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Relationship between latitude and growth of bluegill *Lepomis macrochirus* in Lake Biwa, Japan

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Seasonal changes in body size and stable isotope ratios of bluegill *Lepomis macrochirus* were monitored at three sites in Lake Biwa in an attempt to investigate the latitudinal variation in the fish growth pattern. $\delta^{13}C$ values of bluegill tended to decrease as latitude increased, implying the presence of a thermal gradient across the lake. In contrast, $\delta^{15}N$ values of bluegill increased with increasing latitude. Better digestive performance of the fish at higher latitudes was assumed to explain this result, whereas the discharge from a sewage treatment plant seemed to have a more direct impact on the extremely high $\delta^{15}N$ values of bluegill at the highest latitude site. Length–weight relationships were used to assess the changes in the body weight of fish with a normalized body size. Bluegill at higher latitudes exhibited greater body weights with a prolonged duration of body weight gain. Bluegill at lower latitudes may have adapted to grow rapidly from late spring to early summer when feeding activity increases in response to increasing water temperature, while the catabolic activity remains at a low level. In contrast, bluegill at higher latitudes can continue to grow until the midsummer months owing to the lower water temperature. The seasonal growth pattern of bluegill was analyzed using a logistic-type equation. The assumption that the selection of growth rate or final body size depends on temperature may reasonably explain the latitudinal variation in the growth pattern of bluegill in Lake Biwa.

Introduction

Bluegill *Lepomis macrochirus*, a temperate freshwater fish species native to central and eastern North America, is now a cosmopolitan species as a consequence of transplantation (Welcomme 1992). The importance of bluegill as game fish has motivated investigators to examine how abiotic and biotic factors influence fish growth. As with most other species, prey availability and temperature are of principal importance in determining the growth of bluegill (Mittelbach 1988, Tomcko & Pierce 2001, Hoxmeier *et al*. 2009). Other than these two factors, population density may strongly influence bluegill growth, usually negatively (Osenberg *et al*. 1988, Belk 1993). Vegetation is another crucial factor in various stages of the bluegill life history. In general, vegetation is well accepted to promote bluegill recruitment since vegetated areas may serve not only as feeding grounds (Crowder & Cooper 1982), but also as refuges from predators (Savino & Stein 1982). Vegetated environments are potentially suitable for the efficient growth of bluegill (Belk 1993), but the fish congestion may accelerate the conspecific competition, resulting in stunted growth (Mittelbach 1988).

Due to the above reasons, heterogeneity of vegetation may induce sectional differences in bluegill growth even in a single water body. For example, the south basin of Lake Biwa of Japan is covered by heavy vegetation, and the body weights of bluegill found there are significantly lower than those in the north basin with less vegetation (Yamamoto *et al*. 2010). This phenomenon may be attributed to the density-dependent growth characteristics of bluegill (Mittelbach 1988, Osenberg *et al*. 1988, Belk 1993), given the overwhelming propagation of bluegill in the south basin (Mizuno *et al*. 2007). However, a significant positive correlation between bluegill body weight and latitude is evident across the lake (Yamamoto *et al*. 2010), implying the presence of environmental factor(s) that varies with latitude and critically influences fish growth.

This study explores the potential mechanism that underlies the latitudinal gradient in the body weight, or growth, of bluegill in Lake Biwa. Fish samples were collected from three sites at different latitudes from March to December 2007. Such time series monitoring allowed seasonal changes in fish body weight to be identified. Stable carbon and nitrogen isotope ratios were measured to examine whether the primary food sources or the trophic position of bluegill varies among the sites.

Material and methods

Study site and sampling

Lake Biwa, the largest lake in Japan, is located at latitudes of 34°58´–35°31´N and longitudes of 135°52´–136°17´E. It can be topographically divided into two sections, a large deep north basin (surface area 618 km^2, maximum depth 104 m, mean depth 43 m) and a small shallow south basin (surface area 52 km^2, maximum depth 7.0 m, mean depth 3.5 m). The annual mean water temperature normally varies, decreasing with increasing latitude (Fig. 1, *see* also Yamamoto *et al*. 2010).

