

Prey selection and diets of bluegill *Lepomis macrochirus* with differing population characteristics in two Nebraska natural lakes

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Abstract Environmental prey samples and stomach contents of bluegill *Lepomis macrochirus* (Rafinesque) were collected in spring and summer 2000 from two Nebraska Sandhill lakes. Watts Lake contained a low-density bluegill population, whereas Cozad Lake contained a high-density bluegill population. Bluegill diets from both lakes were compared to determine if bluegill prey preference differed between the two populations. The highest median per cent (by calories) of zooplankton in the diet was 1.3%; the remainder was macroinvertebrates. Watts Lake bluegills preferred (based on Manly's alpha) amphipods in spring and chironomids in summer. Cozad Lake bluegills did not show a strong preference (compared with Watts Lake) for any macroinvertebrates, but still utilized amphipods and chironomids during both seasons. Larger bluegills in Watts Lake preferred chironomids in summer, but Cozad Lake bluegills did not exhibit this relationship. The higher density Cozad Lake bluegill population appeared to be more opportunistic than the lower density Watts Lake population, but both preferred macroinvertebrates.

KEYWORDS: bluegill, diets, food habits, *Lepomis macrochirus*, Nebraska.

Introduction

Bluegill *Lepomis macrochirus* (Rafinesque) food habits have been well documented throughout its geographical range, incorporating zooplankton (Mittelbach 1981; Harris, Galinat & Willis 1999), macroinvertebrates (Schramm & Jirka 1989; Dewey, Richardson & Zigler 1997), and small fish (Flemer & Woolcott 1966; Applegate, Mullen & Morais 1967; Engel 1988). Their diets may differ temporally (Gerking 1962; Keast & Welsh 1968; Keast 1978). Larger bluegills typically select larger prey (Hall, Cooper & Werner 1970); and Engel (1988) found that larger bluegills (i.e. > 210 mm) primarily preyed upon larger aquatic insects and even fish fry.

Optimal foraging theory suggests that bluegill will select for prey items based on the net energy gain, which is affected by prey type, searching time for prey, habitat type, and predator avoidance (Werner & Hall

1974; O'Brien, Slade & Vinyard 1976). In addition, feeding habits may be related to bluegill population density (Kitchell, O'Neill, Shutgart, Magnuson & Booth 1974). When prey density is held constant, higher density bluegill populations typically have slower growth (Weiner & Hanneman 1982), presumably because of intraspecific competition for food resources. Higher density fish populations may exhibit less selective feeding habits, apparently because they need to forage on less-preferred prey (Schindler, Hodgson & Kitchell 1997). Therefore, we compared the food habits and prey selection of two contrasting Nebraska Sandhill bluegill populations to determine if differences in bluegill density affected their food habits and prey selection. We hypothesized that the higher density Cozad Lake bluegill population may exhibit more opportunistic feeding compared with the low-density Watts Lake bluegill population, which would specifically select preferred prey items.

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Study area

Watts Lake and Cozad Lake are both located in the Sandhills of north-central Nebraska (USA), approximately 80 km apart. Both lakes are relatively shallow (mean depth: 1.3 m for Watts Lake; 1.9 m for Cozad Lake), are highly vegetated (72% coverage for Watts Lake and 95% coverage for Cozad Lake), and relatively clear (Secchi depth readings: 122 cm for Watts Lake and 213 cm for Cozad Lake). Although both lakes were shallow and vegetated, groundwater springs prevented winterkills. Both lakes were moderately productive, with chlorophyll *a* values of 2.7 $\mu\text{g L}^{-1}$ in Cozad Lake and 7.5 $\mu\text{g L}^{-1}$ in Watts Lake (Paukert & Willis 2000). Watts Lake is 93 ha in surface area while Cozad Lake has an area of 32 ha. Both catchments are primarily grasslands and have no agricultural crops. Angling pressure and harvest are presumably minimal, based on these lakes being in remote locations and poor access (Paukert, Willis & Gabelhouse 2002).

Watts Lake contained a low-density bluegill population compared with Cozad Lake. The mean total number of bluegills collected per trap (i.e. modified fyke) net night was 32 ($n = 10$ nets, SE = 4.1) in Watts Lake and 233 ($n = 10$ nets, SE = 29.0) in Cozad Lake (Paukert & Willis 2000). Watts Lake bluegills reach a mean length of 168 mm by age 3 whereas Cozad Lake bluegills only attained 126 mm by age 3. Watts Lake bluegills also had slightly higher body condition than did Cozad Lake bluegills (Paukert & Willis 2000). Both lakes contained largemouth bass, *Micropterus salmoides* (Lacépède), black bullhead, *Ameiurus melas* (R), and yellow perch, *Perca flavescens* (Mitchill). Black crappie, *Pomoxis nigromaculatus* (Lesueur), were also present in Cozad Lake; Watts Lake contained saugeye, *Stizostedion vitreum* (M) \times *S. canadense* (Smith). Although they were not sampled in our study, muskellunge, *Esox masquinongy* (M) were last stocked in 1997 and are presumably present in Watts Lake in low numbers (Nebraska Game and Parks Commission, unpublished data). However, largemouth bass appear to be the primary predator on bluegill in Sandhill lakes (Paukert, Willis & Klammer 2002). Both lakes had moderately abundant populations of largemouth bass, with the number of 200 mm and longer largemouth bass collected per hour of electric fishing being 38 ($n = 12$ stations, SE = 4) in Cozad Lake and 96 ($n = 12$ stations, SE = 13) in Watts Lake (Paukert & Willis 2000). In addition, there was little evidence that bluegill interspecific competition with other fish species (e.g. yellow perch, black bullhead, and black crappie) was detrimental to bluegill growth, condition, or stock structure (Paukert & Willis 2000).

