

Food sources contributing to the diet of common and crucian carps in a shallow, temperate, eutrophic lake

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Abstract

We determined the carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in the tissues of three omnivorous cyprinid species: the common carp *Cyprinus carpio*, the silver crucian carp *Carassius* sp. and the Japanese crucian carp *Car. cuvier* collected from a shallow, temperate, eutrophic lake (Izunuma) in Japan. We used Bayesian mixing model to determine the potential contributions of (i) four groups of potential food sources (particulate organic matter [POM], epiphyton + sedimentary organic matter, larval chironomids and the snail) to the diet of common carp, and (ii) five groups of potential sources (the four sources and zooplankton) to the diets of silver crucian and Japanese crucian carps. The isotopic signals suggested that snails were important food sources for carps, but larval chironomids were minor dietary components for these species in this lake. Although Japanese crucian carp is reportedly a phytoplankton feeder, we found that it assimilated snail and zooplankton rather than POM and other food sources. Macroinvertebrates such as snails could be important food sources for carps in shallow water bodies, likely because they were valuable and readily accessible food sources.

Keywords : stable isotope, invasive species, omnivorous fish, benthos

Introduction

Common *Cyprinus carpio* and crucian (*Carassius* complex) carps are widely distributed in Eurasia [Bănărescu & Coad 1991]. Because they are important species for the food and fishing industries, the carps have been introduced to water bodies within and outside their native ranges [Taniguchi 2001; Jang et al., 2002; Zambrano et al., 2006; Tarkan et al., 2012]. Carps could have negative impacts on native ecosystems and the native fish communities by competing with indigenous species [Zambrano et al. 2010; Tarkan et al. 2012; Córdova-Tapia et al. 2015], elevating water turbidity and reducing the biological diversity of zoobenthos and macrophytes through their feeding activities [Miller & Crowl 2006].

Although common and crucian carps are both omnivorous, they differ in behaviors and morphologies related to feeding [Nakamura, 1969]. For example, common carp and some species of *Carassius* forage

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preferentially on benthic dietary items but *Car. cuvieri*, which has large numbers of gill rakers, is adapted to feeding on phytoplankton [Nakamura 1969]. The opportunistic feeding of carps promotes variability in their selectivity among different food sources in different lakes [e.g. García-Berthou 2001; Kanaya et al. 2009; Jackson et al. 2012]. The negative impacts of common carp on native ecosystems have been well studied [e.g. Zambrano et al. 2010; Córdova-Tapia et al. 2015]. In contrast, less is known about the negative effects of crucian carp, although there has been some theorizing about these possible negative impacts [Richardson et al. 1995; Povž & Šumer 2005]. Therefore, comparative study of the diets of different carp species will help provide an understanding of the possible negative impacts of these species on native communities.

Previous studies based on conventional gut contents analyses have reported that common and crucian carps forage on diverse food sources, such as detritus, plants, algae and invertebrates [Nakamura 1969; García-Berthou 2001; Hosoya 2001; Taniguchi 2001]. However, gut contents give only snapshots of individual diets. The content of a gut may be affected by differential digestibility among food items; the quantity of refractory items may skew estimates of consumption. Carbon and nitrogen stable isotope ratios in animal tissues have been used in dietary studies because they reflect the composition of the assimilated food and provide long-term integration of an animal's feeding history. Although a mixing model has been widely used to estimate the isotopic contribution of each food source to consumer diets [Phillips et al. 2005], application of such a conventional simple mass balance approach to stable isotope ratios has limitations because the number of sources cannot exceed the number of elemental tracers by more than one [Layman et al. 2012]. Consequently, the trophic roles of omnivorous common and crucian carps in lake food webs have not been fully investigated due to their having a large number of potential food sources. Recently, Bayesian mixing models, which enable estimation of the relative contributions of large numbers of resources to consumers, have been applied to dietary studies [Jackson et al. 2012; Lopes et al. 2015].