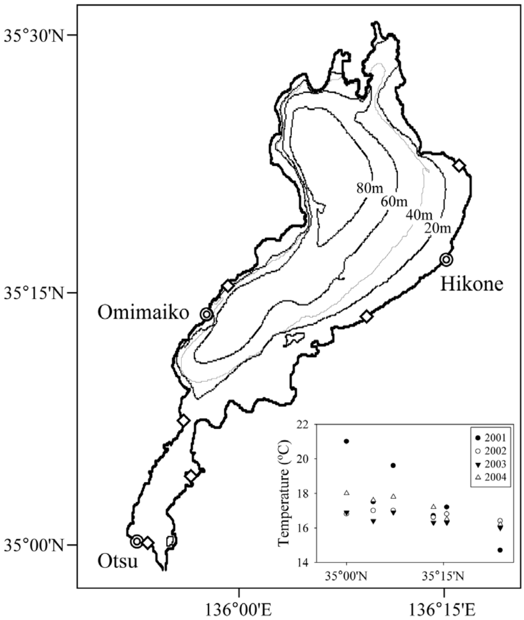

Fig. 1. Sampling sites in Lake Biwa. Inset shows annual mean water temperatures measured at six stations (open diamonds) from 2001 to 2004. Significant negative correlations between annual mean water temperature and latitude were detected in 2001, 2003 and 2004 ($p < 0.05$).

Bluegill have inhabited the lake for over four decades (Terashima 1977). In recent years, they have become dominant in the coastal regions (Mizuno *et al*. 2007). Since bluegill are easily captured by angling, all fish samples were collected by hook and line. Bluegill were collected monthly from March to December 2007 at two sites (Hikone and Omimaiko) in the north basin of the lake (Fig. 1). Fish from the south basin were sampled at Otsu (Fig. 1) from April to November 2007, 1–3 times per month, as a part of another study (Yamamoto 2011). Captured fish were placed in a bucket filled with ice-water slurry.

Sample analyses

The total length and body weight of the bluegill

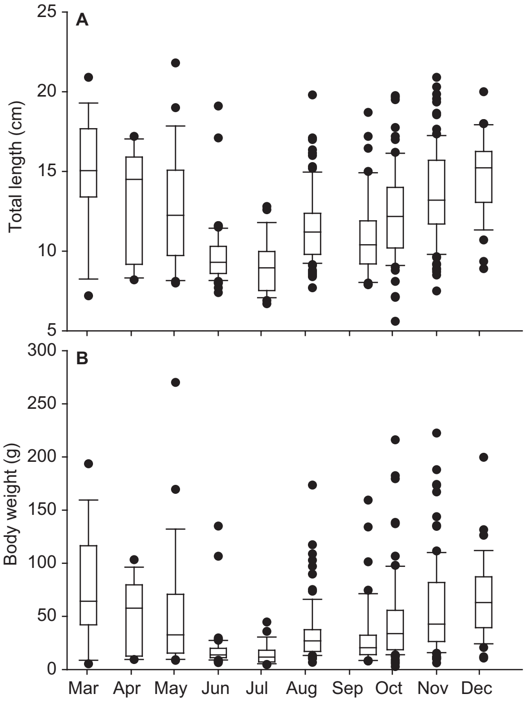

Fig. 2. Box plots showing ranges of (**A**) total length and (**B**) body weight of bluegill captured at Hikone. The 25th, 50th and 75th percentiles are represented by horizontal lines and the 5th and 95th percentiles are represented by error bars. Dots represent outliers.

were measured to the nearest 0.1 cm and 0.1 g, respectively. The length–weight relationships were estimated by fitting an allometric power function $W = aL^b$ to the data, where W is the body weight, L is the total length, a is the initial growth coefficient and b is the relative growth coefficient. Males and females were pooled for determining the length–weight relationships because of small numbers of available samples.

One to three fish with a standard length of around 11 cm were subsampled for stable-isotope analysis. A small specimen of flesh (white muscle tissue, free of bone and skin) was cut from just under the dorsal fin of the left side of the fish, and then placed on a glass Petri dish to dry at 60 °C for 24 hours. The dried flesh was ground to a fine powder and stored in glass vials. Samples were treated with 1 N HCl for 16 h to remove carbonate; the residue was centrifuged and freeze-dried. The carbon and nitrogen stable-isotope ratios were measured with a Thermo Finnigan Deltaplus Advantage isotope ratio mass spectrometer that was connected to a Flash EA 1112 automatic elemental analyzer. Isotope-ratio data are expressed using standard δ notation as $\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$ (‰), where X is ^{13}C or ^{15}N, and R is ^{13}C/^{12}C for carbon and ^{15}N/^{14}N for nitrogen. Pee dee belemnite (PDB) and atmospheric nitrogen were used as δ^{13}C and δ^{15}N standards, respectively. The U.S. Geological Survey standard #40, which has a certified δ^{13}C value of –26.24‰ and a δ^{15}N of –4.52‰, and acetanilide (Merck) with a δ^{13}C of –29.76‰ and a δ^{15}N of –1.52‰, were used as working standards. The reproducibility of both carbon and nitrogen isotopic measurements was better than 0.15‰ — much smaller than the wide distribution of isotopic compositions in bluegill in our study.

