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Latitudinal Gradient in the Body Weight of Bluegill *Lepomis macrochirus* in Lake Biwa, Japan

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Yoshimasa Yamamoto, Hajime Tsukada, and Daisuke Nakai (2010) Latitudinal gradient in the body weight of bluegill *Lepomis macrochirus* in Lake Biwa, Japan. *Zoological Studies* **49**(5): 625-631. Variations in the body weight of bluegill *Lepomis macrochirus* among 10 coastal regions of Lake Biwa and 11 lagoons of the lake were studied in Oct. 2005 and Oct. 2007, respectively. The body weights of fish with a normalized total length were estimated from length-weight relationships determined at each site. Body weights of bluegill from the lake and lagoons increased linearly with latitude. Additionally, there was a negative correlation between the calculated body weight and the number of sampled bluegill per unit time from the lagoons, implying that the population density of bluegill may strongly influence its growth in lagoons. Increasing numbers of submerged plants have covered the lake area in recent years, especially in the shallow southern basin. Moreover, as a predator of bluegill, the largemouth bass *Micropterus salmoides* appears to flourish at higher densities in the northern basin of the lake than in the southern basin. These biotic factors seem to be somewhat responsible for the significant difference between the northern and southern basins in terms of the body weight of bluegill. However, water temperature and population density of the bluegill appear to be more directly responsible for the latitudinal variation in bluegill growth in Lake Biwa. http://zoolstud.sinica.edu.tw/Journals/49.5/625.pdf

Key words: Bluegill, Body weight, Length-weight relationship, Latitude, Lake Biwa.

Understanding the growth performance of fish and factors regulating their growth is essential for the success of aquaculture and leisure angling, and has been one of the central topics in fish research. In particular, the growth of freshwater fish has attracted considerable attention, since certain species with various ranges of morphology and interspecific interactions appear in numerous aquatic systems with different water qualities. Bluegill *Lepomis macrochirus* Rafinesque has been extensively studied due to its widespread distribution and importance as a game fish in North America, the place of its origin. Comparing the growth rates and size structures of bluegill from numerous water bodies suggested how biotic and abiotic factors may impact bluegill growth. For instance, prey availability is of critical importance when determining fish growth (Hoxmeier et al. 2009). Temperature positively influences bluegill growth (Tomcko and Pierce 2001, Hoxmeier et al. 2009), which is assumed to be related to feeding behavior. That is, as bluegill is a thermophylic species, its feeding activity is promoted at higher temperatures. Clear water may also enable bluegill to find prey more easily, subsequently enhancing growth (Hoxmeier et al. 2009), although high productivity with low transparency may facilitate early growth (Tomcko and Pierce 2005). Increased

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population density intensifies intraspecific competition for diet materials, and can restrict growth (Wiener and Hanneman 1982, Osenberg et al. 1988). How predators impact bluegill growth seems to vary depending on the predator species and their abundances (Tomcko and Pierce 2005).

These conclusions were normally drawn by comparing bluegill populations among numerous geographically separated water bodies under the assumption that each water body has distinct limnological features, which are reflected in the growth and size structure of bluegill. However, an environment may vary from section to section within the same water body. Moreover, the feeding habits of bluegill can vary within a population. Yonekura et al. (2002) found trophic polymorphism in the bluegill population in Lake Biwa, Japan, and the 3 morphs, i.e., benthivorous, herbivorous, and planktivorous types, exhibited identifiable morphological variations. Considering the presence of various environmental conditions in Lake Biwa and trophic polymorphism of bluegill within a given population, it is no wonder that bluegill growth may vary from section to section in this water body.

Many previous studies of fish growth often categorized fish based on their ages, as estimated from scales or otoliths. However, considering that not only growth (Putman et al. 1995, Shoup et al. 2007), but also shifts in diet and habitat, relationship with predators, and onset of sexual maturation of bluegill are strongly related to the body size rather than age (Mittelbach 1981, Osenberg et al. 1988, Werner and Hall 1988, Belk 1995), size-based investigations are expected to provide more-significant information on various aspects of bluegill ecophysiology.

The aim of present study was to consider whether bluegill growth varies within a lake, depending on the habitat. We collected fish samples from 21 sites within Lake Biwa, and length-weight relationships were determined for each site. Body weights of fish with a normalized length were calculated from power functions and compared among sites.

