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# Potential factors affecting the body weight of bluegill *Lepomis macrochirus* in Lake Biwa, Japan

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**Abstract.** Lake Biwa consists of a large, deep north basin and a small, shallow south basin, and the body weights of bluegill *Lepomis macrochirus* in the north basin tend to exceed those in the south basin. To elucidate the cause of this phenomenon, the physical characteristics of the fish in the two basins were compared. The fish in the north basin had larger gonads and stomachs than did the fish in the south basin, but the contributions of these organs to the body weight were very small. The body weights of the fish in the north basin still exceeded those in the south basin after the subtraction of the weights of the gonad and stomach. Bluegill in the north basin had deeper bodies than those in the south basin. The heavier body tissues of bluegill in the north basin appear to be an adaptive response to the colder environment. Given the flourishing of largemouth bass *Micropterus salmoides* in the littoral zone in the north basin, the deeper bodies of bluegill there may contribute to their increased survival rate by reducing their vulnerability to predation by largemouth bass.

**Key words:** morphological variation, length-length relationship, length-weight relationship, adaptation, thermal condition

## Introduction

Bluegill *Lepomis macrochirus* Rafinesque, a temperate freshwater fish species that is native to North America, has been extensively transplanted to numerous countries (Welcomme 1992). Bluegill were introduced into Japan in 1960. They are now distributed countrywide and dominate many water systems, including Lake Biwa, the largest lake (surface area 670 km<sup>2</sup>) in Japan. Bluegill have flourished in the littoral zone of the lake following their introduction into the lake in 1965 (Nakai & Hamabata 2002).

Lake Biwa can be divided into two sections – a large, deep north basin (surface area 618 km<sup>2</sup>, maximum depth 104 m, mean depth 43 m) and a small, shallow south basin (surface area 52 km<sup>2</sup>, maximum depth 7.0 m, mean depth 3.5 m). The south basin is more eutrophic than the north basin, and is characterized by the presence of dense vegetation that covers over 80 % of the area (Haga 2008). Vegetated areas are known to favour the recruitment of bluegill, which can cause overcrowding, resulting in stunted growth (Mittelbach 1988). The same situation appears to prevail in Lake Biwa, in which bluegill

overwhelmingly flourish in the south basin (Mizuno et al. 2007) and the body weights of the fish with a normalized body length in the south basin are significantly lower than those in the north basin (Yamamoto et al. 2010).

The topographical characteristics of the lake cause the south basin to warm up more rapidly than the north basin in the spring and to cool down more rapidly in the autumn. Consequently, the annual mean water temperature in the north basin is lower than that in the south basin (Yamamoto & Kao 2012). Such variation in the thermal condition appears to be responsible for the variations in not only the gonadal maturation (Yamamoto et al. 2011), but also the spawning season (Yamamoto & Shiah 2013) of bluegill in the lake. Likewise, the larger body weight of bluegill in the north basin may perhaps be viewed as a consequence of their adaptation to a colder environment (see Atkinson 1994, Angilletta et al. 2004).

The aim of the present study was to elucidate the cause of variation in the body weight of bluegill in Lake Biwa. The physical characteristics of bluegill after the spawning and growing seasons were compared between the two basins.

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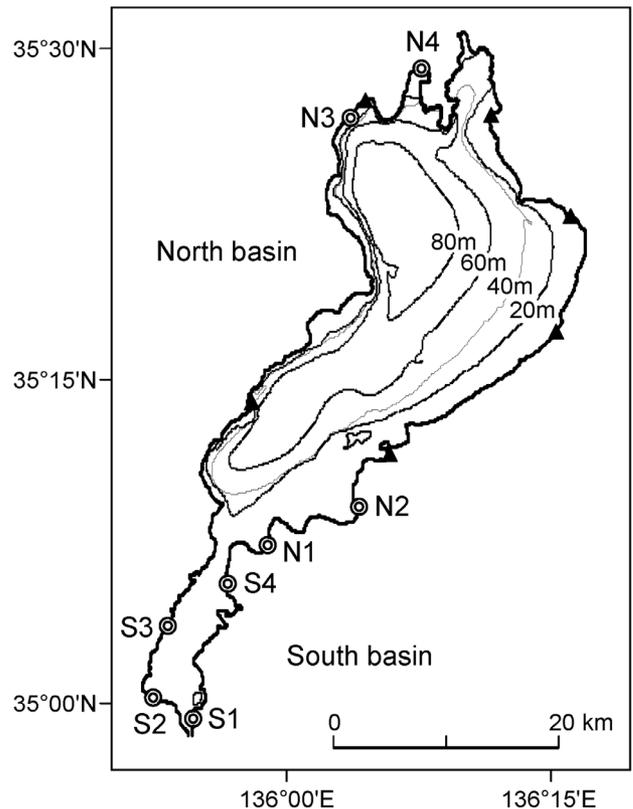
## Material and Methods

