in 2005 than in 2004. Moreover, there was a significant difference between the $\delta^{13}C$ values in 2004 and those in 2005. Firstly, there was a difference between the isotopic compositions at the base of the pelagic food web (Zhou *et al.* 2008). This difference could be transferred to silver carp and bighead via the food chain. On the other hand, prey items and the corresponding isotopic compositions should also be taken into account. Gut content analyses indicated that, in 2004, both silver carp and bighead tended to preferentially utilize zooplankton. However, an obvious increase in phytoplankton biomass was found in the guts of both silver carp and bighead in 2005. Different percentage compositions of phytoplankton and zooplankton implied a difference in the isotopic compositions of the diet, which can be transferred to silver carp and bighead through stable isotope fractionation.

$\delta^{13}C$ of seston (phytoplankton), zooplankton and muscle tissue of silver carp and bighead yielded very little difference (0.2–1.7‰), indicating that silver carp and bighead fed on both phytoplankton and zooplankton (Zhou *et al.* 2008). Thus, the trophic level of silver carp was compared frequently with that of bighead carp based on their $\delta^{15}N$ (Gu *et al.* 1996; Xu & Xie 2004). However, there were not enough isotopic data of the basal source (phytoplankton) to evaluate the trophic level of each carp. Still, an interspecific comparison of trophic level can be performed based on their $\delta^{15}N$ because silver carp and bighead shared the same baseline (phytoplankton) each year. Previous studies suggested that bighead carp possessed a higher trophic level than silver carp (Gu *et al.* 1996; Xu & Xie 2004). This conclusion was in agreement with our result in 2004. Nevertheless, in 2005, $\delta^{15}N$ of bighead carp was 1.1‰ lower than that of silver carp, indicating a slightly lower trophic level for bighead carp than silver carp. Gut content analysis indi-

cated that, in 2005, both silver carp and bighead obviously decreased the proportion of zooplankton due to the deficiency in zooplankton.

Firstly, we assumed that the deficiency in zooplankton resulted in a lower trophic level of bighead carp than silver carp in 2005. However, a decrease in zooplankton biomass occurred in both silver carp and bighead. Moreover, silver carp lost more zooplankton than bighead carp in their guts in 2005. On the other hand, zooplankton was the preferential food of both silver carp and bighead, indicating the importance of zooplankton for both silver carp and bighead. If so, a decrease in zooplankton can cause greater collapse in the trophic level of silver carp than bighead carp. Thus, this hypothesis did not work well. Secondly, we assumed that, in 2005, the initial lower $\delta^{15}N$ led to a lower trophic level in bighead carp than in silver carp. In 2004, bighead carp occupied a lower trophic level in April and May and thereafter a higher trophic level than silver carp. This can be explained by the fact that the isotopic ratio of carps gradually reflected that of their diet due to the isotopic turnover associated with fast growth. Likewise, although bighead carp exhibited a lower trophic level than silver carp in April and May in 2005, isotopic turnover driven by fast growth can make isotopic ratios of both carps equal to those of their diet. Moreover, gut content analysis showed that bighead carp fed mainly on zooplankton and ingested more zooplankton biomass than silver carp in 2005. Thus, we can infer that bighead carp should occupy a higher trophic level than silver carp in 2005. However, this conclusion was in contradiction with the current result using stable isotope analysis. Accordingly, this hypothesis was logically unreasonable.

Stable isotope ratios in the proteins of consumers reflected those of the proteins in their diet in a predictable manner (Hobson & Clark 1992; Hobson 1999). Algae were shown to have a low nutritional benefit and remain undigested during incubation in the gut fluid of stomachless fish like silver carp and bighead (Bitterlich & Gnaiger 1984). Although zooplankton was reported to have good digestibility (Bitterlich 1985), some rigid species (e.g., cladoceran) could not be digested easily by stomachless fish (Kajak, Spodniewska & wisniewski 1977). In this case, gut content analysis failed to show the substantial diet assimilated by silver carp and bighead. Furthermore, food quality was reported to influence the isotopic shift between diet and consumer (McCutchan Jr, Lewis, Kendall & McGrath 2003). Silver carp and bighead preferentially selected zooplankton under a condition where food was abundantly available. In contrast, silver carp and bighead lacked a selective strategy and had to feed on food with low digestibility (e.g., phytoplankton) when zooplankton was deficient. Although the biomass of zooplankton was unavailable, we found a higher biomass of phytoplankton in the lake water in 2005 than in 2004 (Fig. 9), suggesting that phytoplankton was more abundant for both carps in 2005 than in 2004. This conclusion supported our results of gut content analyses that both silver carp and bighead increased the biomass of phytoplankton in their diet in 2005 compared with that in 2004. Consequently, the difference in the prey species and food quality may be responsible for the lower trophic level of bighead carp than silver carp in 2005.

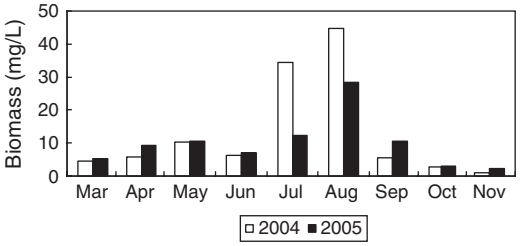

Figure 9 Comparison between biomass of phytoplankton in 2004 and 2005 in the lake water of the fish pen. Biomass of phytoplankton was higher in 2005 than in 2004 except July and August. However, there was no significant difference between biomass of phytoplankton in 2004 and 2005 ($P = 0.38$).

Conclusion

There were probably two factors that could be responsible for the depletion of carp ^{13}C in 2004 than in 2005: (i) the difference between isotopic compositions at the base of the pelagic food web (generally speaking, phytoplankton) and (ii) the difference between the compositions of prey items and stable isotopes. Different growth patterns of silver and bighead carps in 2 consecutive study years could be attributed to the deficiency in the zooplankton percentage in their guts in 2005 compared with that in 2004. Based on two possible presumptions, the difference in prey species and food quality possibly induced an interspecific variance in the annual trophic level of silver carp and bighead.

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