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Food habits of bluegill *Lepomis macrochirus* populations in reservoirs in Kagawa, Japan

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ABSTRACT

Food habitats of bluegill *Lepomis macrochirus* populations in Hachiman and Saburo Reservoirs, Japan, were examined. In both populations, stomach content weights reduced relative to an increase in body weight, there being no gender-specific differences. However, relative stomach weights of males were significantly greater than those of females, a sexually dimorphic characteristic of bluegill. Feeding amounts of bluegills in Hachiman Reservoir tended to be low in winter–spring, and high in summer–autumn. Stomach contents, including insects, zooplankton, crustaceans, fishes, plants and inorganic debris, showed highly generalized feeding, although insects were frequently taken, particularly during spring–summer, with chironomids being a principle dietary item. In spring, numerous eggs of the crucian carp were ingested, suggesting a significant impact upon reproduction of the latter. In summer, many bluegill stomachs were filled with green algae. However, similar cramming of the intestinal tract suggested no digestive ability of bluegill for plant materials, including algae. In both habitats examined, the stomach contents of small bluegills (ca. 20–50 mm TL) comprised almost entirely zooplankton, diets subsequently diversifying gradually with growth. The almost complete absence of zooplankton in bluegills greater than ca. 110 mm in TL indicated a growth-related food habit shift from planktivory to omnivory.

Introduction

Bluegill, *Lepomis macrochirus*, a centrarchid freshwater fish originating from North America (e.g. Hubbs and Lagler 1970; Near and Koppelman 2009), has been widely introduced and become naturalized around the world, including Japan (Lever 1996). In Japan, extensive research has been conducted on bluegills, due to the inherent problems that have arisen from the introduction of exotic species for Japanese native freshwater ecosystems (e.g. NFIFC 1992).

However, although bluegill food habits have been examined in several populations (e.g. Azuma 1992; Katano et al. 2005; Yamaguchi 2007), they have not addressed the impact of sex-related differences, or seasonal and growth-related changes. In particular, relative stomach weight differences between sexes has been recognized as an important issue (OPFFES 1976) because it may concern differences in feeding amount, which can affect the growth rate. In addition, monthly comparisons of food habit are highly desirable, having not been carried out in all previous studies, including those of North American populations. Further, more issues on bluegill food habits have been suggested by previous works, i.e. the nutritional value of plant materials for

bluegills (Gerking 1954), food habit shift from planktivory to omnivory and its 'shift back' (e.g. Spotte 2007), and 'bluegill trophic polymorphism' in Lake Biwa, Japan (Yonekura, Nakai, and Yuma 2002).

Accordingly, the present study undertook detailed food habit examinations so as to address the above oversights and issues, on bluegill populations inhabiting reservoirs in Kagawa, Japan, in which commercial fishes (mainly the crucian carp *Carassius cuvieri*) were cultured. The ecological impacts of the former upon the cultured fishes were also discussed.

Materials and methods

Study sites

Hachiman Reservoir (Figure 1(A)). An artificial middle scale reservoir (maximum surface area 154,000 m², maximum water stock 532,000 m³ and maximum depth 4.9 m) located in a hilly region of eastern Kagawa, also known as Miyaike Reservoir. The reservoir is believed to have been constructed in the 14th century for irrigation, its water still being utilized for agriculture. The reservoir is also utilized for aquaculture, crucian carp seeds being stocked in spring, cultured with supplemental feeding,
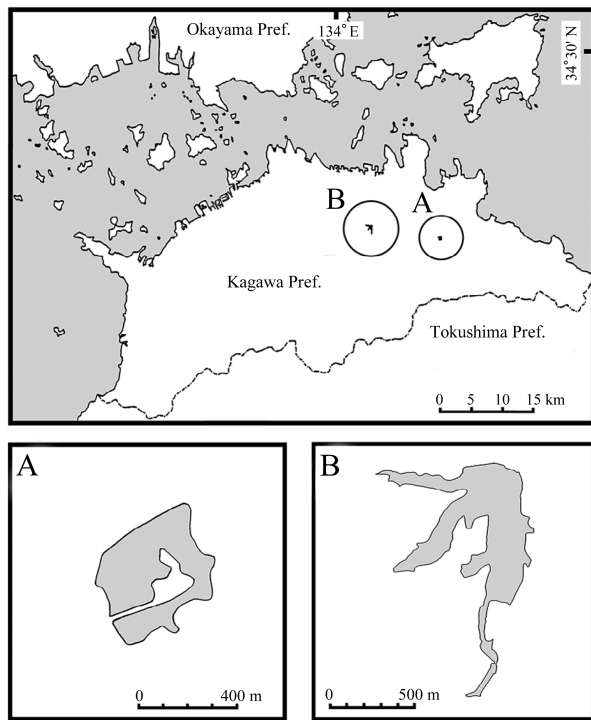

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[icon] Supplemental data for this article can be accessed https://doi.org/10.1080/21658005.2018.1474309.

Figure 1. Location of study sites. (**A**) Hachiman Reservoir, (**B**) Saburo Reservoir. (Maps were drawn by K.Yokogawa). http://d-maps.com/carte.php?num_car=11472&lang=en

and harvested in autumn / winter. Bottom materials include sand, gravel and mud. Although macrophytes are generally less abundant throughout the year, some

green algae may be dominant in summer. Bluegills have been observed in the reservoir since the 1970s, propagating strongly, as have largemouth bass, a more recent arrival (from an upstream dam lake).

Saburo Reservoir (Figure 1(B)). An artificial large scale reservoir (maximum surface area 400,000 m^2, maximum water stock 1,768,000 m^3 and maximum depth 10.1 m) located in a hilly region of central Kagawa. Although the date of establishment of the reservoir is uncertain, the latter is mentioned in 17th century documents. The reservoir is very important for irrigation, supplying water to nearby rice fields. It is also utilized for aquaculture, crucian and common carp, and catfish being cultured with supplemental feeding. Such fishes are harvested during the agricultural off-season, when the reservoir is occasionally emptied for remedial work. Following such activities, water is introduced from small nearby river systems. By such agency, bluegills entered the reservoir and became well established.

Sampling, measurements and stomach content analysis

The main collection site of bluegill examined in the present study was Hachiman Reservoir (Figure 1(A)), specimens being sampled at least once every month from March, 1990 to January, 1991 (Table 1), mainly by angling (hook and line) (Table 1) (boiled marine krill, used as a bait, enabled the distinction of the latter from

Table 1. Collection data for examined bluegill specimens from two reservoirs in Kagawa, Japan.

Date	Total length (mm)			Number of individuals				Sampling method
	Average	Range	Males	Females	Sex-unidentified	Pooled		
Hachiman Reservoir								
29 Mar, 1990	157.1	102.0–205.5	12	6	0	18		Angling
6 Apr, 1990	146.4	117.2–207.6	13	8	0	21		Angling
12 Apr, 1990	151.0	122.7–212.1	6	2	0	8		Angling
19 Apr, 1990	134.6	100.6–198.3	20	20	0	40		Angling
25 Apr, 1990	147.7	100.9–210.5	22	15	0	37		Angling
2 May, 1990	162.0	82.0–208.2	25	9	0	34		Angling
10 May, 1990	137.7	92.8–211.9	44	50	0	94		Angling
16 May, 1990	148.5	91.6–201.0	49	32	0	81		Angling
24 May, 1990	156.3	126.6–204.0	20	15	0	35		Angling
30 May, 1990	136.2	85.6–202.0	22	21	0	43		Angling
7 June, 1990	154.1	108.0–213.4	21	16	0	37		Angling
13 June, 1990	138.5	77.2–193.4	37	15	0	52		Angling
19 June, 1990	152.6	78.3–199.4	26	25	0	51		Angling
28 June, 1990	144.7	97.2–200.3	10	4	0	14		Angling
5 July, 1990	135.1	71.1–198.3	41	55	0	96		Angling
12 July, 1990	123.5	70.0–191.4	38	34	0	72		Angling
18 July, 1990	126.4	69.2–204.6	49	31	0	80		Angling
26 July,1990	117.3	64.8–201.4	56	34	0	90		Angling
1–2 Aug, 1990	104.4	52.1–194.6	35	23	0	58		Angling
6 Sep, 1990	124.8	69.6–198.0	36	14	0	50		Angling
21 Sep, 1990	129.6	81.1–180.8	4	9	0	13		Angling
4 Oct, 1990	128.1	80.6–196.3	21	19	0	40		Angling
24 Oct, 1990	107.1	69.8–171.0	28	21	0	49		Angling
2 Nov, 1990	111.6	79.8–190.8	31	13	0	44		Angling
26 Nov, 1990	127.6	82.7–203.2	15	8	0	23		Angling
28 Dec, 1990	106.5	28.2–229.6	25	51	10	86		Surrounding net
16–17 Jan, 1991	144.3	83.6–212.8	48	76	0	124		Surrounding net
Hachiman R. total	132.6	28.2–229.6	754	626	10	1390		
Saburo Reservoir								
26–29 Oct, 1990	85.3	23.4–182.2	65	55	24	144		Reservoir emptied

normal stomach contents). At Saburo Reservoir (Figure 1(B)), many bluegills (over 40,000) were collected on 26–29th, October, 1990, when the reservoir was emptied (Yokogawa 1992a). Subsequently, variously-sized 114 specimens, which represented the throughout size classes, were selected for the present study (Table 1).

The collected specimens were immediately fixed on site with 10% formalin and preserved. Subsequently, measurements of total length (TL), standard length (SL) and body weight (BW) were made. Because the lengths of body portions and body weight of bluegill adults (including fingerlings) have been reported as unchanging following fixation with 10% formalin (Yokogawa 2009), no subsequent adjustments of the measured values were made. For stomach content analysis, the abdomen of each specimen was dissected and the stomach removed. The latter, including contents, was weighed (to 1 mg) and subsequently opened with a scalpel and the total contents removed. The empty stomach weight (SW) was noted and the wet stomach content weight (SCW) determined as the difference between the former weights.

In addition, a gonad was removed for sex determination (whether testis or ovary), although the sex could not be determined for a few individuals from Saburo Reservoir due to immaturity of the gonad. Those specimens were excluded from sex-based analyses. Size class analyses were based on three size classes, defined as large class (>160 mm TL), middle class (120–160 mm TL) and small class (≤120 mm TL).

Among the stomach content items, insects, including larvae (Figures S1(A)–(H), S2(A)–(H), S3(A)–(D), see supplemental data), were identified to Order, following Tsuda (1962), Shiraki (1981a, 1981b), Kawada (1984) and Kawai (1985), although dipterans, which frequently occurred, were further classified into chironomid larvae, chironomid pupae and other Diptera. Fishes in the stomach contents were generally identified following Miyadi, Kawanabe, and Mizuno (1976), larval centrarchids (bluegill and largemouth bass) following Wang (1986). Fish eggs (Figure S5(B) and (C)) were identified on the bases of diameter and presence or absence of oil globules, following Akazaki, Matsuoka, and Arasaki (1970), Merriner (1971) and Miyadi, Kawanabe, and Mizuno (1976) and fish scales from morphology (cycloid or ctenoid) and size. Other animal remains were identified following Okada (1974). Plant materials (Figures S5(D)–(H), S6(A) see supplemental data) were generally classified into terrestrial or aquatic phanerogams, fungi or algae. Inorganic debris, including gravel, plastic and glass chips (Figure S6(B) –(G)) were also treated as stomach content items.

The removed stomach contents were examined in a laboratory dish with a quadrat grid, being spread flat over the dish by the addition of water. Observations were made by light microscope and the stomach content items identified by individual. The area on the dish occupied by each item was visually measured and the percentage of the total area occupied by the stomach contents regarded as the volumetric percentage of the stomach contents.

Data analysis

The relationship between BW and SCW was demonstrated by natural logarithm-transformed regressions ($\ln SCW = a \ln BW + b$) for both sexes using the least-squares method. Individuals with no stomach contents ($SCW = 0$) were omitted from the regression because ln 0 was not calculable. Subsequently, parameters of the regressions (a and b) between male and female pairs were compared by analysis of covariance (ANCOVA) (t test), following Yamada and Kitada (2004). The same analytical procedure was applied to inter-sexual comparisons of the TL–SW and BW–SW regressions ($\ln SW = a \ln TL + b$ and $\ln SW = a \ln BW + b$).

Relationships between BW and SCW were evaluated so as to determine whether they were isometric or allometric, i.e. a t test was performed for the logarithm-transformed regressions ($\ln SCW = a \ln BW + b$) to examine the significance of the slope for a null hypothesis ($a = 1$), according to Zar (2010). When a was significantly different from 1, SCW was allometric for BW, being otherwise isometric. The same analytical procedure was applied to the BW–SW regression ($\ln SW = a \ln BW + b$).

