

Fish Predation: Its Effects on Littoral Zone Invertebrates

Robert J. Hallahan

Submitted to: Martin B. Berg, Ph.D.

December 1, 1989

## ABSTRACT

A fish exclusion study was conducted in Bay Lake, in Michigan's northern peninsula. The lake featured a well-developed littoral zone with large, diverse fish and macroinvertebrate populations. Two, 32 m perimeter areas were established in the lake, adjacent to the shore. One was a control, the other, an experimental area. Both were marked off with a wooden frame, to which a screen was attached for the experimental area. This screen prevented fish from entering the experimental area. Benthic invertebrates were sampled in both areas with an Ekman grab at the beginning and end of the 6-week experiment.

A comparison of the invertebrate populations sampled showed no differences in benthic densities, individual sizes, or taxon richness, between the experimental and control areas on either sampling date. Also, no differences were found comparing the population of either area at the beginning of the study with the population of the same area at the end of the study.

The null hypothesis, which stated that no differences would be found between the control and experimental plots, was not rejected for several possible reasons: 1) the experiment was too short, 2) fish predation pressure was not strong enough to effect a change and/or, 3) the change that occurred was too small to be detected with the number of samples taken.

## INTRODUCTION

The freshwater littoral zone fauna is controlled by many complex interactions. Previous studies have found the distribution and abundance of macroinvertebrates to be affected in various ways by a variety of sunfish (*Lepomis* spp.) species (Ball and Hayne 1952, Hayne and Ball 1956, Mittelbach 1981, 1988, Thorp and Bergy 1981, Werner et al. 1981). Studies have found that Amphipoda, Chironomidae, Ephemeroptera, Trichoptera, and Zygoptera make up the vast majority of a bluegill's (*Lepomis macrochirus*) diet (Ball and Hayne 1952, Gilinsky 1984, Mittelbach 1988). This predation has a direct effect on a taxon's density; it is clear that when a fish eats an insect, insect density decreases. However, in a lake containing a variety of insect taxa, these densities may be affected differently (Mittelbach 1988). Clearly, there are other factors at work. For instance, it is known that bluegills seek refuge in vegetation in response to piscivore presence (Mittelbach 1981, Werner et al. 1983a). This may lead to a depletion of only vegetation-associated macroinvertebrates. Hall and Werner (1977), however, showed that large bluegills are less affected by piscivore predation than small bluegills. Therefore, they tend to use vegetation as a refuge much less (Mittelbach 1981). Further, large fish encounter more prey per unit time than smaller fish, and feed selectively on larger prey (Mittelbach 1981, 1988, Werner and Hall 1974, 1977, Werner et al. 1983b). Thus, the presence, and presumably density, of piscivores in a lake indirectly affects macroinvertebrate populations by changing the size structure of the

primary predators, and therefore their collective feeding preferences, as well as their habitat use (and therefore, again, their feeding). Further complications arise from diel habits of both fish and invertebrates. Bluegills generally feed diurnally, especially around sunrise (Mittlebach 1981, Sarker 1977), and move towards shore during the night (Baumann and Kitchell 1974, Werner et al. 1977). Crappie (*Pomoxis* spp.), however, are more nocturnal than bass (*Micropterus* spp.) and bluegills (Childers and Shoemaker 1953, as cited in Werner et al. 1977, Werner et al. 1977), and move offshore during the night, feeding at the surface (Werner et al. 1977). Daily vertical migrations of plankton such as the downward movement of *Chaoborus* in the water column (Fedorenko and Swift 1972) are thought to be causally related to these changes (Carter and Kwik 1977). However, bluegills also may be less restricted to the vegetation during darkness when piscivores either are not present or are not able to see well enough to be a predatory threat.

There are yet more complex factors affecting macroinvertebrate populations. Mittelbach (1988) found that "mean invertebrate size decreased significantly as fish density increased, owing to a reduction in the number of large invertebrates." It may be that fish feed on larger individuals of each taxa, or that they feed on taxa with larger individuals. Crowder and Cooper (1982) found that upon introducing bluegills to a small fishless pond, certain large taxa (*Hyaella*, *Zygoptera*) were reduced in density, but small invertebrates increased in abundance. It seems likely that removing larger prey items allows more resources for smaller invertebrates, perhaps due to lessened competition from large, more dominant

consumers. Hall et al. (1970) maintained that mean body size of a population of insects is more indicative of invertebrate response to predation than is taxonomic group. Thus, to get an accurate picture of benthic response to size-selective fish feeding, it is important to measure not only density, but mean body size as well.

Certain studies point to invertebrate predation as being another factor controlling benthic populations. Odonate larvae and certain chironomids (subfamily Tanyptodinae) have been singled out as important predators (Bay 1974, Gilinsky 1984, Pritchard 1964). Menzie (1978, as cited in Gilinsky 1984) and Crowder and Cooper (1982) documented higher densities of odonates and lower densities of their prey in fish exclusion studies.