Materials and methods

Bluegills were collected along the vegetated, nearshore zones of Watts Lake in May (i.e. spring) and August (i.e. summer) 2000 and from Cozad Lake in April (i.e. spring) and August (i.e. summer) 2000. Spring water temperatures in Watts and Cozad Lakes were 17 and 13 °C, respectively, whereas summer water temperatures were 25 °C in both lakes. Daytime electric fishing was used in spring; however, short-term (< 4 h) sets of modified fyke nets (i.e. trap nets) were used in summer because of the difficulty in collecting bluegills in these lakes by electric fishing. All bluegills collected in summer were from modified fyke nets. When possible, five bluegills per centimetre length group were collected to obtain a diversity of fish lengths.

Bluegills were weighed (g), total length measured (TL; mm), and stomach contents removed nonlethally using an acrylic tube (Kamler & Pope 2001) and were subsequently released alive. Stomach contents were preserved in 10% formalin and returned to the laboratory for identification. Laboratory procedures consisted of examining the entire stomach sample for diet items under a dissection microscope with 40 \times magnification. Prey species were identified and counted only if the entire organism or prominent body feature (i.e. heads) was present. Because the use of other body features (e.g. spines, segments, carapaces, segmented legs, etc.) would not accurately reveal a quantitative number of a specific organism, they were not included in laboratory analyses. All diet items were identified to the class, order, or family level and prey frequency of occurrence was calculated (Bowen 1996). Because caloric content may better estimate energetic content of diets compared with other methods (Hyslop 1980), the analysis was conducted using per cent of the diet by calories.

To estimate environmental prey abundance, zooplankton and benthos (i.e. macroinvertebrates) samples were collected at six locations in each lake each season. These collections were along the same transect as bluegill sampling immediately following the fish collections. Two composite benthic grabs were taken at each site with a 156-cm² Ekman dredge, sieved in the field, and preserved in 10% formalin. Zooplankton samples were collected using a 2-m integrated tube sampler, sieved through a 65- μm Wisconsin plankton net and preserved in 10% formalin. All invertebrate samples were returned to the laboratory, identified to the lowest possible taxon and enumerated.

For prey items in the stomach and the environment, weight-length regressions obtained from Dumont, Van de Velde & Dumont (1975) and Smock (1980) were

used to calculate dry weight values. These values were then converted to calorie content using equations from Cummins & Wuycheck (1971). To estimate bluegill prey selection, Manly's alpha for constant prey populations (Chesson 1978; Krebs 1989) was used in terms of calorie content:

$$\alpha_i = (r_i/n_i)[1/\sum(r_i/n_i)]$$

where α_i = Manly's alpha (i.e. preference index) for prey type i , r_i = proportion (in calories) of prey item i in the stomach, and n_i is the proportion (in calories) of prey item i in the environment. Preference values $> 1/m$, where m is the total number of prey types available, suggest selective feeding for that prey type. Values below $1/m$ suggest that the prey item is avoided in the diet. Because some taxa were found in the environment and not in the stomachs (or vice versa), values of m for each lake and season were calculated by summing the total number of taxa found in both the environmental samples and the diets. Preference values were calculated for each prey item for each fish. The preference indices were calculated for macroinvertebrates and zooplankton separately because different gears were used to collect these organisms from the environment.

Because each individual fish had preference values for several taxonomic groups, a repeated-measures analysis of variance was used to test if preference indices differed among taxa for each season and lake. t -Tests were used to determine if the mean total calories consumed differed between seasons for each lake. Pearson correlations were used to determine relationships between prey abundance in diets and bluegill total length (TL). Normality was assessed using the Wilk-Shapiro test prior to all parametric analyses. All statistical analyses were completed in SAS (SAS Institute 1996) with an alpha level of 0.10.

