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Predator-Prey Interaction between Largemouth Bass and Bluegills as Influenced by Simulated, Submersed Vegetation

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Abstract

Data from the literature suggest that predatory success declines as habitat complexity increases. To explain this phenomenon, we studied the predator-prey interaction between largemouth bass *Micropterus salmoides* and bluegills *Lepomis macrochirus* in four laboratory pools (2.4-3.0 m diameter, 0.7 m deep), each with a different density (0, 50, 250, 1,000 stems/m²) of artificial plant stems. Behavior was quantified for both predator and prey during largemouth bass feeding bouts lasting 60 minutes. Predation success (number of captures) by largemouth bass was similar at 0 and 50 stems/m², then declined to near zero at 250 and 1,000 stems/m². As stem density increased, predator activity declined due to a decrease in behaviors associated with visual contact with prey. Reduced predation success by largemouth bass in habitats of increased complexity apparently is related to increases in visual barriers provided by plant stems as well as to adaptive changes in bluegill behavior.

Littoral zones, with their associated vegetation, are important areas of fish production in north temperate aquatic communities. In particular, these areas provide habitat for many fishes, including members of the sunfish family, Centrarchidae (DiCostanzo 1957; Hall and Werner 1977; Werner et al. 1977; Keast 1977, 1978; Laughlin and Werner 1980).

Juvenile sunfishes might live in vegetation for at least two reasons: availability of forage or avoidance of predators. Based on relative habitat profitabilities measured in a natural lake and optimal-foraging considerations, Mittelbach (1981) predicted that all sizes of bluegills *Le-*

pomis macrochirus should move out of the vegetated littoral zone into open water and feed on *Daphnia* during much of the summer. Because bluegills smaller than 100 mm total length do not move offshore as predicted, Mittelbach (1981) suggested that fish of this size remain in the vegetation to avoid predation by largemouth bass *Micropterus salmoides*. This is a reasonable hypothesis because a variety of studies suggest that prey vulnerability decreases as environmental complexity increases (Huffaker 1958; Glass 1971; Stein and Magnuson 1976; Saiki and Tash 1979). However, no one has demonstrated explicitly that vegetation reduces vulnerability of bluegills. To test this assumption, we completed a series of experiments that quantified the relationship between predation mortality and vegetation density, using largemouth bass as predators and bluegills as prey.

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If vulnerability of bluegills declines with increasing structural complexity, selection of this habitat by bluegills, even in the face of poor foraging return, could be explained on the basis of higher survival in vegetation than in open water.

A variety of mechanisms might be involved in reducing prey vulnerability in complex habitats. For example, vulnerability could be reduced in vegetation simply because random visual encounters between predator and prey are reduced (Cooper and Crowder 1979). Alternatively, behavioral responses of the prey to the predator could alter the probability of prey detection and capture. And certainly, predator behavior could be modified by vegetation. To distinguish among these competing hypotheses in our experiments, we quantified the behavioral interactions between largemouth bass and bluegills with increasing stem density. If the random model explains our results, then these data could be generalized to many predator-prey interactions in the vegetation. However, if prey vulnerability is strongly influenced by behavioral interactions, then our results may be specific to this particular predator-prey system.

Methods

We conducted 1-hour observational experiments in a shaded outdoor area during two summers. Four circular, plastic pools (3 m diameter, 0.7 m deep) with dark inside walls were used the first year, whereas circular, steel pools (2.4 m diameter, 0.7 m deep) with white inside walls, which facilitated viewing of fish, were used during the second year. Water temperatures ranged from 16 to 24 C during the study, but fluctuated only 2 C during any 24-hour period. Between experiments, water was circulated through a sand-floss filter to improve water clarity and maintain dissolved oxygen concentrations at about 7 mg/liter. Algal blooms were controlled by an algicide (containing monuron, simazine, and atrazine) applied twice per summer.

Lengths of yellow polypropylene rope (4 mm diameter, 0.5 m long) simulated natural plant stems. Periphyton covered these rope strands after a few weeks, causing them to resemble aquatic macrophytes. Rope ends were fastened, in a uniform distribution, to wire mesh that was covered with sand on the pool bottom; free ends floated to the water surface. Attached strands

remained flexible, allowing largemouth bass freedom of movement through the pool. Each pool contained a different density of these rope strands (0, 50, 250, 1,000 stems/m²), hereafter referred to as zero, low, medium, and high stem density. Inter-stem distances were about 14, 6, and 3 cm for low, medium, and high stem density, respectively. These densities were chosen to reflect the range of macrophyte densities found in natural communities (Ozimek et al. 1976; Sheldon and Boylen 1977; Crowder and Cooper 1979). To permit observers to estimate distances in the pools, we laid colored stones 0.3 m apart on the sand bottom. Experiments were run only in the morning to eliminate time-of-day effects.