The above studies have added the most recent dimension to the current literature on littoral interactions. Overall, some conclude that fish significantly decrease macroinvertebrates (Ball and Hayne 1952, Hayne and Ball 1956, Morin 1984, Werner et al. 1981), while others conclude that there are either no large effects (Thorp and Bergey 1981) or that there are variable effects (Gilinsky 1984, Mittlebach 1988). Perhaps these contradictory findings are the result of incomplete studies: most of these studies were specifically examining only a few factors at a time and not all the interactions. While specificity is important in determining the basic who-eats-whom relationships, relative importances of each relationship in an ecosystem cannot be determined without looking at the whole. Further, most of the studies involved introducing fish to fishless or man-made ponds, where fish are likely to have an inflated effect compared to looking at the fish effect in a system

where predators and prey have coexisted for generations (Mittlebach 1988). Also, Collins (1989) showed that "patchiness in benthic invertebrate compositions might be generated by patchy fish exploitation," an effect not eliminated by studying very small areas of a lake. The present study proposed to fill these gaps--to study each of these relationships--at once--in a natural, diverse, and complete ecosystem.

## MATERIALS AND METHODS

This experiment was conducted in Bay Lake, on UNDERC (University of Notre Dame Environmental Research Center) property, in Gogebic county, Michigan. The lake was chosen for its large size and well-developed fish and insect assemblages.

Two areas were involved: one a control, the other a large fish exclusion cage, the experimental. Both areas were located on a southerly-facing shoreline in a northern bay of the lake. A frame was constructed around each area with wooden 2x4's driven into the sediments every 1-1.5 m. Each post extended out of the water. The complete frame formed a semi-ovoid shape with the two ends of the arc in contact with the shore. The length of each arc was about 21 m, covering 11 m of shoreline. The arc extended about 8 m out into the lake, perpendicular to the shore, enclosing an area with depths ranging from 0 to 2.5 m. Depths were measured at each post of the experimental area, and were used to construct an appropriately shaped screen from fiberglass window screening. The screen was attached to the posts from in the water and without disturbing the sediments. The screen extended from 0.5 m above the waterline, to the sediments, being anchored with rocks pushed into the substrate. No screen was attached to the posts delineating the control area.

Fish were chased from the cage before it was completely attached to the frame, and minnow traps were set throughout the summer to remove any remaining fish. It was necessary to scrub the cage during the experiment to remove periphyton. The cage was in place for six weeks: from June 3, 1989 to July 16, 1989.

To determine the macroinvertebrate fauna, benthic samples from both areas were collected at randomly-determined locations on June 17 and July 15. In June, 5 samples were taken from each area, and in July, 7 samples were taken. To preclude cage effects, no locations near posts were sampled. A 15 cm Ekman grab was used to collect each sample, which was then preserved in 70% ethyl alcohol. In the lab, organisms were separated from the detritus by floating them in a saturated sugar solution. Larval macroinvertebrates were identified and counted. Adult insects, including aquatic Coleoptera, were not considered benthic and therefore were not counted. The area between the control and the experimental enclosures was sampled (4 samples) prior to the initiation of the experiment. The same enumeration techniques were used to estimate sample variability, and this estimate was then used to determine the number of samples required on each date to detect an 80% difference in macroinvertebrate composition between the populations of the control and experimental areas.

To establish fish feeding pressure, two approaches were used. First, fish diets were examined (on June 25 and July 11-14 at different times of the day) by angling and using enlarged minnow traps to collect fish whose stomach and intestine contents were then examined by dissection. A partial list of fish species present in the lake was established from the collections. Second, fish littoral zone activity was quantified in two ways, by direct observation and by use of minnow trap catch per unit effort values. The direct observation was conducted visually from a boat. Three replicates involved a 1 m<sup>2</sup> quadrat being set in different locations on the

bottom of each area and being observed for 15 minutes. Whenever a fish crossed into the area over the quadrat, it was counted and its species noted. The second method of quantifying fish activity involved using bread-baited, modified minnow traps (with enlarged openings for larger fish such as bluegill) that were set in both areas overnight on 4 different occasions. The traps were removed from each area the next day and numbers of fish caught provided a catch per unit effort value. Separate collections with gill and fyke nets set for 1 night each were used to supplement the fish species list. The growth of macrophytes was observed throughout the summer, and a species list was compiled.

## RESULTS

### *Macroinvertebrates*

Tables 1-4 list the benthos collected on the two sampling dates. Members of six aquatic insect orders were collected, the most numerous ones being Diptera, Ephemeroptera, Odonata, and Trichoptera. No Plecoptera, Neuroptera, or Hemiptera were collected. A genus of fingernail clams, *Musculum*, was counted, as this was seen to be an important element of fish diets. Insects were usually identified to genus, except Chironomidae which were identified to subfamily. For the purposes of the tables, however, only the more numerically important genera are presented. The other genera are presented as members of their higher respective taxa. For instance, a small number of odonates was represented by a relatively large number of genera; no significant pattern could emerge from such a wide distribution of organisms among taxa, but considering all dragonflies as a group is more likely to provide meaningful information. For this reason, in most cases, several genera are represented under one more-inclusive taxon. In some cases, both were done: a genus was considered separate of its order, and the order itself was considered. For example, in Ephemeroptera, *Caenis* was often quite numerous, but *Hexagenia* and *Stenonema* occurred occasionally. When the latter two were present, their numbers were added to those of *Caenis*, and this total is listed under Ephemeroptera. For example, in the July control sample #5, eight *Stenonema* and one *Caenis* were collected, giving a total of 9 mayflies. The same procedure was also used for Diptera and Trichoptera. In the Chironomidae, the subfamilies Chironominae and

Orthocladiinae were considered together in June, but separately in July. Also in July, first instar dragonflies had appeared which were not present in June; these were considered separately from later instar dragonflies. Table 5 presents a summary of the means and standard deviations of each sample.