Results

The total number of bluegill that were captured at Hikone was 471; their total length and body weight ranged from 5.6 to 21.8 cm with a mean of 12.1 cm, and from 2.8 to 270.1 g with a mean of 43.2 g, respectively (Fig. 2). The mean size of the captured fish decreased from March to July and then gradually increased until December. The total number of bluegill captured at Omimaiko was 556; their total length and body weight ranged from 6.4 to 21.8 cm with a mean of 13.2 cm, and from 3.7 to 256.0 g with a mean of 48.5 g, respectively (Fig. 3). The mean size of the captured fish was lowest in August, and then increased from September to December. The total number of bluegill captured at Otsu was 865; their total length and body weight ranged from 6.9 to 18.1 cm with a mean of 10.7 cm, and from 4.9 to 124.6 g with a mean of 22.7 g, respectively. The mean sizes of the captured fish were small during the summer months, and the percentage of large fish increased from May (Yamamoto 2011).

To elucidate the seasonal pattern of the body weight of bluegill collected from the different sites, length–weight correlation equations were established for all sampling dates at each site (Table 1). All correlation coefficients of the power law regressions were significant at $p = 0.01$ (Table 1). After these empirical equations were obtained, body weights of fish with a normalized total length of 11.8 cm (the mean total length of 1892 samples) were determined to enable comparisons across seasons.

Greater body weights were always observed at higher latitudes (Fig. 4). At Hikone, the body weight exhibited a dome-shaped pattern with the greatest weight around late September and early October, and the lowest body weight in winter, although the curve included a small spike in early May. Overall, the body weight of bluegill at Hikone increased continuously from March to September. At Omimaiko, the body weight of bluegill also exhibited a dome-shaped curve, but with a plateau of 29.3–30.0 g that lasted for over four months from mid-June to late October. The body weight gain of fish at Omimaiko proceeded faster than that at Hikone from March to June. At Otsu, the seasonal variation in body weight was weaker (< 2.45 g). A significant jump in body weight was observed in May, but with no data collected prior to April, the explanation is elusive. Nevertheless, the plateau of large body weight persists for longer than that at Omimaiko. Notably, a temporary drop in body weight was observed at both Omimaiko (in August) and Otsu (from July to August). In the course of the study, positive correlations between calculated body weight and latitude were identified. The specific growth rates, which were calculated by fitting a least-square linear regression to the natural logarithm of the calculated body weights during the growing season and then multiplying the slope by 100, decreased significantly with

Table 1. Length–weight relationships ($W = aL^b$) of bluegill in 2007. All correlation coefficients are significant at $p = 0.01$.

Site/Date	*n*	*a*	*b*	*r*
Hikone				
2 March	16	0.0064	3.402	0.997
3 April	13	0.0090	3.269	0.997
2 May	24	0.0073	3.379	0.997
1 June	55	0.0097	3.256	0.996
5 July	28	0.0094	3.277	0.993
6 August	85	0.0071	3.401	0.993
14 September	43	0.0065	3.447	0.996
3 October	72	0.0083	3.348	0.994
1 November	99	0.0054	3.484	0.997
4 December	36	0.0047	3.519	0.995
Omimaiko				
14 March	6	0.0119	3.125	0.977
10 April	40	0.0059	3.417	0.986
15 May	45	0.0041	3.580	0.989
13 June	71	0.0099	3.245	0.996
12 July	62	0.0087	3.298	0.996
13 August	50	0.0071	3.373	0.995
18 September	61	0.0062	3.438	0.991
18 October	33	0.0064	3.416	0.995
13 November	96	0.0045	3.527	0.995
12 December	92	0.0052	3.462	0.994
Otsu				
18 April	27	0.0050	3.460	0.978
3 May	46	0.0087	3.267	0.992
16 May	75	0.0160	3.016	0.984
3 June	63	0.0107	3.186	0.991
17 June	72	0.0107	3.186	0.996
1 July	78	0.0086	3.276	0.995
19 July	64	0.0115	3.150	0.996
1 August	67	0.0101	3.202	0.992
16 August	59	0.0119	3.134	0.995
3 September	62	0.0112	3.170	0.993
16 September	66	0.0145	3.059	0.984
2 October	71	0.0088	3.256	0.996
15 October	60	0.0086	3.261	0.996
28 October	31	0.0097	3.195	0.994
8 November	24	0.0076	3.307	0.997