MATERIALS AND METHODS

Study site

Lake Biwa is located in Shiga Prefecture, Japan, at latitudes of 34°58'N-35°31'N and longitudes of 135°52'E-136°17'E (Fig. 1). Topographically, the lake can be divided into a deep northern basin (surface area 618 km^2, maximum depth 104 m, mean depth 43 m) and a shallow southern basin (surface area 52 km^2, maximum depth 7.0 m, mean depth 3.5 m). Having successfully adapted to the lake after being transplanted over 4 decades ago (Terashima 1977), bluegill has become the overwhelmingly dominant species in coastal areas, including lagoons, in terms of population and distribution (Mizuno et al. 2007). The dominance of bluegill in Lake Biwa can be attributed to its distinct survival strategies such as a wide range of diet, the ability of females to deposit tens of thousands of eggs at a time and of males to guard eggs and fry, and diverse reproductive behaviors in males (Dominey 1981, Gross 1982, National Federation of Inlandwater Fisheries Cooperative 1992). Additionally, the lack of congeneric competitors in the lake seems to have facilitated the propagation of bluegill (Azuma 1992).

Sampling of bluegill in the lake and lagoons

Bluegill were sampled on 16, 17, 24, and 26 Oct. 2005 from 10 sites along the shores of Lake Biwa (N1, N2, N3, N4, and N5 in the northern basin, and S1, S2, S3, S4, and S5 in the southern basin; Fig. 1). All lakeshores where the sampling sites are located were paved with concrete or stone. Fish were collected with a rod and line by 1 or 2 of the authors, spending less than 1 h per site due to considerations of efficiency. Angling was stopped once the number of captures reached 30 within 1 h. Captured fish were stored in a cooler with ice. The total length (L) and body weight (W) of each specimen were measured to an accuracy of 0.1 cm and 0.1 g, respectively. Length-weight relationships were estimated by adjusting an allometric power function $W = aL^b$ to the data, where a and b are the initial growth coefficient and relative growth coefficient, respectively. Since the number of available samples was low, males and females were not separated to determine the length-weight relationship. Sampling was performed twice at N1, N2, N4, N5, and S4 on different days, and the data of samples obtained from each site were mixed to estimate the length-weight relationships of bluegill.

Likewise, bluegill were sampled on 13, 16, and 18 Oct. 2007 from 11 sites within lagoons of Lake Biwa (NW1, NW2, and NW3 along the west coast of the northern basin; NE1, NE2, NE3, and NE4 along the east coast of the northern basin;

SW1 along the west coast of the southern basin; and SE1, SE2, and SE3 along the east coast of the southern basin; Fig. 1). Each lagoon is connected to the lake by canals that allow the movement of fish. Sites NE3 and NE4 used to be parts of the same lagoon: they were separated after most of the original enormous lagoon was reclaimed over 4 decades ago to create farmland, explaining why these sites are separated from the main lake. Angling was performed by 2 of the authors for 1 h regardless of the number of captures, but by one of the authors for 2 h at site NW3. Length-weight relationships of the bluegill were determined by the aforementioned method.

RESULTS

The number of collected fish samples from each site ranged from 9 to 60 (Table 1). Large fish were frequently captured from the northern basin of the lake (Fig. 2). Latitude and size structure of bluegill from the lagoons did not appear to be related (Fig. 3). The *L* and *W* of bluegill from the lake (n = 398) ranged 6.0-18.4 cm with a mean of 11.0 cm and 3.0-133.7 g with a mean of 26.7 g,