No significant differences were found between the populations sampled in each area on any date. The densities, in fact, were extremely similar. For any particular taxon, mean densities on a given date were within one standard deviation. For instance, the midges collected in the two areas numbered: 104 and 118 (June), and 115 and 127 (July). The standard deviations were 71 and 50 (June), and 67 and 35 (July). Similar results were found comparing Diptera, Ephemeroptera, or Trichoptera at the ordinal level, or any other combination of taxonomic level including total animals per sample. Not only were no significant differences found between the experimental and control on any on date, but none were found between the June control and the July control or the June experimental and the July experimental. Even the dragonfly hatching, which added an average of seven animals per sample to the July control did not produce significant results.

The lack of significant treatment effects is a function of high standard deviations. In many cases, especially those in which a taxon is not represented in every sample, the standard deviation is much greater than the mean. For example, consider Ephemeroptera in the July control samples. Because the fifth sample had a cluster of eight *Stenonema* (none were found in any other sample), the mean number of mayflies (+/- standard deviation) in the July control

samples was 1.6+/-4.1. High standard deviations were also evident in analyzing total animals per sample. The average total was 149 animals per sample over the whole summer, with the standard deviation ranging from 53 to 80.

No substantial differences in taxa richness were observed in this study. A more detailed consideration of the generic and species-level taxa is necessary to make further conclusions.

A consideration of individual animal sizes throughout the experiment also showed no predation effect. Size-based fish effects are often based on taxonomic differences between two sample sets (Crowder and Cooper 1982). Occasionally it can be shown that such an effect is due to the larger members of each taxa being eliminated (Mittlebach 1988). Though no size measurements were taken, observational data showed a relatively constant taxonomic composition of the insect assemblage and no obvious differences in insect size. These results showed that body size measurements would be highly unlikely to show a predation effect.

#### *Predation Pressure Analysis*

This lack of significance is somewhat surprising in light of results from the determination of fish predation pressure. Fish species collected in the lake included largemouth bass, *Micropterus salmoides*; smallmouth bass, *M. dolomieu*; bluegill sunfish, *Lepomis macrochirus*; pumpkinseed sunfish, *L. gibbosis*; yellow perch, *Perca flavescens*; northern pike, *Esox lucius*; white sucker, *Catostomus commersoni*; rock bass, *Ambloplites rupestris*; and Iowa darter, *Etheostoma exile*. The first part of the predation pressure analysis

involved the examination of fish stomach/intestine contents. The results collected, identified to the lowest taxonomic level possible, are presented in Table 6. It shows a representative list of fish dissected, by species and size. Dates and times the fish were collected showed no obvious correlation with diet. No obvious correlation between benthos composition and gut contents was found. Some fish were collected soon after sunrise and some later in the afternoon, correlating with peak bluegill feeding activity (Mittelbach 1981, Sarker 1977). Diets were generally as expected, with the smallest size classes eating mostly zooplankton, the intermediate size classes feeding primarily on benthic material, and the largest fish being piscivorous. There were some surprising observations, however. Only four fish included fingernail clams as integral parts of their diets. From Thorp and Bergey (1981), it was expected that more would do so. Another surprising result was that it seemed, from looking specifically at clam ingestion, that some fish preferred eating certain animals to others. For instance, of the four fish that ate clams, three were bluegills (6.5-18 cm) and one was a yellow perch (7.5 cm). The two larger fish (both were bluegills) though, had eaten tremendous numbers of clams--nineteen clams were found in just one third of the contents removed from the gut of the 18 cm fish. There were several other bluegills of the same size that had eaten none. Some fish also showed a preference for *Oxyethira* and *Bezzia*. Although this could be a function of nonheterogeneous insect distribution such as that shown in the previously discussed *Stenonema* example (although clams do not appear to have exhibited such grouping), it is possible that

experience played a role in this, such as that mentioned in Werner et al. (1981). They showed that bluegills could become more efficient eaters with experience, and that specialists of eating from one habitat type ate more efficiently than did generalists. A large number of Trichoptera were eaten; often their cases were found in the stomachs along with the other debris.

The question of actual fish numbers now arises, and this is partially answered by the second part of the predation pressure analysis. First, direct observation showed that, as expected, many more fish appeared in the control area than in the experimental (Table 7). In each of the three replicates in the experimental area, no fish were observed. However, for the replicates done in the control area, relatively large numbers of fish were observed. The minnow trapping part of this analysis also strongly suggests that predation pressure was much higher in the control area (Table 8). From observations conducted earlier in the summer, it was expected that the number of fish caught in the control traps would be much higher. The same procedure as that used in July (and presented in Table 8) was used in June. In June, however, 10-15 fish were caught in each control trap, while only 1-2 fish were caught in each experimental trap. This data, unfortunately, was not recorded, and is therefore somewhat unreliable. The difference between these numbers and those recorded in Table 8 may be due to seasonal fish migrations into and out of the littoral zone.

