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Comparison of food habits between native Amur three-lips (*Opsariichthys uncirostris uncirostris*) and non-native largemouth bass (*Micropterus salmoides*) in Lake Biwa, Japan

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Abstract – The Amur three-lips (*Opsariichthys uncirostris uncirostris*) is an endemic subspecies in Japan and native to the river systems of the Lake Biwa–Yodo River. The population of three-lips in Lake Biwa has decreased, primarily due to habitat degradation and introduction by competitive, non-native predators, such as largemouth bass (*Micropterus salmoides*). However, the effects of bass introduction on the three-lips are unclear. We investigated the food habits of the three-lips and compared them with those of sympatric non-native largemouth bass in Lake Biwa. A total of 145 three-lips and 178 largemouth bass were sampled during the summer and fall of 2013. Fish prey, particularly ayu (*Plecoglossus altivelis altivelis*), was predominant in the three-lips diet, followed by terrestrial insects. Decapods (*i.e.*, prawn and shrimp), ayu and demersal fish (*e.g.*, gobids) composed a substantial proportion of bass diets. No significant dietary overlaps were found between the two predators. Our results suggest that differences in food habits between the two species may result from differences in feeding behavior; the three-lips is a mobile predator that forages mainly on nektonic and suspended food, whereas largemouth bass is an ambush predator that forages on both nektonic and benthic prey. We referred the results of three-lips diets in Lake Biwa in a previous study and suggest that changes in fish fauna, due to introduction by non-native largemouth bass, may have affected prey availability for the three-lips.

Key words: Dietary overlap / gut contents / non-native fish / piscivorous fish / prey availability

Introduction

Fish introductions are one of the most serious threats to freshwater biodiversity (Rahel, 2000, 2002; Clavero and Garcia-Berthou, 2005). Non-native predatory species have often been introduced intentionally into non-indigenous habitats for recreational purposes (Rahel, 2000, 2002; Alcaraz *et al*., 2005; Eby *et al*., 2006; Moyle and Marchetti, 2006) and have had a significant effect on the aquatic biota as apex predators in food webs (Jackson *et al*., 2001; Eby *et al*., 2006). Invasion of non-native predatory fish not only directly affects species composition and abundance of native animals by predation, but also indirectly alter food web structures and ecosystem processes, *e.g*., trophic cascades to lower trophic levels (*i.e*., small benthos and algae; Eby *et al*., 2006) and food source competition with native predators (Vander Zanden *et al*., 1999).

Largemouth bass (*Micropterus salmoides* Lacepède, 1802) are native to North America but have been introduced and are successfully established in more than 50 countries in Europe, Africa, South America and Asia (Welcomme, 1992). Largemouth bass are predatory, and mainly forage on fish and large crustaceans. Previous researches demonstrated that largemouth bass have negatively affected native species and altered food web structures throughout the globe where they have been introduced (Godinho *et al*., 1997; Azuma and Motomura, 1998; Weyl and Hecht, 1999; Gratwicke and Marshall, 2001; Jackson, 2002; Maezono and Miyashita, 2003; Yonekura *et al*., 2004; Maezono *et al*., 2005; Jang *et al*., 2006; Tsunoda *et al*., 2010; Tsunoda and Mitsuo, 2012; Natsumeda *et al*., 2015). Largemouth bass may also compete with and replace native predatory species

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(*e.g.*, Lorenzoni *et al.*, 2002; Bacheler *et al.*, 2004; Jang *et al.*, 2006).

