ALTERED FEEDING ELECTIVITY OF THE BLUEGILL FROM INCREASED PREY ACCESSIBILITY FOLLOWING MACROPHYTE REMOVAL

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Species diversity and biomass of invertebrates in stomachs of young-of-the-year, 1- and 2-year-old bluegill (*Lepomis macrochirus*) were examined in relation to variation in the benthos of a pond treated with a herbicide. Vascular plant biomass, mainly *Potamogeton* spp, were nearly eliminated by the treatment; at the 0-1 m depth stratum, the biomass dropped from 481.2 g dry weight per m^2 to 0.3 g dry weight per m^2. Density of the phytomacrofauna declined but the abundance of detritivorous invertebrates increased in post-treatment collections. Averages of total numbers and biomass of zooplanktonic and benthic organisms in stomachs were larger in the sampling period following treatment. Species diversity ($\bar{d}$) of macroinvertebrates in the fish stomachs increased following the herbicide application even though the diversity of macroinvertebrates in the environment declined. Species diversity of the total food ration, including the zooplankton, diminished following treatment because of predator electivity for only the cladoceran species in the zooplankton. The authors suggest that both prey density and vulnerability are of importance in predator selection and that a preferred species, if vulnerable, may be selected even when not relatively abundant.

INTRODUCTION

The concept of accessibility (1) or vulnerability (2) of prey has important applications to understanding resource utilization by predators. Ivlev (1) focused on laboratory simulations of protective mechanisms (cover or shelter) utilized by prey, and Lewis and Helms (3) studied the vulnerability of prey fishes to piscivorous fishes in ponds. Lewis (2) proposed that vulnerability of the prey was more important than morphological and behavioral characteristics of the predator.

This report describes population density and composition of phytomacrofauna and substrate-dwelling invertebrates in a pond before and after treatment with a herbicide, and the food of three age groups of bluegill (*Lepomis macrochirus*). The purpose is to evaluate the relation among habitat structure, the invertebrate assemblages, and feeding electivity of bluegill, to determine if changes in vulnerability of two types of invertebrate assemblages, the phytomacrofauna dwelling among the vascular aquatic plants and the substrate-dwelling macroinvertebrates, affect selectivity by the bluegill.

STUDY AREA

The study was conducted on Sanborn Lake, located adjacent to the Stillwater Municipal Airport, Payne County, Oklahoma. The pond, constructed in 1962, has a surface area of 4.58 hectares, an average depth of 1.7 m, and a maximum depth of 3.8 m (Figure 1). The water is normally clear (<20 Jackson Turbidity Units).

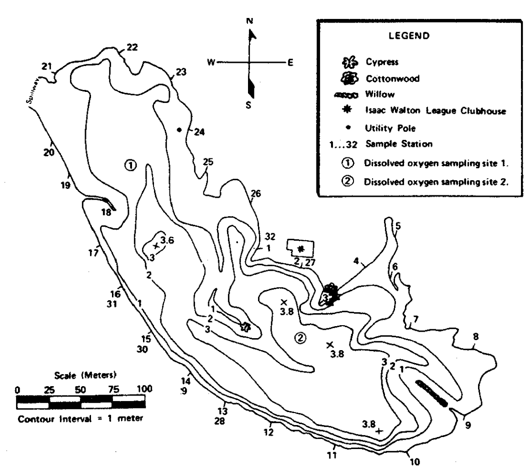

FIGURE 1. Bathymetry of Sanborn Lake, showing sampling sites for invertebrates and dissolved oxygen.

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In September 1971, macrophytes, mainly *Potamogeton nodosus* and *P. amplifolius*, covered approximately 68% of the lake's surface area (Figure 2).

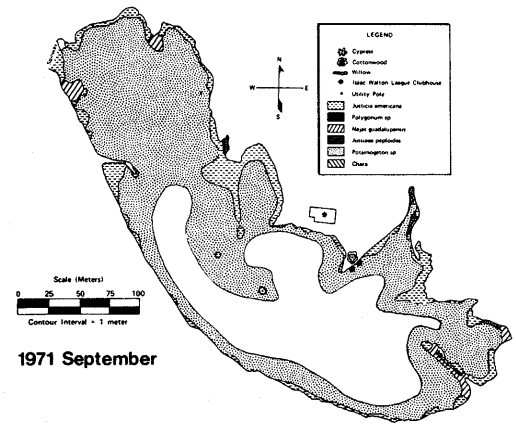

FIGURE 2. Sanborn Lake hydrophyte distribution in September 1971.