Common carp and two species of crucian carp (silver crucian carp *Carasius* sp. (*ginbuna* in Japanese) and Japanese crucian carp *Car. cuvieri*) inhabit Lake Izunuma, in northeastern Honshu, Japan [Fujimoto et al. 2008]. Although common carp is native to Japan, populations of the indigenous strain have been negatively impacted by introductions of morphologically similar non-native domestic strains [Mabuchi et al. 2010]. Silver crucian carp of which the taxonomic identity has yet to be ascertained [Nakabō 2013]. Since the native range of silver crucian carp includes Honshu, they are considered to be native to Lake Izunuma. The Japanese crucian carp *Car. cuvieri* is endemic to Lake Biwa, which is the largest lake in west-central Honshu, Japan. This species has been introduced to many lakes and ponds in Japan and in neighboring countries such as Korea for fishing [Taniguchi 2001; Jang et al. 2002]. Lake Izunuma is shallow and relatively small, and may be representative of water bodies into which common and crucian carps are frequently introduced. Thus, Lake Izunuma could be a suitable place in which to study the possible effects

of carps on native communities.

Our objectives were to compare feeding habits of co-occurring carps and to examine whether they have different possible effects on prey organisms in shallow lakes. In this study, we (i) measured the carbon and nitrogen stable isotope ratios in the tissues of three fish species—common carp, and two species of crucian carp (silver crucian carp *Carasius* sp. and Japanese crucian carp *Car. cuvieri*)—and their potential food sources in a temperate eutrophic shallow lake in northern Japan; (ii) estimated the dietary contribution of each food source using the Bayesian mixing model SIAR [R Development Core Team 2009, SIAR; Parnell et al. 2010], and (iii) determined the most important food sources for each fish species.

Materials and methods

Study site: We conducted field surveys in Lake Izunuma, which is in northeastern Honshu, Japan (38°43'N, 141°06'E, Fig. 1). The lake was temperate, eutrophic, shallow (maximum depth: ca. 1.6 m; area: 3.69 km²) and located 6 m above sea level on an alluvial lowland [Shidara, 1992]. Stratification was rare [Yasuno et al. 2012] because the entire water column was frequently overturned by wind forcing. The water surface was sometimes covered by ice during winter. We calculated Carlson's trophic state indices [TSIs; Carlson 1977] from the annual average chlorophyll *a* concentration and Secchi depth and found that the waters were within the range reported for eutrophic lakes [Yasuno et al. 2009]. Benthic algae and submerged plants had restricted distributions, likely due to the high water turbidity. The emergent macrophyte *Nelumbo nucifera*, which has floating leaves, covered 19.4% of the lake area in 2006 [S. Shikano unpublished data]. Other macrophytes with floating leaves, such as *Trapa natans*, *Nymphoides indica*, and *Nym. peltata*, were also found. *Chironomus plumosus* (Chironominae) was the predominant component of the benthic fauna during 2006 to 2008 [152 ± 114 individuals m⁻²; Yasuno et al., 2009]. Common carp (*Cyp. carpio*) and two species of crucian carp (silver crucian carp, *Carassius* sp., and Japanese crucian carp, *Car. cuvieri*) inhabited the lake [Fujimoto et al., 2008].

Sample collection: We collected the snail *Radix auricularia japonica* (n = 3) by hand near the south shore in June 2006 (Fig. 1). We dissected snail and removed a sample of muscle tissue for freeze-drying and subsequent stable isotope analysis.

We collected the three fish species (*Cyp. carpio* (n = 7), *Carassius* sp. (n = 7), *Car. cuvieri* (n = 5)) using gill nets set near the south shore of the lake in the following time periods: May, August–September, and December, 2006 (Fig. 1, Table 1). We measured the total lengths (TL, mm) to the nearest 1 cm in the laboratory. We then dissected each fish and removed a sample of dorsal muscle tissue for freeze-drying and subsequent stable isotope analysis.

To determine stable isotope ratios, we ground freeze-dried samples of all invertebrates and fishes,

