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Morphological variation in largemouth bass *Micropterus salmoides* in Lake Biwa, Japan

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Abstract – Largemouth bass, *Micropterus salmoides*, have inhabited Lake Biwa in central Japan for over three decades as top predators. Lake Biwa consists of two basins – a large, deep north basin and a small, shallow south basin. Since the mid 1990s, vegetation and bluegill sunfish, *Lepomis macrochirus*, have thrived in the lake – especially in the south basin. Because dense vegetation can mediate the predator-prey relationship between largemouth bass and bluegill, the largemouth bass in the south basin are assumed to be under less favorable conditions than those in the north basin. The length-weight relationship of the largemouth bass in the two basins differed; the body weights of largemouth bass in the north basin significantly exceeded those in the south basin. Moreover, largemouth bass in the south basin appeared to have significantly larger gapes than those in the north basin. Such fish in the south basin were likely selected during and after the ontogenetic diet shift stage, probably because they are capable of handling bluegill more efficiently than those with normal-sized gapes.

Key words: Largemouth bass / morphology / length-weight relationship / mouth gape / Lake Biwa

Introduction

As predacious fish, largemouth bass, *Micropterus salmoides* Lacépède, can adapt to a wide range of freshwater ecosystems. Although native to the eastern United States and south-central Canada, the fish have been transplanted to a wide region of North America and are now distributed worldwide (Jackson, 2002). Largemouth bass were first introduced to Japan in 1925; the population had expanded by the late 1960s, and have now become a common species countrywide (Takamura, 2007). Because of their feeding habits, the introduction of largemouth bass can adversely and severely impact native ecosystems (Jackson, 2002). For instance, in Lake Biwa, which is the largest lake in Japan (surface area 670 km^2, maximum depth 104 m), the presence of largemouth bass was first verified in the northeast part of the lake in 1974, although the time of the introduction of the fish into the lake is uncertain. Soon thereafter, largemouth bass became common across the entire lake and dominated in the 1980s. As pointed out by Nakai and Hamabata (2002), the propagation of largemouth bass is responsible for the disappearance of some small native fish species in the coastal regions of the lake.

Fish are generally distributed unevenly in a water body, in a manner that depends on the relationship between the distribution of environmental resources and such characteristics of the habitat as depth, sediment type, temperature, water clarity, and availability of refuge and food resources. Fish growth and population size reflect both qualitative and quantitative variations in habitat (Hayes *et al*., 1996). Topographically, Lake Biwa consists of two basins – a large, deep north basin (surface area 618 km^2, mean depth 43 m) and a small, shallow south basin (surface area 52 km^2, mean depth 3.5 m). Each basin has a distinct environment, which is reflected in the biotic communities, possibly influencing the dynamics of the largemouth bass population. Recently identified ecological features in Lake Biwa, clearly observed in the south basin, are the propagations of submerged plants (Hamabata and Kobayashi, 2002), and bluegill sunfish, *Lepomis macrochirus* Rafinesque, an exotic fish species that is native to North America and has inhabited Lake Biwa for over four decades (Mizuno *et al*., 2007). Largemouth bass frequently

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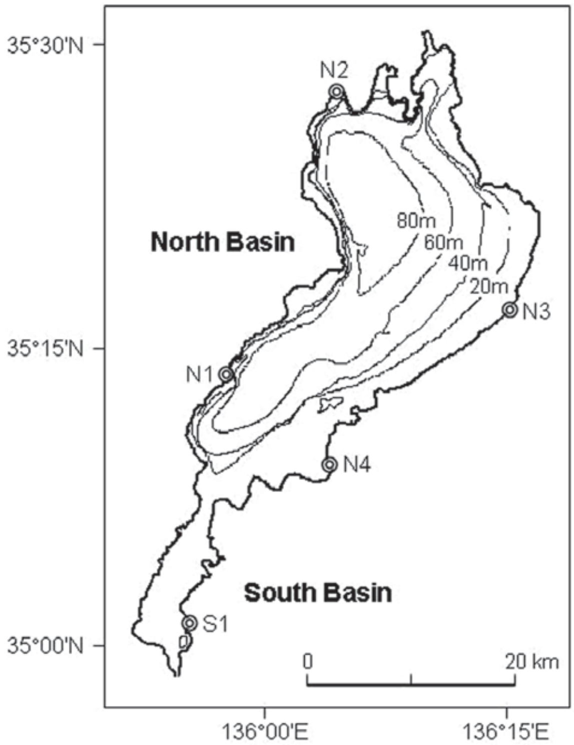

Fig. 1. Sampling sites at Lake Biwa.

prey on bluegill, and the efficiency of their foraging for bluegill is reduced by dense vegetation (Savino and Stein, 1982). Since largemouth bass are the dominant predators in Lake Biwa, clarification of the regional variation in their ecophysiological features is valuable in elucidating the structure of the ecosystem in the lake.