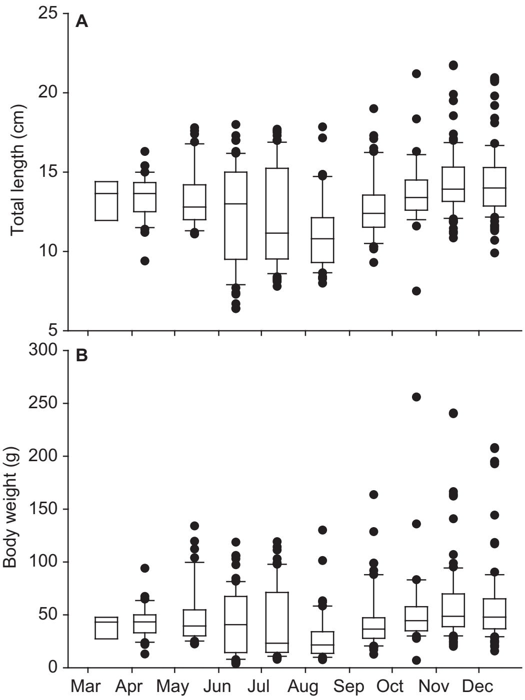

Fig. 3. Box plots showing ranges of (**A**) total length and (**B**) body weight of bluegill captured at Omimaiko. Other information as in Fig. 2.

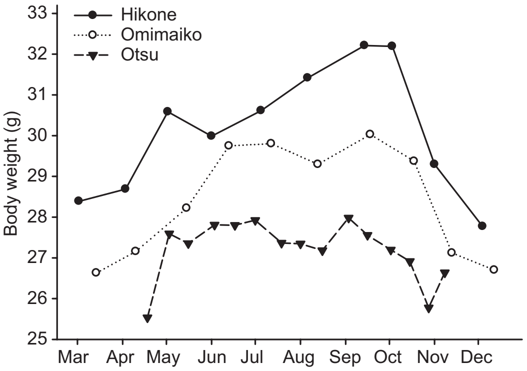

Fig. 4. Changes in the calculated body weight of bluegill with a total length of 11.8 cm.

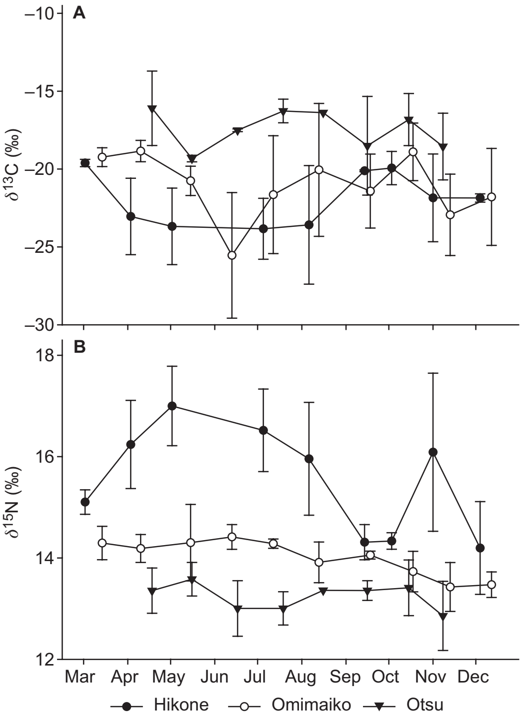

Fig. 5. Changes in the (**A**) δ^{13}C and (**B**) δ^{15}N values of bluegill. Error bars denote standard deviations (n = 2 or 3).

latitude: 0.52% at Otsu, 0.12% at Omimaiko and 0.06% at Hikone.