Largemouth bass used in our experiments were collected from Ross Lake, Ross County, Ohio, and ranged from 33 to 37 cm total length. In all, five largemouth bass were used, one individual per experiment. Bluegills used ranged from 35 to 44 mm total length and were obtained from local ponds and Hebron National Fish Hatchery, Ohio. Bluegills of this size commonly are found within the littoral vegetation of natural lakes (Hall and Werner 1977; Mittelbach 1981), and thus should be most affected by changes in stem density.

Largemouth bass and bluegill behavior categories were determined from preliminary observations. Largemouth bass behaviors were separated into six mutually exclusive categories:

- Search: moving, but not orienting to the prey.
- Follow: moving, and orienting to particular prey.
- Pursue: following at burst speed.
- Attack: striking at prey.
- Capture: ingesting prey.
- Inactive: resting and motionless.

Bluegill behavior and position in experimental pools was categorized as follows:

Behavior

- Schooled: individuals aggregated and moving about as a unit.
- Dispersed: individuals not associating strongly with one another.

Position

- Top edge: upper 0.25 m of the water column and within 0.3 m of the pool side.

Bottom edge: lower 0.25 m of the water column and within 0.3 m of the pool side.

Top center: upper 0.25 m of the water column and beyond 0.3 m from the pool side.

Bottom center: lower 0.25 m of the water column and beyond 0.3 m from the pool side.

Experiments generally consisted of observing feeding behavior of largemouth bass and anti-predator behavior of bluegills in the four stem densities. In each experiment, one largemouth bass was combined with 35 prey. Before any experiment, largemouth bass were acclimated to the experimental pool for 2 to 7 days. Individuals were considered acclimated when they fed regularly in the presence of an observer. Largemouth bass were starved for 24 hours before each experiment. Immediately before testing, bluegills (previously untested) were added and isolated from the predator by a small wire-mesh cage (1 m diameter) for 5 minutes. When the cage was removed, experiments began and continued for 60 minutes. At the end of 60 minutes, largemouth bass either were satiated or had quit trying to capture prey. Observations were made from 2-m-high ladders placed next to the pools. The first year, only predator behavior was recorded; the next year, a second observer documented antipredator behavior of bluegills. Largemouth bass behaviors were coded directly into a Datamyte 900 (Electro/General Corporation, Minnetonka, Minnesota). An entry was made each time the largemouth bass exhibited a change in behavior. The Datamyte records time of each entry, thereby providing a record of time spent in each behavior and number of occurrences during each experiment. Bluegill behavior was recorded on coded data sheets at 5-minute intervals, providing instantaneous observations of their behavior twelve times during each experiment. At each observation, we recorded the percentage of bluegills either schooled or dispersed and in each of the four locations. At the same time, distances between the largemouth bass and the bluegill closest to it were recorded. Behavior, location, and initial distance from the predator were recorded for bluegills attacked during experiments. From these data, we compared behavior of bluegills attacked with those not attacked. After an experiment, largemouth bass were permitted continued access to the remaining bluegills for 24 hours; after 24 hours, blue-

gills were removed and counted. Modifications in bluegill behavior across stem density could be influenced either by the presence of the largemouth bass predator or stem density itself. To distinguish between these two effects, we also quantified the behavior of bluegills without a predator at all stem densities.

Analysis of largemouth bass and bluegill behaviors differed because of the different types of data collected for each fish: that is, continuous versus instantaneous observations. We analyzed predator data on the basis of number of occurrences and time spent in each activity and bluegill data on the basis of the percent of individuals participating in each behavior at each observation. Walsh averages were used to calculate medians and 95% confidence intervals for behaviors and positions (Hollander and Wolfe 1973).

To provide for replication we tested at least two different largemouth bass a total of seven times at each stem density. For bluegills, each treatment was replicated at least five times with a predator and two times without a predator. About 60% of the replicates for the largemouth bass were run in the first year; all replicates of the low-density treatment were run in the second year. Results obtained in the 2 years were not significantly different ($P > 0.05$) nor were the three major behaviors among individual largemouth bass (two-way layout):

Behavior	Years (P)	Individuals (P)
Captures (number)	0.11	0.26
Activity (minutes)	0.28	0.82
Visual contact (minutes)	0.15	0.38

Because some fish were used in experiments more often than others, we tested each individual against the others (combined as a group) to determine if any one of them might bias our results. In these comparisons, no individuals tested were different from the group ($P > 0.05$, two-way layout). Furthermore, we added data from preliminary experiments (in which we recorded behaviors in a slightly different fashion) to the group of final experiments and again compared behavior of single fish with that of the group. As before, the behavior of single fish did not differ from that of the group ($P > 0.05$, two-way layout). Thus, data from both years for individual largemouth bass were lumped for presentation and analysis.