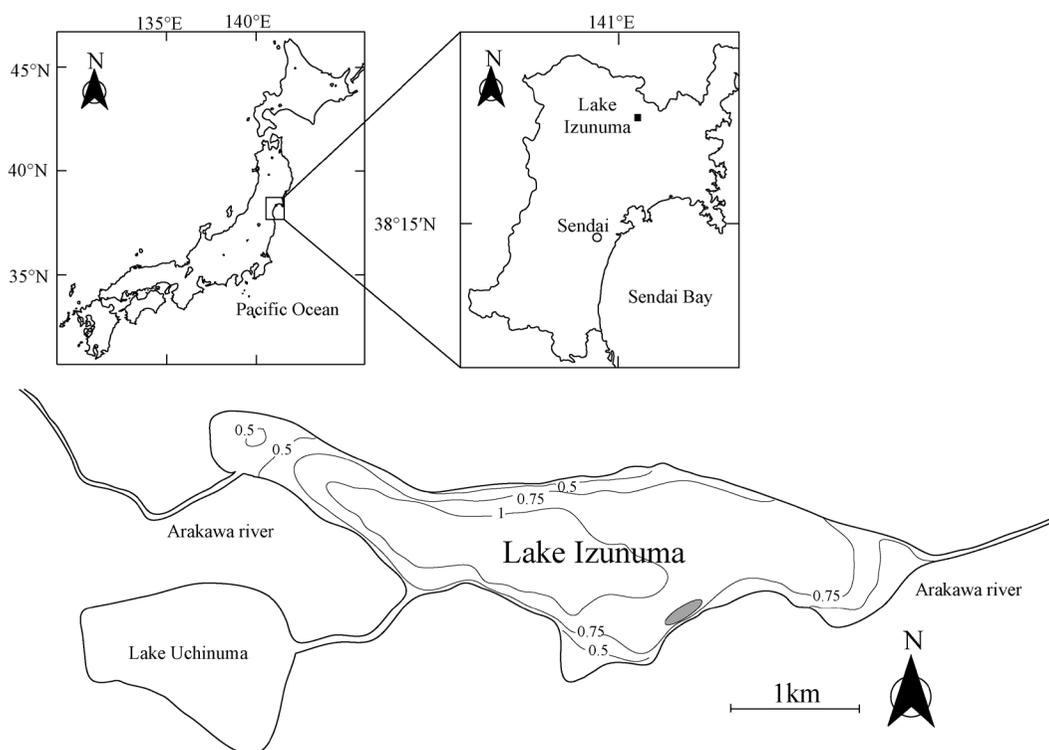


Fig 1 Sampling locations in Lake Izunuma. Solid lines indicate the isobath in meters. Gray area represent the locations where fishes, snails and epiphyton were collected.

homogenized them in a pre-combusted (500°C, 2 h) agate mortar and pestle, and then treated them with a chloroform:methanol mixture (2:1, v/v) to remove lipids. The samples were concentrated onto Whatman GF/C glass filters (pre-combusted at 500°C for 2 h), which were then freeze-dried.

Stable isotope analyses: The stable isotope ratios of the samples were determined with a Finnigan MAT Delta-plus mass spectrometer (Thermo Finnigan, San Diego, CA, USA) connected to an elemental analyzer (NA2500; CE Instruments, Wigan, UK). Stable isotope ratios are presented here in the standard delta notation

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 (\text{‰}),$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. We report isotope ratio values relative to the following standards: Vienna Pee-Dee belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen gas for $\delta^{15}\text{N}$. The analytical error was within $\pm 0.1\text{‰}$ for carbon and $\pm 0.2\text{‰}$ for nitrogen.

Table 1 Carbon and nitrogen stable isotope ratios of potential food sources for common and crucian carps.

Samples	Sampling season	n	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)	
			mean	SD	mean	SD
primary producers and organic matter						
POM ¹⁾	Apr – Dec 2006	27	-30.0	0.9	8.2	0.7
epiphyton ²⁾	Jul 2006	6	-28.0	1.1	8.5	0.8
SOM ¹⁾	Apr – Dec 2006	27	-27.4	0.4	8.2	0.6
epiphyton + SOM mean		33	-27.5	0.6	8.3	0.7
invertebrates						
zooplankton ²⁾	Jun – Dec 2006	17	-31.5	1.2	12.1	2.1
Copepod zooplankton		9	-31.9	1.1	13.8	1
<i>Eodiaptomus japonicus</i>	Jun – Sep 2006	4	-31.2	0.8	13.3	0.9
<i>Eodiaptomus japonicus</i> + <i>Cyclops</i> sp.	Oct 2006	1	-32.7		13.7	
<i>Cyclops</i> sp.	Nov, Dec 2006	4	-32.3	1.2	14.3	1.0
Cladoceran zooplankton		8	-31.1	1.2	10.1	1.1
<i>Sida crystallina</i>	Jun, Jul, Sep 2006	5	-31.0	0.7	10.0	1.1
<i>Sida crystallina</i> + <i>Diaphanosoma brachyurum</i>	Jul, Aug 2006	2	-30.7		11	
<i>Diaphanosoma brachyurum</i>	Sep 2006	1	-32.4		9.1	
benthos ¹⁾						
<i>Chironomus plumosus</i> ¹⁾	May – Dec 2006	41	-35.8	6.2	10.2	2.6
snail						
<i>Radix auricularia japonica</i>	Jun 2006	3	-26.1	1.1	12.6	0.4