Following Hayashi and Yamaguchi (1960), the proportion SCW to BW was regarded as a feeding index (FI). However in bluegills, the relationship between BW and SCW was revealed as allometric (SCW reducing relative to BW increase) (Figures 2(A) and 3(A); Tables 2 and 3(A)), being expressed by the formula $SCW = a\,BW^b$. Accordingly, BW^b was adopted for the FI calculation instead of BW, as follows.

$$FI = (SCW / BW^{\,b}) \times 100$$

where b values were peculiar to habitat, i.e. 0.936 and 0.893 applied to bluegill populations from Hachiman and Saburo Reservoirs, respectively.

FI was also used to weigh the volumetric percentage (VP) of the stomach contents, VP multiplied by FI was taken as the diet score (DS), the diet score proportion (DSP) of the stomach content item being calculated by the sum of individual DS divided by total DS of all individuals in the sample, as follows.

$$DSP = \left[\sum_{i=1}^{n} (xi \times yi) \middle/ \sum_{i=1}^{k} \sum_{i=1}^{n} (xi \times yi) \right] \times 100$$

where xi = individual VP of a stomach content item; yi = individual FI; n = number of individuals; k = number of stomach content items appeared.

The DSP values of stomach content items were calculated by month, size class and sex. A few individuals with completely empty stomachs or unidentifiable solid
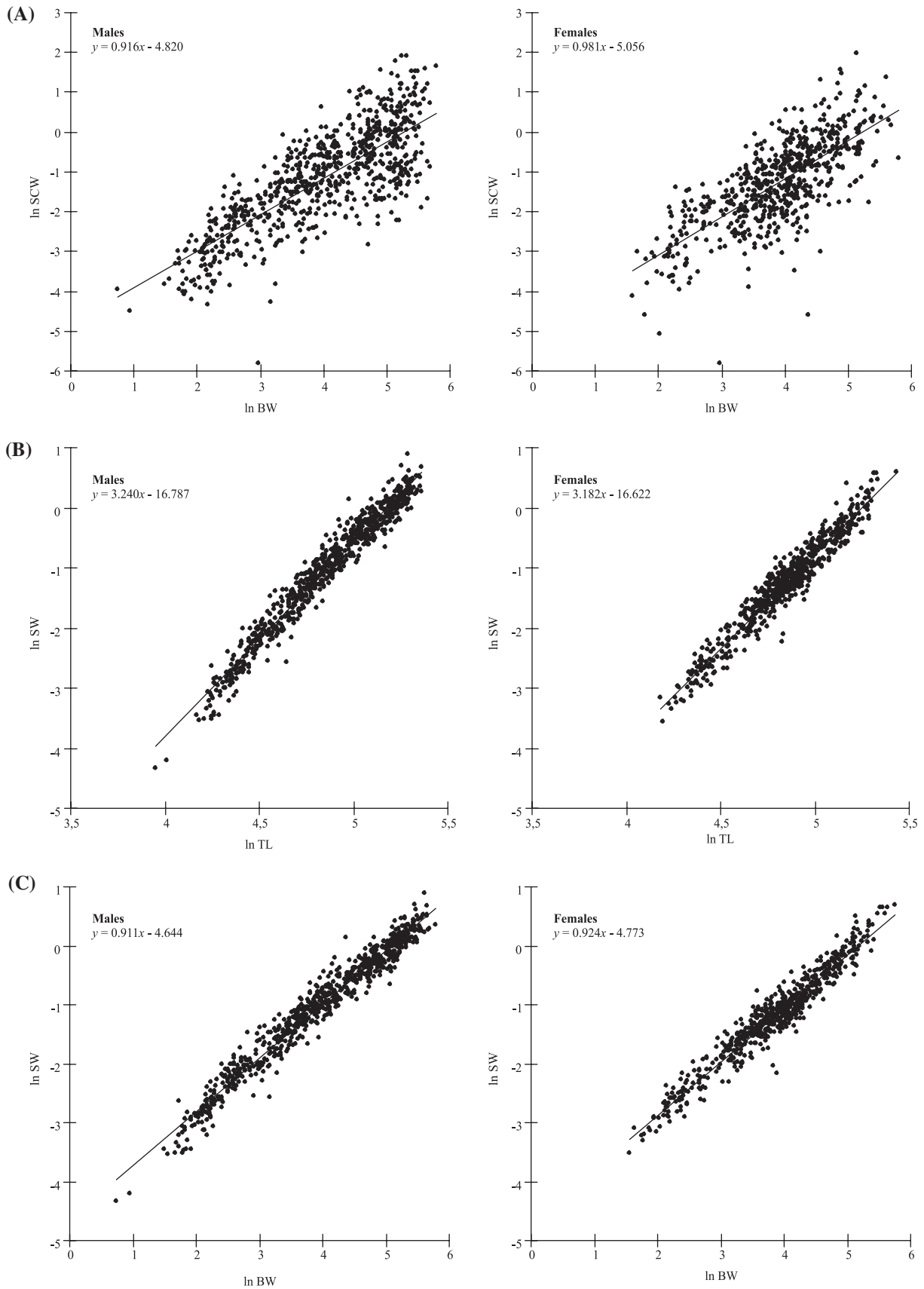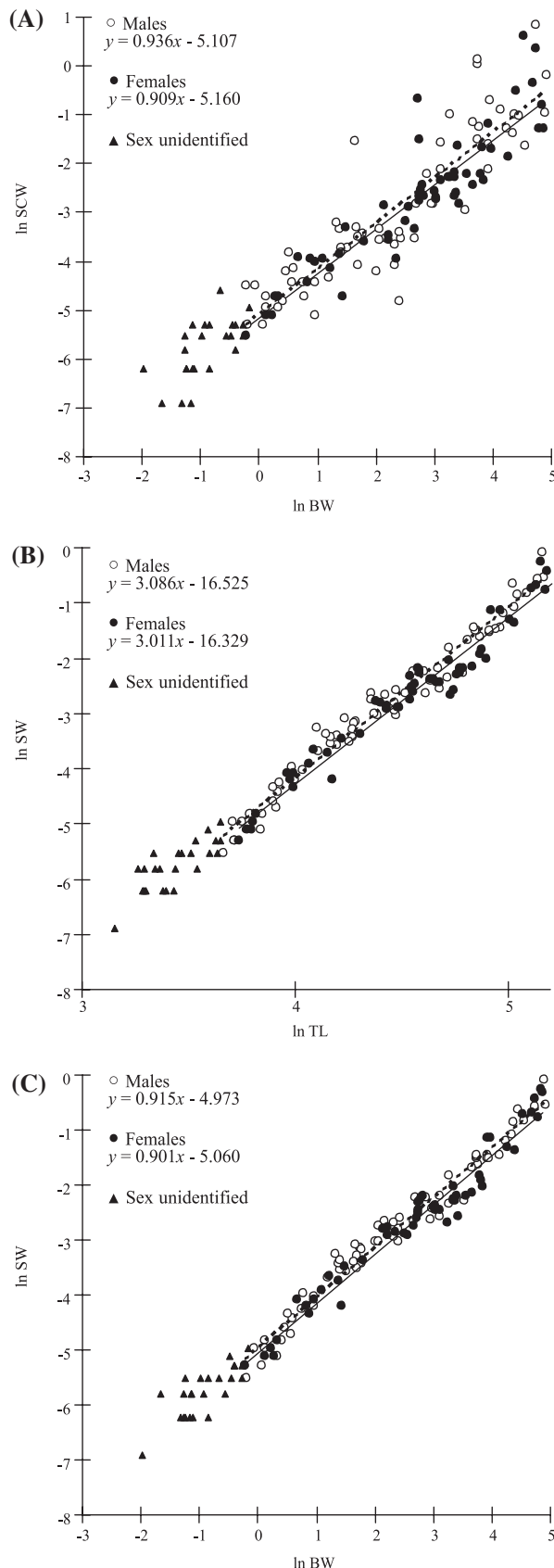
(A)

(B)

(C)

Figure 2. Distribution graphs of relationships between logarithm-transformed total length (TL), body weight (BW), stomach content weight (SCW) and stomach weight (SW) of bluegills inhabiting Hachiman Reservoir, collected during from March, 1990 to January, 1991. (**A**) lnBW–lnSCW, (**B**) lnTL–lnSW, (**C**) lnBW–lnSW.

Figure 3. Distribution graphs of relationships between logarithm-transformed total length (TL), body weight (BW), stomach content weight (SCW) and stomach weight (SW) of bluegills inhabiting Saburo Reservoir, collected during 26–29th, October, 1990. (**A**) lnBW–lnSCW, (**B**) lnTL–lnSW, (**C**) lnBW–lnSW.

stomach contents due to digestion, were omitted from the DSP calculations.

Seasonal changes in stomach content composition (DSP) of the three size classes of each sex of the Hachiman Reservoir bluegills are shown in polygonal charts. In addition, growth-related stomach content compositions in 10 mm TL interval size classes of Hachiman bluegills, including juveniles, based on data for October–December, are shown in a polygonal chart, together with data for bluegills from Saburo Reservoir.

The Shannon index (H'), usually used as an index for species diversity (Krebs 1989), was used to evaluate variability of the stomach content items. Variates (based on DSP values) to calculate the index included all animal stomach content items, summarized at ordinal rank, all plant items, and all inorganic items, summarized as a single variate.

Results

Feeding amount

Distribution graphs of the relationships between logarithm-transformed body weight (BW) and stomach content weight (SCW) showed linear plot clusters for both the Hachiman and Saburo Reservoir bluegills (Figures 2(A) and 3(A)), linear regressions being fitted with comparatively high correlations (Table 2). Because inter-sexual comparisons by analysis of covariance (ANCOVA) showed no significant differences for the regression parameters (slope and intercept) for bluegills from both habitats (Table 2), no inter-sexual difference in feeding amount was suggested.

Subsequently, all individuals were pooled by habitat (males + females + sex-unidentified), regressions between lnBW and lnSCW being re-calculated, and their slopes tested for a null hypothesis (slope = 1). The slopes were significantly less than 1 for bluegills from both habitats (Table 3(A)), inferring that SCW was allometric for BW (relatively reducing with increasing BW).

The feeding index (FI), which standardized the individual feeding amount, showed most individuals to be distributed within a range of 0–2 (Figure 4). Maximum FI values were ca. 6 and 5 (Figure 4), with average FI values being 0.966 and 0.813 for the Hachiman and Saburo Reservoir bluegills, respectively. Very few individuals had completely empty stomachs [indicated by FI = 0 (stomachs completely empty) (Figure 4)], percentages being 0.003 and 0 for the Hachiman and Saburo Reservoir bluegills, respectively.

Seasonal FI changes in the Hachiman Reservoir bluegills (Figure 5) were generally high in March–April, occasionally exceeding 1.5. Subsequently, FI declined gradually until September (minimum value ca. 0.3), before spiking in early October and thereafter increasing gradually towards January (Figure 5).

Table 2. Results of analysis of covariance (ANCOVA) (*t* test) to compare regressions of logarithm-transformed total length (TL), body weight (BW), stomach weight (SW) and stomach content weight (SCW) between sexes of bluegills inhabiting Hachiman and Saburo reservoirs (see also Figures 1 and 2).

Regression	Males			Females			Adjusted intercept		*t*	
	Slope	Intercept	*r*	Slope	Intercept	*r*	Males	Females	Slope	Intercept
Hachiman Reservoir										
ln BW–ln SCW	0.916	−4.820	0.791	0.981	−5.056	0.742	−4.904	−4.885	1.473	0.488
ln TL–ln SW	3.240	−16.787	0.979	3.182	−16.622	0.966	−16.735	−16.853	1.381	11.404***
ln BW–ln SW	0.911	−4.644	0.980	0.924	−4.773	0.967	−4.669	−4.750	1.058	7.968***
Saburo Reservoir										
ln BW–ln SCW	0.936	−5.107	0.891	0.909	−5.160	0.908	−5.082	−5.201	0.312	0.998
ln TL–ln SW	3.086	−16.525	0.985	3.011	−16.329	0.978	−16.383	−16.525	0.684	3.066**
ln BW–ln SW	0.915	−4.973	0.987	0.901	−5.060	0.978	−4.958	−5.083	0.458	2.768**

Note: Asterisks indicate significance of *t* values; double and triple asterisks indicate 1% and 0.1% levels, respectively.

Differences in relative stomach weight between sexes

The distribution graphs of relationships between logarithm-transformed total length (TL) and stomach weight (SW) for both Hachiman and Saburo Reservoir bluegills showed sharp linear clusters (Figures 2(B) and 3(B)). In addition, very similar graphs were obtained for relationships between logarithm-transformed BW and SW (Figures 2(C) and 3(C)), the highly significant regression slopes ranging from 0.901 to 0.924 for both sexes (Tables 2 and 3(B)). Similarly significant slope values were obtained for BW versus SCW (Table 3(A)).