Lake Biwa is located in Shiga Prefecture, Japan, at 34°58′–35°31′ N and 135°52′–136°17′ E. This study was conducted between 6 and 13 October 2010, following the normal breeding season (Nakao et al. 2006) and, presumably, the growing season (Yamamoto & Kao 2012) of bluegill in the lake. Fish samples were successfully obtained from eight sites (S1–S4 in the south basin and N1–N4 in the north basin as shown in Fig. 1). Although an attempt was made to collect fish samples at sites whose latitudes were between those of sites N2 and N3 (Fig. 1), no fish were found at those sites. All samples were collected using a rod and line; this sampling method was effective for the selective collection of specimens with a body size above a particular threshold in a short period. Captured fish were immediately euthanized with an overdose of ethyl 3-aminobenzoate methanesulfonate salt (MS-222).

The standard length and body depth of the specimens were measured to the nearest 0.01 mm using a digital caliper CD-8<sup>™</sup>CSX (Mitsutoyo, Kanagawa, Japan). Body weight was measured to the nearest 0.1 g using a portable digital scale MP-1000 (Ashiba, Taipei, Taiwan). Gonads and stomachs were isolated and weighed to the nearest 0.002 g using a portable digital scale 1210N (Tanita, Tokyo, Japan). Three specimens collected at site N2 contained soft plastic lures in their stomachs, and were excluded from all analyses. One female collected at site S1 had an exceptionally large

**Table 1.** Minimal, maximal and mean standard length (mm) of bluegill specimens at each site.

Sex	Site	<i>n</i>	min	max	mean	SE
Male	N4	35	63.54	137.22	93.64	3.56
	N3	22	53.93	134.12	98.11	4.52
	N2	39	58.10	150.30	115.39	3.79
	N1	29	52.32	120.37	88.93	3.25
	S4	40	68.77	107.80	87.08	1.52
	S3	43	57.22	141.23	87.86	2.69
	S2	52	60.10	110.06	87.55	1.58
	S1	28	58.40	120.10	87.99	2.78
Female	N4	27	61.15	136.04	98.28	4.04
	N3	14	54.51	119.93	84.34	4.98
	N2	24	50.60	126.34	103.56	4.18
	N1	28	74.80	112.13	86.87	1.99
	S4	20	62.47	112.96	81.85	2.22
	S3	19	58.15	98.73	77.43	2.71
	S2	18	59.30	128.72	88.44	3.82
	S1	37	63.48	101.73	86.00	1.65

