

Behavioural interactions between fish predators and their prey: effects of plant density

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Abstract. Prey-specific anti-predatory behaviour under different degrees of structural complexity determines foraging success of predators. The behaviour of piscivorous fish (largemouth bass, *Micropterus salmoides*, and northern pike, *Esox lucius*) and their prey (bluegills, *Lepomis macrochirus*, and fathead minnows, *Pimephales promelas*) were quantified in 60-min experiments in laboratory pools (2.4 m in diameter, 0.5 m deep) with artificial vegetation at densities of 0, 50, 250 and 1000 stems/m². Largemouth bass switched predatory tactics from searching to ambushing as plant density increased whereas northern pike always used ambushing. At high plant density, both predators captured minnows, but not bluegills. Bluegills modified their behaviour more than minnows in response to predators, thereby avoiding predation at high plant densities. Structural complexity alone did not always provide refuge for prey; prey must use the structure to avoid predators. Predators may seek vegetated areas if appropriate, vulnerable prey are present.

Structural complexity in aquatic communities mediates the type and intensity of the interactions between predators and their prey (Helfman 1986). When piscivorous largemouth bass, *Micropterus salmoides*, occur with bluegills, *Lepomis macrochirus*, in ponds, the small vulnerable bluegills are relegated to vegetated areas for refuge (Werner et al. 1983). Similarly, crayfish, *Orconectes propinquus*, co-occurring with smallmouth bass, *M. dolomieu*, live in substrates with large interstices that provide protection (Stein 1977). Largemouth bass become less effective as predators on various fish prey species as structural complexity in a variety of forms increases (Glass 1971; Saiki & Tash 1979; Savino & Stein 1982; Anderson 1984). The predatory success of both blennies, *Helcogramma medium*, and bluegills foraging on invertebrates is reduced as habitat complexity increases (Coull & Wells 1983; Gilinsky 1984). Hence, predatory success in aquatic systems decreases as vegetation density increases. Regardless of a possible reduction in capture success, some freshwater predators prefer to occupy vegetated areas within the littoral

zone (Chapman & MacKay 1984; Holland & Huston 1984). Given that predators and prey reside in vegetated areas, we simulated these habitats and quantified behavioural interactions between predators and their prey.

Inasmuch as both body form and plant density influence relative vulnerability (Lewis & Helms 1964; Vinyard 1980) and capture rate (Vinyard 1980; Laur & Ebeling 1983), we explored how increasing plant stem density influences the behaviour of two predators, different in body form, foraging on two distinctly different prey types. We worked with largemouth bass and northern pike, *Esox lucius*, two predators commonly associated with vegetation (Fish & Savitz 1983; Holland & Huston 1984) but characterized by markedly different body forms. Largemouth bass are strong swimmers with a compressed fusiform body and anteriorly placed paired fins that increase manoeuvrability (Keast & Webb 1966). Northern pike, with an elongated, tubular body, are able to move easily through vegetation (Keast & Webb 1966), and to accelerate rapidly, as during pursuit of prey (Webb 1984).

To assess the relative importance of prey type on foraging success, we chose two prey types (bluegills, fathead minnows) that differ in body design and may differ in vulnerability (Moody et al. 1983). Commonly found in ponds and lakes with largemouth bass (Werner et al. 1977), bluegills are

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facultative shoalers (Savino & Stein 1982; Moody et al. 1983) with a gibbose body that facilitates hovering and with spiny rays for defence (Keast & Webb 1966). Also widely distributed in ponds and small lakes, fathead minnows, *Pimephales promelas*, are typically found without predators (Rahel 1984). Fathead minnows have soft-rayed fins and rounded fusiform bodies (Keast & Webb 1966); they are not strong swimmers but rely on shoaling for defence (Sullivan & Atchison 1978). This difference in co-occurrence with predators suggests that bluegills and fathead minnows differ in their ability to avoid predation.

Similarities or differences in foraging response and success between the two predators on the two prey types at different plant densities should provide insight into the generalized response of predators to structural complexity. Specifically, our objectives were to assess the behavioural response of predators to prey type and plant density, and of prey to plant density and predator type. We sought to explain why and how some predators typically live in areas of high structural complexity.