The objective of this study was to find evidence of differences in the growth or foraging efficiency of largemouth bass between the north and south basins in Lake Biwa. The relationship between the length and weight of each fish can generally be expressed as a simple power function (Santos *et al*., 2002). Therefore, regional variation in the growth of largemouth bass is expected to be reflected in the difference in the length-weight relationship. Moreover, mouth gape is the primary determinant in the selection of largemouth bass prey (Webb, 1986; Hambright, 1991; Huskey and Turingan, 2001). Consequently, information on mouth gape is valuable in evaluating the foraging efficiency of largemouth bass. In this study, fish samples were collected from five sites (four in the north basin and one in the south basin) in Lake Biwa, and the morphological variation of largemouth bass between the two basins was evaluated.

Materials and methods

Largemouth bass were sampled on 19 November 2005 at five sites along the coast of Lake Biwa (Fig. 1). Sites N1, N2, N3 and N4 are located in the north basin, and site S1 is located in the south basin. Largemouth bass were angled using freshwater shrimp, *Palaemon paucidens* De Haan, as bait. Samples were collected from the five sites; the maximum number of captures was limited to 20 per site and the duration of fishing at each site, except site S1, was limited to one hour. Sampling began at site N1 in the early morning, and proceeded in a clockwise direction. Sampling at site S1 was conducted for an extended period of about three hours. Captured fish were placed on ice.

The total length (*TL*) and body weight (*BW*) of each specimen were measured to accuracies of 0.1 cm and 0.1 g, respectively. Length-weight relationships were determined by fitting an allometric power function $BW = aTL^b$ to the data, where a and b denote the initial growth coefficient and the relative growth coefficient, respectively. Males and females were not separated in the determination of the length-weight relationships for two reasons: the number of available samples was low, and male and female largemouth bass are barely distinguishable morphologically, including in their length-weight relationships (Yoshizawa, 1992; Lorenzoni *et al*., 2002). The body depth, standard length, and gape of the fish were also measured. All measurements were made within 18 hours of sampling.

Analysis of covariance (ANCOVA) was used to evaluate the regional variation in the relationships between total length and body weight, standard length and body depth, and standard length and mouth gape. Data on total length and body weight were $\log_{10}$ transformed in the analysis of length-weight relationship.

Results

Twenty largemouth bass were successfully collected from each site in the north basin, whereas the number of samples collected from site S1 was six. Significant length-weight relationships (Pearson's product moment correlation coefficient, $p < 0.01$) were identified at all sites sampled (Table 1, Fig. 2). ANCOVA indicated that the $\log_{10}$-total length *versus* $\log_{10}$-body weight regressions did not vary significantly among the samples in the north basin (slope: $F_{3,72} = 1.62$, $p = 0.19$; intercept: $F_{3,75} = 0.40$, $p > 0.99$). The slopes of the regression lines of $\log_{10}$-body weight against $\log_{10}$-total length of the largemouth bass collected from the two basins did not differ ($F_{1,82} = 0.02$, $p = 0.88$), but the intercept of the regression line for the largemouth bass from the south basin was significantly lower than that for those from the north basin ($F_{1,83} = 112$, $p < 0.001$). The body depth of largemouth bass increased linearly with the standard length (Table 2, Fig. 3A). The regression lines of the standard length *versus* body depth of largemouth bass did not vary significantly among the four sites in the north basin (slope: $F_{3,72} = 0.80$, $p = 0.50$; intercept: $F_{3,75} = 0.96$, $p = 0.57$). The body depths of largemouth bass in the south basin were significantly lower than those in the north basin (slope: $F_{1,82} = 1.15$, $p = 0.29$; intercept: $F_{1,83} = 24.3$, $p < 0.001$). The mouth gape of largemouth bass also increased linearly with standard length (Table 3, Figs. 3B and 3C). The regression lines of standard length *versus* gape height

Table 1. Relationship between total length (TL) and body weight (BW) of largemouth bass. a and b are constants in $BW = aTL^b$. N(1–4) represents combined data from the four sites in the north basin. All correlation coefficients (r) were significant at $p = 0.01$.