Largemouth bass has also been introduced into water bodies throughout Japan (Kiryu, 1992). The first introduction of largemouth bass into Lake Biwa, the largest ancient lake of Japan, was recorded in the 1970s (Kiryu, 1992) and irruption of largemouth bass may be the main cause for the decline in Lake Biwa fishes, particularly in littoral cyprinid and gobid species (Maehata, 1993; Nakai and Hamabata, 2002). In Lake Biwa, there is a native predatory fish, the Amur three-lips (*Opsariichthys uncirostris* Temminck and Schlegel, 1846; family Cyprinidae). The Amur three-lips, sometimes called piscivorous chub, ranges over East Asia in the Korean Peninsula; the Amur River, south of the Yangtze River and Hainan Island in China; and Honshu Island in Japan (Tanaka, 2001). The subspecies, *O. u. uncirostris*, is endemic to Japan and native to the river systems of the Lake Biwa–Yodo River in the Kinki Region and Lake Mikata in Fukui Prefecture on Honshu. The Amur three-lips have been used by local people for traditional food and recreation (Fujioka and Maehata, 2012; Kawanabe *et al.*, 2012). However, declines in the annual catch of three-lips in Lake Biwa have been a concern (see Appendix 1 in electronic-only material), and the Lake Mikata population may be extinct (MOE, 2010). Thus, native three-lips are listed as a vulnerable species in the Red List of the Ministry of the Environment, Japan (MOE, 2010). The main reason for the decline of Lake Biwa three-lips is thought to be habitat degradation by alterations in the littoral zone and river improvements (MOE, 2010; Imamura, 2014). However, the introduction of competitive, non-native predatory fish species, such as largemouth bass, is another possible reason (MOE, 2010). One study conducted a DNA analysis of bass feces and found proportionally higher consumption of three-lips juveniles by largemouth bass (Sugiura and Taguchi, 2011); however, food resource competition between these two species has not been reported. Previous studies showed Amur three-lips and largemouth bass have similar diets (*i.e.*, mainly consumed fish preys) in allopatric environments in Japan (three-lips, Tanaka, 1964; Kurita *et al.*, 2008; Sano, 2012; largemouth bass, Azuma and Motomura, 1998; Yodo and Kimura, 1998; Kuge *et al.*, 2004; Tsunoda *et al.*, 2009; Sugiura and Taguchi, 2011; Taguchi *et al.*, 2014) and a stable isotope analysis indicated a similarity in those species trophic levels in Lake Biwa (Okuda *et al.*, 2012). Therefore, largemouth bass could negatively affect the three-lips as a potential competitor for food resources, while no study has directly observed and compared the diets of the two species.

The present study is the first report of a food habit comparison between the Amur three-lips and largemouth bass in Lake Biwa. We compared food habits and estimated diet overlap of the two species by analyzing their gut contents. We also compared Amur three-lips food habits data to other food habits data collected before the introduction of largemouth bass in Lake Biwa to determine potential shift that may have occurred in the presence of a new predator.

Materials and methods

Study area

Lake Biwa (34°58′–35°30′N, 135°51′–136°16′E) is located in Shiga Prefecture, the central part of Honshu, Japan (Fig. 1). Lake Biwa is the largest lake in Japan (ca. 670 km^2 and 103 m in maximum depth) and is one of the most ancient lakes in the world, as it was formed about 4.5 million years ago (Kawanabe *et al.*, 2012). Numerous endemic species and a relatively high biodiversity are found in Lake Biwa; 46 indigenous fish species and subspecies occur there, of which 17 species/subspecies are endemic to the lake (Maehata, 2012).

Field surveys

We sampled fish in the littoral zone (< 5 m depth) between summer and early autumn (mid-July to early October 2013) as this period had the greatest potential for resource overlap between the two species (Sunaga, 1980; Nakamura, 1992). Six sampling sites were established in the estuarine areas of rivers that flow into Lake Biwa (Fig. 1), which have mud, sand and/or gravel substrates and are partially covered with emergent (*e.g.*, *Phragmites australis* Trin. ex Steud.) and submergent aquatic plants (*e.g.*, *Potamogeton maackianus* A. Been and *Elodea nuttallii* (Planch.) H. St. John). Fish were caught by lure angling throughout the study period, and cast nets (4.1-m diameter with 9.5-mm mesh and 4.7-m diameter with 12.5-mm mesh) were used in July and early August. Angling or cast netting for either species was not prohibited in Lake Biwa during the study season. However, because catch of several fish species (*e.g.*, ayu, *Plecoglossus altivelis altivelis* Temminck and Schlegel, 1846) were restricted from mid-August to November by local fishery regulation, we sampled only by angling to avoiding bycatch of the restricted species. Fish were sampled by five researchers for 2 h at each site. The sampled fishes were killed immediately. The gut was injected with 10% formalin to fix the contents, and the fish were held on ice *in situ*. All samples were transported to the laboratory and frozen at $-20\,^{\circ}C$ until the dietary analysis.