ANCOVA analysis of the lnTL–lnSW regression parameters (slope and intercept) between sexes showed no significant slope *t* values for either of the Hachiman and Saburo Reservoir bluegills, although the intercepts showed high levels of significance for both (Table 2). Because the adjusted intercept values of the males were greater than those of the females from both localities (Table 2), male SW was regarded as being relatively heavier. Similar results were obtained for the parameters of lnBW–lnSW regressions (Table 2).

Seasonal changes in stomach contents of Hachiman Reservoir bluegills

Table 4 summarizes monthly stomach contents as indicated by food score proportions. The wide diversity of items, including animal, plant and inorganic material, indicated that bluegills have a broad foraging habit. In particular, insects representing a range of taxa (Figures S1(A)–(H), S2(A)–(H), S3(A)–(D)) appeared throughout the year, chironomid larvae and pupae (Figure S3(C) and (D)) being well represented in each month, and, in fact, the dominant food proportion during winter and spring (approaching 70% in December), but less so in summer (3.6% in July). Several different chironomid species were recognized, the dominant species changing by season. Considering insect food items overall, the great majority of species were aquatic, although some terrestrial forms, including lepidoptera, coleoptera and hymenoptera, were also recorded.

Table 3. Regression parameters (slope and intercept) and correlation between logarithm-transformed body weight (BW), stomach content weight (SCW) and stomach weight (SW), together with results of *t* tests to examine significance of slopes for a null hypothesis (slope = 1) of bluegills inhabiting Hachiman and Saburo reservoirs (see also Figures 1 and 2).

Regression	Slope	Intercept	*r*	*t*
A ln BW–ln SCW				
Hachiman Reservoir				
Pooled	0.936	−4.893	0.773	−3.082**
Saburo Reservoir				
Pooled	0.893	−5.041	0.935	−9.290***
B ln BW–ln SW				
Hachiman Reservoir				
Males	0.911	−4.644	0.980	−13.825***
Females	0.924	−4.773	0.967	−8.204***
Saburo Reservoir				
Males	0.915	−4.973	0.987	−4.495***
Females	0.901	−5.060	0.978	−3.820***

Note: Asterisks indicate significance of *t* values; double and triple asterisks indicate 1% and 0.1% levels, respectively.

Planktonic crustaceans, including cladocerans and copepods (Figure S3(F) and (G)), also occurred frequently, being a significant food proportion in winter and spring [23.4–29.9% (all copepods) in November–January]. Cladocerans dominated over copepods in spring (April–June), the proportion of the former exceeding 10%.

Although fishes (including eggs and scales) appeared throughout the year, they generally constituted a small proportion of the stomach content. However, fish egg numbers (Figure S5(B) and (C)) climbed in March–May (proportion 26.4% in March), due to spawning of the crucian carp *Carassius cuvieri*. Up to ca. 3500 crucian carp eggs were recorded from a single bluegill stomach. Some crucian carp eggs appeared with aquatic plant leaf chips, to which they had been attached, indicating that bluegills had swallowed both eggs and their spawning bed. Larval or juvenile fish remains of several species were recorded, including freshwater gobies, *Rhinogobius* spp. (Figure S4(H), see supplemental data), largemouth bass, *Micropterus salmoides*, and bluegills. Despite being in low frequencies, fish scales (mainly cyprinids and centrarchids) appeared consistently throughout the year.

Other animal remains recorded from time to time included amphipods, isopods (pill-bugs), decapods
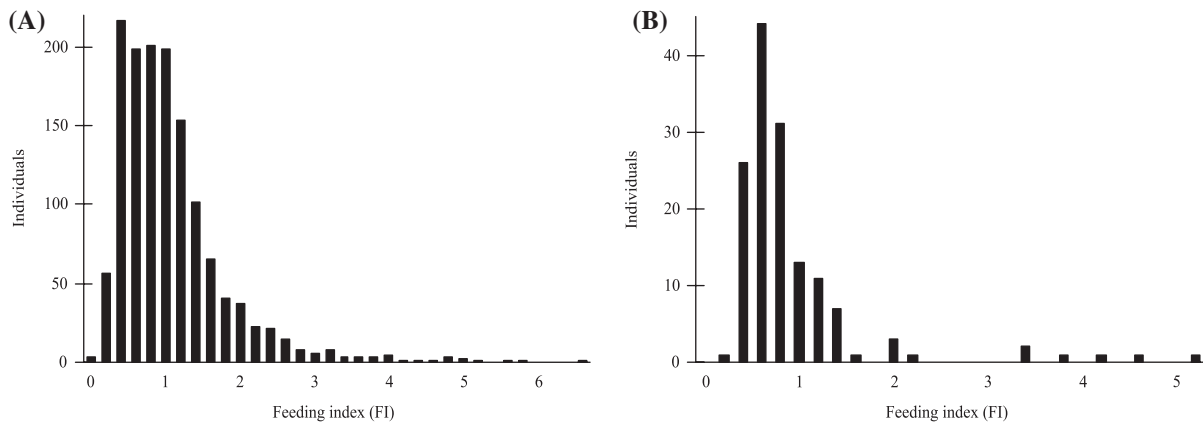
Figure 4. Frequency distribution histograms of feeding indices (FI) of bluegills inhabiting Hachiman Reservoir (**A**) and Saburo Reservoir (**B**).
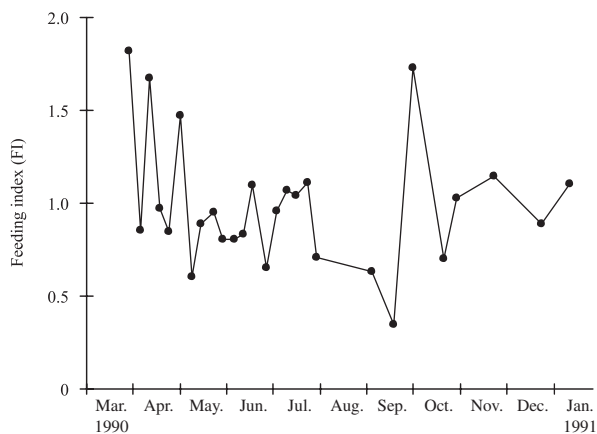

Figure 5. Seasonal changes of feeding indices (FI) of bluegills inhabiting Hachiman Reservoir. Dark dots indicate average values of example lots, in which the males and females were pooled.

(shrimps), arachnids (spiders), chilopods (centipedes), annelids (earthworms, leeches), and mollusks (freshwater snails) (Figures S3(H) and S4(A)–(G)) usually in low proportions, although commercial shrimps (*Macrobrachium nipponense* and *Palaemon paucidens*) appeared constantly throughout the year, sometimes up to ca. 10% proportion.

Plant material predominated in some months, the proportion being particularly high in summer and autumn (exceeding 40% in July). Terrestrial phanerogams (remnants of leaves and stems (Figures S5(F)–(H), S6(A)) were recorded constantly throughout the year, with aquatic phanerogams and algae (mainly green algae) (Figure S5(D) and (E)) appearing during summer and autumn in considerable proportions. In particular, the algal proportion of stomach contents approached 30% in July, the stomachs of many of the specimens collected at the time being filled with green algae, which also crammed their intestinal tract continuously from their stomachs.

Inorganic debris recorded in stomach contents were primarily man-made, including plastic worms, rubber bands and glass (Figure S6(B)–(G)). Although gravel appeared constantly throughout the year, the proportion of the stomach content was low. Flour paste (Figure S6(H)), frequently identified in bluegill stomach contents throughout the year, had been provided as an artificial dietary supplement for the cultured fish in the reservoir.

The organic stomach content composition in bluegill relative to body size (Figure 6(A)) differed by size class. It was also noted that although inorganic debris occupied considerable proportions in the largest size class, they occupied much lesser proportions in the middle and small classes. By contrast, planktonic crustaceans (mostly cladocerans and copepods) were found in considerable proportions in the smallest class, but in gradually reduced proportions in the middle and large classes. Notably, copepods, which were dominant in the small and middle classes during November–January, were scarcely represented in the largest class (Figure 6(A); Table 4). However, despite the lower amounts, cladocerans were recorded in spring from the largest bluegill size class (Figure 6(A); Table 4), indicating that even large individuals ingested such zooplankters. Also, it was notable that the proportions of plant material in the smallest class were less than those in the middle and large classes.

The stomach content compositions of bluegill males and females were similar to each other (Figure 6(B)), despite some small differences in proportion or fluctuation patterns of planktonic crustaceans and inorganic debris, indicating similar food habits between the sexes.

Seasonal changes in the Shannon index (*H'*) (Figure 7), *H'* values of the largest class being generally higher than those of the middle and small (generally lowest) classes in March–July, indicated that large individuals foraged on a more varied diet than smaller ones during spring and summer. Nevertheless, the *H'* values of the three classes fluctuated in a similar manner to one another, gradually increasing through spring and summer, reducing rather rapidly through autumn and winter, and subsequently rebounding in January (Figure 7(A)). In addition, the fluctuation patterns of males and females were very similar to each other (Figure 7(B)).

Table 4. Monthly-summarized stomach contents (diet score proportions) of bluegills inhabiting Hachiman Reservoir.

Year	1990										1991
Month	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.
Number of fish	18	103	274	147	322	56	55	85	66	75	118
ARTHROPODA											
INSECTA											
Orthopoda		+	+	0.5	0.2			0.9	1.0		
Mantodea									1.0		
Dermaptera						2.1			0.9		
Ephemeroptera					+	0.3			+		
Odonata			0.6	5.1	1.3	10.8	5.3	0.8	0.5		0.9
Plecoptera			0.5	+	+	0.4	0.5				
Hemiptera		+	0.9	4.1	1.3	2.4	0.1	0.4	1.1		
Megaloptera					+						
Trichoptera	2.2	+	1.6	2.6	0.3				0.4		
Lepidoptera		0.3	0.5	1.3	+	0.4	2.3	6.5	1.4		
Coleoptera	12.0	0.9	5.2	10.2	4.7	5.0	4.6	2.4	3.6		
Hymenoptera		2.7	2.9	6.2	15.2	7.1	8.6	11.0	3.8		
Diptera											
Chironomid larvae	9.6	30.8	25.4	11.0	4.1	10.9	25.9	6.2	16.8	67.4	49.3
Chironomid pupae	4.0	16.7	2.7	1.8	0.2	+	5.1	6.2	23.1	1.3	
Other diptera	0.4	0.2	0.3	0.4	1.6	0.2	1.2	2.0			
Unidentified insects		0.9	0.4	2.4	0.4	4.5	0.5	0.8			
CRUSTACEA											
Anostraca				2.2							
Cladocera		13.6	12.6	2.3	+		1.9	5.1			
Ostracoda					0.7						
Copepoda	5.0	5.2	1.2				2.7	5.1	24.6	23.4	29.9
Amphipoda	1.1	1.1	0.9	0.4	+			0.2	+		
Isopoda	0.8		4.6	2.4	4.7			7.3	1.7		
Decapoda											
Macrobrachium nipponense										3.2	12.6
Palaemon paucidens	2.0	0.7	0.4	0.3	1.0	10.4	2.4		1.4	2.6	
Unidentified decapods											0.9
ARACHNIDA		+	1.2	1.9	0.9	1.1		1.3	0.6		
CHILOPODA					0.4				+		
ANNELIDA											
OLIGOCHAETA			0.2	1.1	4.1						
HIRUDINEA			0.3	0.3				0.7		1.6	
MOLLUSCA											
GASTROPODA											
Cipangopaludina chinensis			0.4		1.0	0.1		+			
Polypylis hemisphaerula		0.1	0.6		3.1	+	0.2	0.6	1.5		
Other gastropods				0.5	+			+	0.3		
VERTEBRATA											
OSTEICHTHYES											
(Larvae and juveniles)											
Rhinogobius spp.				0.8	0.7	0.5	9.8		0.9		
Micropterus salmoides			+	0.5							
Lepomis macrochirus			13.8	8.4	0.4		1.8	1.4			2.9
Unidentified fishes			0.1	0.5	0.3	0.2			1.1		2.7
(Eggs)											
Carassius cuvieri	26.3	9.5	5.0								
Carassius carassius		2.1	+	+							
Lepomis macrochirus			2.5		0.2						
(Scales)											
Cyprinid		0.2	0.2	+	+	0.4	1.0	+		0.2	
Centrarchid		0.4	0.3	+	+				0.2		0.2
Unidentified scales			+								+
PLANTAE											
Terrestrial phanerogams	29.4	5.1	7.8	9.0	4.4	15.0	15.7	5.0	3.9	0.2	0.5
Fungi						0.4			0.3		
Aquatic phanerogams			+	1.9	8.1	0.3	4.7	22.3	+		
Algae		+	0.3	5.2	30.4	16.8	0.6	3.8	6.4		
INORGANIC DEBRIS											
Gravel	2.4	6.8	4.6	3.5	0.8	2.4	0.9	+	0.2	0.1	+
Plastic worm chips			1.0	4.0	2.8	2.8	1.6				
Rubber band chips			0.1		0.2	0.2					
Vinyl chips			0.3		0.3	1.8					
Plastic chips		+	+		+			+			
Iron chips			+								
Glass chips							0.3				
Feathers			+		+		0.9				
Flour paste	4.8	2.7	0.5	7.8	5.6	3.3	1.5	8.6	4.5		

Note: Plus signs indicate values between 0 and 0.1.