METHODS

To determine how plant density influences foraging success of piscivorous fish and the escape behaviour of their prey, we conducted 163 1-h observational experiments. Polypropylene line (0.5 m long, 4 mm diameter, yellow) simulated a stand of plant stems in four tree-shaded outdoor pools (0.5 m deep, 2.4 m diameter, with white walls). Periphyton grew on the line, causing it to resemble closely natural vegetation. Line sections were fastened to wire mesh, covered with bottom gravel, and extended to the water surface. Stem density in the pools was 0, 50, 250 or 1000 stems/m², herein referred to as zero, low, medium and high plant densities. Temperatures in pools averaged 20°C and varied less than 2°C in 24 h. Submersible pumps circulated and oxygenated (to 7 mg O₂/litre) the water between experiments.

Feeding behaviour and capture success of a predator were monitored continuously during experiments that began after 35 naive prey (acclimated in a 1-m² cage within the pool for 5 min) were released into a pool containing one predator, starved for 24 h. Predator and prey densities were slightly higher in the experimental pools than in most ponds or littoral areas of lakes (Ming 1974;

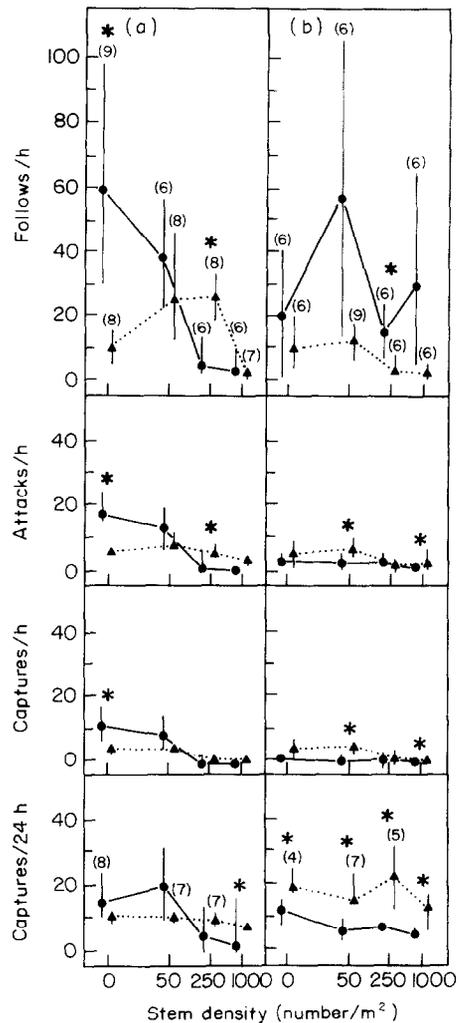


Figure 1. Frequency of occurrence of behaviour of largemouth bass (a) and northern pike (b) during a foraging hour or day with bluegills (—) or fathead minnows (.....), at four plant stem densities. Plant density is displayed in logarithmic scale. Sample sizes as in top panel unless otherwise indicated. Medians and 95% confidence intervals are presented. Differences ($P \leq 0.05$) between prey within a treatment are indicated by an asterisk.

Hackney 1979). Before experiments were started, predators had to be feeding actively in a pool. We observed predators and prey from ladders placed beside the pool and recorded predator behaviour with a Datamate event recorder. Predator behaviour, directed at specific prey fish (as described by Savino & Stein 1982) included: (1) search: moving

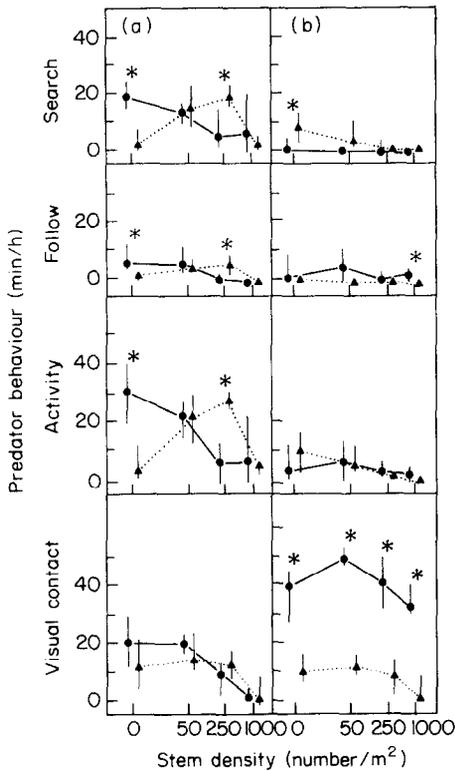


Figure 2. Duration of behaviour of largemouth bass (a) and northern pike (b) during a foraging hour with bluegills (—) or fathead minnows (.....), at four plant stem densities. Details and symbols as in Fig. 1. Sample sizes as in top panel of Fig. 1.