					Total length (cm)		Body weight (g)	
Sites	a	b	n	r	Mean ± SD	Range	Mean ± SD	Range
N2	0.0068	3.20	20	0.993	14.6 ± 2.37	10.6–18.3	39.9 ± 19.7	13.3–72.4
N3	0.0060	3.25	20	0.993	16.7 ± 2.13	14.0–22.5	59.6 ± 29.1	31.8–153
N1	0.0059	3.25	20	0.995	13.1 ± 1.98	8.70–17.4	27.4 ± 14.3	6.90–66.3
N4	0.0033	3.47	20	0.990	15.1 ± 1.98	11.4–18.2	44.3 ± 18.8	15.2–90.5
N(1–4)	0.0056	3.27	80	0.994	14.9 ± 2.46	8.70–22.5	42.8 ± 23.8	6.90–153
S1	0.0045	3.26	6	1.000	15.4 ± 5.64	11.1–26.2	50.3 ± 68.4	11.3–188

(slope: $F_{3,72} = 2.07$, $p = 0.11$; intercept: $F_{3,75} = 1.33$, $p = 0.11$) and standard length *versus* gape width (slope: $F_{3,72} = 0.094$, $p = 0.96$; intercept: $F_{3,75} = 1.45$, $p = 0.051$) of largemouth bass did not vary significantly among the four sites in the north basin. Both the gape height (slope: $F_{1,82} = 5.54$, $p = 0.02$; intercept $F_{1,83} = 51.8$, $p < 0.001$) and the gape width (slope: $F_{1,82} = 20.0$, $p < 0.001$; intercept $F_{1,83} = 18.8$, $p < 0.001$) of the largemouth bass differed significantly between the two basins.

Discussion

Collecting largemouth bass from the south basin appeared to be more difficult than collecting them from the north basin, probably owing to the difference between their population densities in the two basins. The population density of fish is commonly difficult to determine, and so researchers often use catch-per-unit-effort (CPUE) as an index of fish density (*e.g.* He and Lodge, 1990; Guy and Willis, 1995). The lower density of the largemouth bass in the south basin can be inferred from recent environmental changes in the south basin as well as identified using CPUE. In the summer of 1994, the water level in Lake Biwa underwent an unusual decline, to a lowest recorded level of −1.23 m. (The standard lake water level of 0 m corresponds to 84.37 m above sea level.) The drastic changes in water quality associated with the decline in the water level caused a regime shift from phytoplankton-dominated turbid water to macrophyte-dominated clear water (Hamabata and Kobayashi, 2002). This shift was particularly evident in the shallow, eutrophic south basin; the area of the south basin of Lake Biwa that was covered by submerged macrophytes was less than 6 km^2 between 1964 and 1994, but increased to 9 km^2 in 1995, 16 km^2 in 1997, 29 km^2 in 2000 and 43 km^2 in 2002 (Haga *et al.*, 2006). Interestingly, the decline in the abundance of largemouth bass and the proliferation of bluegill in the south basin became obvious around 1995 (Nakai and Hamabata, 2002). According to a test survey that was conducted in 1998 at the northern part of the south basin, the percentage of bluegill in all catches by a set net was 87%, whereas that of largemouth bass was 2% (Kuwamura, 2001). As is well known, competitive and predator-prey relationships exist between largemouth bass and bluegill depending on the growth stage of largemouth bass; although bluegill are strong competitors with young-of-year (YOY) largemouth bass, bluegill become a prey source when the largemouth bass shift to piscivory as they grow (Olson *et al.*, 1995; Olson, 1996; Huskey and Turingan, 2001). Macrophytes provide a habitat for invertebrates that serve as a prey source for both YOY largemouth bass and bluegill. Accordingly, macrophyte beds may induce competition between these species. Before shifting to piscivory, YOY largemouth bass experience severe competition for invertebrates in a vegetated environment not only with bluegill, but also within the species, and their growth tends to be adversely impacted by the population densities of both bluegill and largemouth bass (Olson *et al.*, 1995). Reduced growth can be fatal to YOY largemouth bass since their overwintering success is dependent on the body size (Ludsin and DeVries, 1997; Fullerton *et al.*, 2000). Dense vegetation also affects the predator-prey interaction between largemouth bass and bluegill, usually in favor of bluegill, by providing a valuable refuge for bluegill from predatory largemouth bass (Colle and Shireman, 1980; Savino and Stein, 1982; Wiley *et al.*, 1984); under such conditions, insufficient food intake may delay the growth of largemouth bass. Additionally, the flourishing of bluegill can potentially accelerate the decline of the largemouth bass population, since bluegill actively consume largemouth bass eggs and larvae (Yoshizawa, 1992). In light of these findings, the recently prevailing environment of the south basin of Lake Biwa is thought to be unfavorable to largemouth bass.