Overall, though, the predation pressure aspect of this study does establish that there were many more fish present in the control area than in the experimental area; and that these fish, most likely,

did eat while they were in the control area. This conclusion agrees with the summer-long observation that many fish were actually observed in the control area, and that very few fish were actually seen in the experimental area. There is one troublesome exception, however. Approximately two weeks after the cage was sealed, a large school of largemouth bass fingerlings was seen in the experimental area. Due to their small size (4 cm by the end of the experiment), it was thought that they would not feed benthically and were therefore not removed. However, as shown in Table 6, these fish were, by the length of 4 cm, eating benthos. It is not known at what size (and therefore how far into the study) they began to eat benthic organisms, but considering each fish's relatively small diet, the large size of the experimental area, and the likeliness that they ate from the benthos for only a short time during the experiment, their effect was probably minimal.

### *Macrophytes*

Macrophytes collected during the experiment in both areas included: *Nuphar variegatum*, *Sparganium fluctuans*, *Brasenia schreberi* (very small amounts), and *Eriocaulon septangulare* (small amounts). All of these species were present at the end of the experiment, however there were no mature plants in either area at the beginning of the experiment, due to the unusually long Spring of 1989. No quantitative measure of plant abundance was made. Some *Oxyethira* specimens were found firmly attached to the grasses collected with the Ekman dredge, and this may have affected their susceptibility to vertebrate predation.

## DISCUSSION

The experiment's null hypothesis was not rejected: no important fish effect was discovered. There could be many causes for this result. The most likely ones include: the experiment was of too short a duration; predation pressure measurements were inaccurate or; the population shift that did occur was too small to be detected with the sample size used. Each of these will be explored below.

### *Experiment Length*

The duration of the experiment is one of the most important variables in experiments where two populations are separated, and the effects are observed. In the case of insects, it may take several generations for equilibrium to reestablish itself after such a drastic change as fish exclusion. Ball and Hayne (1952), for instance, carried out a fish exclusion experiment lasting 30 months which involved observing the macroinvertebrate population in a lake for 30 months. The fish population was removed from the lake after the first 17 months. Later, Hayne and Ball (1956) conducted a fish exclusion study which involved moving the fish population of one pond to a similar pond and observing the benthic faunas' reactions to this. The entire experiment lasted over 11 weeks and the significant fish effect may have been magnified by a necessity "to hold the fish without food for 18 days before beginning the experiment." Thorp and Bergey (1981) carried out a fish exclusion study involving three, 3-month test periods over an entire year. Gilinsky (1984) conducted a study which lasted 14 months, and even

Morin's (1984) fish exclusion study, which he titled "...results of short-term experiments...", lasted 3 full months. All of these studies dwarf the present study in length. This is a likely indicator that the effects of fish exclusion require long time periods to manifest themselves.

### *Predation Pressure Analysis*

Even if the experiment was long enough to elicit an effect, fish predation pressure may have been insufficient to effect a change. The fish observation counts were conducted on a sunny day from a boat; the fish may have been attracted to the shelter offered by the boat, in turn crossing over the quadrat more often than they otherwise would have. Also, the quadrat may have induced the fishes' curiosity by its presence alone, drawing them towards it. It was of a bright orange color, offering substantial contrast to the sediment, one which fish would be able to detect (Hoar and Rendall 1971, as cited in Healy 1984). Both of these factors may have artificially inflated the fish count for the control area. Even considering this fish count as accurate, though, there is no evidence that any of the fish actually ate from the control area. The only fishes ever caught actually feeding in the control area were those caught in the minnow traps; presumably, they went into the traps to eat the bread bait. The numbers given for fish feeding in the control (Table 8), however, are much smaller than those given for fish swimming through the control (Table 7), indicating that while fish may frequent the area, it is possible that few actually forage there. This possibility is supported by Collins (1989), who wrote: "data

indicate that risk of fish predation varies greatly among lakes, seasons, days, and sites within lakes." He cited this as a difficulty in detecting the effects of fish predation on benthos and a possible reason for the inconsistency in the results of fish exclusion experiments.

The only two ways to guarantee that fish will eat food from the study area are: 1) study the entire lake (e.g. Hayne and Ball 1956), an impossibility in the present case or, 2) enclose fish in a small area, forcing them to feed in that area (e.g. Mittlebach 1988), although this unnatural burden on fish necessarily changes their diet habits and probably puts a stress on them in other ways, possibly causing them to feed with unnatural patterns, thereby eliminating the entire purpose of enclosing them.