MATERIALS AND METHODS

Diuron, 3-(3,4-dichlorophenyl)-1,1-dimethylurea, is a nonspecific systemic herbicide that controls most aquatic plants at concentrations of 0.2-1.5 mg/*l*, and its toxicity to nontarget organisms is low (4). When diuron was applied to this pond, it was registered by the Oklahoma Department of Agriculture under the product name Aqua-trol, a preparation containing 70 percent diuron. Aqua-trol was applied to Sanborn Lake as an aqueous solution by spraying from a boat on 22 April 1972. The application rate, 2.01 kg/ha, produced a concentration of 0.07 mg/*l* diuron. Because hydrophytes were not killed, a second application was made 3 June 1972 to the northwest half of the pond that contained densely growing *Potamogeton* (Figure 2). This time, Aqua-trol powder was hand-broadcast at the rate of 3.04 kg/ha, which gave a concentration of 0.18 mg/*l* diuron in the treated area.

Thirty-four macroinvertebrate samples were taken, randomly selected from 26 predetermined points equidistant around the lake shore (Figure 1): six samples were taken from 0—1-m stratum in September 1971 and again in October 1972; ten and twelve samples were taken in September 1971 and October 1972, respectively, from the 1—3-m stratum.

Macroinvertebrate samples were obtained from the sediment and vegetation contained inside a galvanized steel cylinder (1.22 m tall, 0.44 m in diameter, and 0.15 m^2 in cross-sectional area) pushed into the lake bottom. All vegetation and attached organisms were removed from within the cylinder and placed in a bucket. Organisms attached to the vegetation were separated from the plants with running water over a 35-mesh, 420-micron sieve. Organisms suspended in the water column contained in the cylinder were collected by sweeping the water column with a 1 mm^2 mesh aquatic net. Organisms in the sediment were collected with three Ekman dredge samples taken within the cylinder after the vegetation was removed. Invertebrates removed from the vegetation were pooled with those obtained from net and dredge samples and preserved in 10 percent formalin. Hereafter, use of the term "benthic macroinvertebrates" refers to both the clinging phytomacrofauna and organisms dwelling in the bottom silt.

Preserved samples of macroinvertebrates were sorted by sugar flotation (5). The organisms were identified, counted, and their dry weights determined. Keys used for identification were Usinger (6), Pennak (7), Edmondson (8), and Mason (9).

Species diversity indices ($\bar{d}$) of the macroinvertebrate assemblages were calculated for each collection date and depth stratum by the formula of Shannon (10). Pooled $\bar{d}$ values were used, rather than mean $\bar{d}$ values, because the pooled, $\bar{d}$, is less variable as it approaches the asymptote (11).

Bluegills were collected in September 1971 and October 1972, by electrofishing. Length, weight, and scale samples were obtained from all fish. Stomachs were extracted and placed in 70% isopropyl alcohol. Ten fish were randomly selected for stomach analysis from each age group in 1971 and five fish from each age group in 1972. The age groups studied were young-of-the-year (YOY), age 1, and age 2.

Macroinvertebrates and zooplankton in the fish stomachs were identified to genus and counted. Dry weights were determined for macroinvertebrate, zooplankton, and plant portions of the stomach contents. Average number and relative abundance of the various food items were compiled for each age class of fish. Species diversity values were determined for stomach contents. Ivlev's index (1) was used as a measure of electivity (E) for various macroinvertebrate taxa in the fish rations: $E = (r_i - p_i)/(r_i + p_i)$ where r_i = % of food item in the ration, and p_i = % of food item in the environment. Values of Ivlev's index (1) range from –1.00 (complete avoidance) to +1.00 (exclusive selection).

Dissolved oxygen in the lake was measured with a galvanic cell oxygen probe (standardized) by the Winkler procedure (12).