The δ^{13}C values ranged from –28.11‰ to –14.61‰ with no clear seasonal pattern (Pearson's product moment correlation coefficient: $r^2 = 0.011–0.026$, $n = 22–30$, $p > 0.05$), but differed significantly among the three sites (ANOVA: $F_{2,74} = 19.1$, $p < 0.001$) (Fig. 5). The mean δ^{13}C values of bluegill at Otsu, Omimaiko and Hikone were –17.53‰, –21.11‰ and –21.87‰, respectively, decreasing as latitude increased. The δ^{15}N of bluegill exhibited no clear seasonal pattern at Hikone ($r^2 = 0.151$, $n = 25$, $p > 0.05$) or Otsu ($r^2 = 0.036$, $n = 22$, $p > 0.05$), but it tended to decrease gradually at Omimaiko ($r^2 = 0.410$, $n = 30$, $p < 0.001$). The δ^{15}N values varied significantly among the three sites (ANOVA: $F_{2,74} = 52.2$, $p < 0.001$). The mean δ^{15}N values of bluegill increased with latitude; the values at Otsu, Omimaiko and Hikone were 13.23‰, 14.01‰ and 15.54‰, respectively.

Discussion

Bluegill are generally assumed to be poorly mobile (Fish & Savitz 1983, Bayne *et al*. 2002, but Paukert *et al*. 2004). The low mobility of bluegill in Lake Biwa was inferred from the significant differences in the fish stable isotope ratios among the three sites. The δ^{13}C values of bluegill depended strongly on the sampling sites, exhibiting a negative correlation with latitude. Bluegill would exhibit similar δ^{13}C values as their food items owing to the inability of predators to influence the carbon content of their prey. Yamada *et al*. (1998) demonstrated that the main carbon source of the food chain in the coastal region in the north basin of Lake Biwa was benthic algae. Given that the south basin is more eutrophic than the north basin and suits for the development of phytoplankton blooms (Nakanishi & Sekino 1995, Yamamoto 2011), the contribution of phytoplankton to the food chain is expected to be greater in the south basin. The δ^{13}C values of consumers using benthic algal carbon are higher than those of the consumers in a phytoplankton-based food chain (France 1995). However, the δ^{13}C values of bluegill in the south basin exceeded those in the north basin, and the fish at lower latitudes tended to exhibit higher δ^{13}C values, making it difficult to explain the local difference in the δ^{13}C values of bluegill based on the basin-dependent environment. Rau *et al*. (1991) identified a positive correlation between the δ^{13}C values of marine particle organic matter and water temperature, and therefore δ^{13}C values tend to fall with latitude. This decline in δ^{13}C values with increasing latitude can occur also in larger oceanic animals (Takai *et al*. 2000, Cherel & Hobson 2007). The latitudinal gradient in the δ^{13}C values of bluegill together with the variation in the annual mean water temperature among sites (Fig. 1) strongly suggest the presence of a significant latitudinal thermal gradient across the lake, despite its narrowness on a global scale (*see* also Akitomo *et al*. 2009).

The δ^{15}N value serves as an indicator of a consumer's trophic position, and is enriched by approximately 3.4‰ over that of its diet organisms (Vander Zanden & Rasmussen 2001). Unlike the δ^{13}C values, the δ^{15}N values of bluegill herein increased with latitude. Two explanations can be offered for this result. First, Lake Biwa receives discharge from a sewage treatment plant at Hikone, which makes Hikone an extremely nitrogen-rich environment; the mean concentrations of dissolved inorganic nitrogen, summed over ammonium, nitrite and nitrate, from April to November 2007 at Hikone, Omimaiko and Otsu were 55.9, 5.38 and 6.66 μmol l^{-1}, respectively (first author's unpubl. data). Given the impact of sewage input to increase δ^{15}N values of aquatic organisms (DeBruyn & Rasmussen 2002, Hadwen & Arthington 2007, Lin *et al*. 2007), the high δ^{15}N values of bluegill at Hikone are reasonably assumed to be caused by the discharge from the sewage treatment plant.