1)Data from Yasuno et al. (2013)

2)Data from Yasuno et al. (2016)

Isotopic data of potential food sources for common and crucian carps: Since common, silver crucian and Japanese crucian carps are able to forage on diverse food sources [Nakamura 1969; Hosoya 2001; Taniguchi 2001]; we recognized seven end members as potential food items: particulate organic matter (POM; mainly phytoplankton), sedimentary organic matter (SOM), epiphyton, zooplankton, larval chironomids (*C. plumosus*) and snails (*R. auricularia japonica*) (Table 1). We used the isotopic data for POM, SOM and larval chironomids provided by Yasuno et al. [2013], and the isotopic data for epiphyton and zooplankton provided by Yasuno et al. [2016]. Surface lake water was collected for analysis of particulate organic matter (POM) at the center of Lake Izunuma. Water samples were filtered through Whatman GF/F glass filters (precombusted at 500°C for 2 h) to concentrate the POM onto GF/F. Zooplankton was collected using a 0.4 mm-mesh net at the center of the lake [Yasuno et al., 2016]. Floating macrophyte leaves (*Nelumbo nucifera* and *Nymphoides indica*) for epiphyton were collected near the south shore in July 2006. Epiphyton were detached from the undersides of floating leaves by brushing it into the distilled water, and the water was filtered through the pre-combusted glass filters to concentrate the epiphyton. SOM and larval chironomids *Chironomus plumosus* were collected using an Ekman grab and