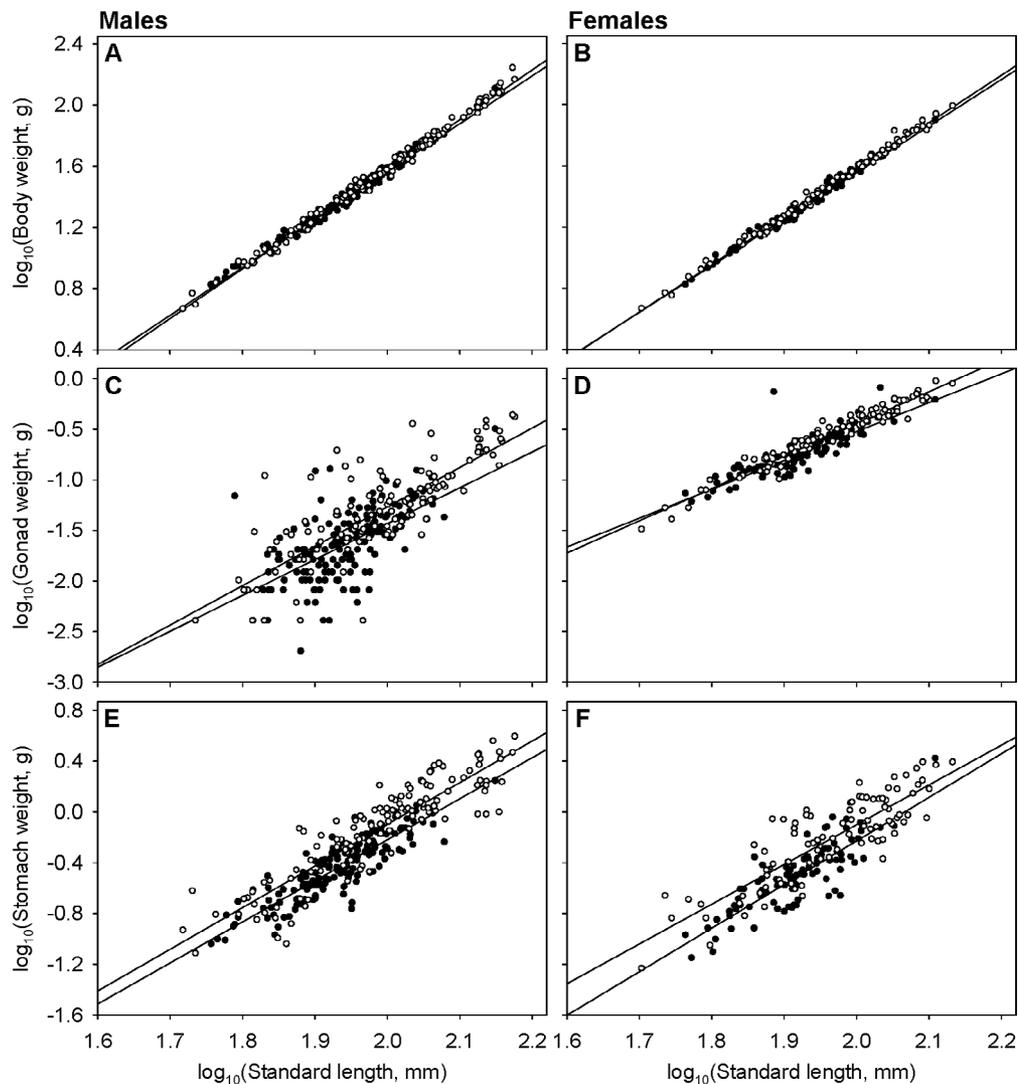


**Fig. 1.** Map of Lake Biwa showing sampling sites. Fish samples were successfully collected at sites indicated by double circles (sites S1–S4 and N1–N4); no samples were collected at any sites indicated by closed triangles. Lines on map indicate depth of lake.

ovary (see Results); it was included in the analyses unless otherwise stated. The specimens collected from sites S1–S4 and sites N1–N4 were pooled as specimens from the south and the north basins, respectively. The binomial test was used to compare the numbers of males and females collected from each basin. The standard lengths of the specimens were compared between the two basins using the *t*-test. The relationships of body weight, gonad weight, stomach weight and body depth with standard length were assessed by Pearson's correlation coefficients, and the difference in the regression lines between the basins was assessed by ANCOVA. The *t*-test was performed to compare the ratios of gonad weight to body weight and of stomach weight to body weight between the basins. The level of statistical significance was set at  $P < 0.05$ .

## Results

A total of 257 fish (163 males and 94 females) were collected from the south basin, and 218 fish (125 males and 93 females) were collected from the north basin. In each basin, the number of males significantly exceeded the number of females (binomial test,  $P < 0.05$ ). The standard lengths of males and females