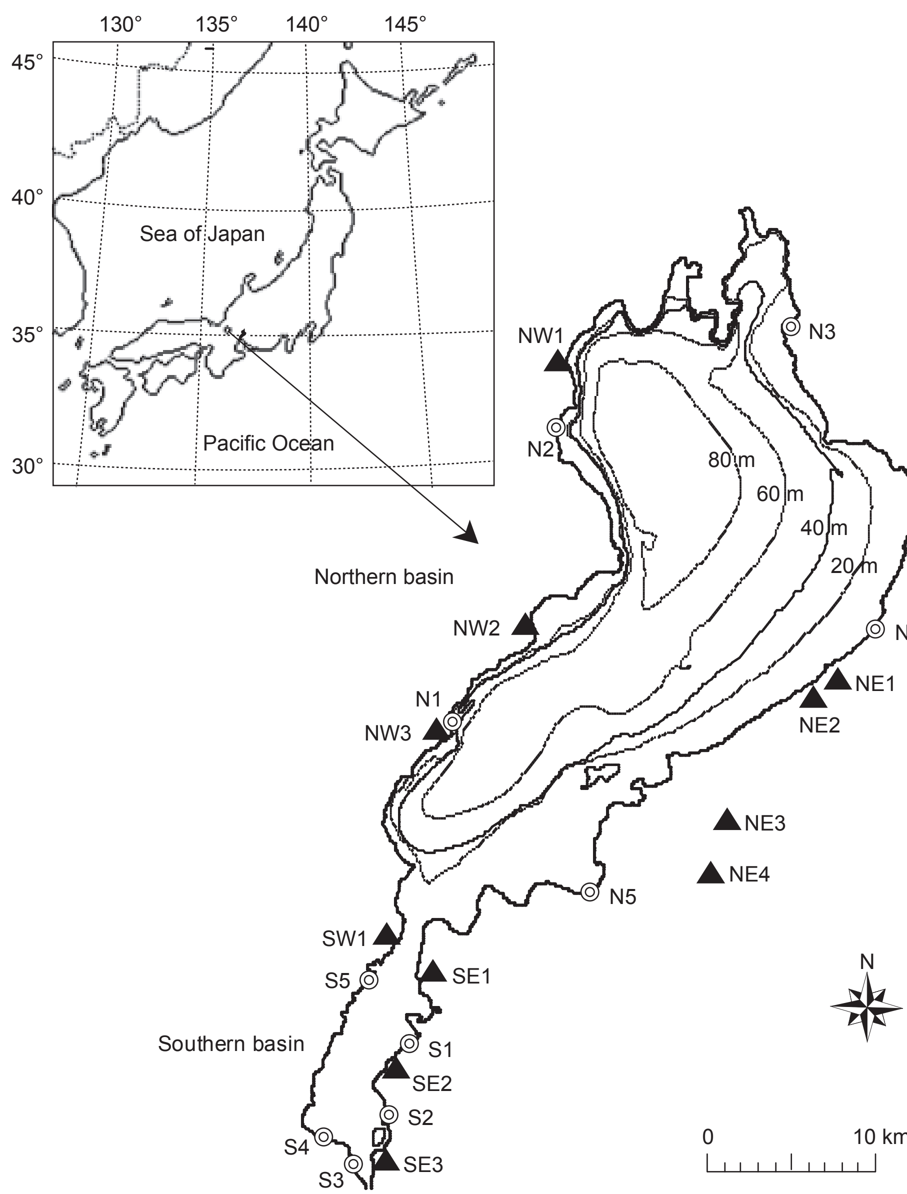

Fig. 1. Location of Lake Biwa and sampling sites. Double circles and closed triangles represent sites on the lake and in lagoons, respectively.

respectively. The *L* and *W* of bluegill from lagoons ($n = 341$) ranged 6.0-21.8 cm with a mean of 11.3 cm and 3.2-251.8 g with a mean of 28.2 g, respectively.

Figure 4 shows the relationship between latitude and calculated *W* of bluegill with an *L* of 11.1 cm (the mean *L* of all specimens in this study, $n = 739$) in the lake and lagoons. *W*s of bluegill from the northern basin of the lake surpassed those from the southern basin of the lake (*t*-test, $p < 0.01$). The calculated *W* of bluegill from the lake clearly increased with latitude (Pearson's product moment correlation coefficient, $r^2 = 0.960$, $n = 10$, $p < 0.01$). A significant positive correlation was also found between latitude and calculated *W* of bluegill from the lagoons (Pearson's product moment correlation coefficient, $r^2 = 0.375$, $n = 10$, $p < 0.05$) if site NE1 data were excluded because it was calculated using an extremely small sample size, possibly making the estimated value unreliable. Furthermore, the calculated *W* and number of sampled bluegill from lagoons were negatively correlated (Spearman's rank correlation coefficient, $r = -0.750$, $n = 9$, $p < 0.05$) when data from sites NE1 and NW3 were excluded, owing to either being too small of a sample size or using a different angling method to collect the bluegill samples.