Results

In May 2000, 55 bluegills (range 74–227 mm TL) were collected with electric fishing from Watts Lake with 21 (38%) having empty stomachs. August modified-fyke-net samples resulted in 17 bluegills (78–176 mm TL) sampled with only one (6%) stomach empty. Twenty-one bluegills (43–193 mm TL) were sampled in April using electric fishing from Cozad Lake, with three (14%) having empty stomachs, and 78 bluegills (74–178 mm TL) were sampled using modified-fyke nets during August with 24 (31%) having empty stomachs. Relative weight was not related to fish length in Cozad Lake for either April (range, 70–107, $r = -0.352$, $n = 11$, $P = 0.289$) or August (range, 82–133, $r = -0.027$, $n = 48$, $P = 0.856$), or Watts Lake in May

(range, 88–193, $r = 0.258$, $n = 31$, $P = 0.161$). However, relative weight did increase with fish length for the few fish collected in August (range, 69–117, $r = 0.825$, $n = 14$, $P = 0.0003$). The weight of individual macroinvertebrate prey item and number of calories of each prey item were strongly associated ($r = 0.896$, $n = 1255$, $P < 0.0001$), suggesting that analysis by weight instead of calories likely would yield similar results.

The four most abundant macroinvertebrates (i.e. chironomids, amphipods, trichopterans, and gastropods) accounted for 77.4% of the total calories of macroinvertebrates consumed. Therefore, only these diet items will be further discussed. However, additional taxa collected include Hymenoptera, Ostracoda, Pelecypoda, and Ephemeroptera. Although zooplankton were found in up to 87.5% of the stomachs analysed (depending on season and lake), they accounted for very few calories found in the stomach (Table 1). The median percentage of zooplankton calories in the stomach ranged from 0.0% (Cozad Lake in spring) to only 1.3% (Watts Lake in spring). Because zooplankton apparently contributed little to the caloric content of the diets, they will not be further discussed.

The total number of macroinvertebrate taxa found in these lakes differed by season and lake. Nine taxa were collected in either the stomachs or environmental samples from Watts Lake in spring, whereas 11 were collected in summer. Cozad Lake samples revealed 13 taxa collected in spring and 11 in summer. Based on these samples, Manly's alpha values > 0.111 for Watts Lake spring sampling suggested bluegills were selecting for a taxon whereas values > 0.077 suggested preference for a taxon in spring Cozad Lake samples. Values > 0.091 suggested preference in both Watts and Cozad Lakes in summer.

Total calories in the stomach did increase with increasing fish length for bluegills collected during spring in Cozad Lake when water temperatures were 13°C ($r = 0.776$, $n = 18$, $P < 0.001$). However, this relationship was not evident for Cozad Lake bluegills collected in summer when water temperature was 25°C ($r = -0.005$, $n = 54$, $P = 0.973$), or for Watts Lake bluegills collected during spring at a water temperature of 17°C ($r = -0.030$, $n = 34$, $P = 0.880$) or summer with a water temperature of 25°C ($r = 0.386$, $n = 16$, $P = 0.140$). From Watts Lake, the mean total calories consumed by bluegills were higher in summer (mean = 39.8 cal fish⁻¹) than spring (mean = 14.9 cal fish⁻¹) ($t = -2.94$, d.f. = 76, $P = 0.002$). However, Cozad Lake bluegills exhibited an opposite relationship, with significantly more calories consumed during the spring (mean = 42.8 cal fish⁻¹) than summer (mean = 11.7 cal fish⁻¹) ($t = 6.95$, d.f. = 73, $P < 0.001$).

Table 1. Frequency of occurrence (%) and per cent of diet by calories for prey items found in bluegills collected in spring and summer 2000 from Watts and Cozad Lakes, Nebraska

Taxon	Spring		Summer	
	Frequency of occurrence (%)	Per cent of calories	Frequency of occurrence (%)	Per cent of calories
Watts Lake				
Chironomidae	11.8	11.5	93.8	83.4
Amphipoda	64.7	30.5	50.0	2.0
Odonata	5.9	5.9	0	0
Trichoptera	61.8	43.6	50.0	1.2
Pelecypoda	0	0	0	0
Gastropoda	0	0	6.3	4.8
Coleoptera	2.9	0.2	12.5	7.4×10^{-2}
Ephemeroptera	14.7	1.5	0	0
Other macroinvertebrates	17.6	4.2	56.3	3.0
Plant material	0.0	0	25.0	4.0
<i>Daphnia</i>	73.5	2.5	37.5	9.4×10^{-2}
<i>Chydorus</i>	0	0	75.0	1.4
<i>Bosmina</i>	0	0	25.0	0.1
<i>Cyclops</i>	8.8	0.1	6.3	7.3×10^{-4}
Cozad Lake				
Chironomidae	88.9	24.7	44.4	7.4
Amphipoda	88.9	25.8	59.3	9.7
Odonata	22.2	12.2	1.9	20.2
Trichoptera	22.2	7.8	33.3	10.1
Pelecypoda	16.7	0.2	0	0
Gastropoda	16.7	16.5	7.4	26.7
Coleoptera	16.7	0.5	18.5	3.3
Ephemeroptera	1.9	1.1	11.1	10.4
Other macroinvertebrates	61.1	11.1	20.4	7.7
Plant material	0.0	0.0	27.8	4.4
<i>Daphnia</i>	11.1	3.7×10^{-3}	13.0	0.1
<i>Chydorus</i>	11.1	9.2×10^{-3}	0	0
<i>Bosmina</i>	0	0	0	0
<i>Cyclops</i>	5.6	1.9×10^{-2}	3.7	1.9×10^{-2}