Gut content analysis

Standard length (SL, mm) and body wet weight (BW, g) of each individual were recorded before the gut was removed. Gut contents were examined by sight or using a microscope (10 ×) and identified to the level of order, family, or species, if possible. The total wet weight (0.001 g) of each prey item in the gut was recorded, except nonfood material, such as plants, sand, gravel or plastic fishing lures.

For describing the proportion of a prey item in gut contents, we used the percent frequency of occurrence

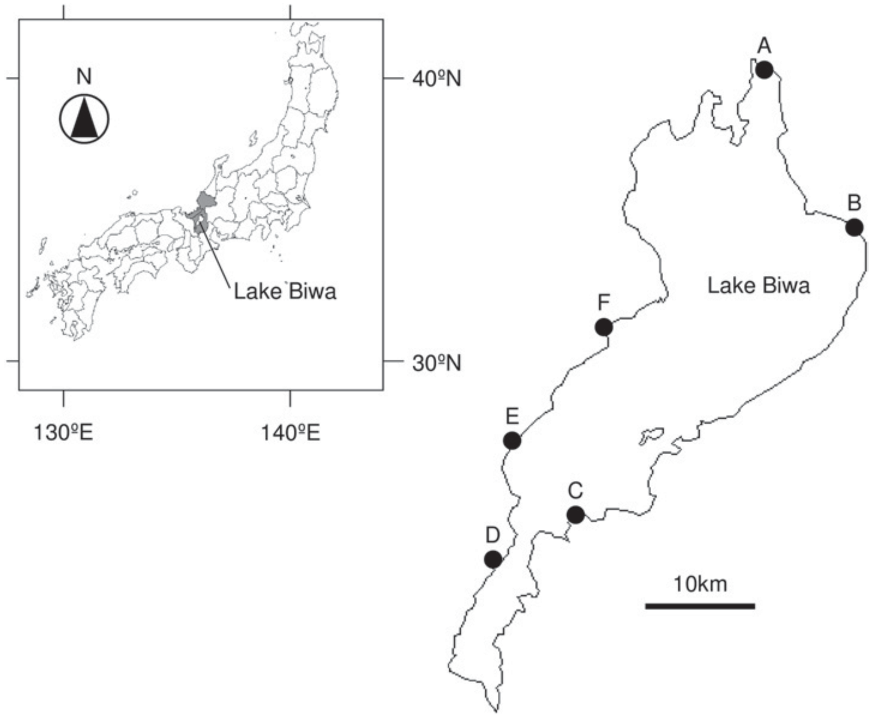

Fig. 1. Lake Biwa and sampling site locations (solid circles; A–F).

(%F) and percent by prey weight (%W). We calculated %F and %W for each prey item as follows:

$$\%Fi = (\text{number of guts containing a prey item } i / \text{number of guts with any contents}) \times 100;$$

and

$$\%Wi = (\text{total weight of a prey item } i / \text{total weight of all prey items}) \times 100.$$

For the food habits analysis, we divided the samples into three body-size classes (small, < 120 mm SL; medium, 120–180 mm SL; and large, > 180 mm SL) to determine ontogenetic changes in food habits for both species. We used the age class size categories for the Amur three-lips, as reported previously for Lake Biwa (Tanaka, 1964), to assess potential competitive effects of largemouth bass on Amur three-lips at different age classes. Both the Amur three-lips (Tanaka, 1964; Sano, 2012) and largemouth bass (Olson, 1996; Garcia-Berthou, 2002) show ontogenetic shifts in diet and change to piscivory at juvenile stage: 1 + year-classed fish (ca. > 70 mm SL) of the three-lips starts to prey on fishes (Tanaka, 1964), while yearlings of largemouth bass start piscivory with 30–50 mm of body length (Azuma and Motomura, 1998; Yasuno *et al.*, 2012; Taguchi *et al.*, 2014), indicating that two species may be potentially competitive after 1 + year. The sampled fishes were included within the size-classes in potentially piscivorous for both species (*i.e.*, > 70 mm SL for three-lips and > 50 mm for largemouth bass; see Fig. 2). For the analysis, we combined all monthly data because of short study period (*i.e.*, 3 months) and small sample size (see Appendix 2).