### *Sample Size*

Even if, considering these factors, predation pressure was strong enough to effect a change in 6 weeks, the change may have been too small to be detected by the sample size used. The estimate of sample variability (variability in each Ekman) derived from the presampling conducted in early June was used to determine the number of samples to be taken in each area necessary to observe a population shift of 80%. The required number of samples was calculated to be five Ekmans in each area. This was done for the June 17 sample. Upon sorting these and finding no differences, the sample number was increased to seven (for the July samples) in each area, in hopes of detecting a smaller change--70%. Lack of significant predator effects indicates that perhaps seven samples

were not enough. For comparison, Hayne and Ball's (1956) study required twenty Ekman collections each week, an amount of work far beyond the scope of this study.

Clearly, the complexity of the present subject, predator-prey interactions, lends itself to many different kinds of studies. Some must determine basic who-eats-whom relationships. Others must determine how much predation pressure actually exists in a system and why. When these elementary factors are known, more mature studies, such as the present one, can be carried out to determine the overall susceptibility of such systems to disturbance. This will give us a better idea as to how much concern we, as humans, must act with in order to guarantee that ecosystems persist in such a rapidly changing world as the one in which we now live.

## ACKNOWLEDGEMENTS

I would like to thank the Bernard J. Hank Foundation for the generous donation which made this study and the associated summer ecology course possible. Thanks also to the Notre Dame Biology Department professors George Craig, David Lodge, Sunny Boyd, Ronald Hellenthal, and postdoc Mike Dini for their devotion to us, students. Thanks to CAPT G. H. Dewherst, USN, Commanding Officer, NROTC Unit, University of Notre Dame, for permission to postpone my summer training, something without which, I would not have been able to participate in the ecology course. Kim McNaughton deserves recognition for her patience in lab and field help. Finally, a special thanks to Marty Berg for guidance and support during the entire UNDERC experience.

## LITERATURE CITED

- Ball, R. C. and D. W. Hayne, 1952. Effects of the removal of the fish population on the fish-food organisms of a lake. *Ecology* 33: 41-48.
- Bay, 1974. Predator-prey relationships among aquatic insects. *Annual Review of Entomology* 19: 441-453.
- Baumann, P. C., and J. F. Kitchell, 1974. Diel feeding in bluegills. *Transactions of the American Fisheries Society* 103: 255-260.
- Benke, A. C., 1978. Interactions among coexisting predators--a field experiment with dragonfly larvae. *Journal of Animal Ecology* 47: 335-350.
- Carter, J. C. H. and J. K. Kwik, 1977. Instar succession, vertical distribution, and interspecific competition among four species of *Chaoborus*. *Journal of the Fisheries Research Board of Canada* 34: 113-118.
- Childers, W., and H. H. Shoemaker, 1953. Time of feeding of the black crappie and white crappie. *Illinois Academy of Science Transactions* 46: 227-233.
- Collins, N. C., 1989. Daytime exposure to fish predation for littoral benthic organisms in unproductive lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 11-15.
- Crowder, L. D. and W. E. Cooper, 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63: 1802-1813.
- Fedorenko, A. Y. and M. C. Swift, 1972. Comparative biology of *Chaoborus americanus* and *Chaoborus trivittatus* in Eunice Lake, British Columbia. *Limnology and Oceanography* 17: 721-730.
- Gilinsky, E., 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* 65: 455-468.

- Hall, D. J., W. E. Cooper, and E. E. Werner, 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnology and Oceanography* 15: 839-928.
- Hayne, D. W. and R. C. Ball, 1956. Benthic productivity as influenced by fish predation. *Limnology and Oceanography* 1: 162-175.
- Healy, M., 1984. Fish predation on aquatic insects, pp. 255-288 in Resh, V. H., and D. M. Rosenberg, Eds., *The Ecology of Aquatic Insects*. Praeger: New York.
- Hoar, W. S. and D. J. Randall (eds.), 1971. *Fish physiology*. Vol. 5. Sensory systems and electric organs. Academic Press, Inc., New York, NY. 600 pp.
- Menzie, C. A., 1978. Productivity of chironomid larvae in a littoral area of the Hudson River estuary. Dissertation. City University of New York, New York, USA.
- Mittelbach, G. G., 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62: 1370-1386.
- 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. *Ecology* 69: 614-623.
- Morin, P. J., 1984. The impact of fish exclusion on the abundance and species composition of larval odonates: results of short-term experiments in a North Carolina farm pond. *Ecology* 65: 53-60.
- Pritchard, G., 1964. The prey of dragonfly larvae (Odonata: Anisoptera) in ponds in Northern Alberta. *Canadian Journal of Zoology* 42: 785-800
- Sarker, A. L., 1977. Feeding ecology of the bluegill, *Lepomis macrochirus*, in two heated reservoirs of Texas, III. Time of day and patterns of feeding. *Transactions of the American Fisheries Society* 106: 596-601.
- Thorp, J. H., 1986. Two distinct roles for predators in freshwater assemblages. *Oikos* 47: 75-82.