To relate our findings to a more natural sit-

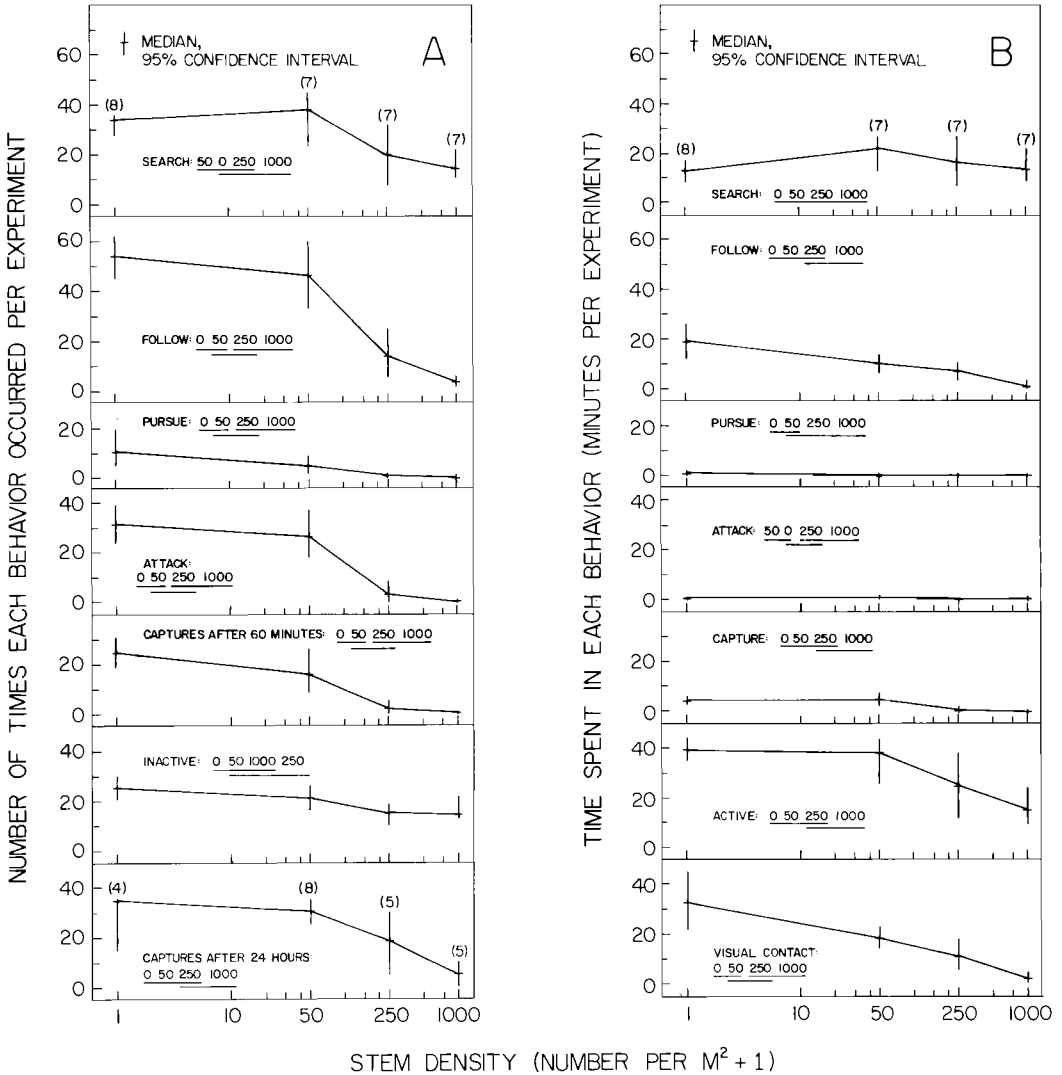


FIGURE 1.—(A) Number of times each of several largemouth bass behaviors occurred with increasing stem density during an experiment. (B) Time spent in each behavior by largemouth bass with increasing stem density during an experiment. Visual contact was the sum of time the predator spent motionless while observing bluegills, and following, pursuing, attacking, and capturing bluegills. Medians not significantly different from each other are underlined (Kruskal–Wallis test, $P > 0.05$). Sample sizes (in parentheses) for each treatment for all behaviors are given in the top panel, except where indicated differently.

uation, we compared the amount of cover provided by polypropylene line with that provided by a natural aquatic macrophyte *Potamogeton natans*, by quantifying the percent cover provided by each at the same stem density. Percent cover was defined as the percent vertical area of the water column occupied by vegetation (artificial or natural). If refuge for prey is re-

lated to the amount of visual isolation between predator and prey, percent cover should provide some measure of protection available to prey at any given stem density. To measure percent cover, we photographed from the side a 0.5-m strip (extending 12.5 cm into an aquarium) of each stem type (artificial or natural) at the three experimental densities. Photographs