Another possible explanation is the latitudinal variation in the food sources and/or digestive performance of bluegill. Even in the same species, larger fish may exhibit higher δ^{15}N values, because they have more available food sources (Ménard *et al*. 2007). Therefore, it is tempting to assume that bluegill at higher latitudes may eat wider range of prey species than those at lower latitudes. However, informal measurement showed no clear qualitative variation in the bluegill diet among the sites; the major ingested materials throughout the study were filamentous green algae and chironomid larvae (data not shown). Although algae and aquatic plants are frequently detected in bluegill stomachs, they are assumed to be defecated without being digested (Yokogawa 1992, Uchii *et al*. 2007). Nicieza *et al*. (1994) demonstrated that the high-latitude population of Atlantic salmon *Salmo salar* has better digestive performance than the low-latitude population. One possible explanation may involve the inherited metabolic difference between the two populations; the relative anabolic activity is assumed to decline with rising temperature because of the marked increase in the catabolism (Von Bertalanffy 1960, Perrin 1995), hence the population at higher latitude may have better digestive performance. In Lake Biwa, the animal food that is ingested by bluegill may be more efficiently digested at higher latitudes owing to lower temperatures, resulting in the latitudinal gradient in the δ^{15}N values of bluegill.

In the present study, fish samples were not collected from higher latitudes than Hikone, making the evaluation of the mechanisms that underlie the latitudinal variation in the δ^{15}N values of bluegill difficult. However, given the fact that a strong positive correlation between latitude and the body weight of bluegill was observed over a wide range of latitudes that covered almost all of Lake Biwa (Yamamoto *et al*. 2010), the variation in body weight, or physiological activity, of fish should be attributed to environmental factor(s) that regularly varies with latitude, rather than to an artificial regional cause, such as sewage input. Notably, despite their higher body weight, the body weight gain of bluegill at higher latitudes proceeded more slowly than at lower latitudes. As is well known, numerous ectotherms exhibit a lower growth rate and a greater body size in colder regions (Atkinson 1994, Angilletta *et al*. 2004). Given the lower mean annual water temperatures at the higher latitudes in Lake Biwa, the variation in the bluegill growth in the lake is likely caused by the temperature difference. The difference in temperatures among the sites is small, but it may be sufficient to affect the physiological status of bluegill, given the potential capacities of fish to respond to a slight change in temperature (Bull 1936, Bardach & Bjorklund 1957) and to adapt to a new temperature by adjusting metabolic processes (Kelsch & Neill 1990). The temporary declines in the calculated body weights of bluegill at Omimaiko and Otsu in the summer are possibly owing to the increased catabolic activity (Von Bertalanffy 1960, Perrin 1995).

To increase anabolic efficiency, bluegill at these sites may have adapted to grow quickly from spring to early summer when feeding activity increases gradually in response to the increasing water temperature, but the catabolic activity remains relatively low. In contrast, owing to the lower water temperature, the anabolic activity of bluegill at Hikone may remain relatively high even in the summer months, enabling them to grow slowly but steadily until September.

Although a study of seasonal patterns in fish should depend on monitoring the physical attributes, such as length and weight of individual fish, an attempt is made to infer the growth pattern of bluegill from the results presented herein. Yamamoto and Nakai (2009) analyzed the growth pattern of tilapia (*Oreochromis niloticus* and *Tilapia zillii*) in an artificially heated river by monitoring the length and weight of individual fish, and demonstrated that fish body weight estimated from the length–weight relationship increased during the spring and summer when the lengthwise growth was occurring, subsequently decreasing during the autumn and winter when no lengthwise growth occurred. Booth and Keast (1986) demonstrated that the lengthwise growth of bluegill in Lake Opinicon occurred greatly during the summer months, but stopped entirely during the winter. Based on these results, the annual lengthwise growth of bluegill in Lake Biwa is assumed to proceed from late spring to summer when the body weight that is estimated from the length–weight relationship is increasing, and to approach an asymptote thereafter, including the period when the calculated body weight is decreasing. Such a growth pattern can be described by the following equation:

$$\frac{dx}{dt} = r'x\left(1 - \frac{x}{K'}\right)$$

where x is the fish body size, r' is the growth rate during the growing season and K' is the final body size at the end of the plateau phase. The form of this equation is the same as that of the logistic model of population growth. Note that the equation presented here describes the annual growth pattern of individual fish.

The supposition of r'/K' selection with reference to temperature seems to be useful in explaining how bluegill adapt to a wide range of temperatures. Since bluegill are temperate fish, they are fundamentally thought to adapt well to warm environments. However, the summer temperatures in these environments can be too high to allow bluegill to grow continuously. Hence, bluegill use energy to grow quickly from spring to early summer when the catabolic activity remains relatively low. When adapting to colder environments, bluegill allocate energy to increase their final body size at the expense of a reduction in growth rate. This strategy seems to be reasonable for reducing the mortality rate during the winter months, since acquiring a large body is critical to successful overwintering by bluegill, especially those in juvenile stages (Cargnelli & Gross 1996).