but not orienting to prey; (2) follow: moving and orienting to prey; (3) pursue: following prey at burst speed; (4) attack: striking at prey; (5) capture: engulfing and handling prey; and (6) motionless: no movement; we also noted whether the predator was observing or not observing prey by the orientation and movement of the predator's eyes. The activity of predators and visual contact of predators with prey were based on these behaviours and defined as follows: (1) activity: sum of all active behaviour (search, follow, pursue, attack and capture); and (2) visual contact: sum of all behaviour associated with observing prey (follow, pursue, attack, capture and motionless while observing prey). After a 1-h experiment, predator and prey were left in the pool for 24 h; prey were then removed and counted. This design of short- and long-term observations, which was also used by Sullivan & Atchison (1978) and Savino & Stein (1982), reinforces behavioural

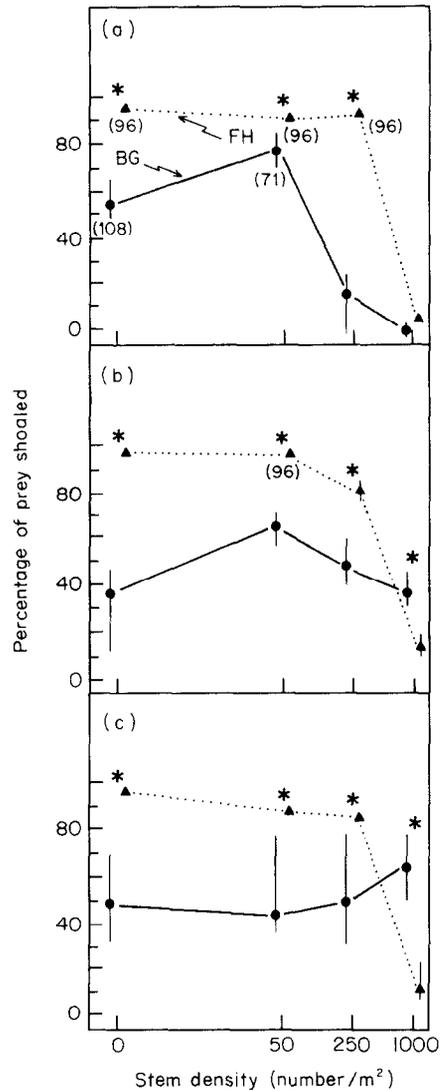


Figure 3. Shoaling behaviour of prey (BG: bluegills; FH: fathead minnows) with (a) largemouth bass, (b) northern pike and (c) no predator, in four plant stem densities. Medians and 95% confidence intervals presented. Sample sizes are 24 observations/treatment without a predator and 72 observations/treatment with a predator unless otherwise indicated. Differences ($P \leq 0.05$) between prey within a given treatment are designated by an asterisk. Bluegills with no predator are taken from Savino & Stein (1982).

observations if hourly feeding trends reflect daily feeding trends.

All combinations of predators and prey were tested across all vegetation densities. We compared experiments with largemouth bass (23–27 cm) and

Table 1. Comparisons between the percentage of shoaled and dispersed bluegills and fathead minnows attacked by largemouth bass and northern pike, for all plant densities combined

Predator/Prey	Attacks (number observed)	% Shoaled†	% Dispersed	± 95% Confidence interval*
Bass/Bluegills	193	31.6	68.4	6.6
Bass/Minnows	190	62.7	36.3	6.8
Pike/Bluegills	41	61.0	39.0	14.9
Pike/Minnows	119	59.7	40.3	8.8

* For both shoaled and dispersed prey. Determined by the Clopper-Pearson method for binomial data (Hollander & Wolfe 1973).

† Medians presented.

northern pike (23–27 cm) across treatments to determine how predator shape influenced foraging efficiency. To determine the effect of prey shape on foraging efficiency and behaviour, we tested bluegills (35–45 mm) and fathead minnows (50–60 mm) with each predator type. These size ranges of prey are those commonly encountered by the predators in lakes (Werner et al. 1977, 1983). We tested at least two fish (of a given predator type) at least six times at each vegetation treatment. At least four individuals (for a given predator type) were tested in each set of experiments among the four vegetation densities. Analysis of variance in each vegetation density for three major behaviours (captures, activity, visual contact) showed one or no behaviours with significant differences ($P \leq 0.05$) among individuals in 14 of 16 comparisons. As no individual consistently differed from others in these behaviours, data were combined for analysis.