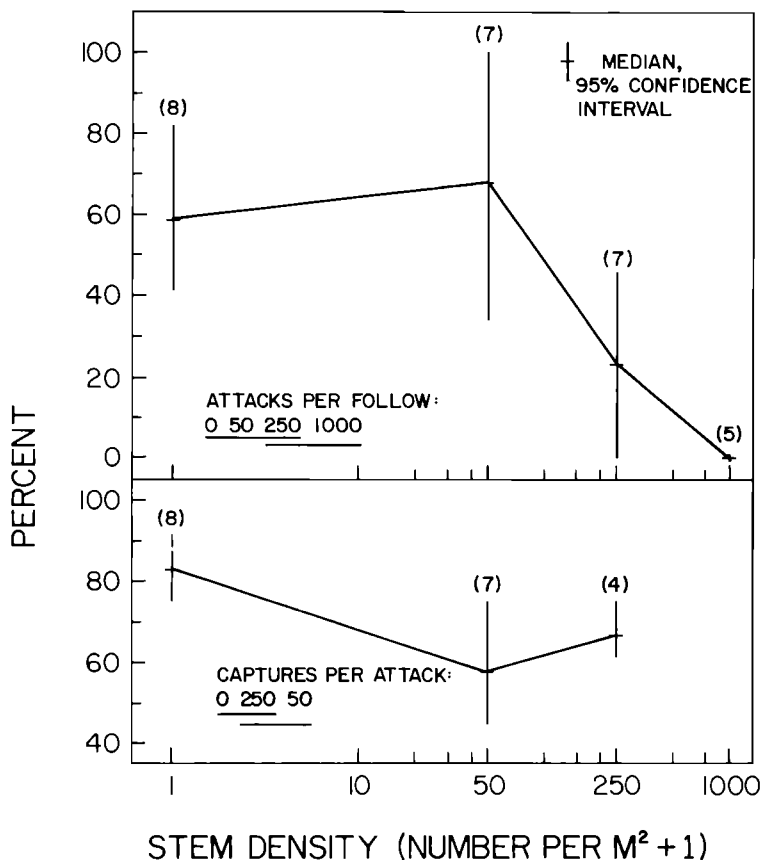


FIGURE 2.—Percent of attacks on bluegills per follow and percent of captures per attack in an experiment with largemouth bass under conditions of increasing stem density. Number of experiments per treatment is indicated in parentheses. Medians not significantly different (Kruskal-Wallis test, $P > 0.05$) from each other are underlined. No attacks were observed at high stem density.

then were digitized (Hewlett-Packard Digitizer, Model 9874) and percent cover was calculated for each stem density.

Results

Changes in stem density modified the predatory tactics of largemouth bass. Predator behavior, as measured by number of occurrences or time spent, did not change from zero to low density, nor did it change from medium to high (Fig. 1). However, nearly all predatory behaviors declined significantly as stem density increased from zero to medium or from low to high, suggesting that these behavioral patterns were modified between densities of 50 and 250 stems/m².

Participation by largemouth bass in predatory behaviors, as measured by number of oc-

currences of the behaviors, declined as stem density increased (Fig. 1A). As these behaviors decreased, so did the number of bluegills captured by largemouth bass, during both 1-hour and 24-hour feeding bouts. Consistent with the results of Glass (1971), increasing stem density reduced the predatory ability of largemouth bass.

Time spent in each predator behavior did not reflect the number of its occurrences. Search time remained constant whereas follow time decreased as stem density increased (Fig. 1B). When active, largemouth bass spent most of their time searching and following. Pursuing, attacking, and capturing contributed little to total feeding times at zero and low stem density. As these behaviors declined and approached zero at medium and high stem density, signif-

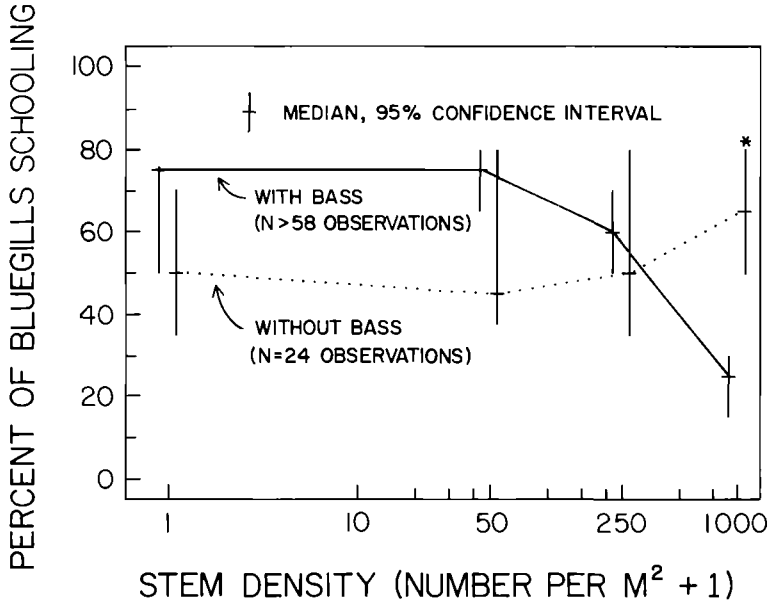


FIGURE 3.—Percent schooling of bluegills with and without a largemouth bass present, in relation to stem density. Significant differences (Kruskal-Wallis test, $P \leq 0.05$) between the percentages of schooling with and without largemouth bass within a treatment are designated by an asterisk (*).