RESULTS

Plant biomass

The herbicide application reduced the biomass of higher aquatic plants to approximately 0.1% of the pretreatment standing crop. In September 1971, plant biomass was 481.2 gm/^{3} in the 0—1-m stratum and 150.3 m/g^3 in the 1—3-m stratum. Most of the biomass for both strata was due to *Potamogeton amplifolius* and *P. nodosus,* but the 0—1-m stratum also contained substantial quantities of *Justicia americana* and *Najas guadalupensis.* In the October following treatment, the live plant

TABLE 1. *Biomass, density, and species diversity (pooled $\bar{d}$) of benthic macroinvertebrates September 1971 and October 1972 for two depth strata.*

	0—1-m. stratum		1—3-m. stratum	
	Sept. 1971	Oct. 1972	Sept. 1971	Oct. 1972
Biomass (g/m^2)	1.62	4.49	1.32	1.02
Numerical density/m^2	4009	4496	1264	771
No. of samples	6	6	10	12
No. of species	62	37	57	33
Pooled $\bar{d}$	4.03	3.76	4.59	3.70

TABLE 2. *Numerical density (no/m^2) and biomass (g/m^2) of macroinvertebrate taxa between September 1971 and October 1972 for two depth strata.*

	0—1-m. stratum		1—3-m. stratum	
Taxon	Sept. 1971	Oct. 1972	Sept. 1971	Oct. 1972
Oligochaeta	554[1] 0.1599[2]	515 1.4922	127 0.6866	66 0.4020
Gastropoda	65 0.2589	2 0.0001	22 0.0786	1 0
Pelecypoda	13 0.0016	432 2.1016	103 0.2127	67 0.2785
Amphipoda	1081 0.1009	5 0.0007	128 0.0164	0 0
Hydracarina	119 0.0085	2 0.0001	5 0.0003	0 0
Coleoptera	230 0.4202	0 0	44 0.0718	0 0
Trichoptera	105 0.0086	24 0.0062	76 0.0148	1 0.0001
Odonata	965 0.4626	39 0.1211	229 0.1189	6 0.0248
Ephemeroptera				
Baetidae (*Caenis*)	253 0.0198	75 0.0070	21 0.0032	16 0.0024
Ephemeridae (*Hexagenia*)	0 0	32 0.2762	0 0	1 0.0040
Diptera				
Chironomidae	404 0.0299	3055 0.4172	301 0.0456	524 0.2631
Culicidae (*Chaoborus*)	16 0.0013	0 0	118 0.0127	7 0.0012
Tabanidae (*Chrysops*)	39 0.0797	0 0	32 0.0381	1 0.0008
Ceratopogonidae (*Palpomyia*)	8 0.0006	297 0.0376	24 0.0021	77 0.0147

biomass was 0.3 g/m^3 in the 0—1-m stratum and 0.4 g/m^3 in the 1—3-m stratum.

Plant decomposition following treatment reduced dissolved oxygen; only the upper 2-3 meters of the water column contained more than 3 mg/*l* dissolved oxygen. After treatment, water samples taken near the lake bottom (3.8 m) had no more than 1.5 mg/*l* dissolved oxygen, and frequently the concentration approached 0 mg/*l*, whereas prior to treatment, the dissolved oxygen averaged 8 mg/*l* in the surface layers and 6 mg/*l* near the bottom.

Benthic macroinvertebrates

There was a significant increase in average biomass of macroinvertebrates in the 0—1-m stratum between September 1971 and October 1972 ($p<0.05$). There was also an increase in average numerical density, but the increase was not statistically significant (Table 1). When the Pelecypoda were omitted from the biomass calculations, the increase in biomass was no longer significant. In the 1—3-m stratum, there was a decrease in both numbers and biomass in the post-treatment collections. The decrease in numerical density was significant ($P<0.05$). The species diversity of the macroinvertebrates declined in the post-treatment collections at both the 0—1 and 1—3 m strata (Table 1) due to a decrease in several species of phytomacrofauna and an increase in the numbers of a few species of the silt-dwelling detritivores.

Substantial changes occurred in both average biomass and numerical density for most taxa of macroinvertebrates (Table 2). Organisms found in greatest abundance clinging to the higher plants, such as the Amphipoda, Hydracarina, Gastropoda, Trichoptera, Odonata, and Coleoptera, were substantially diminished. Among the Ephemeroptera, the bottomsprawling *Caenis* decreased in numbers following treatment, while the burrowing, debris-feeding *Hexagenia,* which was not present before treatment, appeared in the samples in 1972.