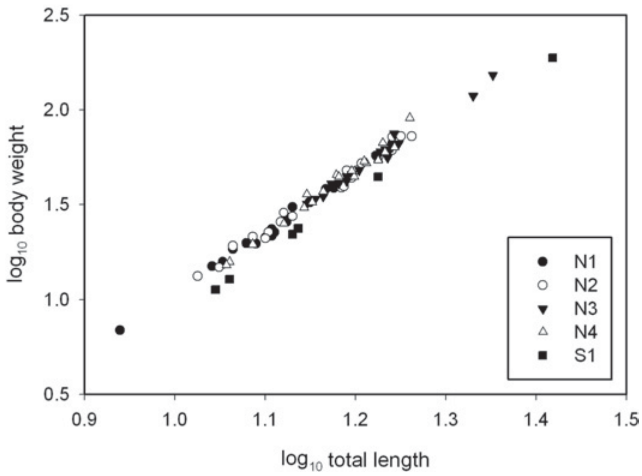

Fig. 2. Relationship between $\log_{10}$ total length and $\log_{10}$ body weight of largemouth bass.

Table 2. Relationship between standard length (*SL*) and body depth (*BD*) of largemouth bass. *a* and *b* are constants in $BD = aSL + b$. N(1–4) represents combined data from the four sites in the north basin. All correlation coefficients (*r*) were significant at $p = 0.01$.

Sites	*a*	*b*	*n*	*r*
N2	0.324	– 0.225	20	0.959
N3	0.324	– 0.258	20	0.954
N1	0.310	– 0.106	20	0.966
N4	0.361	– 0.632	20	0.960
N(1–4)	0.329	– 0.285	80	0.968
S1	0.308	– 0.398	6	0.995