Growth-related stomach content changes

In both Hachiman and Saburo Reservoir bluegills, the stomach contents of small individuals (20–50 mm TL) comprised almost solely planktonic crustaceans (mostly copepods), with other dietary items, including chironomids, shrimps and fishes, becoming apparent and increasing gradually with increasing bluegill body size (Figure 8(A) and (B)). In individuals larger than 110 mm TL, zooplankton was hardly recorded in Hachiman Reservoir individuals (Saburo Reservoir not at all) (Figure 8(A) and (B)), indicating that food habits of bluegills apparently shift from planktivory to omnivory with growth. On the other hand, large bluegills (ca.>100 mm TL) from Saburo Reservoir frequently foraged upon shrimps (mostly *Macrobrachium nipponense*) and fishes (mostly freshwater gobies, *Rhinogobius* spp.) (Figure S4(H)), the proportions of those species in the stomach contents being rather greater than in the Hachiman Reservoir bluegills (Figure 8(A) and (B)).

Discussion

The stomach content weight (SCW) of bluegill reduced relative to an increase in body weight (BW), although the slope values of the lnBW–lnSCW regressions were close to 1 (0.893–0.936) (Figures 2(A) and 3(A); Table 3(A)). This may be closely related to the stomach weight (SW) also reducing relative to BW increase (Figures 2(C) and 3(C); Table 3(B)), the slope values of the lnBW–lnSW regressions being 0.901–0.924 (Table 3(B)), i.e. very similar to those of the lnBW–lnSCW regressions. However, the relative reduction in SW with BW increase does not necessarily indicate that the stomachs of bluegill become relatively smaller with growth because the slope values of the logarithm-transformed regressions between TL and SW were all greater than 3 (Table 2), which indicates a stable relationship. This may be related to the BW of bluegill increasing relative to growth due to associated increases in body depth and width (Yokogawa 2013). Therefore, the relative reduction in SW with BW increase may be simply explained by a greater rate of increase in the latter.

On the other hand, relative SW differed significantly between the sexes, male SW being greater than that of females, as evident in the regressions of lnTL–lnSW and lnBW–lnSW (Table 2). Although this has been reported previously in cultured bluegill (OPFFES 1976), no significant inter-sexual SW difference was recognized in bluegill populations in Manno and Sendai Reservoirs (Yokogawa 1986). However, the latter may have been due to the small sizes of the specimens examined (<140 and <70 mm TL in Manno and Sendai Reservoirs, respectively).

Although greater SW of males implies a larger stomach, containing a greater volume of contents than in females, such is inconsistent with the lack of inter-sexual SCW difference (Table 2). However, this may be explained by the relative BW of males being significantly greater than that of females, a sexually dimorphic feature of bluegill (Yokogawa 2013), i.e. although males may consume more food than females, the rate of consumption relative to BW may not differ from that of females, more food being necessary for the gaining of greater BW in the former. The inter-sexual SW difference is also regarded as a sexually dimorphic characteristic, being more prominent in larger individuals with prominent secondary sexual traits. Therefore, it may be reasonable to conclude that significant inter-sexual SW differences were not recognized in bluegill from Manno and Sendai Reservoirs, because only small individuals were examined, in which sexually dimorphic features were not prominent.

Very few of the specimens examined had completely empty stomachs (Figure 4), as found in bluegill populations from other localities, including their native habitat (Couey 1935; Bennett 1948; Seaburg and Moyle 1964; Turner 1966; Minckley 1982; Katano et al. 2005; Sugiura and Taguchi 2012), apparently a common characteristic. Although Windell (1966) demonstrated experimentally that ingested natural food organisms required about 18 h for complete digestion by bluegills, such low empty stomach rates suggest that bluegills continually forage for food, supported by SCW being relatively closely correlated with BW (Figures 2(A) and 3(A)). Almost all of the bluegill individuals examined contained food items digested to varying degrees, unlike another centrarchid, the largemouth bass *Micropterus salmoides*, individuals of which were found to frequently have empty stomachs (Turner 1966; Yoshizawa 1992).

An ecological implication may lie in bluegill stomach capacity being much less than that of other omnivorous centrarchids, including white and black crappies (*Pomoxis annularis* and *P. nigromaculatus*), as well as typical carnivorous freshwater fishes, including spotted bass, *Micropterus punctulatus*, channel catfish, *Ictalurus punctatus* and white bass, *Morone chrysops* (Gosch, Pope, and Michaletz 2009), and possibly related to gape size, bluegill having one of the smallest within Centrarchidae (Collar and Wainwright 2009). Accordingly, bluegills have difficulty swallowing large prey, Keast (1978a) finding that most prey items (ca. 65–80%) in bluegill stomachs had a body width less than a quarter of the predators' gape width. Consequently, bluegill feeding behavior may have evolved as frequent pecking, so as to secure sufficient nutrition.

The feeding index (FI), reflecting seasonal changes in feeding quantities, of the Hachiman Reservoir bluegills was generally higher during winter–spring and lower during summer–autumn (Figure 5). This pattern may not necessarily be common to bluegill populations in other habitats due to feeding conditions being largely affected by environmental factors. However, it was notable that the Hachiman Reservoir bluegills actively foraged in
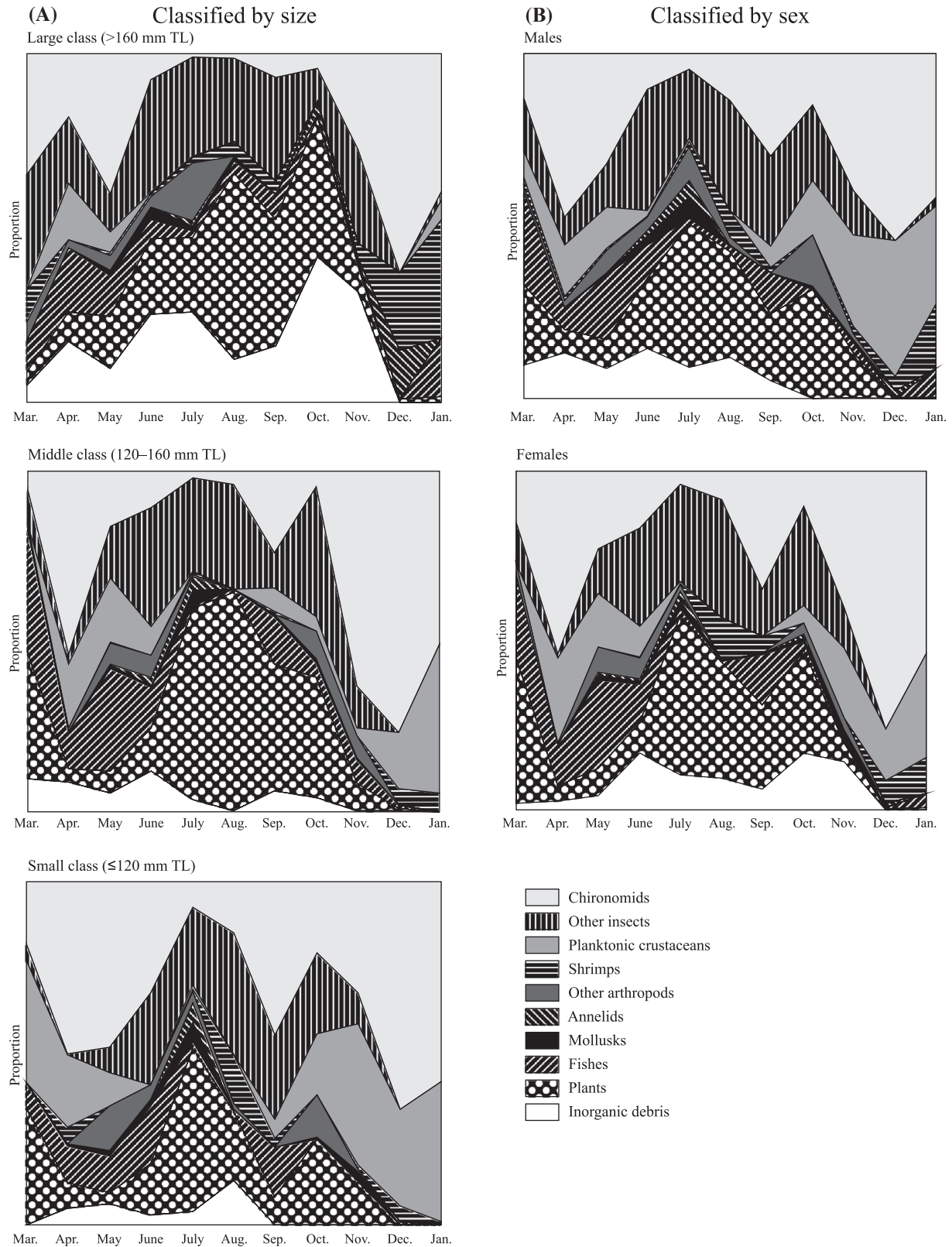
(A) Classified by size

Large class (>160 mm TL)

Middle class (120–160 mm TL)

Small class (≤120 mm TL)

(B) Classified by sex

Males

Females

- Chironomids
- Other insects
- Planktonic crustaceans
- Shrimps
- Other arthropods
- Annelids
- Mollusks
- Fishes
- Plants
- Inorganic debris

Figure 6. Seasonal changes in stomach content compositions (diet score proportions) of bluegills inhabiting Hachiman Reservoir. Fish were classified by size (**A**) (see text) and sex (**B**).

winter, when ambient water temperatures (WT) fell to ca. 5 ℃ in January (Figure 9). In contrast, FI decreased in summer, when WT exceeded 33 ℃ in August (Figure 9), indicating better tolerance of bluegill to cold stress than heat stress. This is further evident by annulus formation in the scales of the Hachiman Reservoir bluegills

occurring in autumn due to summer heat stress, but not in winter (Yokogawa 2001), although they may occur as 'winter rings' due to cold stress in many other fishes (Kubo and Yoshihara 1969).

Hathaway (1927) experimentally compared food consumption of bluegill under 10 and 20 ℃, finding
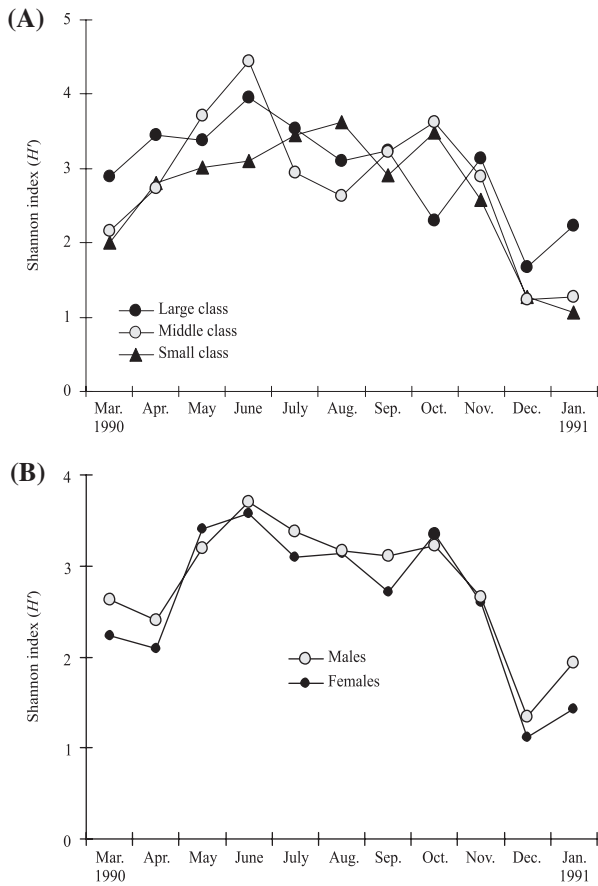
Figure 7. Seasonal changes of the Shannon indices (*H'*) of bluegills inhabiting Hachiman Reservoir. Fish were classified by size (**A**) (see text) and sex (**B**).
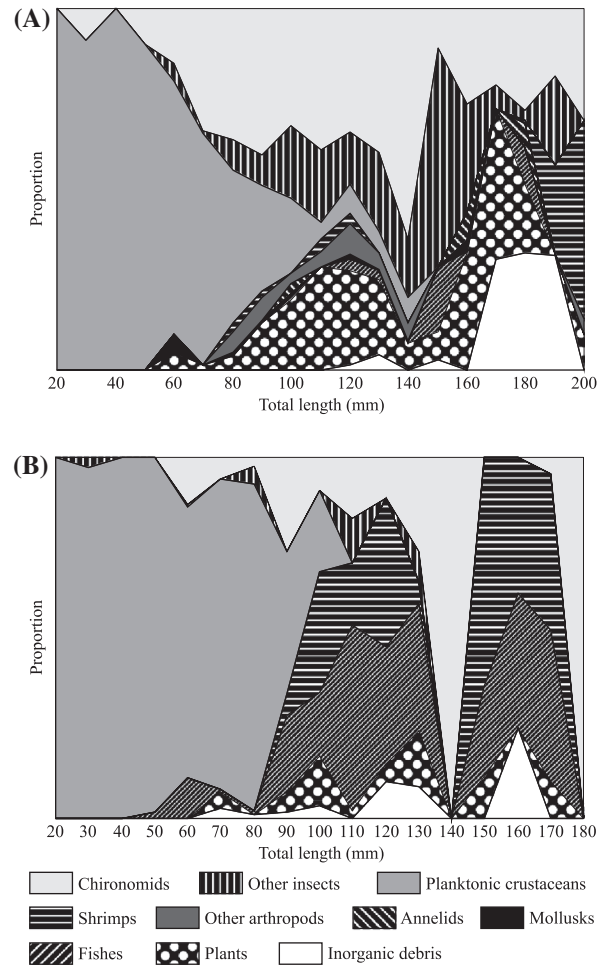