Spring bluegill prey selection

In both Watts and Cozad Lakes, only a few macroinvertebrate taxa dominated the environmental samples. Gastropods accounted for 91% of the 181.95 calories m^{-2} in the Watts Lake macroinvertebrate samples, whereas chironomids accounted for 53% of the 6.70 calories m^{-2} in Cozad Lake (Table 2). Trichopterans and amphipods were also common in both Watts and Cozad Lakes (Table 2). Despite the abundance of gastropods in the environment, bluegill stomach samples from Watts Lake contained no gastropods. Over 61% of the bluegills sampled from Watts Lake consumed trichopterans whereas 64.7% consumed amphipods (Table 1). Nearly all bluegills sampled in Cozad Lake consumed chironomids and amphipods (88.9%).

Bluegills in the Watts Lake preferred amphipods (mean Manly's alpha [α] = 0.52) over other macroin-

vertebrates ($F = 16.10$, d.f. = 3, 33, $P < 0.0001$; Fig. 1). Bluegills in Cozad Lake had the strongest preference for chironomids ($\alpha = 0.36$) and amphipods ($\alpha = 0.29$), no preference for gastropods ($\alpha = 0.10$), and an avoidance of trichopterans ($\alpha = 0.04$; $F = 7.85$, d.f. = 3,29, $P = 0.0006$; Fig. 1).

Correlations between bluegill total length and Manly's preference indices for amphipods, chironomids, and trichopterans revealed no meaningful pattern for either Watts or Cozad Lakes in spring (Fig. 2). However, the majority of the preference values in Watts Lake were either near 0 or near 1.0, suggesting two somewhat distinct feeding strategies, regardless of bluegill length. Some bluegills had very strong preferences for these macroinvertebrates, whereas others had relatively strong avoidance, with few fish indicating moderate preference (Fig. 2). Cozad Lake bluegills did not show the same trend, with preference values

Table 2. Mean (\pm SE) calories per litre (cal L^{-1}) for zooplankton or calories per square metre (cal m^{-2}) for macroinvertebrates collected in spring and summer 2000 from Watts and Cozad Lakes, Nebraska

Taxon	Spring		Summer	
	Watts	Cozad	Watts	Cozad
Macroinvertebrates (cal m^{-2})				
Amphipoda	1.15 (0.64)	0.03 (0.02)		0.02 (0.01)
Chironomidae	3.40 (3.26)	3.53 (1.66)		0.55 (0.30)
Gastropoda	164.87 (72.13)	2.56 (1.62)	215.17 (96.33)	100.78 (19.08)
Pelecypoda	0.002 (0.001)		0.00 (0.00)	0.003 (0.001)
Odonata	1.20 (1.15)	0.01 (0.01)		12.71 (12.71)
Trichoptera	11.33 (4.31)	0.57 (0.53)		8.79 (6.86)
Total	181.95 (81.49)	6.70 (3.84)	215.17 (96.33)	122.84 (38.96)
Zooplankton (cal L^{-1})				
<i>Bosmina</i>	0.005 (0.005)	0.031 (0.011)	0.020 (0.010)	0.006 (0.002)
<i>Chydorus</i>	0.095 (0.039)	0.069 (0.010)	0.323 (0.072)	0.020 (0.007)
<i>Cyclops</i>	0.050 (0.019)	1.049 (0.147)	1.104 (0.355)	0.210 (0.137)
<i>Daphnia</i>	3.884 (1.319)	0.021 (0.015)	0.161 (0.045)	0.101 (0.050)
Copepoda nauplii	0.005 (0.002)	0.002 (0.001)	0.007 (0.001)	0.008 (0.005)
Total	4.04 (1.38)	1.17 (0.18)	1.62 (0.48)	0.35 (0.20)

typically distributed throughout the index range (0–1), regardless of bluegill length (Fig. 2).

Summer bluegill prey selection

Gastropods were the most abundant macroinvertebrate in summer environmental samples from Watts Lake (99%; 215.17 calories m^{-2}) and Cozad Lake (89%; 100.78 calories m^{-2} ; Table 2). No chironomids, amphipods, or trichopterans were collected in Watts Lake, but they were common in Cozad Lake (Table 2). Gastropods made up only 4.8% of all calories consumed by the bluegills collected from Watts Lake, with chironomids dominating the diets (83.4% by calories; Table 1). In contrast, gastropods were the most abundant macroinvertebrate consumed by bluegill in Cozad Lake (26.7% by calories; Table 1).