Among the silt-dwelling organisms, numerical density of oligochaetes diminished

TABLE 3. *Mean number and percent abundance (in parentheses) of food organisms in bluegill ration, 1971 and 1972.*

Food organism	Age 1 Fish		Age 2 Fish	
	1971	1972	1971	1972
Chironomidae	2.4 (49)	7.8 (72)	10.3 (81)	22.8 (80)
Trichoptera	0.8 (16)	0.2 (2)	0.3 (2)	0.4 (1)
Odonata	0.7 (14)	0.2 (2)	0	0
Hydracarina	0.6 (12)	1.0 (9)	0.7 (13)	1.0 (4)
Ephemeroptera	0.2 (4)	0.2 (2)	0.2 (2)	0.4 (1)
Ceratopogonidae	0.2 (4)	0.6 (6)	0	0.2 (0.7)
Mollusca		0.6 (6)	0.1 (1)	0
Culicidae (*Chaoborus*)			0.1 (1)	0
Amphipoda				0.2 (0.7)
Oligochaeta				0.2 (0.7)
Annelid cocoons				3.2 (11)

TABLE 4. *Electivity indices for benthic macroinvertebrates in fish rations, 1971 and 1972.*

Food organism	Age 1 Fish		Age 2 Fish	
	1971	1972	1971	1972
Bottom dwellers				
Chironomidae	+0.65	+0.03	+0.78	+0.08
Ceratopogonidae	+0.91	−0.14	−1.00	−0.83
Mollusca	−1.00	−0.27	−0.36	−1.00
Oligochaeta	−1.00	−1.00	−1.00	−0.87
Phytomacrofauna				
Hydracarina	+0.63	+0.99	+0.65	+0.97
Ephemeroptera	−0.28	−0.16	−0.64	−0.30
Trichoptera	+0.66	+0.52	−0.16	+0.40
Odonata	−0.17	+0.31	−1.00	−1.00
Amphipoda	−1.00	−1.00	−1.00	+0.75

somewhat in both strata in 1972, but their biomass density increased significantly in the 0—1-m stratum. Thus, the size of individuals increased by an order of magnitude. Pelecypoda (*Sphaerium* and *Pisidium*) also increased in the 0—1-m stratum, both in numbers and biomass. Among the Diptera, Chironomidae increased significantly, particularly in the 0—1-m stratum. The ceratopogonid *Palpomyia*, also a silt dweller, increased in numbers and biomass in both strata but especially at the 0—1-m depth. Populations of the phantom midge, *Chaoborus*, and the horsefly, *Chrysops*, diminished.

Macroinvertebrates in the bluegill ration

Chironomids constituted the major portion of the macroinvertebrates in the diet of the bluegill in 1971 and 1972 for both age 1 and 2 fish (Table 3). The average number of chironomids per fish increased substantially after treatment. Fewer Trichoptera but more Ceratopogonidae were eaten in 1972 by the age 1 fish. Annelids and annelid cocoons appeared in the diet for the first time in 1972 in the age 2 fish. The young-of-the-year fish fed primarily on zooplankton.

Chironomidae were highly favored by both year classes of fish in 1971 (Table 4). The electivity indices for chironomids declined in 1972; although chironomids were eaten in increased amounts in 1972, consumption did not remain in the same proportion to their abundance in the environment. Ceratopogonidae, Oligochaeta, and Mollusca were generally not favored by fish in proportion to their abundance among the benthos.

Among the phytomacrofauna, Hydracarina were highly favored; even in 1972 when these were extremely scarce in the environment, their vegetation habitat having been destroyed, they continued to constitute a substantial portion of the bluegill diet. Trichoptera (dominated by the small, plant-associated *Ochrotrichia*) were generally favored by the fish, even though the population of Trichoptera was drastically reduced in 1972. Electivity was generally low for the Ephemeroptera, *Caenis* being found in the rations only in 1972.

Species diversity values for macroinvertebrates in the fish ration and in the environment for 1971 and 1972 reflect opposite trends (Table 5). Diversity of macroinvertebrates in the rations of both age classes increased in the year following treatment, while diversity of macroinvertebrates for both depth strata decreased.

TABLE 5. *Species diversity indices (pooled $\bar{d}$) for benthic macroinvertebrates in fish rations and environment preceding and following diuron treatment.*

	Fish		Benthos	
	Age 1	Age 2	0-1 meter	1-3 meter
1971	2.92	3.15	4.03	4.59
1972	3.83	3.49	3.76	3.70

The total ration

When total stomach contents, including both macroinvertebrates and zooplankton, were analyzed, the species diversity in the ration actually diminished in the year following treatment (Table 6). The total amount of food in the fish stomachs increased substantially in 1972 (Table 7). Most of that increase was due to greater consumption of Cladocera.