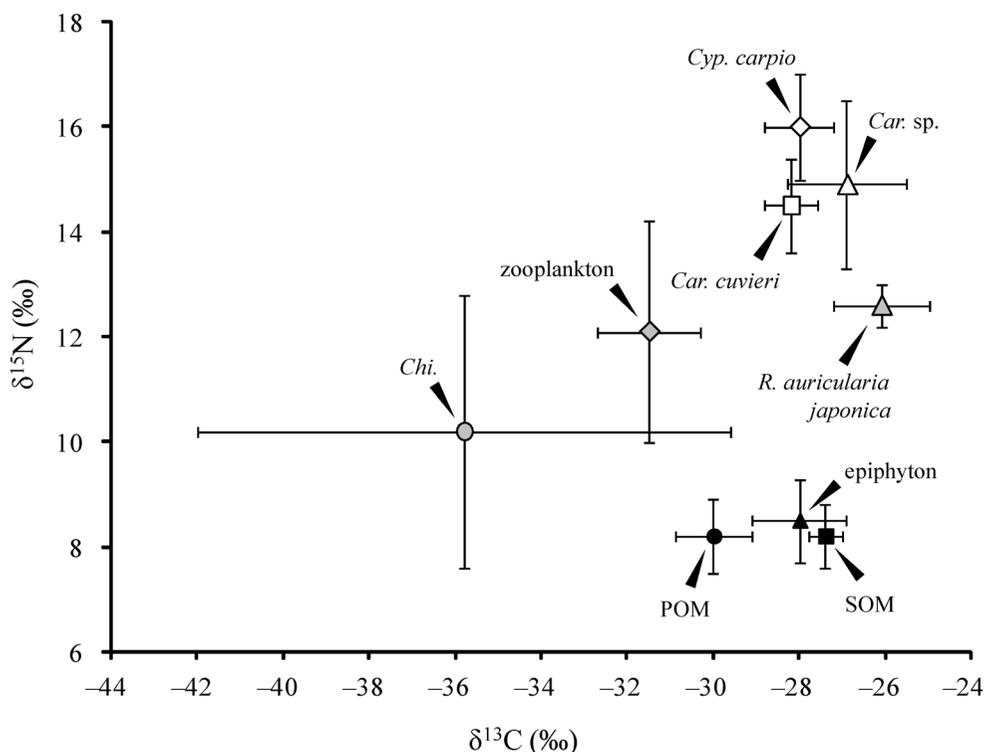


Fig 2 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of fish species and their potential food sources collected in Lake Izunuma. Open, gray and closed symbols represent carps, invertebrates and primary producers or organic matter, respectively. Names of carps and invertebrates are abbreviated. See Table 1 and 2 for full taxon names and sample sizes (n). Bars indicate SD estimates.

larval chironomids were sieved from the surrounding sediment (mesh size 1 mm) [Yasuno et al., 2013]. Crucian carp are able to capture zooplankton with their gill rakers [Nakamura, 1969], but common carp (> ca. 300 mm long) are not because their branchial sieves have a larger mesh width (Sibbing, 1988). Thus, zooplankters were not considered as potential food for common carp. POM deposited on the sediment was considered to be a potential food source for common carp and two species of crucian carp because benthic foragers are able to ingest POM. Since the SOM in Lake Izunuma is derived mostly from dead macrophytes, such as lotus or other plants [Fujibayashi et al., 2013; Yasuno et al., 2013], the SOM isotopic signatures we used in our investigation were those obtained from detritus derived from these macrophytes. Epiphyton and SOM were pooled into one group because they had similar isotopic signatures (Fig. 2, Table 1) and were largely derived from littoral primary producers (macrophytes and their epiphytic algae). Therefore, we recognized five groups of potential food for common carp, and six groups for silver crucian carp and Japanese crucian carp.

Table 2 Carbon and nitrogen stable isotope ratios of common and crucian carps.

Species	Sampling season	Size range (mm TL)	n	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)	
				mean \pm SD	range	mean \pm SD	range
<i>Cyprinus carpio</i>	May 2006	280 – 315	7	-28.0 ± 0.8	-29.5 to -27.1	16.0 ± 1.0	14.4 to 17.0
<i>Carassius</i> sp.	May, Aug, Dec 2006	243 – 335	7	-26.9 ± 1.4	-28.2 to -26.1	14.9 ± 1.6	12.1 to 16.5
<i>Carassius cuvieri</i>	May, Sep, Dec 2006	200 – 280	5	-28.2 ± 0.6	-28.8 to -27.3	14.5 ± 0.9	13.3 to 15.5

Bayesian mixing model: The relative contributions of these food sources to the diets of the three fish species were calculated using the Stable Isotope Analysis routine in R software [SIAR; Parnell et al., 2010, R Development Core Team, 2015], which is a Bayesian mixing model. As indicated, Bayesian mixing models have the advantage of allowing the variation and uncertainties associated with isotopic measurements and trophic enrichment to be propagated through the models, which produce an output that best reflects the natural variability within a system. The SIAR model was fitted with Markov Chain Monte Carlo methods (with the Dirichlet prior distribution) to produce simulated values of the dietary proportions of sources that were consistent with the data (Parnell et al. 2010). Trophic enrichment factors (TEFs) for nitrogen was assumed at 2.55‰ based on: (a) Post [2002]: 3.4 ± 1.0 ‰ (mean \pm SD), $n = 56$; (b) McCutchan et al. [2003]: 2.0 ± 1.8 ‰, $n = 83$, and (c) Vanderklift & Ponsard [2003]: 2.54 ± 1.3 ‰, $n = 134$. TEFs for carbon were assumed at 0.4 ± 1.3 ‰ based on Post [2002] and McCutchan et al. [2003]. The SIAR mixing model was run for 500,000 iterations, discarding the first 50,000 samples.