Table 1. Length-weight relationships of bluegill at each site. Data were collected in Oct. 2005 from the lake and Oct. 2007 from lagoons. All correlation coefficients of regression lines were significant at $p = 0.01$

	$W = aL^b$			
Sites	*a*	*b*	*n*	*r*
Lake				
N3	0.0075	3.38	23	0.998
N2	0.0094	3.29	44	0.997
N4	0.0071	3.38	60	0.997
N1	0.0091	3.25	37	0.997
N5	0.0079	3.31	54	0.998
S5	0.0062	3.36	30	0.995
S1	0.0092	3.20	30	0.993
S2	0.0103	3.14	30	0.992
S4	0.0097	3.16	60	0.996
S3	0.0076	3.27	30	0.992
Lagoons				
NW1	0.0054	3.48	18	0.998
NW2	0.0099	3.21	24	0.998
NE1	0.0073	3.39	9	0.995
NE2	0.0096	3.23	22	0.993
NW3	0.0069	3.38	46	0.987
NE3	0.0110	3.18	19	0.999
NE4	0.0076	3.32	39	0.997
SW1	0.0094	3.25	36	0.991
SE1	0.0079	3.29	60	0.994
SE2	0.0099	3.20	35	0.998
SE3	0.0074	3.33	33	0.990

DISCUSSION

The annual growth of bluegill in North America exhibits a negative trend with latitude (Modde and Scalet 1985, Belk and Houston 2002). This was assumed to be because bluegill, as do many aquatic animals, adapt to warm environments. Low-latitude regions therefore provide preferable climatic conditions for maintaining the high physiological activity of bluegill and supporting the propagation of their prey species. Our analysis indicates that the *W* of bluegill with a standardized *L* increased with latitude across

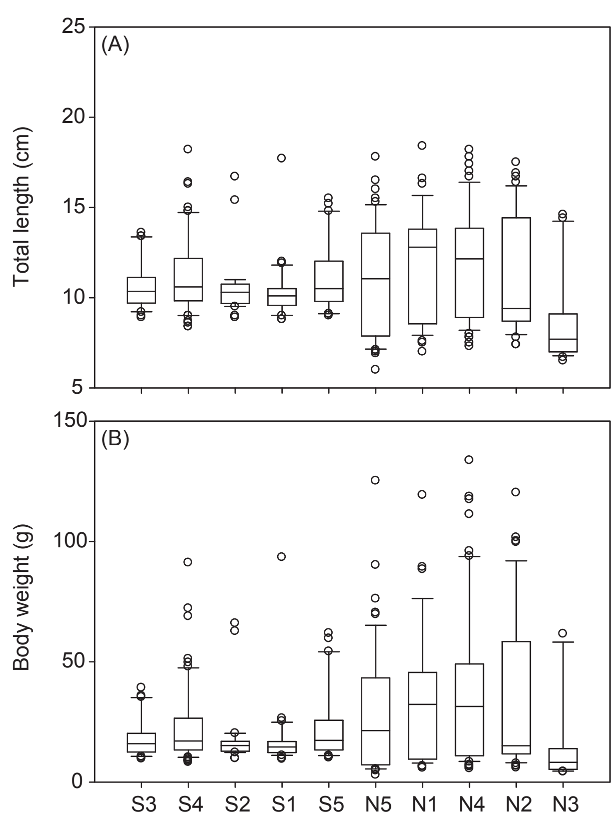

Fig. 2. Box plots showing the ranges of total length (A) and body weight (B) of bluegill captured in the lake. The 25th, 50th, and 75th percentiles are represented by horizontal lines, and the 5th and 95th percentiles are represented by error bars. Open circles represent outliers.

Lake Biwa, implying that bluegill growth, at least in the autumn, is enhanced at higher latitudes in the lake. This finding may conflict with anticipated results from previous studies. Notably, in the present study, a latitudinal size variation of fish was observed within the lake with a narrow latitude range viewed on a global scale. The relationship between the body size of animals and latitude has received considerable attention. Bergmann's rule is a macroecological theory, describing the positive trend of homeothermal animals with latitude (Bergmann 1847). Belk and Houston (2002) indicated that Bergmann's rule does not apply to bluegill populations in North America. However, results of the present study suggest that bluegill can exhibit regional variations within a large water body, in accordance with a Bergmann's rule-like trend.