Consequently, the latitudinal gradients in the body size and growth rate of bluegill in Lake Biwa can be viewed as a result of the dependence of r'/K' selection on temperature condition. The temperature condition in the south basin of the lake is suitable for bluegill to be r' selected, and so they grow rapidly. In contrast, to adapt to higher latitude regions in which the annual mean water temperature is lower, bluegill become subject to be K' selected, and so allocate more of the energy that they obtain during the growing season to increasing the final body size.

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References

Akitomo, K., Tanaka, K., Kumagai, M. & Jiao, C. 2009: Annual cycle of circulations in Lake Biwa, part 1: model validation. — *Limnology* 10: 105–118.

Angilletta, M. J., Steury, T. D. & Sears, M. W. 2004: Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. — *Integrative and Comparative Biology* 44: 498–509.

Atkinson, D. 1994: Temperature and organism size – a biological law for ectotherms? — *Advances in Ecological Research* 25: 1–58.

Bardach, J. E. & Bjorklund, R. G. 1957: The temperature sensitivity of some American freshwater fishes. — *American Naturalist* 91: 233–251.

Bayne, D. R., Reutebuch, E. & Seesock, W. C. 2002: Relative motility of fishes in a southeastern reservoir based on tissue polychlorinated biphenyl residues. — *North American Journal of Fisheries Management* 22: 122–131.

Belk, M. C. 1993: Growth and mortality of juvenile sunfishes (*Lepomis* sp.) under heavy predation. — *Ecology of Freshwater Fish* 2: 91–98.

Booth, D. J. & Keast, J. A. 1986: Growth energy partitioning by juvenile bluegill sunfish, *Lepomis macrochirus* Rafinesque. — *Journal of Fish Biology* 28: 37–45.

Bull, H. O. 1936: Studies on conditioned responses in fishes. Part IV. Temperature perception in teleosts. — *Journal of the Marine Biological Association of the United Kingdom* 21: 1–27.

Cargnelli, L. M. & Gross, M. R. 1996: The temporal dimension in fish recruitment: birth date, body size, and size-dependent survival in a sunfish (bluegill: *Lepomis macrochirus*). — *Canadian Journal of Fisheries and Aquatic Sciences* 53: 360–367.

Cherel, Y. & Hobson, K. A. 2007: Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. — *Marine Ecology Progress Series* 329: 281–287.

Crowder, L. B. & Cooper, W. E. 1982: Habitat structural complexity and the interaction between bluegills and their prey. — *Ecology* 63: 1802–1813.

DeBruyn, A. M. H. & Rasmussen, J. B. 2002: Quantifying assimilation of sewage-derived organic matter by riverine benthos. — *Ecological Applications* 12: 511–520.

Fish, P. A. & Savitz, J. 1983: Variations in home ranges of largemouth bass, yellow perch, bluegills, and pumpkinseeds in an Illinois lake. — *Transactions of the American Fisheries Society* 112: 147–153.

France, R. L. 1995: Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. — *Marine Ecology Progress Series* 124: 307–312.

Hadwen, W. L. & Arthington, A. H. 2007: Food webs of two intermittently open estuaries receiving ^{15}N-enriched sewage effluent. — *Estuarine, Coastal and Shelf Science* 71: 347–358.

Hoxmeier, R. J. H., Aday, D. D. & Wahl, D. H. 2009: Examining interpopulation variation in bluegill growth rates and size structure: effects of harvest, maturation, and environmental variables. — *Transactions of the American Fisheries Society* 138: 423–432.

Kelsch, S. W. & Neill, W. H. 1990: Temperature preference versus acclimation in fishes: selection for changing metabolic optima. — *Transactions of the American Fisheries Society* 119: 601–610.

Lin, H. J., Wu, C. Y., Kao, S. J., Kao, W. Y. & Meng, P. J. 2007: Mapping anthropogenic nitrogen through point sources in coral reefs using δ^{15}N in macroalgae. — *Marine Ecology Progress Series* 335: 95–109.

Ménard, F., Lorrain, A., Potier, M. & Marsac, F. 2007: Isotopic evidence of distinct feeding ecologies and movement patterns in two migratory predators (yellowfin tuna and swordfish) of the western Indian Ocean. — *Marine Biology* 153: 141–152.

Mittelbach, G. G. 1988: Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. — *Ecology* 69: 614–623.