Watts Lake bluegills most strongly preferred chironomids ($\alpha = 0.64$; $F = 11.89$; d.f. = 3,35; $P < 0.0001$; Fig. 1). There was no difference in Manly's alpha for amphipods ($\alpha = 0.10$) or trichopterans ($\alpha = 0.08$; Fig. 1), and bluegills appeared to prey on these taxa in proportion to availability in the environment. Similarly, Cozad Lake bluegills also preferred amphipods ($\alpha = 0.35$) and chironomids ($\alpha = 0.22$), but preference was less for trichopterans ($\alpha = 0.08$; $F = 7.51$; d.f. = 3, 97; $P < 0.0001$; Fig. 1). Although bluegills consumed gastropods, the high environmental abundance and subsequent electivity index suggested gastropods were avoided (Fig. 1).

During the summer, larger bluegills in Watts Lake preferred chironomids more, and amphipods and

trichopterans less, than did smaller bluegills (Fig. 3). As bluegill length increased, preference for chironomids also increased. In contrast, preference for amphipods and trichopterans decreased with bluegill length. Cozad Lake bluegills did not exhibit similar trends, as preference for these macroinvertebrates did not depend on bluegill length. Regardless of bluegill length, preferences for these macroinvertebrates varied (Fig. 3).

Discussion

The results suggest that larger bluegills typically did not have more calories in their stomachs than smaller bluegills except during spring in Cozad Lake. It was expected that warmer summer water temperatures would increase caloric content of the stomachs. This was only evident in Watts Lake. Seaburg & Moyle (1964) found that bluegills may feed more actively during spring; however, Kitchell *et al.* (1974) found the optimum feeding temperature for bluegill was between 27 and 31 °C. In this study, Cozad Lake had a higher proportion of bluegills feeding in spring (based on the per cent empty stomachs) and more calories per stomach when compared with summer, although water temperature was only 13 °C. In fact, water temperatures during the summer samples at both lakes reached only 25 °C, which is below the suggested bluegill feeding optimum. However, lower water temperatures may also suggest lower metabolism and digestion that may result in the increased number of calories documented in the stomach. Jobling (1981) suggested that