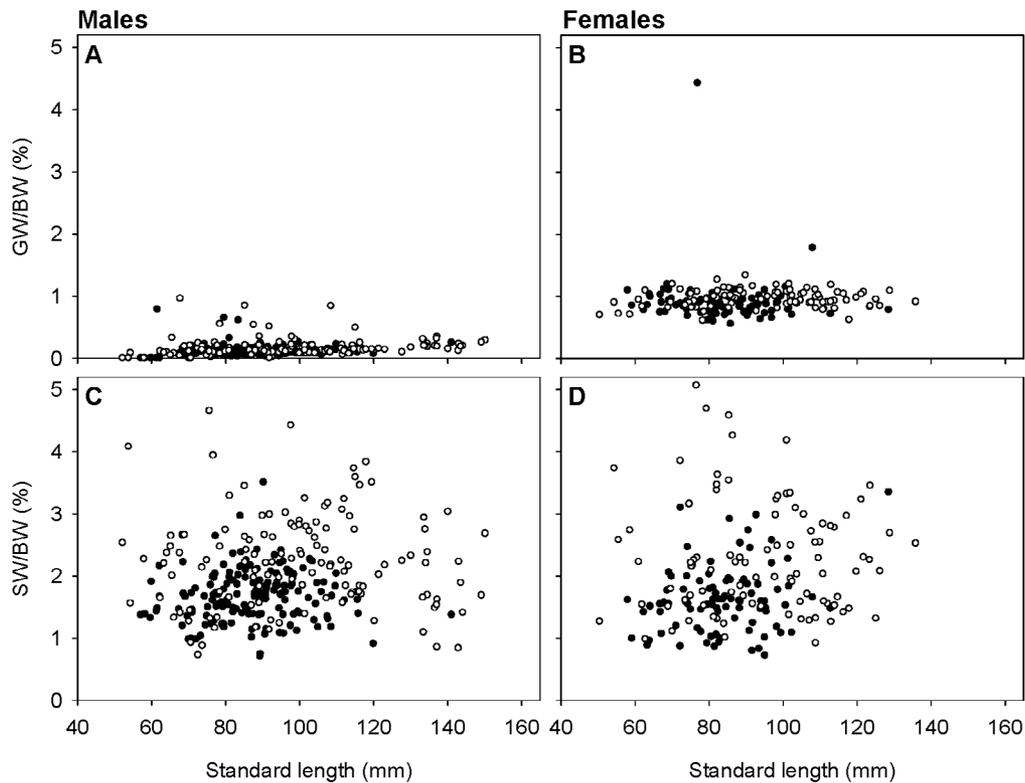


**Fig. 2.** Relationships between body weight and standard length (A, B), between gonad weight and standard length (C, D) and between stomach weight and standard length (E, F) of bluegill in Lake Biwa. Closed circles and open circles denote data for south and north basins, respectively.

ranged from 52.32 to 150.30 mm and from 50.60 to 136.04 mm, respectively (Table 1). The mean standard length of males in the north basin ( $100.12 \pm 2.11$  SE) significantly exceeded the mean standard length of males in the south basin ( $87.59 \pm 1.05$  SE) ( $t$ -test,  $P < 0.001$ ). Similarly, the mean standard length of females in the north basins of the lake ( $94.11 \pm 1.99$  SE) significantly exceeded the mean standard length of females in the south basin ( $83.85 \pm 1.26$  SE) ( $t$ -test,  $P < 0.001$ ).

The  $\log_{10}$ -transformed body weight was significantly correlated with the  $\log_{10}$ -transformed standard length (south basin: males,  $y = 3.13x - 4.70$ ,  $r = 0.99$ ,  $P < 0.001$ , females,  $y = 3.04x - 4.53$ ,  $r = 0.99$ ,  $P < 0.001$ ; north basin: males,  $y = 3.25x - 4.93$ ,  $r = 1.00$ ,  $P < 0.001$ , females,  $y = 3.10x - 4.62$ ,  $r = 1.00$ ,  $P < 0.001$ ) (Fig. 2A-B). ANCOVA revealed that the regression lines significantly differed between the