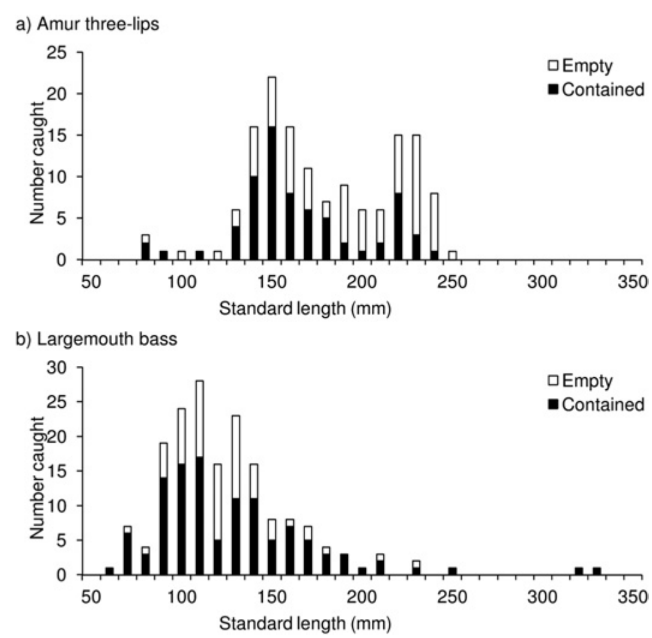

Fig. 2. Size distributions of sampled native Amur three-lips (*Opsariichthys uncirostris uncirostris* (a); and non-native largemouth bass (*Micropterus salmoides* (b) in Lake Biwa.

Analysis of dietary overlap

Dietary overlap was determined using Schoener's index (α; Schoener, 1970) and the null-model test (Winemiller and Pianka, 1990). Schoener's index is the most appropriate and commonly used method to assess overlap of

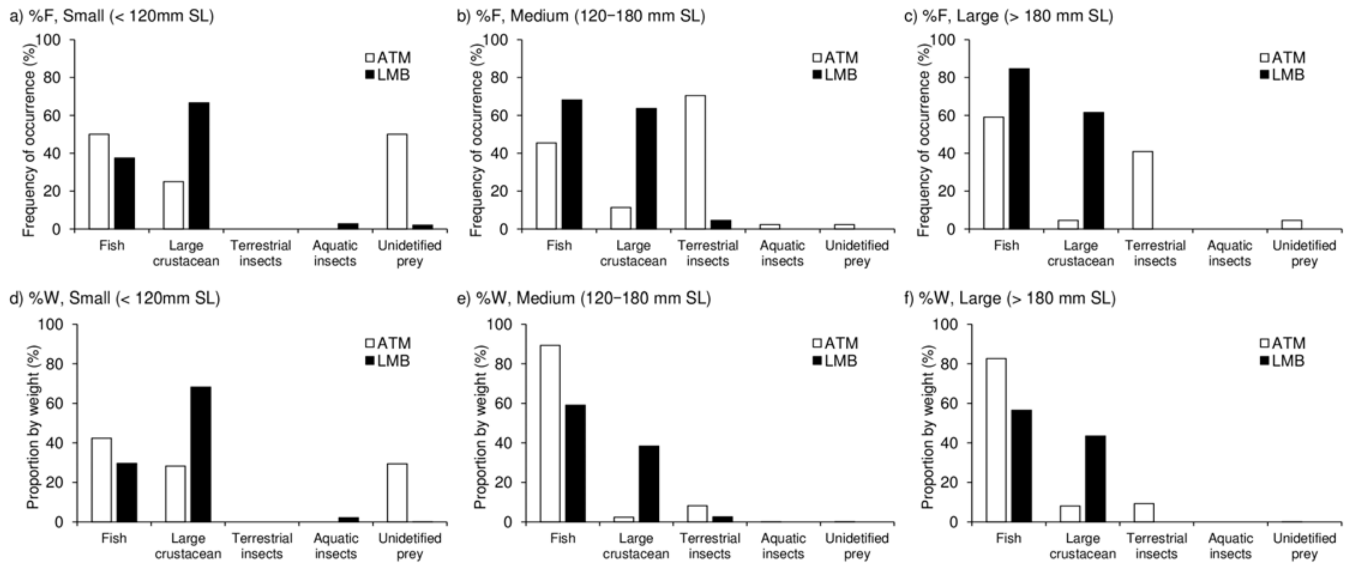

Fig. 3. Food habits comparisons in different size-classes between native Amur three-lips (*Opsariichthys uncirostris uncirostris*; ATL) and non-native largemouth bass (*Micropterus salmoides*; LMB) in Lake Biwa. %F and %W represent the percent frequency of occurrence and the percent by prey weight, respectively.