Results

Stable isotope signatures of potential food sources for common and crucian carps: The mean $\delta^{13}\text{C}$ signatures of the potential food sources ranged from -35.8 ‰ to -26.1 ‰; the $\delta^{15}\text{N}$ signatures ranged from 8.2‰ to 12.6‰ (Fig. 2, Table 1). Larval chironomids (data from Yasuno et al., 2013) had the most depleted $\delta^{13}\text{C}$ signatures (-35.8 ± 6.2 ‰). Snails had the most enriched $\delta^{13}\text{C}$ signatures (-26.1 ± 1.1 ‰). POM and snail had the most depleted (8.2 ± 0.7 ‰) and enriched $\delta^{15}\text{N}$ signatures (12.6 ± 0.4 ‰), respectively. Epiphyton ($\delta^{13}\text{C}$: -28.0 ± 1.1 ‰, $\delta^{15}\text{N}$: 8.5 ± 0.8 ‰) and SOM ($\delta^{13}\text{C}$: -27.4 ± 0.4 ‰, $\delta^{15}\text{N}$: 8.2 ± 0.6 ‰) had closely similar isotopic signatures.

Stable isotope signatures of common and crucian carps: The mean $\delta^{13}\text{C}$ signatures of the three species of fish ranged from -28.2 ‰ to -26.9 ‰; these values fell within the intermediate segment of the $\delta^{13}\text{C}$ signature range that we measured in the potential food sources (Table 2, Fig. 2). The fish species had similar $\delta^{13}\text{C}$ signatures (-28.0 ± 0.8 ‰ in common carp, -26.9 ± 1.4 ‰ in silver crucian carp, and -28.2 ± 0.6 ‰ in Japanese crucian carp), but their $\delta^{15}\text{N}$ signatures differed slightly (16.0 ± 1.0 ‰ in common carp, 14.9 ± 1.6 ‰ in silver crucian carp, and 14.5 ± 0.9 ‰ in Japanese crucian carp). Individual $\delta^{13}\text{C}$ signatures for

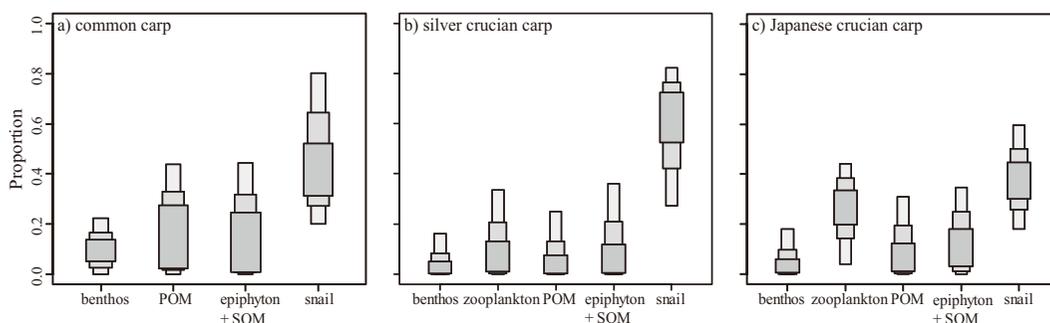


Fig 3 Boxplot and whisker plots constructed by the Stable Isotope Analysis routine (a Bayesian mixing model) in R software to show the contributions of diverse potential food sources to the diets of three fish species based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes. The plots include 95%, 75% and 25% credibility intervals.

common carp, silver crucian carp and Japanese crucian carp ranged from -29.5‰ to -27.1‰ , -28.2‰ to -26.1‰ and -28.8‰ to -27.3‰ , respectively. Individual $\delta^{15}\text{N}$ signatures for common carp, silver crucian carp and Japanese crucian carp ranged from 14.4‰ to 17.0‰ , 12.1‰ to 16.5‰ and 13.3‰ to 15.5‰ , respectively.

Identification of potential food sources in omnivorous fish diets: The SIAR mixing model indicated that snail was one of major food sources for common carp (95% credibility interval: 20–80%), silver crucian carp (28–82%) and Japanese crucian carp (18–60%) (Fig. 3). The benthos less contributed to the diet for common carp (0–22%), silver crucian carp (0–16%) and Japanese crucian carp (0–18%) than other invertebrate food sources. Zooplankton could more contribute to the diet for Japanese crucian carp (34–44%) than that for silver crucian carp (0–32%). The dietary contribution of zooplankton for Japanese crucian carp tended to be higher than POM (0–31%), epiphyton + SOM (0–35%) and benthos.