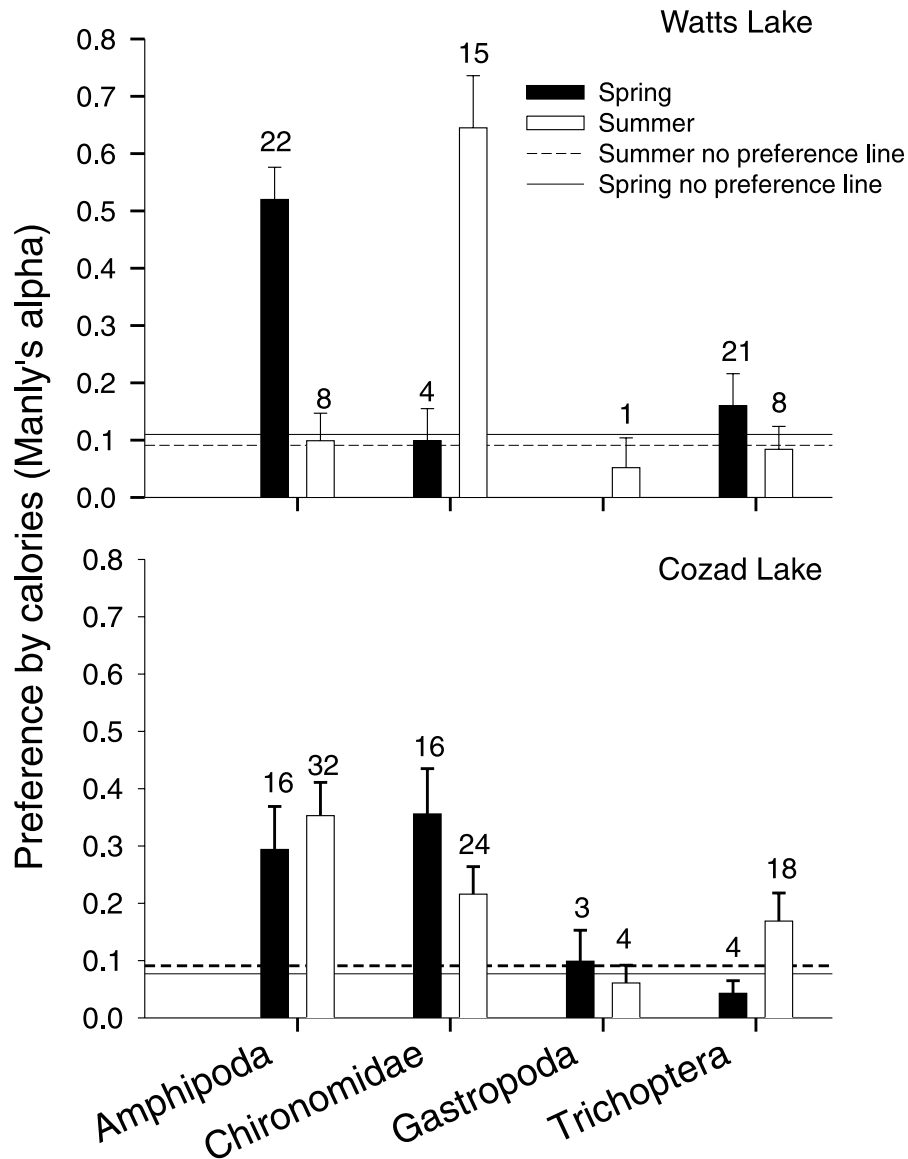


Figure 1. Mean preference values (Manly's alpha \pm SE) for macroinvertebrates consumed by bluegills collected during spring and summer 2000 in Watts and Cozad Lakes, Nebraska. Numbers above the vertical bars indicate the number of fish that had that diet item in their stomach. However, the total number of fish with any diet item in the stomach was used to calculate the index. Values above the horizontal line ($1/m$, where m is the total number of taxa collected in the lake), suggest preference, whereas values below the line suggest avoidance for that taxon.

digestion rates for fishes may be affected by fish size, water temperature, prey type, and meal frequency. In a laboratory study, Pierce & Wissing (1974) documented lower bluegill metabolism in 15 °C water temperatures compared with warmer (up to 25 °C) water temperature. Therefore, the results of this study may also be related to digestion and metabolism in differing water temperatures.

Predators also may affect the feeding habits of bluegills. The primary predator in both study lakes was largemouth bass (Paukert *et al.* 2002). Bluegills that

are susceptible to predation by largemouth bass may feed more extensively in vegetated habitat where predation risk is reduced (Werner, Gilliam, Hall & Mittelbach 1983). Paukert *et al.* (2002) suggested that largemouth bass predation on bluegills had the greatest effect on bluegill quality (e.g. condition, growth, size structure) in Nebraska Sandhill lakes. Although the effects of muskellunge are not well documented in these lakes, Paukert & Willis (in press) suggested that northern pike *Esox lucius* L., a similar species to muskellunge, may also prey on bluegills in Nebraska