A gravimetric analysis of the rations of the three age classes of fish before and after treatment showed the relative importance by weight of each type of food (Table 8). The category defined as plant material included both fragments of decaying higher plants and filamentous algae. By weight, benthic macroinvertebrates constituted the greater portion of the bluegill diet except for YOY fish in 1971 and age 2 fish in 1972. Zooplankton ranked second in importance by weight, although they ranked first in importance by number.

TABLE 6. *Species diversity (pooled $\bar{d}$) of fish rations, including zooplankton and benthos, for three age classes of bluegills, 1971 and 1972.*

	Young-of-Year	Age 1 Fish	Age 2 Fish
1971	1.44	2.54	2.23
1972	0.27	0.70	0.46

DISCUSSION

The ecology of the feeding of fishes relates to density, patchiness, and vulnerability of their prey (1). In the present study, as in other investigations, Cladocera and Chironomidae comprise the greatest portion of the bluegill diet (13, 14, 15, 16). Our gravimetric analysis of the total ration shows that in 1971, YOY fish (39 mm average length) consumed mostly zooplankton, while age 1 fish (68 mm) and age 2 fish (98 mm) consumed more benthic macroinvertebrates. The numerical analysis, however, shows zooplankton comprising the greatest portion of the diet for all three age groups. Some investigators indicate that bluegills switch from a plankton diet to eating macroinvertebrates at 30-40 mm average length (17) while others indicate that bluegills remain planktivorous up to about 200 mm (18). The time at which this shift in diet occurs for any particular bluegill population probably depends to a great extent on density and availability of the prey.

Electivity indices for macroinvertebrate components in the diet of the bluegills before treatment of the lake indicate Chironomidae and Hydracarina were the preferred foods of age 1 and 2 fish, as well as Ceratopogonidae and the small trichopteran *Ochrotrichia* for the age 1 bluegills. Molluscs and oligochaetes do not seem to be favored by bluegills, as Gerking (14) has indicated.

The herbicide treatment in the spring of 1972 affected abundance of macroinvertebrates and zooplankton. Density of Chironomidae increased for both depth strata of the lake, whereas destruction of the hydrophytes reduced the numerical density of the phytomacrofauna — represented by Gastropoda, Amphipoda, Hydracarina, Trichtoptera, and Odonata — by factors ranging from 4 to 216. The Coleoptera, abundant in 1971, were not collected in 1972. Despite major reductions in the phytomacrofauna, species diversity of the macroinvertebrate assemblage in 1972 was only slightly less than that in 1971. The diversity was probably maintained by substitution of silt-dwelling species for the phytomacrofauna. Young-of-the-year, age 1, and age 2 fish had 42.7, 39.6, and 29.5 times more Cladocera per fish stomach in 1972 than in 1971. There was also an increased consumption of benthic macroinvertebrates and plant fragments following treatment. Although the diversity of the total bluegill ration decreased somewhat in 1972 (i.e., feeding was somewhat more selective), simplification of macroinvertebrate diversity in the environment was not reflected by simplification of macroinvertebrate diversity in the diet. This was probably due to substitution of organisms that were made vulnerable to fish predation by the elimination of plant cover.

TABLE 7. *Average number and relative abundance (in parentheses) of organisms found in stomachs of three age classes of fish in 1971 and 1972.*

Food item	Young-of-Year 1971	Young-of-Year 1972	Age 1 Fish 1971	Age 1 Fish 1972	Age 2 Fish 1971	Age 2 Fish 1972
Cladocera	15.3 (77.7)	653.6 (97.0)	11.8 (37.8)	467.0 (90.6)	54.3 (67.9)	1602.2 (96.2)
Cladoceran eggs	0.3 (1.5	3.2 (0.5)	2.4 (7.6)	32.0 (6.2)	4.5 (5.6)	30.0 (1.8)
Ostracoda	1.5 (7.6)	4.8 (0.7)	10.1 (32.4)	2.8 (0.5)	7.6 (9.5)	3.6 (0.2)
Copepoda	0.7 (3.6)	8.6 (1.3)	2.0 (6.4)	3.0 (0.6)	1.9 (2.4)	1.0 (0.1)
Chironomidae	1.3 (6.6)	1.6 (0.2)	2.4 (7.6)	7.8 (1.5)	10.3 (12.9)	22.8 (1.4)
Other[a]	0.6 (4.0)	2.2 (0.3)	2.5 (8.0)	2.8 (0.5)	1.4 (1.8)	5.6 (0.3)

[a]Includes all benthic macroninvertebrates in the rations other than Chironomidae

TABLE 8. *Percent of stomach contents by weight for three major types of food organisms for three age classes of fish.*