Discussion

Our isotopic results suggest that snails were important food sources for common and crucian carps in Lake Izunuma (Fig. 3). These species have developed pharyngeal teeth for crushing hard-shelled food items [Nakamura 1969; Sibbing 1991]. Previous reports indicated that common carp and silver crucian carp foraged mostly on snails [Nakamura 1969; Richardson et al. 1995]. We showed that Japanese crucian carp, previously considered as a phytoplankton feeder, also relied on snails. The high dietary contribution of snails suggested that these were valuable and easily accessible food items for the omnivorous fishes in Lake Izunuma.

Larval chironomids are often major dietary components of common and crucian carps [Lammens and

Hoogenboezem 1991; Richardson et al. 1995; Jones & Waldron 2003]. However, our isotopic results indicated that these fish rarely relied on this potential food source in Lake Izunuma (Fig. 3). The disparity between our work and previous studies may be explained by the presence of more valuable alternative food items (snails) in Lake Izunuma. The total zoobenthos density in the lake was not high [359 ± 329 individuals m^{-2} during 2006 and 2008; Yasuno et al., 2009]; therefore, foraging on snails and may have been more rewarding for the fish than feeding on larval chironomids. *C. plumosus*, which is the dominant chironomid species in Lake Izunuma [Yasuno et al. 2009], assimilates carbon derived from biogenic methane produced in anoxic sediments through feeding on methane-oxidizing bacteria [Yasuno et al. 2012; Yasuno et al. 2013]. The minimal larval chironomid component in the diets of these three cyprinid species suggests that the fish rarely contribute to the transfer of methane-derived carbon to higher trophic levels in the lake.

Zooplankton was also an important food source for Japanese crucian carp, together with snails (Fig. 3). Japanese crucian carp relied more on zooplankton than silver crucian carp in Lake Izunuma (Fig. 3). Japanese crucian carp has a larger number of gill rakers (92–128) than other *Carassius* species [Nakabō 2013]. Thus, Japanese crucian carp is morphologically adapted to foraging on suspension feeders. Morphological differentiation in gill raker numbers may account for differences in the proportional contributions of zooplankton among these fish species.

Although Japanese crucian carp are reportedly phytoplankton feeders [Nakamura 1969; Taniguchi 2001], we found that this fish depended little on POM (mainly phytoplankton) as a food source. Instead, the species utilized diverse food sources, including zooplankton, littoral production (epiphyton and/or SOM [detritus]) and snails in Lake Izunuma (Fig. 3). This fish is able to shift from phytoplanktivory to benthivory in the presence of silver carp (*Hypophthalmichthys molitrix*), which is a specialist phytoplankton feeder likely to avoid interspecific competition [Japan River Front Research Center 1996]. However, no strictly phytoplanktivorous fish inhabited Lake Izunuma [Fujimoto et al. 2008], which was eutrophicated and supported a large abundance of phytoplankton [Yasuno et al. 2009]. Thus, the foraging of Japanese crucian carp on diverse food sources was probably unrelated to (i) competition with a specialist phytoplankton feeder or (ii) low abundances of phytoplankton. Therefore, this fish species appears to function as an omnivore (rather than as a phytoplanktivore) in shallow water bodies where diverse food sources are readily accessed.

In this study, we showed that macroinvertebrates such as snails could be important food sources for carps in shallow bodies of water, even though different carp species are adapted for different foraging strategies (e.g. benthivory or planktivory). Carps have been introduced outside of their native range for food and fishing [Taniguchi 2001; Jang et al. 2002; Zambrano et al. 2006; Tarkan et al. 2012], and they are often introduced to small and shallow bodies of water such as farm ponds. Our results suggested that carps could potentially cause predation pressure and negative impacts on macroinvertebrates community in

shallow bodies of water despite of interspecific differences in foraging strategies, and more attention should be paid to these potential effects when carps are introduced.

Acknowledgments

We sincerely thank Dr. K. Ito, Graduate School of Agricultural Science, Tohoku University, for her assistance in the stable isotope analytical facilities. We thank the Miyagi Prefectural Izunuma–Uchinuma Environmental Foundation for its assistance in the sampling program. This study was supported in part by Grants-in-Aid for Scientific Research (C) from the Japan Society for the Promotion of Science (numbers 20570013). Ethical concerns on all experiments and sampling animals were considered and followed under the current laws in Japan.

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