Figure 8. Growth-related changes of stomach content compositions (diet score proportions) of bluegills inhabiting Hachiman Reservoir (October–December, 1990) (**A**) and Saburo Reservoir (October, 1990) (**B**).
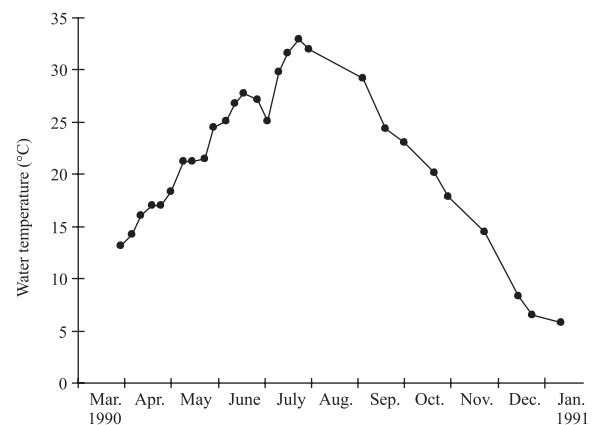

Figure 9. Changes in water surface temperature at Hachiman Reservoir from March, 1990 to January, 1991.

the former level to be about half of the latter. Although this was inconsistent with FI of the Hachiman Reservoir bluegill not declining in December–January (Figure 5), when WT was below 10 °C (Figure 9), such may have been due to stressful treatment, Hathaway's (1927) specimens having been transferred directly to 10 °C after two weeks experimentation at 20 °C. Furthermore, difficulties in keeping specimens alive for long periods at a higher temperature (30 °C) during that study, inferred a lower tolerance to heat stress.

Bluegills have been reported as foraging on various prey during winter in ice-covered Clear Lake (Michigan, USA) (Moffett and Hunt 1945), and continuing to feed in winter and being modestly active (Snow, Ensign, and Klingbiel 1960). On the other hand, experimental studies to gauge bluegill tolerance to heat stress reported 31.2 °C as the uppermost WT preference (Beitinger 1977), with the maximum WT in which they could feed being ca. 35 °C (OPFFES 1975) and mortality due to heat stress beginning at 33.5 °C (Hickman and Dewey 1973).

With the exception of summer (Figure 6; Table 4), the stomach contents of the Hachiman Reservoir bluegills included considerable proportions of chironomid larvae and pupae (Figure S3(C) and (D)), being principle dietary items. This was particularly so in December and January (Table 4). Because many chironomid species

occur naturally in Japan, having varying life cycles (Kondo et al. 2001), the larvae and pupae of different species occur throughout the year in fresh water habit, including Hachiman Reservoir, therefore being available for utilization by bluegills.

High proportions of chironomids (ca. 20–80%) in the stomach contents of Japanese bluegill populations

have been frequently reported from a variety of habitats (Maruyama, Furuta, and Hirabayashi 1972; Yokogawa 1986; Azuma 1992, 2002; Oyama and Ide 2003, 2004; Katano et al. 2005; Yamaguchi 2007) and North America (Forbes 1903; Hankinson 1908; Pearse 1918, 1921a; De-Ryke and Scott 1922; Couey 1935; Bennett, Thompson, and Parr 1940; McCormick 1940; Howell, Swingle, and Smith 1941; Bennett 1948; Parks 1949; Morgan 1951; Huish 1957; Lux and Smith 1960; Gerking 1962; Goodson 1965; Flemer and Woolcott 1966; Turner 1966; Mullan and Applegate 1967; Keast and Welsh 1968; Hall, Cooper, and Werner 1970; Etnier 1971; Laarman and Schneider 1972; Baumann and Kitchell 1974; Kolehmainen 1974; Diggins, Summerfelt, and Mnich 1979; Minckley 1982; Krska and Applegate 1984; Engel 1988; Harris, Galinat, and Willis 1999; Olson et al.2003). In addition, Ball (1948) found that bluegills fed preferentially on chironomid larvae, taking a proportion greater than the relative abundance of the latter in Third Sister Lake (Michigan, USA). The appearance of multiple chironomid species in the stomach contents of Hachiman Reservoir bluegills indicated that chironomids were taken regardless of species (see also Lobinske, Cichra, and Ali 2002).

The Hachiman Reservoir bluegills also exploited planktonic crustaceans (mostly cladocerans and copepods), although their proportions in bluegill stomach contents reduced with body size increase (Figure 6(A)). In the small bluegill class (≤120 mm TL), the dominance of zooplankton was a consequence of the initial planktivorous food habits of the fish (Figure 8(A)). In middle (120–160 mm TL) and large (>160 mm TL) classes, smaller proportions of zooplankton suggested a change to opportunistic or supplemental feeding. Moffett and Hunt (1945) had earlier reported a decreasing proportion of zooplankton taken by increasing size bluegill in winter, whereas Ball (1948) found no evidence that bluegill fed more extensively on zooplankton during periods of abundance, turning to that food source opportunistically when alternative invertebrate food was at a minimum.

However, despite such opportunism, size-dependent prey selectivity was recognized, insofar as large class bluegills occasionally ingested cladocerans in spring in addition to other prey, but hardly took copepods, which were commonly consumed by the other size classes in autumn–winter (Figure 6(A); Table 4). Although it has been reported that bluegills consumed zooplankters in a size-selective fashion (O'Brien, Slade, and Vinyard 1976; Mittelbach 1981b; Bartell 1982; Werner et al. 1983a), this was not the case here.

Sakano and Yodo (2004) compared the food habits of bluegill populations in reservoirs in Nagano, Japan and found that the cladoceran *Daphnia longispina* was selectively consumed in one reservoir whereas the copepod *Cyclopus vicinus* was selectively consumed in the other. Their results were similar to those of the present study because the average body size of the cladoceran feeders

was greater than that of the copepod feeders (126 vs. 97 mm in fork length). Similarly, Radant and Scalet (1975) found that young-of-the-year bluegills (15–55 mm TL) in Abbey Pond (South Dakota, USA) had clear feeding selectivity for copepods rather than cladocerans. Sakano and Yodo (2004) indicated some likely factors for their findings, including differing levels of success by zooplankters in evading predation. Large bluegills may not need to exploit copepods, which are more evasive than cladocerans (Drenner, Stricker, and O'Brien 1978), because they have sufficient ability to catch other prey groups. In addition, Manatunge and Asaeda (1998) pointed out that such selectivity results from fish activity avoiding prey with high evasion capability. It may also be related to suction capability, for although bluegills are high-performance suction feeders (Spotte 2007), their suction capability (= generatable buccal pressure) decreases with increasing body size (Carroll et al. 2004) perhaps due to a reduction of kinematic speed with increasing body length (Wainwright and Shaw 1999). Consequently, large bluegills may not be able to ingest evasive copepods.

On the other hand, bluegills inhabiting open water in some small Michigan lakes (USA) have been reported to feed extensively on zooplankton, primarily *Daphnia* (Mittelbach 1981b, 1984; Werner and Hall 1988; Schneider 1999), a positive correlation between large bluegill growth rates and ambient zooplankton (chiefly *Daphnia*) abundance having been suggested (Osenberg et al. 1988; Mittelbach and Osenberg 1993). However, Shoup et al. (2007) found that large bluegill growth was in fact negatively related to *Daphnia* biomass, based on their investigations in 14 Illinois reservoirs (USA). The above positive correlation may be erroneous because zooplankton have relatively low calorific value and apparently contribute little to the caloric content of the diets (Olson et al. 2003), in particular for larger bluegills with greater body mass. Furthermore, since large bluegills consume much more protein than small ones during their growing season (e.g. age 4 group consumes approximately 3 times the amount of protein as age 2 group) (Gerking 1972), it is unlikely that zooplankton taken by bluegills can supply all of the required protein amount for their growth. In this respect, Lemly and Dimmick (1982) demonstrated that the abundance of adult copepods was frequently correlated with growth and body condition of many age 0 + centrarchids, including bluegill, but that the number of significant correlations dropped sharply as fish age increased to 1 + years.

Even if a positive zooplankton–growth correlation were correct, such large bluegills may not be regarded as permanent planktivores, due to daphnids inhabiting North American inland waters typically having seasonal fluctuations in abundance (Petersen 1983; Engel 1985; Stich and Maier 2007; Havel 2010; Kaemingk et al. 2012; Burdis and Hirsch 2017). Furthermore, the earlier-cited studies that suggested 'planktivory' in large bluegill

were based on fish specimens collected during a limited period (all during summer). Therefore, 'planktivory' in large bluegills may be a seasonal phenomenon, just as the winter / spring food habits of Hachiman Reservoir bluegills (Figure 6; Table 4). Similar food habit seasonality for zooplankton has been further recognized in large bluegills inhabiting other North American lakes (DeRyke and Scott 1922; Lux and Smith 1960; Keast 1985b; Booth 1990; Keast and Fox 1992; VanderKooy, Rakocinski, and Heard 2000). Engel's (1985, 1987) investigations in Halverson Lake (Wisconsin, USA) revealed that zooplankton usually declined in late summer, when *Daphnia*, *Keratella*, and nauplii populations plummeted, thereby removing the planktivorous food option from bluegills.

Hachiman Reservoir bluegills consumed many fish eggs in spring (Table 4), mostly those of the cultured crucian carp, *Carassius cuvieri*, the reproductive success of the latter being impacted accordingly. Although bluegill is known as a predator of centrarchid nests (Aasen and Henry 1980; Bain and Helfrich 1983), depredation may not reach high rates because the nests are protected by territorial males (e.g. Scott and Crossman 1973; Carlander 1977). By contrast, crucian carp eggs, which lack protection, are easily exploited by bluegills, being a good nutritional resource in the bluegill breeding season. In fact, 42% of bluegills in Tamizo Reservoir (Nagano, Japan) fed upon eggs of common carp, *Cyprinus carpio*, and crucian carp in their spawning season (Yamamoto 2005), thereby seriously reducing carp reproductive success. A subsequent experimental study also demonstrated that bluegills fed heavily on common carp eggs (Sano and Ezaki 2007).

Although little work has been published on predation of cyprinid fish eggs by bluegills in North American inland waters, where cyprinids are less dominant, Huish (1957) found that large bluegills in Lake George (Florida, USA) during spring and summer heavily predated fish eggs (ca. 120–140 eggs / individual), possibly those of threadfin shad, *Dorosoma petenense*, a species which undertakes no egg protection.

Despite heavy fish egg predation, fishes generally occurred in low frequencies in bluegill stomach contents, with the exception of centrarchid larvae which may have been predated as 'nestlings' (Table 4). Similarly low preference for fish prey has been found in bluegill populations elsewhere Japan, as well as in North America (see summary in Yokogawa 1992b), suggesting that bluegills are not carnivorous. Earlier, Keast (1985a) defined bluegill as a species in which fish consumption is limited to sometimes taking larvae. However, large bluegills from Saburo Reservoir (ca.>100 mm TL) commonly predated fishes (mostly freshwater gobies) as well as shrimps (Figure 8(B)), possibly due to the reduction of water level during draining of the reservoir, allowing fishes and shrimps to be caught more easily.