- Thorp, J. H. and E. A. Bergey, 1981. Field experiments on responses of a freshwater, benthic macroinvertebrate community to vertebrate predators. *Ecology* 62: 365-375.
- Werner, E. E., J. F. Gilliam, D. H. Hall, and G. G. Mittelbach, 1983a. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64: 1540-1548.
- Werner, E. E. and D. H. Hall, 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55: 1042-1052.
- Werner, E. E., D. J. Hall, D. R. Laughlin, D. J. Wagner, L. A. Wilsmann, and F. C. Funk, 1977. Habitat partitioning in a freshwater fish community. *Journal of the Fisheries Research Board of Canada* 34: 360-370.
- Werner, E. E., G. G. Mittelbach, and D. H. Hall, 1981. The role of foraging profitability and experience in habitat use by the bluegill sunfish. *Ecology* 62:116-125.
- Werner, E. E., G. G. Mittelbach, D. H. Hall, and J. F. Gilliam, 1983b. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. *Ecology* 64: 1525-1539.

Table 1: June Experimental Samples

GROUP	1	2	3	4	5	MEAN	ST. DEV.
COLEOPTERA		1				0.2	0.45
DIPTERA	100	71	22	190	180	112.6	71.82
Ceratopogonidae	8	9	6	9	8	8	1.22
<i>Bezzia</i>	8	8	5	8	7	7.2	1.30
Chironomidae	92	61	15	181	171	104	71.30
Chironominae/Orthoclaadiinae	70	47	10	128	117	74.4	49.00
Tanypodinae	22	14	5	53	54	29.6	22.63
Tabanidae: <i>Chrysops</i>		1	1		1	0.6	0.55
EPHEMEROPTERA	3	9	1	7	3	4.6	3.29
<i>Caenis</i>	2	9	1	7	3	4.4	3.44
MEGALOPTERA: <i>Sialis</i>						0	0.00
ODONATA	0	5	0	5	4	2.8	2.59
Anisoptera		5		5	4	2.8	2.59
Zygoptera						0	0.00
TRICHOPTERA	10	6	5	6	9	7.2	2.17
<i>Neureclipsis</i>						0	0.00
<i>Oecetis</i>	8	6	4	5	9	6.4	2.07
<i>Oxyethira</i>	2		1	1		0.8	0.84
PELECYPODA: <i>Musculum</i>	1	5		12	10	5.6	5.32
TOTALS	114	97	28	220	206	133	79.97

NOTES: The five samples taken for the June experimental area are listed above. Each entry represents the number of animals of that taxon collected with the Ekman dredge. For example, in sample #1 above, 100 Diptera were collected, 8 of which were ceratopogonids (all *Bezzia* spp.), and 92 of which were midges (including 70 Chironominae/Orthoclaadiinae and 22 Tanypodinae). Total number of animals for samples 1-5 is listed at the bottom of those columns. Mean and standard deviation values for Table 1 samples are given for each taxonomic group. Chironominae and Orthoclaadiinae are presented as one group.

Table 2: June Control Samples

GROUP	1	2	3	4	5	MEAN	ST. DEV.
COLEOPTERA	0		2	3		1	1.41
DIPTERA	86	196	169	122	79	130.4	51.18
Ceratopogonidae	11	7	23	14	7	12.4	6.62
<i>Bezzia</i>	11	6	17	14	7	11	4.64
Chironomidae	75	189	146	108	72	118	49.72
Chironominae/Orthoclaadiinae	46	146	102	76	55	85	40.35
Tanypodinae	29	43	44	32	17	33	11.11
Tabanidae: <i>Chrysops</i>						0	0.00
EPHEMEROPTERA	3	3	8	6	6	5.2	2.17
<i>Caenis</i>	2	3	7	6	6	4.8	2.17
MEGALOPTERA: <i>Sialis</i>						0	0.00
ODONATA	4	5	2	2	0	2.6	1.95
Anisoptera	3	5	2	2		2.4	1.82
Zygoptera	1					0.2	0.45
TRICHOPTERA	12	9	5	5	3	6.8	3.63
<i>Neureclipsis</i>			1	1		0.4	0.55
<i>Oecetis</i>	8	8	1	3	2	4.4	3.36
<i>Oxyethira</i>	1	1	3	1	1	1.4	0.89
PELECYPODA: <i>Musculum</i>	5	8	3	1	1	3.6	2.97
TOTALS	110	221	189	139	89	149.6	54.78

NOTES: The five samples taken for the June control area are listed above. Each entry represents the number of animals of that taxon collected with the Ekman dredge. For example, in sample #2 above, 196 Diptera were collected, 7 of which were ceratopogonids (6 of these were *Bezzia* spp.), and 189 of which were midges (including 146 Chironominae/Orthoclaadiinae and 43 Tanypodinae). Total number of animals for samples 1-5 is listed at the bottom of those columns. Mean and standard deviation values for Table 2 samples are given for each taxonomic group. Chironominae and Orthoclaadiinae are presented as one group.