icant differences occurred between zero-low and medium-high stem densities. Because swimming speed and metabolic rate are exponentially related (Glass 1971), the contribution of pursuit, attack, and capture (behaviors that involve fast swimming) to costs of predation may be substantial, even though these behaviors make up a small portion of the time budget. Time spent active by largemouth bass decreased with increasing stem densities; predators did not appear to compensate for reduced captures by increased searching or following.

Largemouth bass could not capture bluegills at high stem density because they could not find or follow them through the artificial vegetation. Visual contact between predator and prey declined precipitously with increasing stem density (Fig. 1B). Both the total number of follows (Fig. 1A) and the percent of follows leading to an attack (Fig. 2) decreased with increased stem density, thereby decreasing the possible number of attacks. However, the percent of captures resulting from an attack did not change with stem density (Fig. 2), a result supported by the work of Glass (1971). Thus, the ability of a largemouth bass to follow and attack was instrumental in determining capture success. Once

begun, attacks led to captures about 70% of the time in a total of 476 attacks. Even given this result, more attacks were required per capture at low than at zero density. Number of captures were similar between these two densities; however, energy required per capture was probably higher at low than at zero stem density.

Bluegill behavior was modified by both stem density and the presence of largemouth bass. Generally, bluegill behavior was less variable when largemouth bass were present. At each stem density except the highest, the percent of fish schooling was similar, whether a predator was present or not (Table 1; Fig. 3). At high density, predator presence significantly reduced the percent of bluegills schooling. Of the bluegills attacked by largemouth bass at zero, low, and medium stem densities, few were schooling (mean = 6.0%; Clopper-Pearson 95% confidence interval = $\pm 2.7\%$; $N = 302$; Hollander and Wolfe 1973). The ratio of attacks on schooled to dispersed bluegills was similar across these three treatments (binomial test: $P \geq 0.14$; $N = 302$; Hollander and Wolfe 1973). Thus, because so few schools were attacked, schooling was advantageous at these densities. Yet, at high stem density, no bluegills were at-

TABLE 1.—Null probabilities^a of changes in behavior and distribution of bluegills across stem densities with and without co-occurring largemouth bass. Plus and minus signs in parentheses indicate whether a behavior of bluegill was enhanced (+) or depressed (-) as stem density increased. Probabilities are from distribution-free multiple comparisons based on Kruskal-Wallis rank sums (Hollander and Wolfe 1973). Within-treatment comparisons can be found on the figures referenced.

Bluegill behavior or distribution	Figure reference	Plant densities (stems per m ²)					
		0 versus 50	0 versus 250	0 versus 1,000	50 versus 250	50 versus 1,000	250 versus 1,000
Schooling (%)	3						
With bass		— ^b	—	*** (-)	—	*** (-)	*** (-)
Without bass		—	—	—	—	—	—
Top edge (%)	4						
With bass		*** (-)	*** (+)	0.06 (-)	—	0.34 (+)	** (+)
Without bass		0.22 (+)	—	—	0.15 (-)	** (-)	—
Bottom edge (%)	4						
With bass		*** (+)	*** (+)	0.10 (-)	—	*** (-)	*** (-)
Without bass		—	—	0.36 (+)	—	* (+)	—
Top center (%)	4						
With bass		—	—	*** (+)	—	*** (+)	*** (+)
Without bass		—	—	—	—	—	—
Bottom center (%)	4						
With bass		—	** (+)	*** (+)	*** (+)	*** (+)	*** (+)
Without bass		—	—	0.22 (-)	—	—	—
Distance to bass (m)	5						
Closest schooled		* (+)	0.39 (+)	** (+)	—	—	0.48 (+)
School attacked		* (+)	—	^c	—	^c	^c
Closest dispersed		—	—	0.07 (-)	—	*** (-)	*** (-)
Dispersed attacked		0.49 (+)	0.39 (+)	^c	—	^c	^c

^a $P \leq * 0.05$; ** 0.01; *** 0.001.

^b All dashes designate $P \geq 0.5$.

^c No attacks on bluegills by largemouth bass occurred at high stem density.

tacked and only schooling bluegills were followed. Apparently, bluegills reduced their susceptibility to the predator by dispersing among the stems at high density and schooling at low densities.