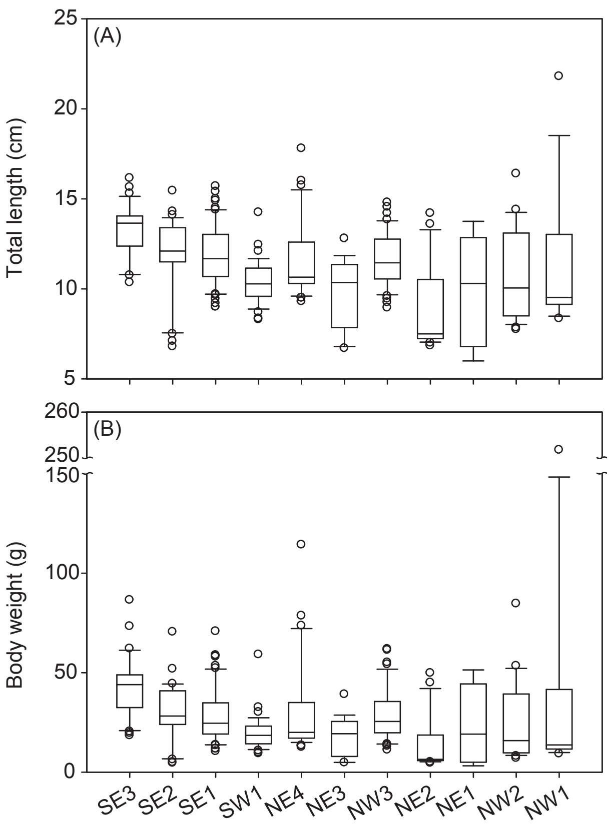

Fig. 3. Box plots showing the ranges of total length (A) and body weight (B) of bluegill capture in the lagoons. The other information is the same as that described in figure 2.

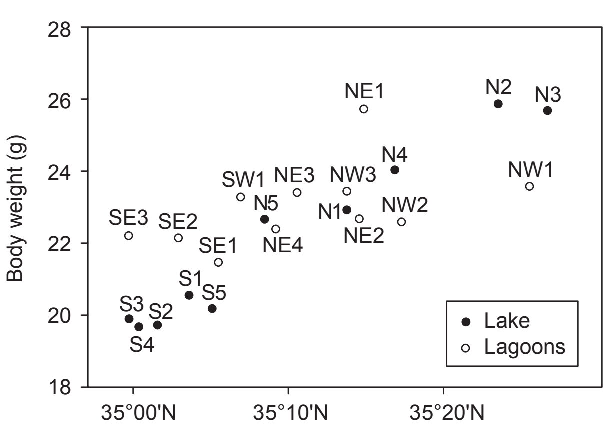

Fig. 4. Relationship between latitude and calculated body weight of bluegill with a total length of 11.1 cm.

Whether a variation in stomach contents or tissue weight is responsible for the latitudinal variation in *W* of bluegill in Lake Biwa remains unclear. In each case, the regular variation in the *W* of bluegill suggests that metabolic activities relating to feeding and growth vary with latitude. As factors that vary with latitude, temperature and day length influence fish growth (Woiwode and Adelman 1991, Boeuf and Le Bail 1999, Ginés et al. 2004). Data collected at 6 sites across the shore of Lake Biwa from 2001 to 2004 (Lake Biwa Environmental Research Institute 2010) show that the annual mean temperatures, except for those in 2002, significantly decreased with latitude (r^2 = 0.703-0.898, n = 6, $p < 0.05$), although the temperature differed only slightly (0.9-6.3°C). In contrast, correlations between latitude and annual hours of sunshine, as measured at 5 sites around Lake Biwa during the same period (Japan Meteorological Agency 2009), were always insignificantly negative (r^2 = 0.002-0.173, n = 5, $p > 0.1$). Accordingly, latitudinal variation in water temperature may be at least partially responsible for why the *W* of bluegill varies.