food habits (Wallace, 1981). The index was calculated as follows:

$$\alpha = 1 - 0.5\left(\sum |\mathrm{ATL}i - \mathrm{LMB}i|\right),$$

where ATLi and LMBi represent the %F and %W of the prey category i in the diets of the Amur three-lips and largemouth bass, respectively. We categorized the prey items into five groups, including fish, large crustaceans, terrestrial insects, aquatic insects and unidentified prey. Dietary overlap was analyzed for each size class. The null-model test is a statistical approach to determine whether niche overlap is significant (Winemiller and Pianka, 1990). The statistical significance of dietary overlap was determined by comparing the observed value of α to the simulated value from the null distribution. The null distribution was created from 1000 randomizations of data provided using the "scrambled-zeros" randomization algorithm (Winemiller and Pianka, 1990). A significant dietary overlap between two species is detected when the observed value is $>95\%$ of the simulated at $P < 0.05$ (Winemiller and Pianka, 1990). We used EcoSim ver. 7.0 for the null-model test analysis (Gotelli and Entsminger, 2001).

Results

A total of 145 Amur three-lips and 178 largemouth bass were sampled, of which 52% (n = 75) and 36% (n = 64) had empty guts, respectively. Length of the sampled fishes ranged from 80 to 252 mm SL for three-lips and from 68 to 332 mm SL for largemouth bass, respectively (Fig. 2). The ratio of empty guts of three-lips increased with increasing body size (Fig. 2 and Appendix 2). For largemouth bass, however, the ratio of empty guts was the highest in medium size class and the lowest in the large size class (Appendix 2).

Unidentified fish were the predominant prey of small-sized three-lips, comprising 50% of the %F and 42% of the %W of the diet, although the sample size was small (n = 4; Fig. 3). In contrast, decapods (*i.e.*, prawn and shrimp) were the predominant prey for small-sized largemouth bass, followed by fish prey (mostly unidentified species but including ayu and some gobid species; Fig. 3 and Appendix 2).

For medium-sized three-lips, terrestrial insects were the predominant prey on the basis of occurrence, followed by fish (Fig. 3), while fish was the predominant prey on the basis of weight (Fig. 3). For medium-sized largemouth bass, fish and large crustaceans were the most dominant on the basis of occurrence (Fig. 3). On the other hand, fish was more predominant than large crustaceans in the bass diet by weight (Fig. 3). For both species, ayu was the most predominant prey in diets on the basis of weight (see Appendix 2).

Fish were the predominant prey for large three-lips by frequency and weight (Fig. 3). The majority of the fish prey was unidentified species on the basis of occurrence (%F = 45%) but ayu comprised 13%. In addition, ayu was the most predominant prey item by weight (%W = 42%; see Appendix 2). Terrestrial insects were secondary in importance by frequency and weight. Fish was more predominant than large crustaceans in the diet of large-sized bass on the basis of occurrence (Fig. 3), while fish and large crustaceans were equally dominant by weight (Fig. 3). For largemouth bass, ayu was the most predominant prey in this class (%F = 31% and %W = 42%, respectively; see Appendix 2).

Dietary overlap indices between Amur three-lips and largemouth bass were estimated 0.46–0.58 on the

Table 1. The dietary overlap index between native Amur three-lips (*Opsariichthys uncirostris uncirostris*) and non-native largemouth bass (*Micropterus salmoides*) in Lake Biwa.

Body-size class	Diet index*	Schoener's index Observed	Schoener's index Simulated (SD)	Null-model test *P*
< 120 mm SL**	%F	0.563	0.412 (0.021)	0.290
	%W	0.579	0.395 (0.017)	0.204
120–180 mm SL	%F	0.464	0.414 (0.028)	0.425
	%W	0.641	0.249 (0.028)	0.060
> 180 mm SL	%F	0.583	0.378 (0.030)	0.102
	%W	0.646	0.263 (0.026)	0.097

*%F, the percentage frequency of occurrence; %W, the percentage of prey weight.
**Standard length.

basis of occurrence (*i.e.*, %F) and 0.58–0.65 on the basis of weight (*i.e.*, %W). Based on the null-model test, however, there were no significant dietary overlaps between three-lips and largemouth bass within each size class (Table 1).