basins (males: slope,  $F_{1,284} = 9.60$ ,  $P < 0.01$ ; females: slope,  $F_{1,183} = 1.17$ ,  $P = 0.28$ , intercept,  $F_{1,184} = 13.9$ ,  $P < 0.001$ ), showing that the fish in the north basin tended to be heavier than those in the south basin. The  $\log_{10}$ -transformed gonad weight significantly increased with the  $\log_{10}$ -transformed standard length (south basin: males,  $y = 3.55x - 8.53$ ,  $r = 0.61$ ,  $P < 0.001$ , females,  $y = 2.85x - 6.23$ ,  $r = 0.85$ ,  $P < 0.001$ ; north basin: males,  $y = 3.90x - 9.06$ ,  $r = 0.81$ ,  $P < 0.001$ , females,  $y = 3.19x - 6.83$ ,  $r = 0.97$ ,  $P < 0.001$ ) (Fig. 2C-D). ANCOVA revealed that the regression lines significantly differed between the basins (males: slope,  $F_{1,284} = 13.3$ ,  $P < 0.001$ ; females: slope,  $F_{1,183} = 3.30$ ,  $P = 0.07$ , intercept,  $F_{1,184} = 13.0$ ,  $P < 0.001$ ), showing that the fish in the north basin tended to have larger gonads than those in the south basin. The  $\log_{10}$ -transformed stomach weight increased significantly with the  $\log_{10}$ -transformed standard length (south



**Fig. 3.** Contributions of gonad weight (A, B) and stomach weight (C, D) to body weight of bluegill in Lake Biwa. BW, GW and SW indicate body weight, gonad weight and stomach weight, respectively. Closed circles and open circles denote data for south and north basins, respectively.

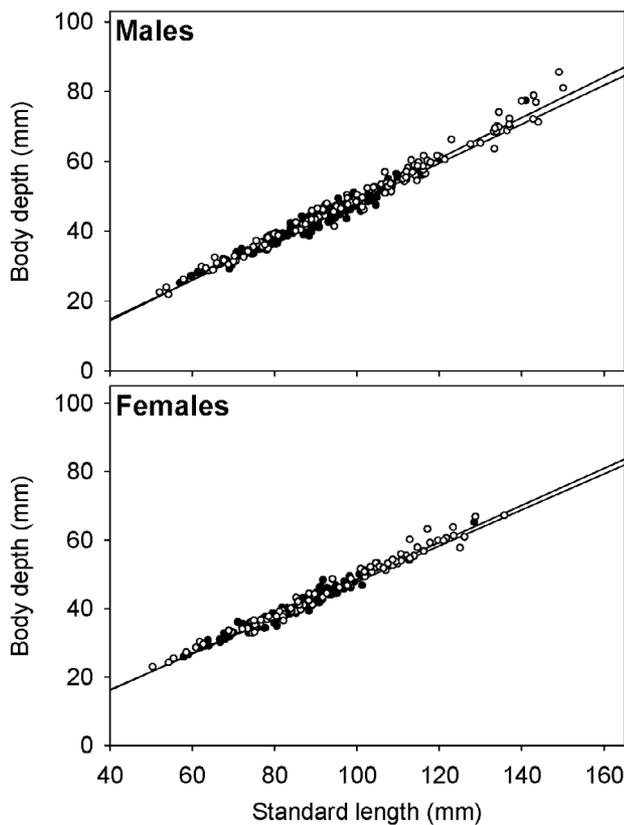
basin: males,  $y = 3.23x - 6.69$ ,  $r = 0.88$ ,  $P < 0.001$ , females,  $y = 3.43x - 7.09$ ,  $r = 0.84$ ,  $P < 0.001$ ; north basin: males,  $y = 3.28x - 6.66$ ,  $r = 0.90$ ,  $P < 0.001$ , females,  $y = 3.13x - 6.36$ ,  $r = 0.86$ ,  $P < 0.001$ ) (Fig. 2E-F). ANCOVA revealed that the regression lines significantly differed between the basins (males: slope,  $F_{1,284} = 0.055$ ,  $P = 0.81$ , intercept,  $F_{1,285} = 47.5$ ,  $P < 0.001$ ; females: slope,  $F_{1,183} = 0.92$ ,  $P = 0.34$ , intercept,  $F_{1,184} = 38.0$ ,  $P < 0.001$ ), showing that the fish in the north basin tended to have larger stomachs than those in the south basin. Neither gonad weight nor stomach weight affected the correlation between body weight and standard length (data not shown). The ratio of the gonad weight to the body weight (GW/BW) for males varied greatly among specimens; 13 specimens had a GW/BW of zero because their testes were minuscule, whereas the GW/BW of some males exceeded the mean by a large factor (Fig. 3A). No significant correlation was found between GW/BW and standard length for males (south basin:  $r = 0.083$ ,  $P = 0.29$ ; north basin:  $r = 0.11$ ,  $P = 0.22$ ), and the mean GW/BW of the fish in the north basin significantly exceeded that of the fish in the south basin ( $t$ -test,  $P < 0.001$ ) (Table 2). With the exception of one specimen with a GW/BW of 4.42 %, which was collected from site S1, the GW/BW of all females ranged from 0.55