The biotic factors in Lake Biwa that may affect bluegill growth are the propagation of submerged plants and the presence of largemouth bass *Micropterus salmoides* Lacépède. The area of the distribution of submerged plants has been increasing in Lake Biwa since 1994 (Hamabata and Kobayashi 2002). In particular, the shallow southern basin provides an ideal environment for the development of heavy macrophyte beds; according to estimates, the area covered by macrophytes reached approximately 80% of the total area of the southern basin in 2006 (Haga 2008). Dense vegetation tends to favor the propagation of bluegill (Bettoli et al. 1993, Cross and McInerny 2005), while possibly suppressing their growth (Olson et al. 1998). This phenomenon can be explained by noting the role of macrophyte beds in providing refuge for bluegill from predators such as largemouth bass, which can potentially improve the growth of bluegill by preventing their surplus production (Savino and Stein 1982, Trebitz et al. 1997). Therefore, the recent overwhelming dominance of bluegill in the southern basin of Lake Biwa may be related to the propagation of submerged plants. The assumption here that the population density of largemouth bass in the northern basin significantly exceeds that in the southern basin (Yamamoto and Tsukada 2010), together with the area of macrophyte beds, could explain why the *W*s of bluegill in the 2 basins show obvious differences. Still, whether these factors are related to the latitudinal gradient in the *W* of bluegill in Lake Biwa remains unclear.

In the present study, bluegill were sampled from lagoons (except for site NW3) by 2 persons for 1 h. Accordingly, the number of fish samples from each site was expected to represent the population size to some extent. Calculated *W* and the number of samples were negatively correlated with each other, implying that population density strongly regulates bluegill growth in lagoons, which corresponds to previous studies (Wiener and Hanneman 1982, Osenberg et al. 1988). This finding implies that the population density also influences bluegill growth in the lake to a certain extent. If so, the population density of bluegill in the lake is expected to decline in the northern compared to the southern basin. The number of bluegill captured from the lake was high throughout the entire southern basin, but low at northern basin sites N1, N2, and N3. However, bluegill were captured quite efficiently at site N4 where the calculated *W* was the 3rd largest among the lake sites, implying that there was a high population density of bluegill at site N4. The above results suggest that the population density somewhat impacts bluegill growth in Lake Biwa, even though it is not the primary factor.

Overall, water temperature and population density of bluegill appear to have certain roles in inducing the latitudinal gradient in the growth of bluegill in Lake Biwa, including its lagoons. The latitudinal gradient of *W* of bluegill in the lake implies that bluegill tend to settle in relatively narrow areas; such a clear relationship between *W* and latitude would not appear if the habitat of each bluegill ranged over a wide area in the lake. It is assumed that the omnivorous bluegill can prey on various diet materials that are available in the local habitat, thus making migration to a wider area unnecessary. Therefore, the quality and/or quantity of bluegill diets may vary according to habitat. A future investigation on the growth pattern of bluegill in Lake Biwa should perform stable carbon and nitrogen isotope analyses to shed light on the long-term diet history of individual fish.

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REFERENCES

Azuma M. 1992. Ecological release in feeding behaviour: the case of bluegills in Japan. Hydrobiologia **243/244:** 269-276.

Belk MC. 1995. Variation in growth and age at maturity in bluegill sunfish: genetic or environmental effects? J. Fish Biol. **47:** 237-247.

Belk MC, DD Houston. 2002. Bergmann's rule in ectotherms: a test using freshwater fishes. Am. Nat. **160:** 803-808.

Bergmann C. 1847. Über die verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Gött. Stud. **1:** 595-708.

Bettoli PW, MJ Maceina, RL Noble, RK Betsill. 1993. Response of a reservoir fish community to aquatic vegetation removal. N. Am. J. Fish. Manage. **13:** 110-124.

Boeuf G, PY Le Bail. 1999. Does light have an influence on fish growth? Aquaculture **177:** 129-152.

Cross TK, MC McInerny. 2005. Spatial habitat dynamics affecting bluegill abundance in Minnesota bass-panfish lakes. N. Am. J. Fish. Manage. **25:** 1051-1066.

Dominey WJ. 1981. Maintenance of female mimicry as a reproductive strategy in bluegill sunfish (*Lepomis macrochirus*). Environ. Biol. Fish. **6:** 59-64.

Ginés R, JM Afonso, A Argüello, MJ Zamorano, JL López. 2004. The effects of long-day photoperiod on growth, body composition and skin colour in immature gilthead sea bream (*Sparus aurata* L.). Aquacult. Res. **35:** 1207-1212.

Gross MR. 1982. Sneakers, satellites, and parentals: polymorphic mating strategies in North American sunfishes. Z. Tierpsychol. **60:** 1-26.