Bluegill distribution was also modified by stem density and predators. In the absence of predators, bluegills moved throughout the pool, although they showed some affinity for edges (Fig. 4). When a largemouth bass was present, bluegills stayed near pool edges (especially bottom edges), except at high density when they dispersed throughout the pool. Largemouth bass responded to this distribution by exclusively attacking individuals at the edge in the three lowest stem densities; only 1% of all attacks ($N = 302$) were on bluegills in the center. Center attacks excluded, largemouth bass did not differentially attack bluegills at the top or bottom edge (binomial test; $P \geq 0.12$; $N = 129$) except at low density, in which largemouth bass showed a

slight preference for attacking bluegills at the top edge (binomial test; $P = 0.05$; mean = 57%; $N = 169$). Given that so few bluegills were found at the top edge (Fig. 4) and about 50% of the predator attacks occurred there, the probability that an individual at the surface would be eaten was high. Thus, bluegills reduced their vulnerability to a predator by congregating near bottom edges in all pools. Typically, bluegills stayed in areas of discontinuity, either air-water or sediment-water interfaces, at the pool edge. In this way, bluegills were protected from two attack directions: dorsally and laterally or ventrally and laterally. Bluegills moved only to center pool when stem density was high enough (1,000 stems/m²) to provide protection from predation.

Occurrence of an attack depended on distances between largemouth bass and bluegills. Largemouth bass generally attacked bluegills within about 0.5 m from the predator; bluegills

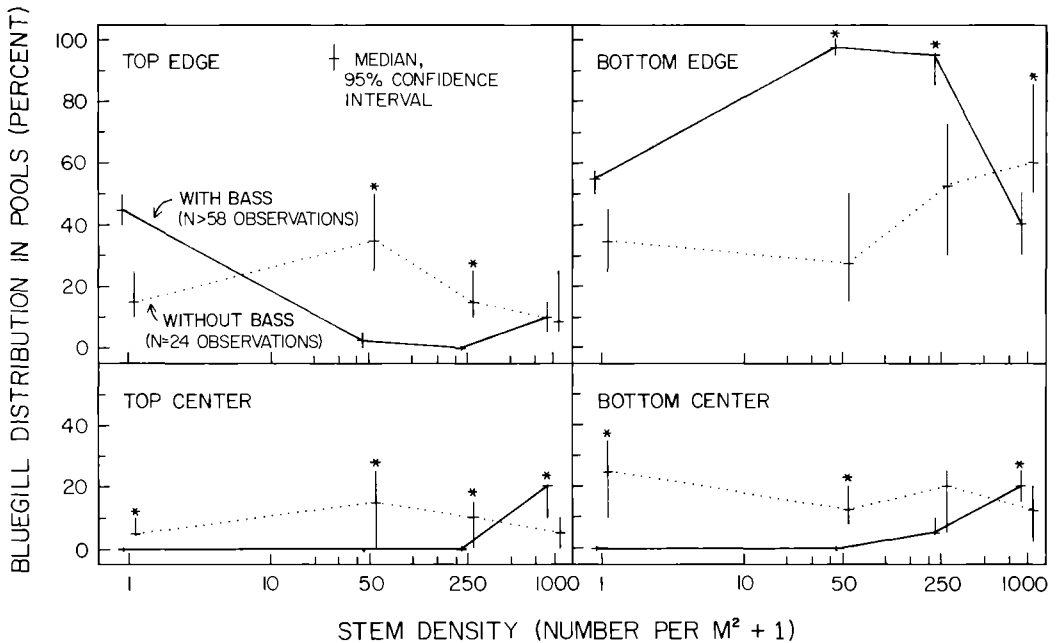


FIGURE 4.—Distribution of bluegills within a pool with increasing stem densities, with and without a largemouth bass present. Significant differences (Kruskal-Wallis test, $P \leq 0.05$) between bluegill distributions with and without a predator in each location within a treatment are designated by an asterisk (*).

were most commonly farther than 0.5 m from the predator (Fig. 5). Generally, schooled bluegills remained farther from largemouth bass than dispersed ones (not attacked; Fig. 5). As stem density increased, schools stayed farther from largemouth bass, whereas individuals were closer. Largemouth bass attacked from about the same distance regardless of stem density or dispersion pattern of bluegills (Fig. 5).

Our comparison of artificial with natural cover showed that *Potamogeton natans* provided more cover than artificial vegetation at similar densities (Fig. 6). From this relationship, we would predict that natural densities of *P. natans* of 130 stems/m² (about 250 artificial stems/m²) or greater would modify predatory behavior of largemouth bass and antipredator behavior of bluegills.