Table 3: July Experimental Samples

GROUP	1	2	3	4	5	6	7	MEAN	ST. DEV.
COLEOPTERA								0.0	0.00
DIPTERA	114	77	158	87	102	239	111	126.9	68.29
Ceratopogonidae	14	3	4	7	14	15	19	10.9	7.53
<i>Bezzia</i>	14	3	4	7	12	13	19	10.3	7.13
Chironomidae	100	74	154	78	88	223	91	115.4	66.64
Chironominae	51	51	113	55	50	160	68	78.3	52.01
Tanypodinae	32	21	19	13	24	48	12	24.1	15.32
Orthoclaadiinae	17	2	22	10	14	15	11	13.0	7.68
Tabanidae: <i>Chrysops</i>				2		1		0.4	0.96
EPHEMEROPTERA					2			0.3	0.93
<i>Caenis</i>					1			0.1	0.46
MEGALOPTERA: <i>Sialis</i>	1	1	1	1	6	2		1.7	2.42
ODONATA	2	9	7	2	5	4	6	5.0	3.16
Anisoptera (large)	2		3		3	2	2	1.7	1.54
Anisoptera (1st instar)		8	4	2	2	2	3	3.0	3.08
Zygoptera		1					1	0.3	0.60
TRICHOPTERA	7	8	9	1	20	12	3	8.6	7.64
<i>Neureclipsis</i>	1	1	7		5	5		2.7	3.52
<i>Oecetis</i>			1			2		0.4	0.96
<i>Oxyethira</i>	6	5		1	15	4	3	4.9	6.06
PELECYPODA: <i>Musc.</i>	2	2	9	6	2	2	3	3.7	3.37
TOTALS	126	97	184	97	137	259	123	146.1	70.75

NOTES: The seven samples taken for the July experimental are listed above. Each entry represents the number of animals of that taxon collected with the Ekman dredge. For example, in sample #2 above, 77 Diptera were collected, 3 of which were ceratopogonids (all *Bezzia* spp.), and 74 of which were midges (including 51 Chironominae, 21 Tanypodinae, and 2 Orthoclaadiinae). Total number of animals for samples 1-7 are listed at the bottom of those columns. Mean and standard deviation values for Table 3 samples are given for each taxonomic group. "*Musc.*" is the genus of fingernail clams, *Musculum*.

Table 4: July Control Samples

GROUP	1	2	3	4	5	6	7	MEAN	ST. DEV.
COLEOPTERA		2				1		0.4	0.96
DIPTERA	162	86	175	108	114	154	152	135.9	40.45
Ceratopogonidae	15	5	15	4	5	9	6	8.4	5.82
<i>Bezzia</i>	15	5	15	3	5	9	6	8.3	6.03
Chironomidae	147	81	160	104	109	141	146	126.9	35.41
Chironominae	94	29	90	35	70	93	50	65.9	34.24
Tanypodinae	22	9	45	20	26	16	30	24.0	14.05
Orthoclaadiinae	31	43	25	49	13	32	66	37.0	21.22
Tabanidae: <i>Chrysops</i>						3		0.4	1.39
EPHEMEROPTERA					9	1	1	1.6	4.05
<i>Caenis</i>					1	1	1	0.4	0.65
MEGALOPTERA: <i>Sialis</i>								0.0	0.00
ODONATA	27	2	8	0	10	12	1	8.6	11.49
Anisoptera (large)	8	1	1			1		1.6	3.53
Anisoptera (1st instar)	18	1	7		10	11	1	6.9	8.17
Zygoptera	1							0.1	0.46
TRICHOPTERA	19	16	21	12	2	6	8	12.0	8.63
<i>Neureclipsis</i>	9	8	13	3	1	4	3	5.9	5.22
<i>Oecetis</i>	4	4	2					1.4	2.33
<i>Oxyethira</i>	6	4	6	8	1	1	5	4.4	3.23
PELECYPODA: <i>Musc.</i>	11	5	15	2	7	6	3	7.0	5.61
TOTALS	219	111	219	122	142	180	165	165.4	53.27

NOTES: The seven samples taken for the July control area are listed above. Each entry represents the number of animals of that taxon collected with the Ekman dredge. For example, in sample #1 above, 162 Diptera were collected, 15 of which were ceratopogonids (all *Bezzia* spp.), and 147 of which were midges (including 94 Chironominae, 22 Tanypodinae, and 31 Orthoclaadiinae). Total number of animals for samples 1-7 is listed at the bottom of those columns. Mean and standard deviation values for Table 4 samples are given for each taxonomic group. "*Musc.*" is the genus of fingernail clams, *Musculum*.