Discussion

Potential resource competition

Our results show that the food habits of the Amur three-lips were different from sympatric, non-native largemouth bass, although both species mainly preyed on fish preys. These dietary differences between the two species may be a result of differences in feeding behavior because three-lips are predominately mobile predators (Tanaka, 2001), whereas largemouth bass switch between ambush and mobile predation (Savino and Stein, 1982). This was reflected in the results of gut contents analysis, as three-lips mainly foraged on nektonic minnows, such as ayu, and suspended terrestrial insects, whereas largemouth bass preyed on benthic prey, such as large crustaceans and gobids relatively larger amounts and more frequently. Similar results were observed in Lake Kawaguchi, central Japan, where non-indigenous Amur three-lips forage for fish and terrestrial insects, and sympatric non-native largemouth bass mainly forage for prawns (Urano *et al.*, 2014).

As the three-lips and largemouth bass have similar diets (*i.e.*, mainly forage on ayu, cypinids and gobids) in allopatric environments in Japan (three-lips, Tanaka, 1964; Kurita *et al.*, 2008; Sano, 2012; largemouth bass, Azuma and Motomura, 1998; Yodo and Kimura, 1998; Kuge *et al.*, 2004; Tsunoda *et al.*, 2009; Sugiura and Taguchi, 2011; Taguchi *et al.*, 2014), their food niches could overlap. Thus, food resource competition between the two species has been a concern where they are sympatric (MOE, 2010). However, our results show no significant dietary overlap between three-lips and largemouth bass in Lake Biwa, indicating little direct competition for food resources between the two species. Food resource partitioning has often been observed among sympatric piscivorous fish (Winemiller, 1989; Liao *et al.*, 2002; Wheeler and Allen, 2003; Pelicice and Agostinho, 2005; Wuellner *et al.*, 2010; Walker *et al.*, 2013) and it can reduce direct interspecific competition for food (Winemiller, 1989). In addition, Ross (1986) suggested that food resource partitioning may be more important in structuring fish assemblages than habitat segregation. Resource partitioning between native and non-native species may contribute to the persistence of the native species after invasion by a non-native competitor. Bacheler *et al.* (2004) suggested that local extinction of the native bigmouth sleeper (*Gobiomorus dormitor* Lacepède, 1800) in some Puerto Rican reservoirs may have been caused by competition with non-native largemouth bass because the food niche overlapped significantly between the two species. In contrast, native lake trout (*Salvelinus namaycush* Walbaum, 1792) in some Canadian lakes coexist with competitive, non-native smallmouth bass (*Micropterus dolomieu* Lacepède, 1802) and rock bass (*Ambloplites rupestris* Rafinesque, 1817), due to a shift from foraging on littoral fish (*e.g.*, cyprinids) to foraging on pelagic fish (*e.g.*, cisco, *Coregonus* sp. or alewife, *Alosa pseudoharengus* Wilson, 1811) or zooplankton (Vander Zanden *et al.*, 1999; Lepak *et al.*, 2006; Morbey *et al.*, 2007). Thus, the food differences between the two species may enable three-lips to coexist with competitive largemouth bass in Lake Biwa.

Changes in the diet of Lake Biwa three-lips after introduction by largemouth bass

The prey of Amur three-lips in Lake Biwa before introduction of largemouth bass (ca. 50 years ago) included ayu, gobid (*Rhinogobius* sp.), and cyprinid (*e.g.*, *Gnathopogon caerulescens* Sauvage, 1883) species between summer to autumn (Tanaka, 1964). The sampling sites (*i.e.*, littoral zone) and the methods of gut content analysis (*i.e.*, the percent frequency of occurrence and the percent by weight) were common between the two studies, while the sampling method of the present study (angling and cast netting) was different from the previous one (beach seines; Tanaka, 1964). Thus, we can compare the results of the gut content analysis between the two studies. Although we found that all body-size classes of the three-lips remained mainly piscivorous, prey composition differed from that reported previously (Tanaka, 1964), particularly in the decline/disappearance of gobids and cyprinids in the diet of the three-lips.