Discussion

Recent work suggests that intermediate structural complexity within a habitat produces optimum conditions for predator growth, because it ensures a long-term supply of prey (Glass 1971; Cooper and Crowder 1979). This prediction depends on a positive relationship

between structural complexity and prey numbers (DiConstanzo 1957; Saiki and Tash 1979) and an inverse relationship between predation rate and structural complexity—assumptions supported by our results and by those of other investigators (Huffaker 1958; Glass 1971; Crowder and Cooper 1979; Saiki and Tash 1979). However, rather than a linear relationship, we found a break in capture rate occurring at a moderately high structural complexity (greater than 15% cover), beyond which largemouth bass predators of greater than 300 mm were severely limited. This limitation was produced by a combination of factors, including the antipredator response of prey and a reduction in visual contact of prey by predators caused by an increasing number of barriers. Largemouth bass also changed their tactics with changes in structural complexity; at low densities they were active searchers whereas at high densities, they became “sit and wait” or ambush predators. These behavioral shifts may operate to minimize energy costs required for prey capture.

Vulnerable prey often seek cover to avoid predation (Stein and Magnuson 1976; Stein 1977; Werner et al. 1977; Saiki and Tash 1979).

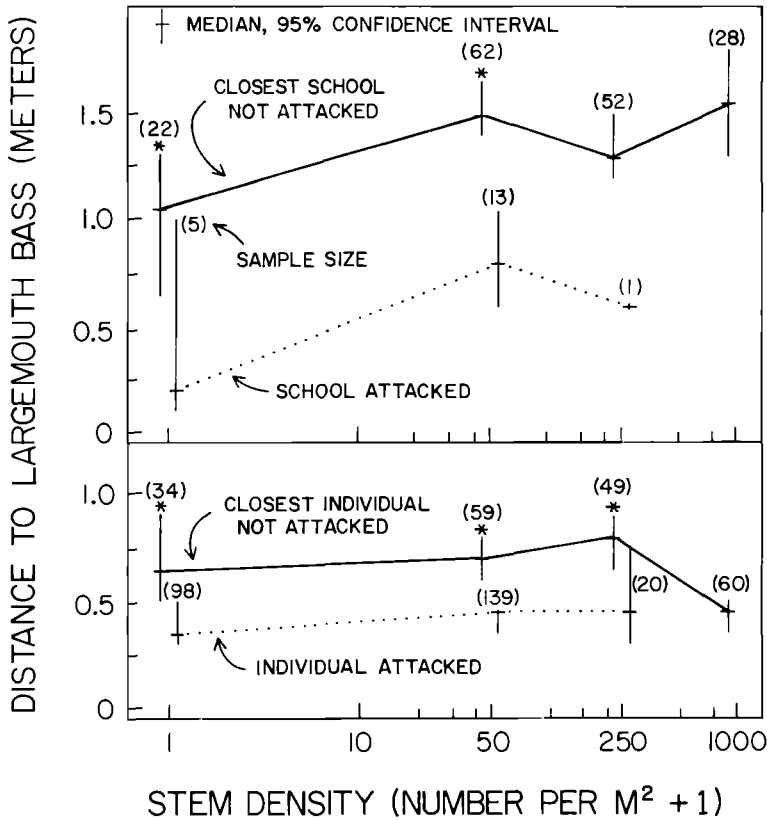


FIGURE 5.—Distances between largemouth bass and bluegills (both schooled and dispersed) with increasing stem density. Bluegills that were attacked are compared with those that were closest to the predator but not attacked. Significant differences (Kruskal-Wallis test, $P \leq 0.05$) between bluegills attacked and not attacked within a treatment are designated by an asterisk (*). The closest schooled bluegill (not attacked) was significantly farther from the largemouth bass ($P \leq 0.05$) than the closest dispersed bluegill (not attacked) in all treatments except for 0 stems/m². Sample sizes indicate the number of times each behavior was observed.

Immobilization or “freezing” (Smythe 1970; Curio 1976) combines with cryptic coloration (Ender 1980) to permit prey to blend in with their background and avoid detection. Although percent cover increased linearly with stem density, it did not afford protection for dispersed bluegills in our experiments until high stem densities were reached (about 40% cover). At high cover densities, bluegills may well be difficult to detect owing to their barred color patterns. These color patterns combine with the antipredator tactic of becoming completely motionless in the presence of a predator to reduce substantially the vulnerability of bluegills, even within striking range of largemouth bass.

At stem densities less than 250 stems/m², bluegills exhibited a different behavioral rep-

ertoire to reduce their susceptibility. Schooling can reduce the probability of capture of a given individual, for as the number of individuals in a group increases, predation success and probability of encounter with a predator decline (Brock and Riffenburgh 1960; Hamilton 1971; Neill and Cullen 1974; Taylor 1976; Major 1978; Shaw 1978). Furthermore, imitation of neighbors in defense movements enables schooling prey to respond to an attack more rapidly than solitary prey (Radakov 1973). As group size increases, it becomes increasingly difficult for a predator to single out and attack an individual (Neill and Cullen 1974; Seghers 1974; Major 1978). In fact, few schooled bluegills in our study were attacked, perhaps owing to the increase in difficulty of capturing schooled