Mizuno, T., Nakao, H., LBM Fish Survey Group & Nakajima, T. 2007: Risk analysis of habitat utilization by bluegill (*Lepomis macrochirus*) in the Lake Biwa Basin. — *Japanese Journal of Conservation Ecology* 12: 1–9. [In Japanese with English summary].

Nakanishi, M. & Sekino, T. 1995: Recent drastic changes in Lake Biwa bio-communities, with special attention to exploitation of the littoral zone. — *GeoJournal* 40: 63–67.

Nicieza, A. G., Reiriz, L. & Braña, F. 1994: Variation in digestive performance between geographically disjunct populations of Atlantic salmon: countergradient in passage time and digestion rate. — *Oecologia* 99: 243–251.

Osenberg, C. W., Werner, E. E., Mittelbach, G. G. & Hall, D. J. 1988: Growth patterns in bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish: environmental variation and the importance of ontogenetic niche shifts. — *Canadian Journal of Fisheries and Aquatic Sciences* 45: 17–26.

Paukert, C. P., Willis, D. W. & Bouchard, M. A. 2004: Movement, home range, and site fidelity of bluegills in a Great Plains lake. — *North American Journal of Fisheries Management* 24: 154–161.

Perrin, N. 1995: About Berrigan and Charnov's life-history puzzle. — *Oikos* 73: 137–139.

Rau, G. H., Takahashi, T., Des Marais, D. J. & Sullivan, C. W. 1991: Particulate organic matter δ^{13}C variations across the Drake Passage. — *Journal of Geophysical Research* 96: 15131–15135.

Savino, J. F. & Stein, R. A. 1982: Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submerged vegetation. — *Transactions of the American Fisheries Society* 111: 255–266.

Takai, N., Onaka, S., Ikeda, Y., Yatsu, A., Kidokoro, H. & Sakamoto, W. 2000: Geographical variations in carbon and nitrogen stable isotope ratios in squid. — *Journal of the Marine Biological Association of the United Kingdom* 80: 675–684.

Terashima, A. 1977: [Exotic fish species in Lake Biwa, especially about bluegill]. — *Tansuigyo* 3: 38–43. [In Japanese].

Tomcko, C. M. & Pierce, R. B. 2001: The relationship of bluegill growth, lake morphometry, and water quality in Minnesota. — *Transactions of the American Fisheries Society* 130: 317–321.

Uchii, K., Okuda, N., Yonekura, R., Karube, Z., Matsui, K. & Kawabata, Z. 2007: Trophic polymorphism in bluegill sunfish (*Lepomis macrochirus*) introduced into Lake Biwa: evidence from stable isotope analysis. — *Limnology* 8: 59–63.

Vander Zanden, M. J. & Rasmussen, J. B. 2001: Variation in δ^{15}N and δ^{13}C trophic fractionation: Implications for aquatic food web studies. — *Limnology and Oceanography* 46: 2061–2066.

Von Bertalanffy, L. 1960. Principles and theory of growth. — In: Nowinski, W. W. (ed.), *Fundamental aspects of normal and malignant growth*: 137–259. Elsevier, Amsterdam.

Welcomme, R. L. 1992: A history of international introductions of inland aquatic species. — *ICES Marine Science*

Symposium 194: 3–14.

Yamada, Y., Ueda, T., Koitabashi, T. & Wada, E. 1998: Horizontal and vertical isotopic model of Lake Biwa ecosystem. — *Japanese Journal of Limnology* 59: 409–427.

Yamamoto, Y. 2011: Indirect impact of bluegill *Lepomis macrochirus* on the development of cyanobacterial blooms in Lake Biwa, Japan. — *Journal of Freshwater Ecology* 26: 323–335.

Yamamoto, Y. & Nakai, D. 2009: Monitoring individual growth of tilapia (*Oreochromis niloticus* and *Tilapia zillii*) in an artificially heated river. — *Aquaculture Science* 57: 109–116.

Yamamoto, Y., Tsukada, H. & Nakai, D. 2010: Latitudinal gradient in the body weight of bluegill *Lepomis macrochirus* in Lake Biwa, Japan. — *Zoological Studies* 49: 625–631.

Yokogawa, K. 1992: [Bluegill-feeding habit]. — In: National Federation of Inlandwater Fisheries Cooperative (ed.), [*The review of exotic largemouth bass and bluegill*]: 92–103. Fisheries Agency, Tokyo. [In Japanese].