Cannibalism was barely evident among Hachiman Reservoir bluegills throughout the year, except for bluegill larvae (probably eaten in the nest) during the breeding season (May–July) (Table 4). Although such bluegill larvae appeared in considerable proportions in May and June (Table 4), they may have been from nests from which guarding males had been removed by sampling. Such nests might have been quickly predated by other bluegills. Previous attempts to measure cannibalism in bluegills via diet analysis have found little evidence of significant consumption of larval bluegills by adults (Breck 1996; Schneider 1999; Rettig and Mittelbach 2002), being consistent with the results of the present study. Although Kim and DeVries (2001) conducted a mesocosm experiment in which they found significant cannibalism by adult bluegills, their experimental design excluded ambient invertebrate prey (except zooplankton), thereby being significantly different from normal field conditions. Accordingly, bluegill may not resort to cannibalism when sufficient ambient prey are present.

This being said, the occurrence of fish scales (in low frequencies throughout the year) in Hachiman Reservoir bluegill stomach contents was interesting (Table 4), suggesting that bluegills either peck the bodies of dead fish, or consume scales while cleaning other fishes (Sulak 1975; Powell 1984). The latter may be in keeping with Powell's (1984) comment that skin fragments taken during cleaning behavior may be of benefit, providing additional nutrition.

Low levels of carnivory in bluegills can also be inferred from the low frequency of shrimps in the stomach contents (Table 4) (see also, results of previous food habit studies on bluegills, summarized by Yokogawa 1992b). In North America, even when abundant in fresh water, shrimps are not consumed by bluegills, although taken by other fishes, including green sunfish, largemouth and smallmouth bass, and catfishes (Applegate, Mullan, and Morais 1966; Keast and Welsh 1968; Minckley 1982). A contrary finding by Terashima (1977, 1980) noted that the stomach contents of bluegills inhabiting Lake Biwa (Shiga, the greatest lake in Japan) comprised mostly shrimps (ca. 80–90% by weight), possibly due to a considerable increase in the shrimp resource due to a mass bloom of large-flowered waterweed, *Elodea densa*, in the 1970s. Although that food resource was effectively utilized by bluegills at the time, the food habits of the latter in Lake Biwa have since changed dramatically, recent studies (Kohashi and Kataoka 2000; Oyama et al. 2001) reporting much lower consumption of shrimps (0.6% occurrence).

The Hachiman Reservoir bluegills also took plant material throughout the year, in particular, grazing on large amounts of green algae in summer (Figure 6; Table 4). Similar dominance of plants in bluegill stomach contents have been recorded from Japan (Kohashi and Kataoka 2000; Oyama et al. 2001; Oyama and Ide

2003, 2004; Yamaguchi 2007; Sugiura and Taguchi 2012) and North America (Pearse 1921b; Couey 1935; Bennett, Thompson, and Parr 1940; McCormick 1940; Rice 1941; Nelson and Hasler 1942; Ball 1948; Morgan 1951; Scidmore and Woods 1960; Seaburg and Moyle 1964; Sadzikowski and Wallace 1976; Krska and Applegate 1984; Michaletz 2006). In particular, plant material was taken by ca. 50 and 70% of bluegills inhabiting Daini-Maze Lake (Saitama, Japan) in June and July, respectively (Yamaguchi 2007).

DeRyke and Scott (1922) found that bluegills inhabiting dense vegetation in Winona Lake (Indiana, USA) consumed four times the amount of plant material than those inhabiting an area of scant vegetation, suggesting opportunistic plant feeding. Furthermore, in some habitats, the proportions of plant material in bluegill stomach contents increased with increasing fish body size (Couey 1935; Bennett, Thompson, and Parr 1940; Huish 1957; Diggins, Summerfelt, and Mnich 1979; Azuma 1998, 2002; Kohashi and Kataoka 2000), as seen in the present study (Figure 6(A)). Similarly, Engel (1985, 1987, 1988) noted that large bluegills consumed vegetation 4–5 times as often as small ones, his summary of over two dozen studies listing vegetation in bluegill diet showing the mean percentage volume of plants as typically 20–30% (Engel 1985).

On the other hand, Forbes and Richardson (1920) considered that the large quantity (24%) of aquatic vegetation found in some bluegills from Illinois, USA had been swallowed accidentally while ingesting prey. Similarly, Scidmore and Woods (1960) questioned whether or not the high proportion of green plant material (ca. 40% by volume) in bluegills from St. Olaf Lake, Minnesota, USA indicated a feeding preference for plant material or simply represented incidental ingestion during regular feeding activities. However, it is now evident that bluegills take plant material purposely, grazing plants continuously year-round and taking particularly large amounts in summer. Although bluegills from Lake George (Florida, USA) fed more on plant material in autumn / winter rather than in spring / summer (Huish 1957), this may be due to plants, including aquatic vegetation, growing year-round in the subtropical Florida climate.

A study in Third Sister Lake (Michigan, USA) by Ball (1948) described bluegills, which fed on aquatic invertebrates during most of the active growing season, as turning to plants as a food supplement or replacement during the midsummer period, when the volume of invertebrates reached its lowest point of the year. In addition, Lux and Smith (1960) found that the volume of food taken by bluegills in Linwood Lake (Minnesota, USA) rose toward summer, with the volume of invertebrates dropping while the plant intake rose sharply. Mittelbach (1981a) also found at Lawrence Lake (Michigan, USA) that the biomass of littoral invertebrates declined dramatically from May to August (late spring–summer).

Laarman and Schneider (1972) found that bluegills in diet-poor lakes contained more plant material than bluegill in diet-rich lakes, suggesting that the former were forced to graze on plant materials instead of animal prey. This may be the case especially during midsummer, when bluegill stomach evacuation rates are so high (Booth 1990) that constant refilling with any kind of material, including plants, is necessary. Bennett, Thompson, and Parr (1940) had earlier considered that the higher percentage of plants eaten by old bluegills implied that older fish were less active in seeking prey, instead using plants as stuffing. This may be likely since their kinematic speed for feeding reduces with growth (Wainwright and Shaw 1999); accordingly, SCW reduces relative to BW with growth (Table 3(A)).

Many Hachiman Reservoir bluegill individuals in summer were characterized by the stomach and intestinal tract crammed with green algae fragments, similar to Reighard's (1915) observations of bluegills in Douglas Lake (Michigan, USA). However, Rice's (1941) examination of the lower intestinal tract of summer bluegills from Reelfoot Lake (Tennessee, USA) showed very little if any digestion of filamentous algae and questioned whether or not the latter had any actual food value. This suggests that undigested algae in the stomachs have been conveyed to the intestine directly, bluegill being unable to digest cellulose. Gerking (1954) also questioned if plant materials taken by bluegill contributed to their protein requirement.

Subsequently, Kitchell and Windell's (1970) breeding experiments suggested that bluegills gained some nutritional value from algae, based on the body weights of experimental fish, to which algae had been given, slightly exceeding those of controls, although not supported statistically. Notwithstanding, the nutritional value of algae may have been too little for utilization as a food resource.

The ingestion of non-nutrient plant materials by bluegills suggests that the species feeds on any material in the environment, regardless of nutritional value, supported by some examined individuals having ingested inorganic debris, including gravel, plastic worms and vinyl chips (Table 4). Such debris suggests that bluegills often peck at the substrate, ingesting bottom material together with benthic prey, as pointed out by Huish (1957). Such behavior seems to be more active in large bluegills, which contained considerable inorganic debris (Figure 6(A)).

Clearly, bluegills are characterized by very wide diet selectivity, unlike other *Lepomis* species (Desselle et al. 1978; Ploskey and Jenkins 1982). Such selectivity is more prominent in larger bluegills (Figures 6(A) and 7(A)), probably due to the increase in gape width with growth, allowing the ingestion of various-sized prey and other materials. On the other hand, zooplankters (cladocerans and copepods), which were exploited predominantly by small bluegills, were also extensively consumed by

middle-sized and large fish (Figure 6(A)), indicating efficient utilization of food resources. Although bluegills may have some prey-size selectivity for zooplankters (see above), such may be a minor characteristic within the overall food habits of the species.

Because the diet diversity of bluegills is environment-dependent (Goodson 1965; Keast and Webb 1966), the Shannon index (*H'*) changes seasonally (Figure 7), probably according to prey variation and abundance. Similarly, the diet composition of bluegills in Florida lakes (USA) has been related to epiphytic macroinvertebrate assemblages (Schramm and Jirka 1989).

Engel (1985, 1987, 1988) found that bluegills evidently 'sampled' many food types, but concentrated on a smaller variety of prey. Feeding descriptions of bluegills as 'generalized feeders' (Keast and Webb 1966), 'dietary generalists' (Paszkowski 1986), 'generalist predators' (Ehlinger and Wilson 1988; Ehlinger 1989) and 'generalist foragers' (Wildharber and Crowder 1991), indicate widespread recognition of the species' very wide diet selectivity, although it may be more appropriate to describe such as virtually no particular diet selectivity.

It was apparent from the diet composition results that the food habits of both Hachiman and Saburo Reservoir bluegills shift from planktivory to omnivory with growth (Figure 8(A) and (B)). Although the present study excluded food habit data of larval bluegills (>20 mm TL), previous studies have revealed that larvae fed mostly upon cladocerans and copepods, as well as rotifers (Pearse 1915; Moore 1920; Werner 1969; Siefert 1972; Lemly and Dimmick 1982; Welker, Pierce, and Wahl 1994; Partridge and DeVries 1999; Harrel and Dibble 2001; Jolley, Willis, and Holland 2010), as did juveniles in this study (ca. 20–40 mm TL) (Figure 8(A) and (B)). Similar growth-related food habit shifts have been inferred by studies from Japan (IPFFRI 1990) and North America (Forbes 1903; DeRyke and Scott 1922; Bennett, Thompson, and Parr 1940; Leonard 1940; Howell, Swingle, and Smith 1941; Rice 1942; Bennett 1948; Patriarche and Ball 1949; Huish 1957; Ridenhour 1960; Flemer and Woolcott 1966; Mullan and Applegate 1967; Sadzikowski and Wallace 1976; Keast 1978a, 1978b; Beard 1982; Keast 1985a; Diggins, Summerfelt, and Mnich 1979; Keast 1985b; Werner et al.1983b; Dewey, Richardson, and Zigler 1997; Harris, Galinat, and Willis 1999; VanderKooy, Rakocinski, and Heard 2000), apparently being a common event in every habitat. Warren (2009) described a bluegill shift from pelagic zoolplanktivory to littoral invertivory at small sizes (12–15 mm SL), although the present study found the food habit shift to occur gradually at a larger size (from ca. 50 mm TL) (Figure 8(A) and (B)).

Despite similar growth-related food habit change patterns reported from Kawahara-oike Lake (Nagasaki, Japan) by Azuma (1998), that data showed somewhat greater proportions of chironomids in the diets of smaller bluegills, rather than zooplankton, possibly due to seasonal abundance of the zooplankton [data were based on specimens collected in June–September, when zooplankters (cladocerans and copepods) are generally less abundant in Japanese inland waters (Mizuno 1964; also see Figure 6)]. Similarly, Collingsworth and Kohler (2010) showed a greater preference for diptera rather than zooplankton in juvenile bluegills (<75 mm TL) in Cedar Lake (Illinois, USA), possibly also a bias of their investigation period (June–October).

On the other hand, it has been found in some Michigan lakes (USA) that large bluegills (>75 mm SL) foraged primarily on open-water zooplankton (*Daphnia*), smaller specimens (≤75 mm SL) foraging predominantly on vegetation-dwelling prey (Mittelbach 1984). A similar shift back to planktivory after a period of growth (>50–83 mm SL and ca.>100 mm TL) was recognized by Werner and Hall (1988) and Schneider (1999), respectively. Although such reversals appear inconsistent with growth-related food habit changes, they may have resulted from seasonal abundance of potential prey, since the reports were based on limited data collection periods (May–August, June–August and June–August, respectively).

The above studies showed that the 'shift back to planktivory' was accompanied by a growth-related habitat shift from littoral to pelagic zones, indicating that large bluegills with greater swimming ability move to the pelagic zone to seek exploitable prey (zooplankton) in summer, when the volume of invertebrates reaches its lowest point of the year (Ball 1948). However, it is unlikely that large habitat-shifted bluegills permanently inhabit the pelagic zone, in which prey comprises almost solely zooplankton. In fact, Engel (1987) found that bluegills in Halverson Lake (Wisconsin, USA) switched to eating zooplankton, especially after spring emergence of chironomids, and then returned to littoral foods, when *Daphnia* numbers dwindled in midsummer. Namely, the event is likely food-driven (Spotte 2007), the 'shift back to planktivory' reflecting feeding plasticity of bluegill.

Yonekura, Nakai, and Yuma (2002) hypothesized trophic polymorphism in bluegill from Lake Biwa, recognizing several morphs [benthivorous, herbivorous and planktivorous (*Daphnia*) morphs for larger bluegills and calanoid and cyclopoid foragers for smaller bluegills] based on stomach contents. Among the larger bluegills, they concluded that the planktivorous morphs (ca. 84 mm SL) were distinguished from the others (ca. 93–95 mm SL), having relatively less midbody length and depth. Although their hypothesis did not consider growth-related morphological changes in bluegill, i.e. body depth (BD) increases relatively with growth (Yokogawa 2013; Bell and Jacquemin 2017), it was supported by the clear shift in food habits of bluegill from planktivory to omnivory with growth, as revealed here (Figure 8). Similarly, their calanoid and cyclopoid foragers

(ca. 50–55 mm SL) are not regarded as 'morphs' because such small bluegills mostly feed on planktonic crustaceans (chiefly copepods) (Figure 8).