Table 5: Summary of Means and Standard Deviations from Tables 1-4

GROUP	1:MEANS	1:ST.DEV	2:MEANS	2:ST.DEV	3:MEANS	3:ST.DEV	4:MEANS	4:ST.DEV
COLEOPTERA	0.2	0.45	1	1.41	0	0	0.4	0.96
DIPTERA	112.6	71.82	130.4	51.18	126.9	68.29	135.9	40.45
Ceratopogonidae	8	1.22	12.4	6.62	10.9	7.53	8.4	5.82
<i>Bezzia</i>	7.2	1.3	11	4.64	10.3	7.13	8.3	6.03
Chironomidae	104	71.3	118	49.72	115.4	66.64	126.9	35.41
Chironominae	75	49	85	40.35	78.3	52.01	65.9	34.24
Tanypodinae	29.6	22.63	33	11.11	24.1	15.32	24	14.05
Orthoclaadiinae	-----	-----	-----	-----	13	7.68	37	21.22
Tabanidae: <i>Chrysops</i>	0.6	0.55	0	0	0.4	0.96	0.4	1.39
EPHEMEROPTERA	4.6	3.29	5.2	2.17	0.3	0.93	1.6	4.05
<i>Caenis</i>	4.4	3.44	4.8	2.17	0.1	0.46	0.4	0.65
MEGALOPTERA: <i>Sialis</i>	0	0	0	0	1.7	2.42	0	0
ODONATA	2.8	2.59	2.6	1.95	5	3.16	8.6	11.49
Anisoptera (large)	2.8	2.59	2.4	1.82	1.7	1.54	1.6	3.53
Anisoptera (1st instar)	-----	-----	-----	-----	3	3.08	6.9	8.17
Zygoptera	0	0	0.2	0.45	0.3	0.6	0.1	0.46
TRICHOPTERA	7.2	2.17	6.8	3.63	8.6	7.64	12	8.63
<i>Neureclipsis</i>	0	0	0.4	0.55	2.7	3.52	5.9	5.22
<i>Oecetis</i>	6.4	2.07	4.4	3.36	0.4	0.96	1.4	2.33
<i>Oxyethira</i>	0.8	0.84	1.4	0.89	4.9	6.06	4.4	3.23
PELECYPODA: <i>Musc.</i>	5.6	5.32	3.6	2.97	3.7	3.37	7	5.61
TOTALS	133	79.97	149.6	54.78	146.1	70.75	165.4	53.27

NOTES: The mean and standard deviation values from Tables 1-4 are listed above. For example, "1:MEANS" represents all of the mean values from Table 1. "*Musc.*" is the genus of fingernail clams, *Musculum*.

Table 6: Fish Stomach/Intestine Contents

Date Caught	Fish Species	Fish Size(cm)	Contents										Notes		
			Coleoptera	Ceratopoda	Bezzia	Chironomidae	Caenis	Odonata	Trichoptera	Oxyethira	Oecetis	Musculum	Insecta fish	zooplankton	
14 Jul	RB	17.0	R												>2 drams volume; little id'able
11 Jul	RB	18.5				R		R	R						also crayfish, snail
13 Jul	YP	4.0				R							A		four 1cm fish
11 Jul	YP	7.0		A		A								R	
13 Jul	YP	7.0				A									17 midges
11 Jul	YP	7.5				C					R				also mayfly
25 Jun	YP	10.0							R						
13 Jul	YP	13.5											R		others unid'able
14 Jul	YP	17.0						R							
12 Jul	LMB	4.0				R								C	
14 Jul	LMB	4.0				R								R	
25 Jun	LMB	20.5				R						R		R	
13 Jul	LMB	29.0											R		16 cm fish
12 Jul	LMB	30.0													full but unid'able
25 Jun	BG	5.5												A	
25 Jun	BG	6.0				R						R		A	
25 Jun	BG	6.5				R			R		R				
11 Jul	BG	6.5				A			R						
12 Jul	BG	10.0			A	C			R	A		A			
11 Jul	BG	11.0	R	A		R		R		A	R				
13 Jul	BG	11.0	R		R	A		C	C	A					18 <i>Oxyethira</i>
14 Jul	BG	18.0	R		R	A		R	R		A				1/3 subsample
11 Jul	BG	19.5					R	R	A						

NOTES: RB= rock bass, YP= yellow perch, LMB= largemouth bass, BG= bluegill. R= Rare (1-2 animals), C= Common (3-4 animals), A= Abundant (>4 animals). Contents are listed only under the lowest taxon to which they were identifiable. Other fish species were not included in stomach/intestine survey. Some of larger fish seemed better able to digest their food than smaller fish. These contents were an unidentifiable ("unid'able") black mass. No fish was found to have both stomach and intestine empty. Some of the fish had only their stomachs examined. All insects listed are larval except Coleoptera, all of which are adult.

Table 7: Direct Observation of Fish Activity

<u>Replicate #</u>	<u>Fish Observed</u>
Experimental 1	none
Experimental 2	none
Experimental 3	none
Control 1	121 YP, 34 BG
Control 2	40 YP, 34 BG
Control 3	1 LMB, 23 BG

NOTES: YP= yellow perch, BG= bluegill, LMB= largemouth bass. Young-of-the-year were not counted in these observations. Each replicate involved 15 minutes of direct observation from a boat. The numbers and species of fish which crossed over a 1 m<sup>2</sup> quadrat placed on the lake bottom, in the respective area, are listed above.

Table 8: Minnow Trap Captures

<u>11 July</u>	<u>Experiment</u>	<u>Control</u>
Trap #1	none	3 YP
# 2	none	1 YP, 1 BG
# 3	none	2 BG
<u>12 July</u>		
# 1	1 LMB fingerling	none
# 2	none	2 YP
# 3	none	none
<u>13 July</u>		
# 1	none	4 YP
# 2	none	2 YP
# 3	none	3 YP
<u>14 July</u>		
# 1	1 LMB fingerling	3 YP
# 2	none	3 YP
# 3	none	3 YP, 1 BG

NOTES: YP= yellow perch, BG= bluegill, LMB= largemouth bass. LMB fingerlings were those fish from the school of largemouth bass found to be living in the experimental area. Only relatively small fish were small enough to fit into the traps, which had inlets about 5 cm wide.