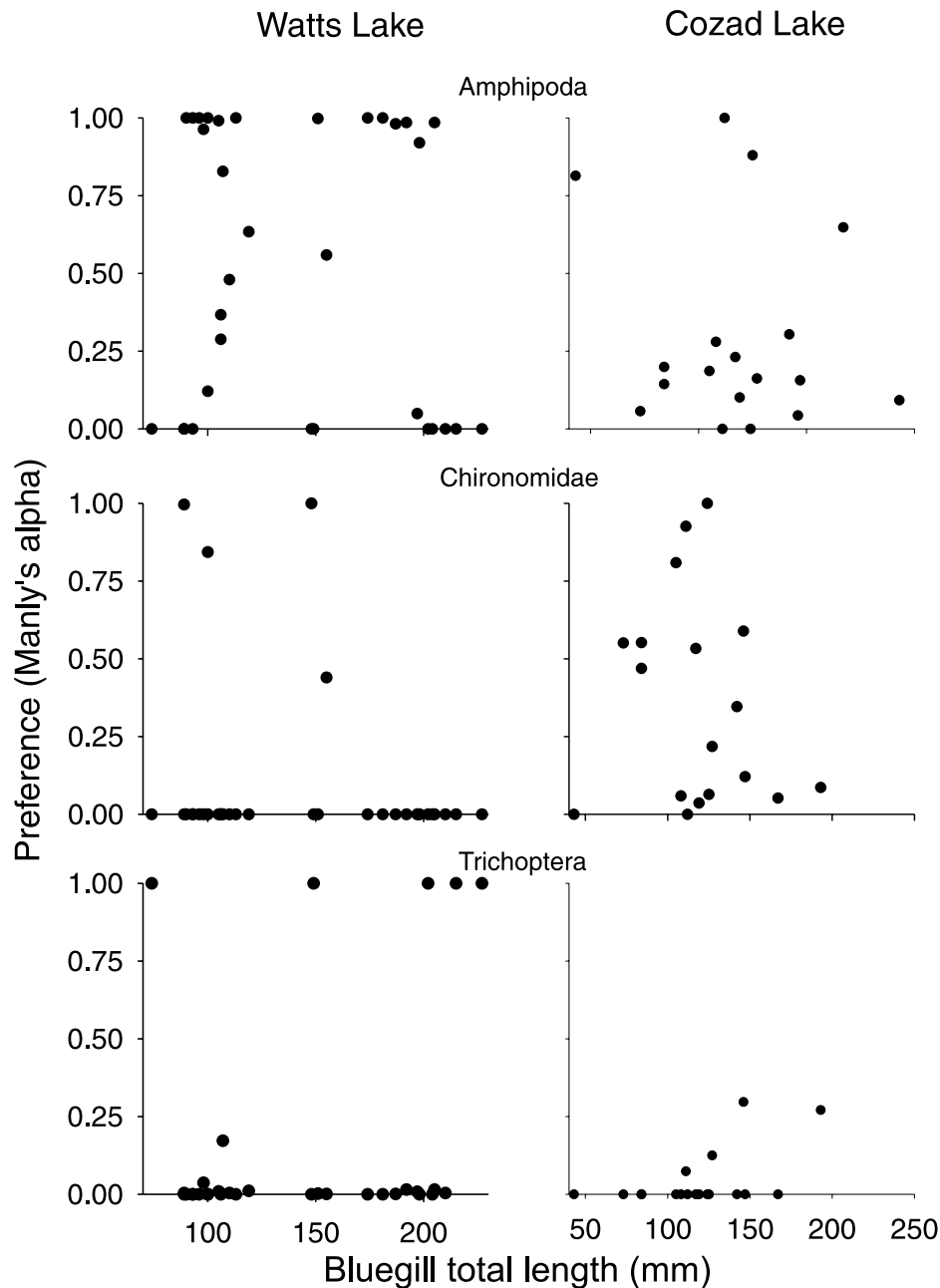


Figure 2. Relationship between bluegill total length and Manly's alpha for amphipods, chironomids, and trichopterans in Watts and Cozad Lakes, Nebraska during spring 2000.

Sandhill lakes. The predator populations in these lakes may have forced the bluegills to move out of open-water habitats where zooplankton may be more abundant to vegetated zones where they feed primarily on macroinvertebrates.

Bluegills from Watts and Cozad Lakes primarily preferred macroinvertebrates (e.g. chironomids and amphipods), which is consistent with other studies (e.g. Schramm & Jirka 1989; Dewey *et al.* 1997;

Schneider 1999). The strong preference for amphipods in the study may be attributed, in part, to the benthic grabs (environmental samples) not effectively sampling epiphytic macroinvertebrates, thus biasing the amphipod preference indices toward higher values. Other studies suggested that bluegills relied more on zooplankton (Werner 1969); however, Werner reported that bluegills only 10–25 mm in total length relied on zooplankton as food. The