A subsequent study by Uchii et al. (2006), which examined intestinal bacterial microbiota of three trophic types (benthivorous, herbivorous and planktivorous) (= morphs sensu Yonekura, Nakai, and Yuma 2002) that might be related to their food habits, asserted some differences among the three types. However, it may be inconclusive because their MANCOVA results for the three types did not involve the multiple comparisons (Uchii et al. 2006, table 2), and plots of the three types in a distribution graph seemed not to well cluster and separate each other (Uchii et al. 2006, figure 4). Thereupon, Uchii et al. (2007) examined the long-term effects of food resource utilization by the three types using stable isotope analysis. They designed the three types with similar sized individuals (ca. 100 mm SL), recognizing no clear difference for BD among the types. And they found that the isotope values of the herbivorous type were distinctly different from expected values, indicating the unlikelihood of aquatic plant utilization by bluegills (see discussion above). Although these results generally failed to support Yonekura, Nakai, and Yuma's (2002) hypothesis, a similarity between isotope values of the planktivorous types and those of zooplankton, suggested otherwise. However, the above planktivorous types may have been individuals that had not switched from initial planktivory to omnivory (Figure 8), implying that their somatic isotope values could have originated from zooplankton, which had been continuously preyed upon. Such fish would therefore have been planktivorous, exhibiting not a trophic morph but a life cycle stage, leading to the conclusion that trophic categorization based upon individual 'temporal' stomach contents (Yonekura, Nakai, and Yuma 2002; Uchii et al. 2006, 2007) is invalid, due to bluegill diets being opportunistic, except in early life stages. Further in these three studies, although all material bluegill specimens were collected by angling, it may be unnatural that the herbivorous and planktivorous morphs (plant and plankton feeders) bit a bait. However, continuous non-lethal investigation of individual fish diets may provide new insights.

In conclusion, despite the wealth of studies concerning the food habits of bluegill, many have been based on data from limited short survey periods (seasons) of the year. Because the diets of bluegill vary strongly and are influenced by the abundance of potential prey, such data therefore reflects just part of what are very extensive food habits. Clearly, discussions of bluegill dietary patterns based only on data from limited periods is so problematic that they necessitate year-round surveys, especially regarding reversal to planktivory. In addition, the occurrence of long-term food habit changes, even in the same habitat such as Lake Biwa (see discussion above) should also be considered.

Disclosure statement

No potential conflict of interest was reported by the author.

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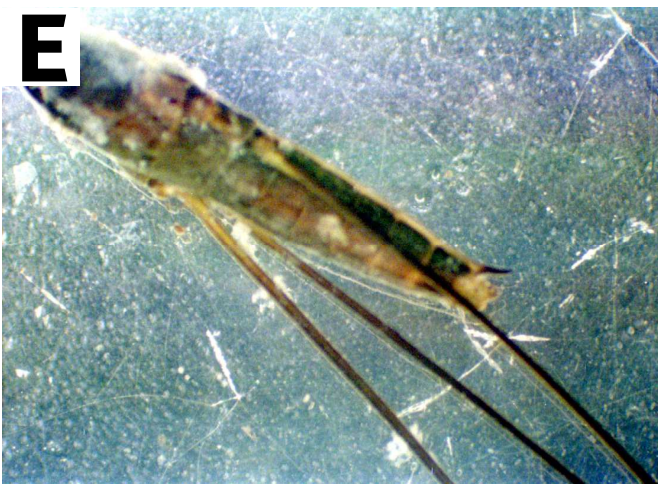Zar, J. H. 2010. *Biostatistical Analysis*. 5th ed. Upper Saddle River: Pearson Education.