to 1.78 % (Fig. 3B). No significant correlation existed between the GW/BW of females and their standard length (south basin:  $r = 0.072$ ,  $P = 0.49$ ; north basin:  $r = 0.076$ ,  $P = 0.47$ ). The aforementioned specimen was clearly responsible for the lack of a significant difference in the mean GW/BW of the fish between the basins ( $t$ -test,  $P = 0.22$ ), since the GW/BW of the fish in the north basin significantly exceeded those of the fish in the south basin ( $t$ -test,  $P < 0.001$ ) when this specimen was excluded from the analysis. For both sexes, the ratio of stomach weight to body weight (SW/BW) greatly exceeded GW/BW (Table 2). The ratio for males ranged from 0.70 to 4.65 % and that for females ranged from 0.72 to 5.06 % (Fig. 3C-D). The correlation between SW/BW and standard length was insignificant for males (south basin:  $r = 0.044$ ,  $P = 0.58$ ; north basin:  $r = 0.022$ ,  $P = 0.80$ ), but was significant for females in the south basin (south basin:  $y = 0.00959x + 0.810$ ,  $r = 0.22$ ,  $P < 0.05$ ; north basin:  $r = 0.032$ ,  $P = 0.76$ ). The mean SW/BW of the fish in the north basin significantly exceeded that of the fish in the south basin ( $t$ -test,  $P < 0.001$ ). Body depth increased linearly with standard length (south basin: males,  $y = 0.558x - 7.49$ ,  $r = 0.98$ ,  $P < 0.001$ , females,  $y = 0.525x - 4.71$ ,  $r = 0.98$ ,  $P < 0.001$ ; north basin: males,  $y = 0.581x - 8.84$ ,  $r = 0.99$ ,  $P <$

**Table 2.** Mean ratio of gonad weight to body weight (GW/BW) and mean ratio of stomach weight to body weight (SW/BW) for bluegill in Lake Biwa.

Sex	Basin	n	GW/BW (%)		SW/BW (%)	
			Mean	SE	Mean	SE
Male	North	125	0.171	0.013	2.241	0.069
	South	163	0.111	0.008	1.680	0.033
Female	North	93	0.959	0.014	2.289	0.094
	South	94	0.906	0.041	1.610	0.054
	South*	93	0.868	0.017		

\* Result when a fish with an exceptionally large ovary was excluded.



**Fig. 4.** Relationship between body depth and standard length of bluegill in Lake Biwa. Closed circles and open circles denote data for south and north basins, respectively.

0.001, females,  $y = 0.540x - 5.45$ ,  $r = 0.99$ ,  $P < 0.001$ ) (Fig. 4). ANCOVA revealed that the regression lines significantly differed between the two basins (males: slope,  $F_{1,284} = 3.83$ ,  $P = 0.051$ , intercept,  $F_{1,285} = 12.5$ ,  $P < 0.001$ ; females: slope,  $F_{1,183} = 1.07$ ,  $P = 0.30$ , intercept,  $F_{1,184} = 6.04$ ,  $P < 0.05$ ), showing that the fish in the north basin tended to have deeper bodies than those in the south basin.

## Discussion

This study showed that the body weights of bluegill collected from the north basin of Lake Biwa tended

to exceed those from the south basin, verifying our earlier finding (Yamamoto et al. 2010). The finding of the larger stomach weight of the fish in the north basin may imply that the fish therein were actively feeding. However, the body weight minus the stomach weight was also larger for the fish in the north basin, suggesting that the contribution of stomach weight to body weight was too small to account for the difference in the body weight of bluegill between the two basins.