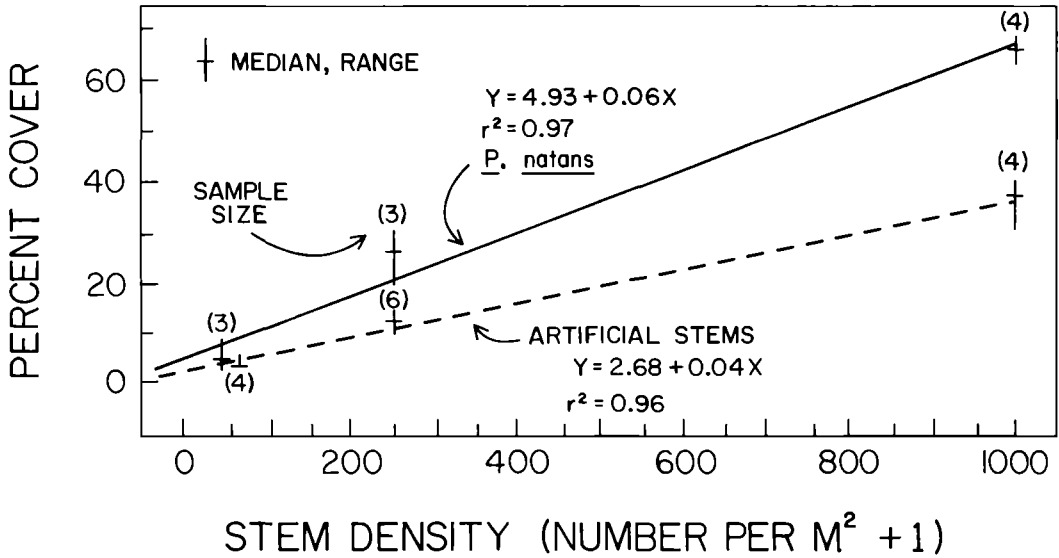


FIGURE 6.—Percent cover provided by different densities of *Potamogeton natans* and single strands of polypropylene line (4 mm diameter, 0.5 m long).

over dispersed prey or to the ability of schooled prey to respond and stay farther from largemouth bass than dispersed prey. Increased structural complexity also increased the distance schools could maintain from largemouth bass. However, bluegills eventually switched their strategy from primarily schooling at low stem densities to dispersing at the highest density, in response to advantages associated with dispersal. At high density dispersed prey could hide effectively; thus fewer advantages accrued to schooling individuals. Indeed, schooling may be disadvantageous at this density as it provided groups large enough for largemouth bass to find and follow.

Optimal foraging theory predicts that strategies will be selected for maximizing net energy intake (providing lowest costs per benefit to a predator: Pyke et al. 1977). Cost often is measured as time spent in active foraging behaviors (Werner 1974). Predator activity may be influenced by the relative costs in searching for, pursuing, and capturing prey (Griffiths 1980). If prey attack and capture is energetically inexpensive, then predators can afford to adopt an active foraging strategy—increasing time spent in search and pursuit. Given that prey attack and capture is energetically costly, then predators should minimize energy expenditures in other activities (such as pursuit) and become

ambush predators. Our results suggest that predators switch strategies as prey vulnerability changes; largemouth bass were far-ranging predators at low stem densities in which prey were highly vulnerable, but ambush predators at high stem densities, when prey vulnerability was low. Thus, we believe that predatory tactics of largemouth bass may be a function of habitat as well as a species-specific characteristic (such as body shape). Clearly, piscivores that typically associate themselves with inshore macrophytes (largemouth bass; northern pike *Esox lucius*) would be ambush predators, whereas open-water species (white crappie *Pomoxis annularis*; white bass *Morone chrysops*) would be active, searching predators. From our perspective, the largemouth bass is probably flexible in its predation strategies. Whether this species is an ambush or an actively searching predator depends on the complexity of the habitat in which it (or its prey) happens to live.

In addition to using different tactics in different stem densities, largemouth bass also reduced costs by attacking only prey with the greatest chance of being captured. Almost always, these prey were dispersed within a rather short striking distance. Once the predator attacked, capture was nearly assured; success rates were high—70–80%—corresponding to the 90% rate measured by Nyberg (1971). The most en-

ergy-costly behaviors are probably pursuit, attack, and capture, and these behaviors were directed at prey within a short distance from largemouth bass. With this strategy, costs per unit of benefit were minimized.

This study demonstrates that vegetation is effective as cover in reducing predation mortality of juvenile bluegills. Therefore, we have at least partly explained the distribution of juvenile centrarchids in natural communities on the basis of predation pressures, which cause prey to move into relatively safe areas of vegetation or areas providing similar amounts of cover. The resultant reduction in vulnerability can be explained by increases in the number of visual barriers (or percent cover), as well as by modifications in prey behavior. The random-encounter model is supported in part by the continual decline in encounter rates as stem density increases. In addition, prey modify their behavior (decreased schooling) in the presence of predators, further reducing their visibility and susceptibility.

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