Figure S1. Stomach contents of bluegills–1. (**A**) mole cricket, (**B**) earwig, (**C**) dragonfly larva, (**D**) dragonfly adult, (**E**) water skipper, (**F**) stink bug, (**G**) caddisfly larva, (**H**) caddisfly adult.
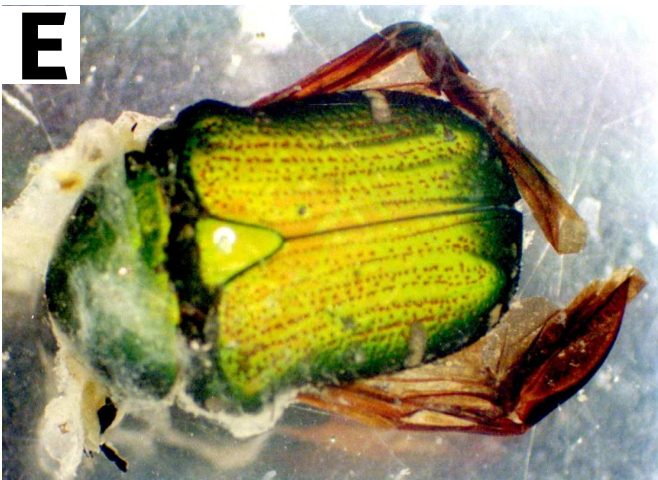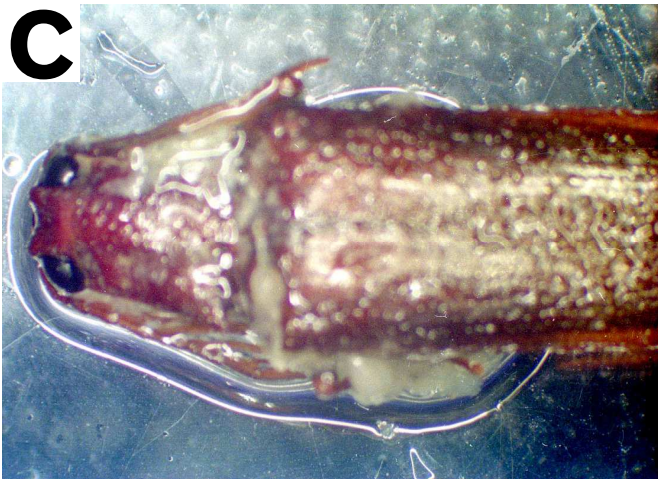
Figure S2. Stomach contents of bluegills–2. (**A**) lepidopterous larva, (**B**) terrestrial beetle larvae, (**C**)–(**F**) terrestrial beetles, (**G**) sand wasp, (**H**) ant.
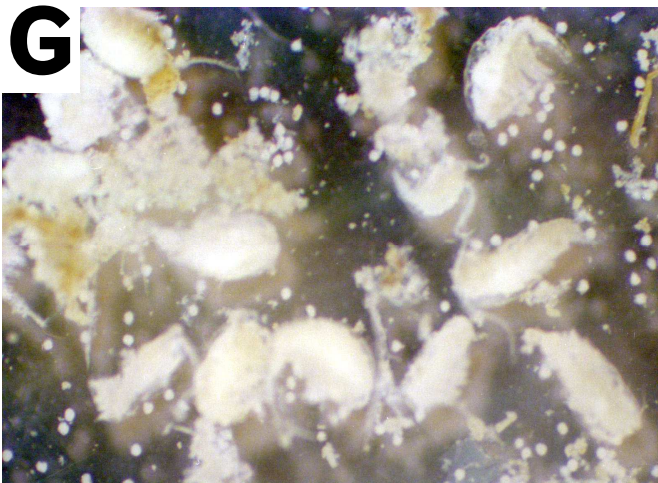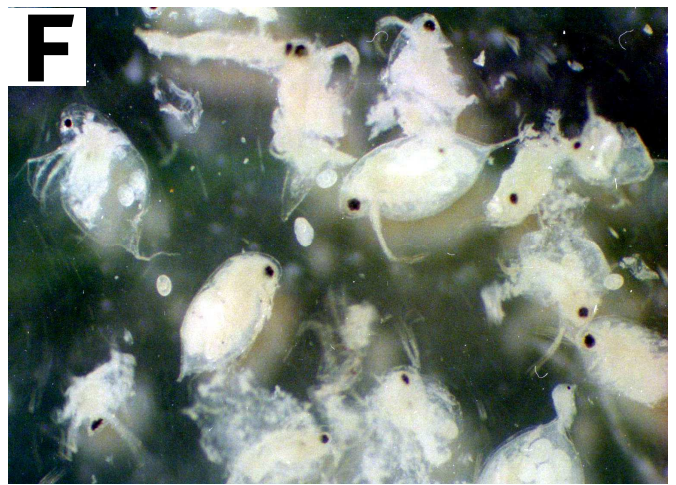
Figure S3. Stomach contents of bluegills–3. (**A**) dipteran larvae, (**B**) dipteran pupa, (**C**) chironomid larvae, (**D**) chironomid pupae, (**E**) ostracods, (**F**) cladocerans, (**G**) copepods, (**H**) amphipod.
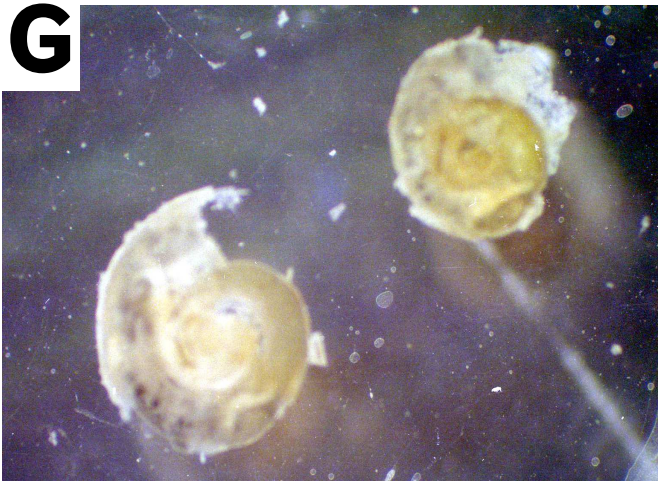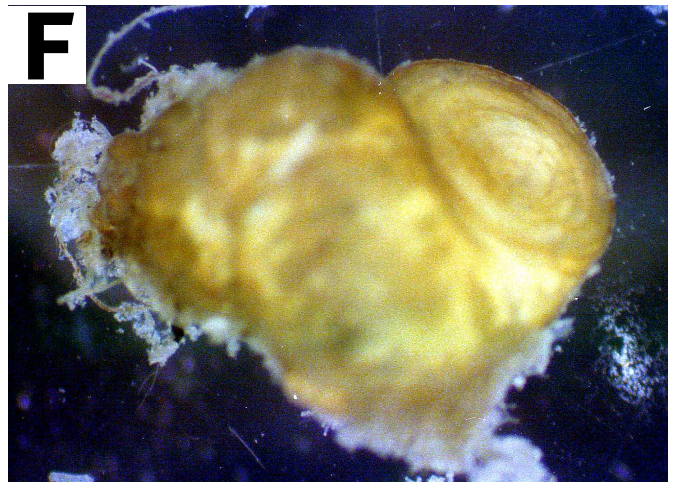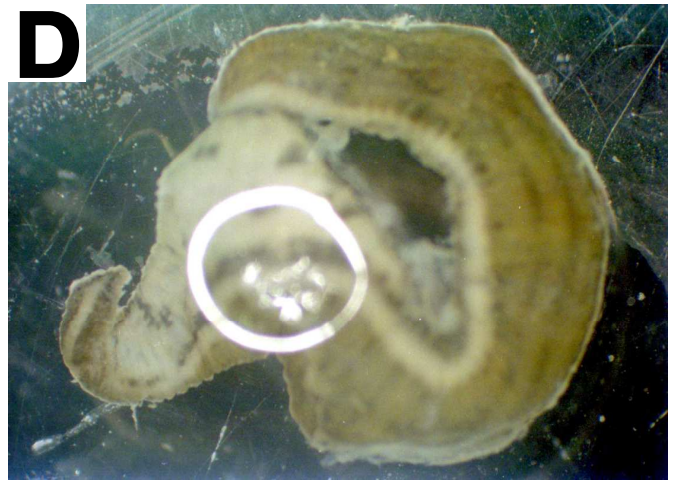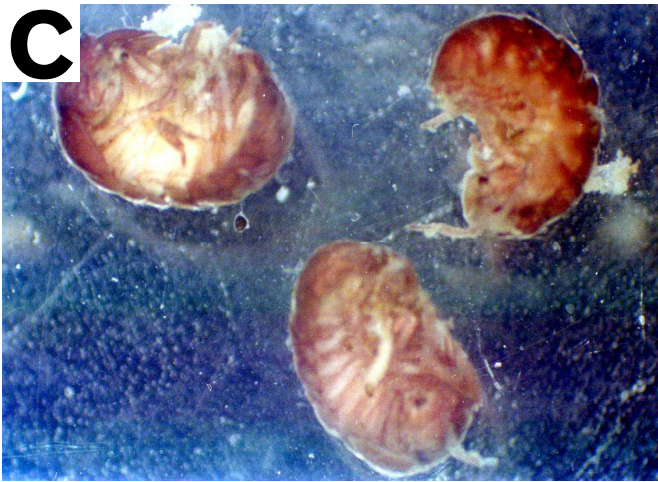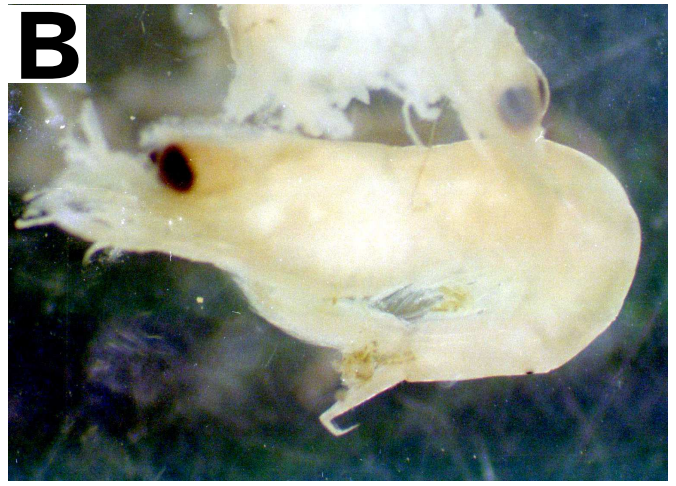
Figure S4. Stomach contents of bluegills–4. (**A**) fairy shrimp, (**B**) fresh-water shrimp, (**C**) pill-bugs, (**D**) leech, (**E**) earthworm, (**F**), (**G**) freshwater snails, (**H**) freshwater goby.
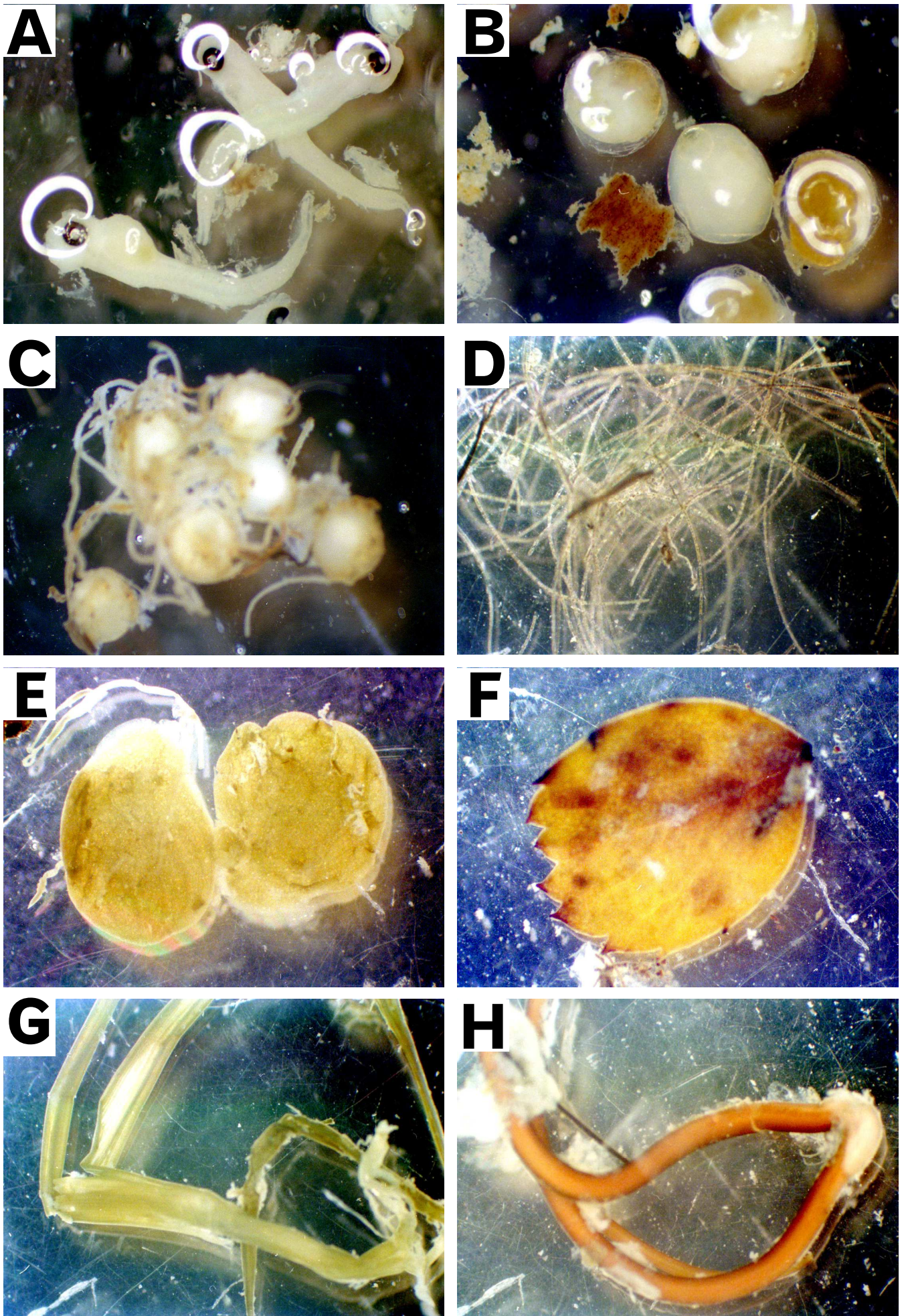
Figure S5. Stomach contents of bluegills–5. (**A**) centrarchid larvae, (**B**) grass carp eggs, (**C**) centrarchid eggs, (**D**) green alga, (**E**) duckweed, (**F**) terrestrial plant leaf, (**G**) plant stem, (**H**) plant root.
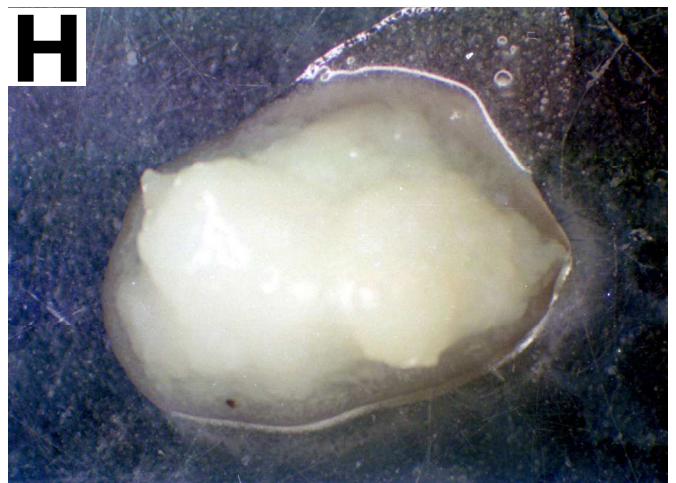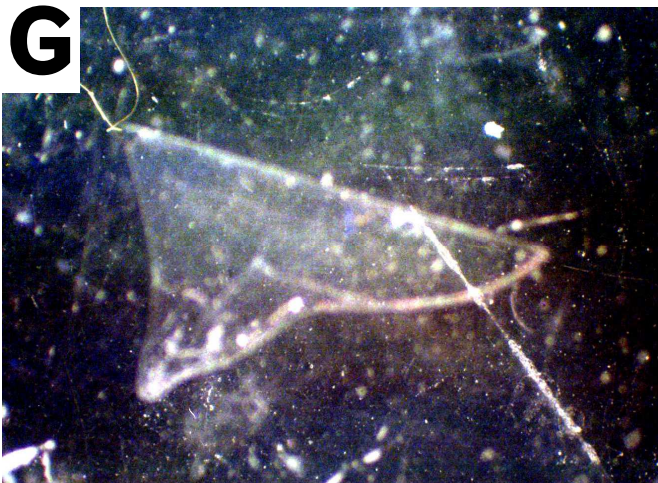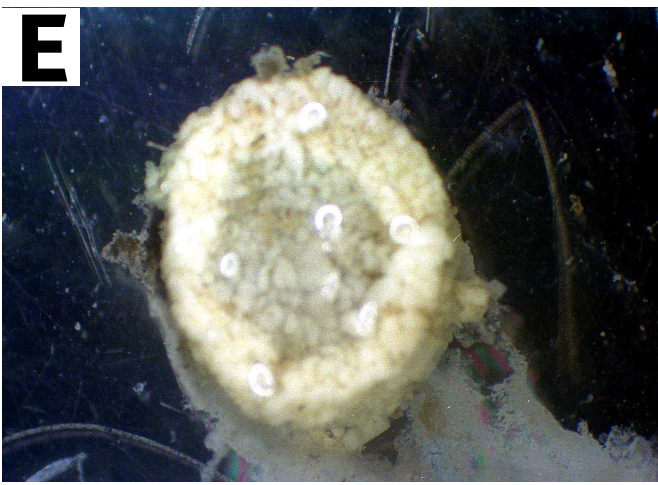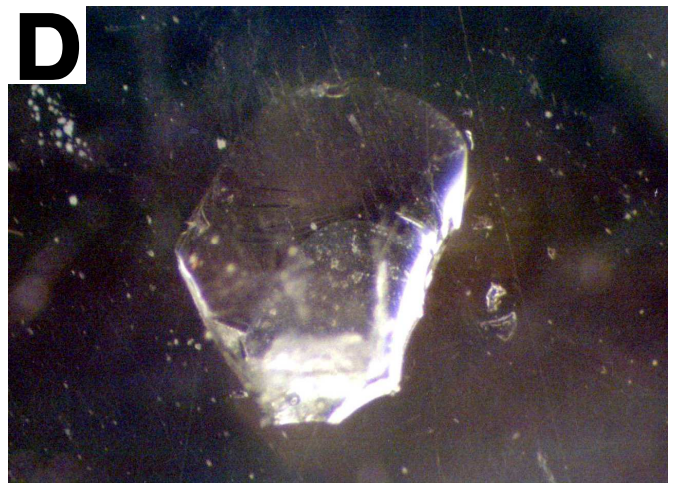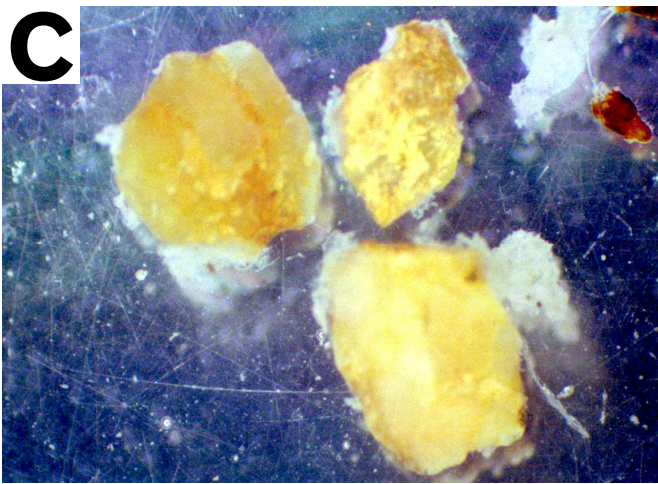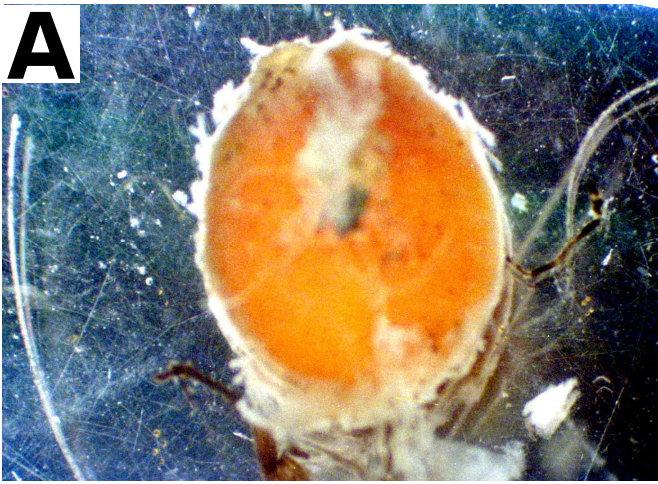
Figure S6. Stomach contents of bluegills–6. (**A**) terrestrial plant seed, (**B**) feather, (**C**) gravel, (**D**) glass chip, (**E**) plastic worm chip (a section), (**F**) rubber band chip, (**G**) vinyl chip, (**H**) flour paste.