Food type	Young-of-Year 1971	Young-of-Year 1972	Age 1 Fish 1971	Age 1 Fish 1972	Age 2 Fish 1971	Age 2 Fish 1972
Macroinvertebrates	26.3	51.0	61.5	69.0	49.5	33.3
Zooplankton	73.7	36.7	38.5	23.2	23.7	16.1
Plant	0	12.3	0	7.8	26.8	50.6

in 1972, electivity was apparently affected by changes in density and vulnerability of the prey. More chironomids were eaten in 1972 and electivity for chironomids decreased. Among the 16 genera of larval chironomids found in the fish stomachs, 3 (subfamily Tanypodinae) typically leave the substrate at times of low oxygen and swim into upper strata. Twelve genera found in the ration belonged to the subfamily Chironominae, which build tubes in the substrate and contain the respiratory pigment hemoglobin for withstanding conditions of low oxygen in their microhabitat (19).

Conversely, bluegill electivity increased for various species of phytomacrofauna in 1972. These were more exposed to fish predation because of destruction of their habitat. The increased electivity for Hydracarina is the most striking example, although increased electivity for trichopterans among age 2 fish is also illustrative. Slightly increased electivity for Ephemeroptera in 1972 appears related to the presence of *Caenis* in the fish stomachs for the first time. Some age-specific differences, however, are evident, such as the increased electivity of age 1 fish for small odonates and the increased electivity of the age 2 fish for the amphipod *Hyallela azteca*.

Electivity in the feeding of fishes depends on a variety of factors: size and their degree of concentration and concealment, and innate preference of the predator for certain foods (1). Size of the food item has been examined for the bluegill by a number of investigators, most notably Werner and his associates (20, 21). Accessibility as used by Ivlev (1) refers to degree of concealment of the prey. Vulnerability as used by Lewis (2) refers to degree of exposure of the prey. Both are expressions of cover or lack thereof. Changes in vulnerability of the prey can be seen by examining the food habits of a given age class of fish preceding and following an environmental perturbation affecting prey habitat or cover.

Ivlev's, (1) expression of accessibility is given by the formula $A = E - Ep$, where E is electivity for the food item under the given conditions and Ep is the innate preference of the predator for the specific food item. Although electivity can range from –1.00 to +1.00, a preference value below 0 would be meaningless. Since innate preferences are always difficult to ascertain, A has utility for comparing environmental situations where cover is altered and E values are available before and after an environmental perturbation affecting cover.

In the present study, the habitat of the phytomacrofauna was nearly eliminated in 1972 by the herbicide treatment. The E value for phytomacrofauna in 1972 is analogous to conditions for Ep, where the predator can freely forage on the unconcealed prey. In 1971, cover was abundant, producing a situation analogous to E. Thus, for Hydracarina: $A = E_{1971} - E_{1972}$ and $A = (+0.63) - (+0.99) = -0.36$ for the age 1 fish. For the age 2 fish, $A = (+0.65) - (+0.97) = -0.32$. The change in electivity provides a measure of changes in vulnerability with decreased cover. Electivity was high for Hydracarina even when they had adequate cover and bluegills preyed upon the brightly colored hydracnids even in dense vegetation.

The abundance of decaying hydrophytes should have increased cover for chironomids in 1972, and the E value in 1971 is somewhat analogous to Ep, and the E value in 1972 to E. Hence for Chironomidae: $A = E_{1972} - E_{I971}$, and $A = (+0.03) - (+0.65) = -0.62$ for age 1 fish. For age 2 fish, $A = (+0.08) - (+0.78) = -0.70$. The change in electivity may be attributed, at least in part, to increased cover in 1972. However, the Chironomidae were not completely without cover in 1971, so the electivity in 1971 is not entirely a matter of bluegill preference. However, there was a change in density of chironomids between 1971 and 1972, and as Ivlev (1) has shown, when the density of a preferred food increases, the electivity for that food declines and remains at a lower level. Although the change in electivity for chironomids in this study is probably the combined effect of changes in density and cover, the increased electivity for hydracnids, despite a 60-fold decline in their density, must be attributed to a substantial increase in vulnerability due to reduced cover. Bluegills demonstrated high selective, not opportunistic, feeding behavior for hydracnids. The study shows that for a preferred prey, increased vulnerability may compensate for a decrease in density. In such a situation electivity in predator feeding behavior can be associated with the relative contributions of prey density and vulnerability.

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