Prey behaviour and position (recorded as the percentage of prey at a certain location or showing a certain behaviour at the time of observation) and distance of closest prey to the predator (± 0.1 m) were recorded instantaneously during experiments by a second observer at 5-min intervals during a 1-h experiment. Prey behaviour and positions were as follows: (1) shoaled: aggregations of individuals moving about as a unit (Pitcher 1983); (2) dispersed: individuals not associating strongly with one another; (3) top or bottom: in the upper or lower half of the 0.5-m water column; and (4) edge or centre: within or beyond 0.3 m from the edge of the pool. Behaviour of prey attacked and their distance from the predator at the start of an attack were also recorded. Behaviour of bluegills and

minnows also were quantified in 1-h experiments without a predator.

We determined medians and 95% confidence intervals by Walsh averages, used Kruskal-Wallis test for multiple comparisons, and determined confidence intervals for binomial data by the Clopper-Pearson method (Hollander & Wolfe 1973). Only frequencies of behaviour directly related to the attack sequence (follow, attack and capture) are presented. Because pursuing, attacking and capturing prey generally required less than 10% of the foraging hour, they were not included in the duration analyses. Statements regarding comparisons, such as increased or decreased response rate, refer to significant differences ($P \leq 0.05$).

RESULTS

Behaviour of Largemouth Bass

In general, increasing plant density reduced the foraging success of largemouth bass on bluegills (Fig. 1). The number of follows, an indication of prey sightings, decreased as plant density increased. Decreased follows led to a reduction in attacks and hence fewer captures during 1 and 24 h. As the number of follows decreased, the time spent following bluegills decreased (Fig. 2). Search time also decreased with plant density. Predator activity of the bass, consisting primarily of searching and following, therefore decreased as plant density increased. In addition, visual contact, influenced primarily by changes in following time, decreased as plant density increased.

Capture rates of largemouth bass foraging on fathead minnows did not change as plant density increased even though the frequency of follows and

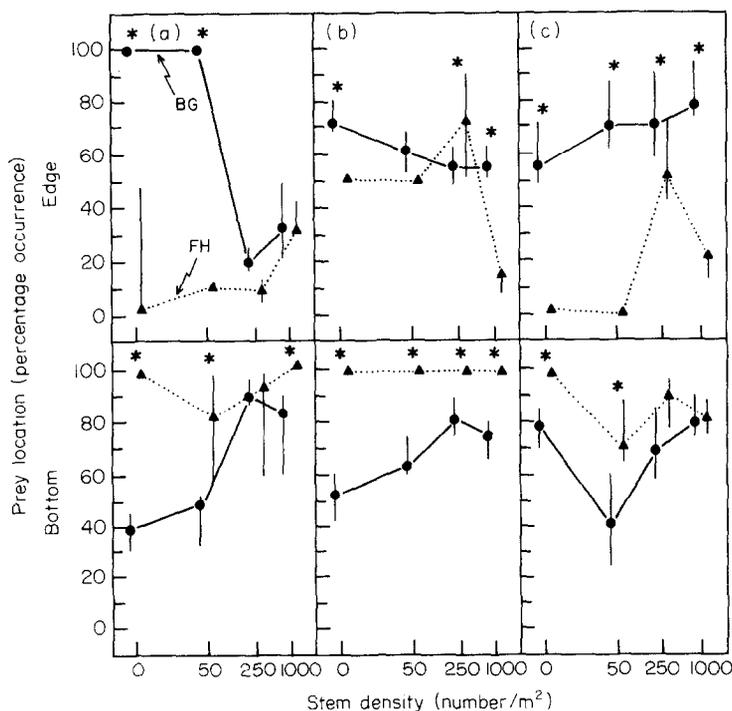


Figure 4. Location of prey with (a) largemouth bass, (b) northern pike and (c) no predator, at four plant stem densities. Details and symbols as in Fig. 3.

attacks did (Fig. 1). Activity, which consisted primarily of searching and following, did change with plant density (Fig. 2). Bass were most active at the medium plant density and relatively inactive at zero and high plant density. Visual contact did not change with plant density; thus, plant density influenced neither visual contact nor capture rate with minnows.

Behaviour of Northern Pike

Capture success of bluegills or minnows by northern pike during 1 h did not change with stem density and changed only slightly with prey type (Fig. 1). However, pike clearly caught more minnows than bluegills during 24 h. Prey vulnerability to pike did not change with the absence or presence of cover, but did change with prey species.

Activity of northern pike changed little with plant density when they foraged on either bluegills or minnows (Fig. 2). Pike attacked and captured more minnows than bluegills per unit of effort (activity) at each plant density. Changes in anti-

predator behaviour between bluegills and minnows may account for this difference in susceptibility.