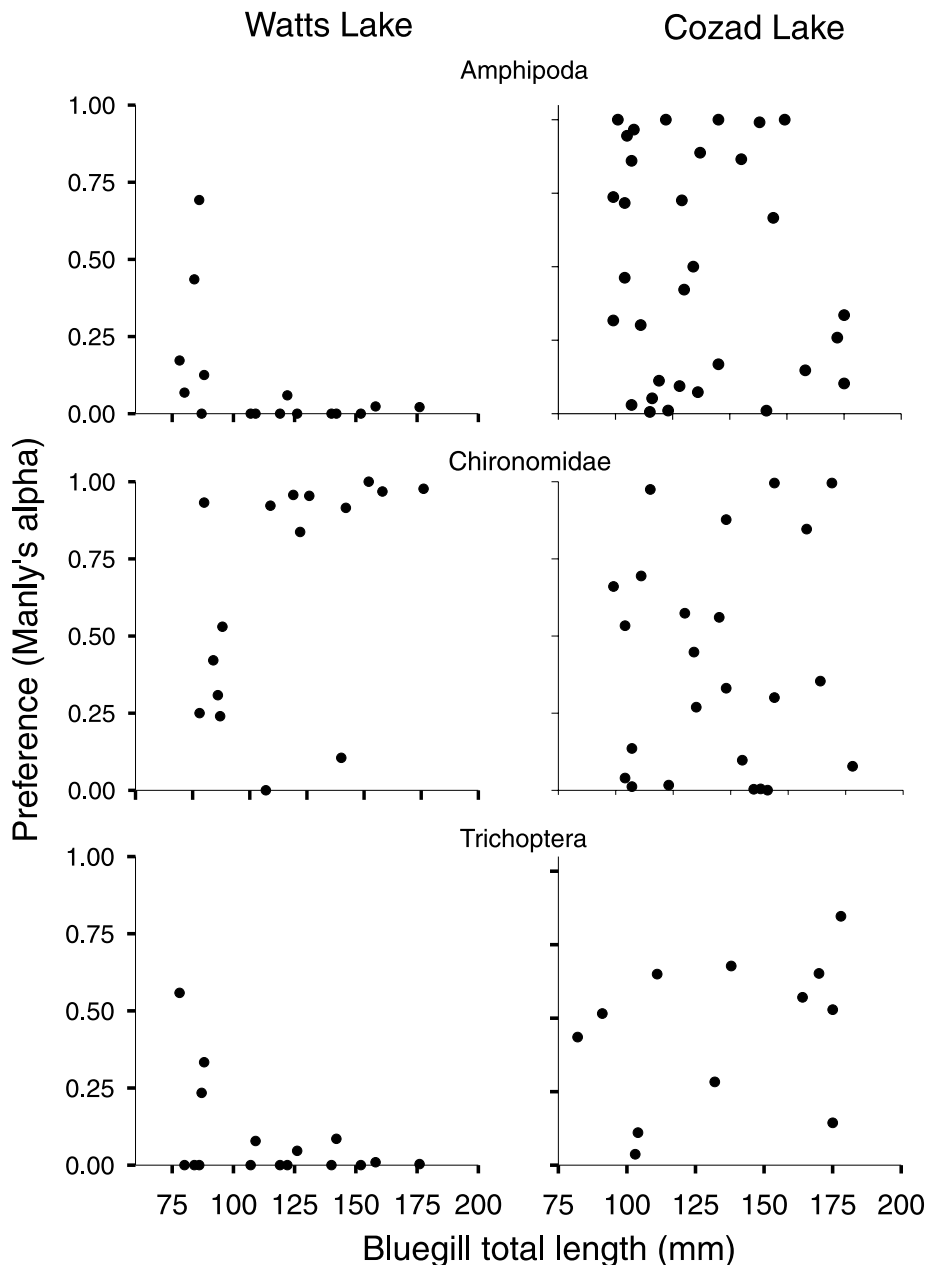


Figure 3. Relationship between bluegill total length and Manly's alpha for amphipods, chironomids, and trichopterans in Watts and Cozad Lakes, Nebraska during summer 2000.

smallest bluegill that we sampled was 43 mm total length.

Harris *et al.* (1999) reported that bluegills of similar lengths to this study collected from Richmond Lake, South Dakota positively selected for zooplankton (i.e. *Daphnia*) and hypothesized that low vegetation coverage (in contrast to these highly vegetated lakes) negatively affected macroinvertebrate abundance, causing bluegills to feed more on zooplankton. Lakes

with higher vegetation abundance may support larger abundances of macroinvertebrates (Dvorak & Best 1982), allowing the bluegills to rely more on macroinvertebrates as prey, which may have occurred in our study. Hall *et al.* (1970) found that as bluegill size increased, prey size increased. In addition, older bluegills may depend less on zooplankton and more on aquatic insects (Keast 1978; Engel 1988). Perhaps diet analyses of smaller bluegills would have revealed

more zooplankton in the diets. In addition, zooplankton tend to be digested more rapidly in the stomach than other diet items (Gannon 1976), which may bias our results to a more dominant diet of macroinvertebrates.

The low-density Watts Lake bluegill population appeared to target only specific organisms, particularly in the summer (based on higher mean preference indices and stronger correlations between preference indices and bluegill length in summer). Although the high-density Cozad Lake bluegill population did show preference for macroinvertebrates, they still appeared to be more generalists than Watts Lake bluegills, with all sizes of fish feeding on different macroinvertebrates. These differing food habits of bluegills in Watts and Cozad Lakes may be because of the higher-density, slower-growing bluegill population in Cozad Lake. High-density populations (e.g. Cozad Lake) may encounter greater intraspecific competition for food resources, possibly causing the bluegills in Cozad Lake to have no alternative but to feed on any available prey, regardless of what is preferred (Schindler *et al.* 1997).

For both spring and summer, Watts Lake had more calories per square metre of substrate compared with Cozad Lake. This may be attributed to Watts Lake having higher primary productivity. Sampling in 1998 determined that chlorophyll *a* levels were $7.6 \mu\text{g L}^{-1}$ in Watts Lake and $2.7 \mu\text{g L}^{-1}$ in Cozad Lake. In addition, total phosphorus levels in Watts Lake were over double the levels in Cozad Lake (Paukert & Willis 2000). Although Watts Lake was more turbid than Cozad Lake, this likely did not affect feeding by bluegills. Gardner (1981) documented reduced feeding rates of bluegills at higher turbidity [i.e. 60 nephelometric turbidity units (NTU)]. However, turbidity was low in these lakes (0 NTU for Cozad Lake and 10 NTU for Watts Lake). Secchi depth readings 213 cm in Cozad Lake and 122 cm in Watts Lake, suggesting water clarity was relatively high in both lakes.

In conclusion, larger (> 150 mm) bluegills collected from Nebraska Sandhill lakes rarely contained more calories than smaller bluegills. Macroinvertebrates were preferred for and utilized as a primary source of prey for bluegill diets. In addition, these two different bluegill populations exhibited different foraging strategies, with bluegills from Watts Lake specializing on more specific prey items and Cozad Lake bluegills being generalists. Although the mechanisms for these differences are not clear, these lakes exhibited relatively similar physical characteristics, suggesting that differences may be related to other factors (e.g. bluegill population density). Further ecological analyses of these bluegill populations may reveal more explana-

tions of why certain prey items are favoured over others.

Acknowledgments

We would like to thank Brian Heikes, Matt Ward, and Andrew Glidden for field and laboratory assistance. The Valentine National Wildlife Refuges allowed access to Watts Lake. The project was funded by the Nebraska Game and Parks Commission through Federal Aid in Sport Fish Restoration Project Number F-118-R. This paper was approved for publication by the South Dakota Agricultural Experiment Station as Journal Series 3279.

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