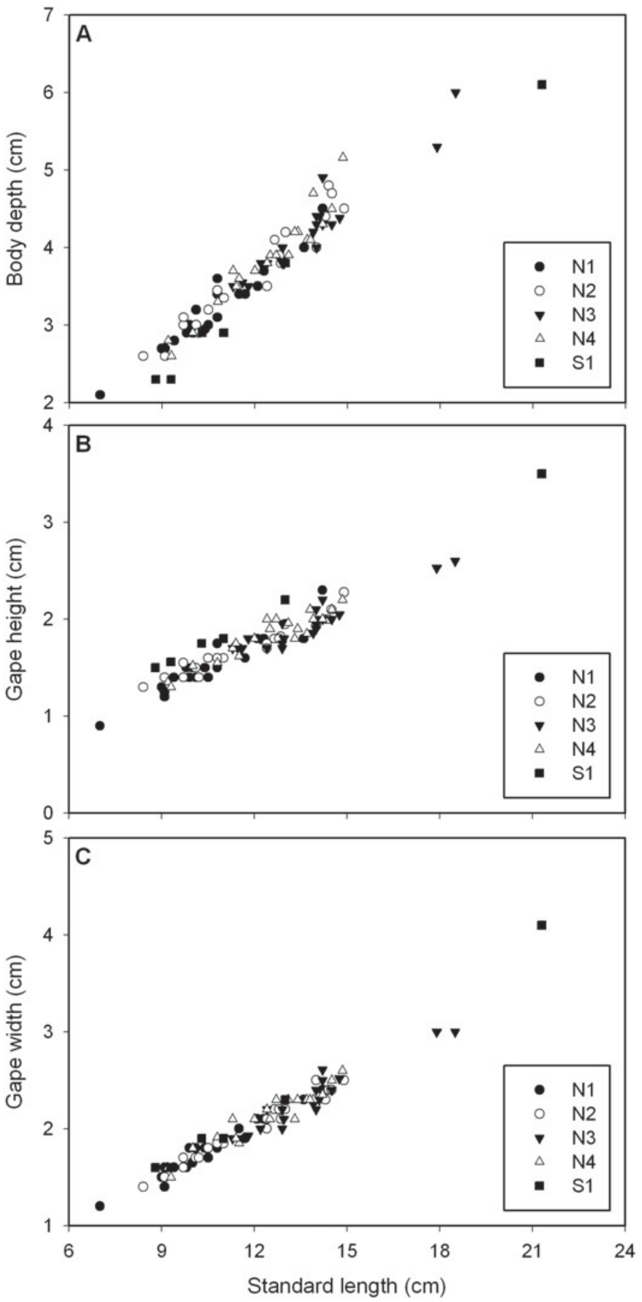

Fig. 3. Relationships between standard length and body depth (A), gape height (B) and gape width (C) of largemouth bass.

Table 3. Relationship between standard length (*SL*) and gape measures (*GM*) of largemouth bass. *a* and *b* are constants in $GM = aSL + b$. N(1–4) represents combined data from the four sites in the north basin. All correlation coefficients (*r*) were significant at $p = 0.01$.

Gape	Sites	*a*	*b*	*n*	*r*
Height	N2	0.128	0.199	20	0.967
	N3	0.131	0.159	20	0.939
	N1	0.165	– 0.218	20	0.942
	N4	0.139	0.094	20	0.937
	N(1–4)	0.138	0.076	80	0.955
	S1	0.162	0.072	6	0.999
Width	N2	0.167	0.019	20	0.986
	N3	0.165	0.025	20	0.954
	N1	0.171	– 0.016	20	0.976
	N4	0.163	0.105	20	0.953
	N(1–4)	0.165	0.047	80	0.976
	S1	0.204	– 0.266	6	0.997

The morphological features of largemouth bass in the north basin, as indicated by the relationships between total length and body weight, standard length and body depth, and standard length and mouth gape, did not significantly vary among the sites. Since the factors that govern the population dynamics of fish, including growth, survival, and reproduction, vary among habitats (Hayes *et al.*, 1996), the similarity of the morphological features of largemouth bass in the north basin suggests that the regional variations in biotic and abiotic factors among sampling sites were small. Additionally, owing to the density-dependence of largemouth bass growth (Olson *et al.*, 1995), variation in the population density of largemouth bass among sites in the north basin appears to be slight.

YOY largemouth bass normally begin to consume fish when their standard length reaches 20–50 mm, thereafter fish become an important part of their diet (Olson, 1996; Huskey and Turingan, 2001). Since bluegill are the overwhelmingly dominant fish species in the south basin of Lake Biwa, they may serve as an important food source for largemouth bass. In the water where bluegill are dominant, an early diet shift to piscivory is critical to the survival of largemouth bass (Olson, 1996). The morphology of some prey fish species – with a ratio of large body depth to body length, as exhibited by bluegill – is thought to serve somewhat as a defense against the predatory behavior of largemouth bass (Webb, 1986; Hambright, 1991). Accordingly, as expected, largemouth bass with a larger gape can consume bluegill more efficiently than those with a normal-sized gape. The mouth gape of the largemouth bass that were collected from the south basin – although the number of samples was small – obviously exceeded that of those sampled from the north basin. The fish in the south basin had a smaller body depth and significantly lower body weights than those in the north basin. Notably, despite the clear morphological difference, the patterns of the weight gain of largemouth bass in the two basins, associated with lengthwise growth, are similar, as suggested by the statistically identical regression slopes of the length-weight relationship. In the south basin of Lake Biwa, only the largemouth bass with a larger mouth are selected during and after the diet shift stage, because the increase in the higher foraging efficiency that is associated with the larger mouth gape may compensate for the disadvantage of low body weight.

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