We speculate that food habits changes in the three-lips was mainly caused by changes in the Lake Biwa fish fauna over the last five decades due to human activities, as human activities have greatly altered the lake environment and affected the biodiversity in Lake Biwa (Kawanabe *et al.*, 2012). The number and abundance of some indigenous Lake Biwa fish species have declined because of overfishing (1969–1991), alteration/destruction of reed zones and littoral areas, *i.e.*, lacustrine fish habitat (by the "Lake Biwa Comprehensive Development Program", 1972–1997), and invasion by non-native fish species (since the late 1980s) (Maehata, 2012; Nakai, 2012). Indeed, a declining trend in the total annual catch (*i.e.*, an indicator of abundance; Nakai, 1999) of some species has been reported, *e.g.*, *Carassius* sp., *G. caerulescens* and *Gymnogobius isaza* Tanaka, 1916 (see Appendix 1 in electronic-only material), and these species were found to be mainly preyed on by three-lips in a previous study (Tanaka, 1964).

It also suggested that irruption of largemouth bass may be the main cause for the decline in Lake Biwa fishes, particularly in littoral cyprinid and gobid species (Nakai and Hamabata, 2002) because those species are susceptible to the predatory impact of bass (Jackson *et al.*, 2001; Maezono and Miyashita, 2003; Yonekura *et al.*, 2004; Tsunoda *et al.*, 2010; Tsunoda and Mitsuo, 2012). In fact, 12 cyprinid species have disappeared, and the populations of eight cyprinid and one gobid species have declined for about 10 years after irruption of largemouth bass in the southern part of Lake Biwa (Maehata, 1993). We speculate that changes in the fish fauna due to irruption of the bass may affect prey availability, resulting in dietary changes by the three-lips before and after the Lake Biwa bass introduction. This assumption is consistent with the results of some studies reporting that reductions in fish prey abundance by the predatory impact of invading smallmouth bass and/or rock bass altered the food habits of native lake trout and facilitated dietary shifts to predominately zooplankton in several Canadian lakes (Vander Zanden *et al.*, 1999; Lepak *et al.*, 2006). Further study using stable isotope analysis is recommended to help clarify the dietary shift of three-lips due to the effects of largemouth bass introduction on prey availability in Lake Biwa. The stable isotope analysis method is appropriate to help understand food web changes and interactions among populations over long periods (Vander Zanden *et al.*, 1999; Galster *et al.*, 2012; Guzzo *et al.*, 2013). In addition, trophic niche shifts in native predator caused by invasion of non-native competitors also affected fitness or fitness-related factors (*e.g.*, fecundity, growth and survival) of the native species (Vander Zanden *et al.*, 1999), indicating that negative (indirect) effects of the non-native competitor were persistent. We also suggest further study and monitoring on fitness or the related factors of the three-lips in Lake Biwa.

Conclusion

Our results indicate little food competition between native Amur three-lips and non-native largemouth bass in Lake Biwa but these differences may be related to a shift in food habits of Amur three-lips after largemouth bass were introduced. Further study is recommended to understand the mechanism of the effects of reduction in the prey fish availability on the three-lips, such as archival specimens analyzed with a stable isotope (*e.g.*, Okuda *et al.*, 2012). In addition, previous studies suggest that reducing suitable prey by introducing competitive predators can affect body condition, growth and reproduction of native predators (Vander Zanden *et al.*, 1999; Lepak *et al.*, 2006). Ontogenetic dietary shifts from planktivory to piscivory are important for growth of young three-lips, and gobids (*e.g.*, *Rhinogobius* sp.) were the most predominant food for them before the Lake Biwa bass invasion (Tanaka, 1964). As mentioned above, gobids are susceptible to bass invasion (*e.g.*, Maezono and Miyashita, 2003; Tsunoda *et al.*, 2010), and our results indicated a reduction in gobids in the diet of young three-lips, compared with that reported previously (Tanaka, 1964). We suggest that both direct predation on juveniles and reduction in preferable prey availability by largemouth bass on growth and survival of young three-lips need to be evaluated in a further study. The Lake Biwa three-lips is not only an endangered species but also an important fishery resource for local traditional food culture (Fujioka and Maehata, 2012). Therefore, future studies will contribute to the planning and development of countermeasures for competitive non-native bass to conserve the three-lips population as a sustainable resource.

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