For females, ovary weight critically influences the total body weight in the prespawning season (Yamamoto et al. 2011). Nakao et al. (2006) reported that the spawning season of bluegill at the northern edge of Lake Biwa (near site N4) starts in early June and ends before September. Although Yamamoto & Shiah (2013) suggested that bluegill in the south basin start to spawn earlier and have a shorter spawning season than those in the north basin, the collection of a specimen with an exceptionally high GW/BW at site S1 may suggest the presence of fish in the south basin that can spawn even in autumn. According to Yamamoto & Shiah (2013), the lowest gonadosomatic index ( $GW/BW \times 100$ ) of a specimen that was considered to be mature, based on the size of the largest oocyte, was 4.90. The possibility that the above specimen had mature oocytes when it was captured cannot be completely ruled out; however, even though it was ready to spawn, it might not actively spawn.

Some males also exhibited an exceptionally high GW/BW. Male bluegill are known to have a discrete polymorphism in life histories that are called “parental” and “cuckolder”. The latter is characterized by precocious maturation with a larger investment in reproduction than the former (Gross 1982). Thus, the males with a GW/BW of greater than approximately 0.6 % appeared to be cuckolders. Regardless of sex, the gonad size generally had little influence on the total body weight of bluegill in October.

The conclusion that can be drawn from the results of this study is that not only particular organs, such as the stomach and gonad, but also the body tissues of bluegill in the north basin become heavier than those in the south basin. Bluegill is generally considered to be a sedentary species (Fish & Savitz 1983), so they appear to adopt optimal physiological patterns depending on their habitats. The environmental conditions differ greatly between the south and the north basins of Lake Biwa, and consequently the bluegill in the lake may exhibit basin-specific adaptive responses. It is well known that numerous ectotherms adapt to colder regions by increasing

their body size at the cost of a reduced growth rate (Atkinson 1994, Angilletta et al. 2004). Yamamoto & Kao (2012) hypothesized that bluegill inhabiting the higher latitudes of Lake Biwa grow slowly during long growing seasons and eventually become larger than the fish at lower latitudes. Therefore, the heavier organs and body tissues of the bluegill in the north basin may be regarded as a consequence of their adaptation to colder environments.

The fish in the north basin had deeper bodies than those in the south basin. If the variation in fish body density in the lake is negligible, the fish in the north basin must be heavier than those in the south basin because of their larger bodies, explaining the difference between the body weights of the bluegill in the two basins. Although the majority of the specimens were assumed to be sufficiently large to reproduce (Yokogawa 1992, Yamamoto & Shiah 2013), any change in body shape owing to the development of a gonad, as typically becomes evident in females in the prespawning season, is clearly negligible in this study. One explanation of this phenomenon is that the deeper bodies of fish in the north basin reflect an adaptive response to the colder environment, as discussed above.

Another hypothetical explanation of the deeper bodies of fish in the north basin involves predators. Largemouth bass *Micropterus salmoides* Lacépède, which are the main predators of bluegill in their native environment, have inhabited Lake Biwa since 1974, and they flourish in the littoral zone (Nakai & Hamabata 2002). Given that the population density of largemouth bass in the littoral zone of the north basin

greatly exceeds that in the south basin (Yamamoto & Tsukada 2010), the bluegill in the north basin are potentially at higher risk of largemouth bass strikes. Combined with the fact that deeper bodies contribute to reduce the vulnerability to predation by largemouth bass (Hambright 1991, Huskey & Turingan 2001), either largemouth bass strikes may have imposed greater selection pressure on bluegill with deeper bodies in the north basin or bluegill in the north basin may have increased their body depths in response to the presence of largemouth bass (see Januszkiewicz & Robinson 2007). Since largemouth bass in the north basin have smaller gapes than those in the south basin (Yamamoto & Tsukada 2010), having deeper bodies seems effectively to increase the survival rate of bluegill in the north basin.

Bluegill are known to adopt the optimal foraging behaviour for their habitat, and this behaviour is closely related to phenotypic variation among individuals in a water body (Ehlinger & Wilson 1988, Ehlinger 1990). Bluegill in Lake Biwa adopt three forms of foraging (benthivorous, planktivorous and herbivorous types) as they grow, and these are associated with particular morphometric characteristics (Yonekura et al. 2002, see also Uchii et al. 2007). Whether the phenotypic plasticity of bluegill explains the difference between the body weights of fish in the south and the north basins warrants testing.

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