Haga H. 2008. Massive expansion of submerged macrophytes in the southern basin of Lake Biwa. Nippon Suisan Gakkaishi **74:** 892-894. (in Japanese)

Hamabata E, Y Kobayashi. 2002. Present status of submerged macrophyte growth in Lake Biwa: recent recovery following a summer decline in the water level. Lake Reserv. Res. Manage. **7:** 331-338.

Hoxmeier RJH, DD Aday, DH Wahl. 2009. Examining interpopulation variation in bluegill growth rates and size structure: effects of harvest, maturation, and environmental variables. Trans. Am. Fish. Soc. **138:** 423-432.

Japan Meteorological Agency. 2009. Statistical weather information. Available at http://www.jma.go.jp/jma/index.html (Accessed 31 Oct. 2009).

Lake Biwa Environmental Research Institute. 2010. Continuous monitoring of water quality of Lake Biwa. Available at http://www.lberi.jp/root/jp/bkjhindex.htm (Accessed 21 Jan. 2010).

Mittelbach GG. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology

62: 1370-1386.
Mizuno T, H Nakao, LBM Fish Survey Group, T Nakajima. 2007. Risk analysis of habitat utilization by bluegill (*Lepomis macrochirus*) in the Lake Biwa Basin. Jpn. J. Conserv. Ecol. **12:** 1-9. (in Japanese with English summary)
Modde T, CC Scalet. 1985. Latitudinal growth effects on predator-prey interactions between largemouth bass and bluegills in ponds. N. Am. J. Fish. Manage. **5:** 227-232.
National Federation of Inlandwater Fisheries Cooperatives, ed. 1992. The review of exotic largemouth bass and bluegill. Tokyo: Fisheries Agency. (in Japanese)
Olson MH, SR Carpenter, P Cunningham, S Gafny, BR Herwig, NP Nibbelink, T Pellett, C Storlie, AS Trebitz, KA Wilson. 1998. Managing macrophytes to improve fish growth: a multi-lake experiment. Fisheries **23:** 6-12.
Osenberg CW, EE Werner, GG Mittelbach, DJ Hall. 1988. Growth patterns in bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish: environmental variation and the importance of ontogenetic niche shifts. Can. J. Fish. Aquat. Sci. **45:** 17-26.
Putman JH, CL Pierce, DM Day. 1995. Relationships between environmental variables and size-specific growth rates of Illinois stream fishes. Trans. Am. Fish. Soc. **124:** 252-261.
Savino JF, RA Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submerged vegetation. Trans. Am. Fish. Soc. **111:** 255-266.
Shoup DE, SP Callahan, DH Wahl, CL Pierce. 2007. Size-specific growth of bluegill, largemouth bass and channel catfish in relation to prey availability and limnological variables. J. Fish Biol. **70:** 21-34.
Terashima A. 1977. Exotic fish species in Lake Biwa, especially about bluegill. Tansuigyo **3:** 38-43. (in Japanese)
Tomcko CM, RB Pierce. 2001. The relationship of bluegill growth, lake morphometry, and water quality in Minnesota. Trans. Am. Fish. Soc. **130:** 317-321.
Tomcko CM, RB Pierce. 2005. Bluegill recruitment, growth, population size structure, and associated factors in Minnesota lakes. N. Am. J. Fish. Manage. **25:** 171-179.
Trebitz A, S Carpenter, P Cunningham, B Johnson, R Lillie, D Marshall et al. 1997. A model of bluegill-largemouth bass interactions in relation to aquatic vegetation and its management. Ecol. Model. **94:** 139-156.
Wiener JG, WR Hanneman. 1982. Growth and condition of bluegills in Wisconsin lakes: effects of population density and lake pH. Trans. Am. Fish. Soc. **111:** 761-767.
Werner EE, DJ Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology **69:** 1352-1366.
Woiwode JG, IR Adelman. 1991. Effects of temperature, photoperiod, and ration size on growth of hybrid striped bass × white bass. Trans. Am. Fish. Soc. **120:** 217-229.
Yamamoto Y, H Tsukada. 2010. Morphological variation in largemouth bass *Micropterus salmoides* in Lake Biwa, Japan. Ann. Limnol. Int. J. Lim. **46:** 41-45.
Yonekura R, K Nakai, M Yuma. 2002. Trophic polymorphism in introduced bluegill in Japan. Ecol. Res. **17:** 49-57.