Visual contact by northern pike differed with prey type, being much greater for bluegills than for minnows at all plant densities (Fig. 2). Pike spent more time motionless (but observing prey) when they were with bluegills than when they were with minnows. For both prey species, visual contact was highest at low plant density and lowest at high plant density. However, in northern pike (in contrast to largemouth bass) high visual contact did not imply high capture rate; visual contact was greatest with bluegills, but capture rate was greatest with minnows at all plant densities.

Behaviour of Bluegills and Fathead Minnows

We now examine the possible influence of different predators on the behavioural response of bluegills and fathead minnows at different plant densities. Bluegill shoaling changed with plant density and with predator presence (Fig. 3). Behaviour of bluegills in the absence of a predator, as

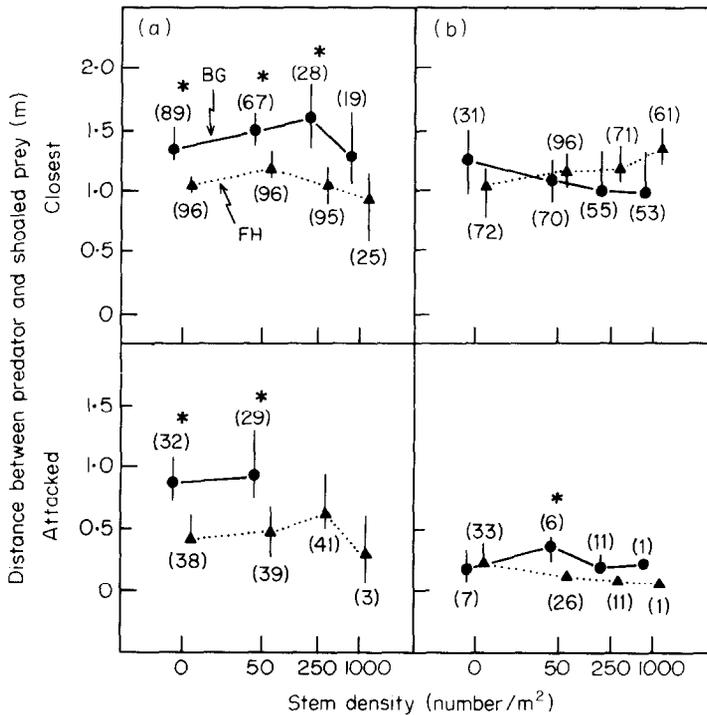


Figure 5. Distance between predator (a: largemouth bass; b: northern pike) and shoaled prey (BG: bluegills; FH: fathead minnows) at four plant stem densities. Plant density is displayed in logarithmic scale. Medians and 95% confidence intervals presented. Number of observations/treatment given in parentheses. Differences ($P \leq 0.05$) between prey in a given treatment are designated by an asterisk.

described by Savino & Stein (1982), is repeated here and in the figures to enable comparisons with behaviour of bluegills in the presence of predators. Without a predator, bluegill behaviour was consistent with about 50% shoaling across all plant densities. With largemouth bass, 50–80% of the bluegills shoaled at low plant densities; bluegill shoaling fell to less than 20% at medium and high plant densities.

In addition to changing with plant density, the percentage of bluegill shoaling also changed with predator type. At zero plant density, bluegills shoaled less with pike than with bass. At low plant density with both predators, more than 60% of the bluegills shoaled. At medium density, however, shoaling was lowest when the predator was a bass. At high plant density, shoaling was greatest in the absence of predators and again lowest when the predator was a bass. Shoaling of bluegills reduced the probability of their being attacked depending on the predator. Bass attacked more dispersed bluegills than shoaled ones (Table I). Northern

pike, however, attacked both shoaled and dispersed bluegills without distinction.

In addition to changes in behaviour, the distribution of bluegills changed with both plant density and predator presence. Bluegills were distributed throughout the pool when no predator was present and when a pike was present (Fig. 4). With a bass present, bluegills moved to areas offering the most cover or protection in each treatment; they stayed at the pool's edge (top or bottom) at low plant densities and moved to the bottom centre at high plant densities.

The behaviour of fathead minnows changed somewhat with plant density but only slightly with predator type. Nearly all minnows (90–100%) shoaled in zero, low and medium density, but shoaled less (10–30%) with or without a predator at high plant density (Fig. 3). Shoaling by minnows generally did not reduce their probability of being attacked (Table I); bass and pike attacked more shoaled minnows than dispersed minnows. Minnow distribution was not as constant as their

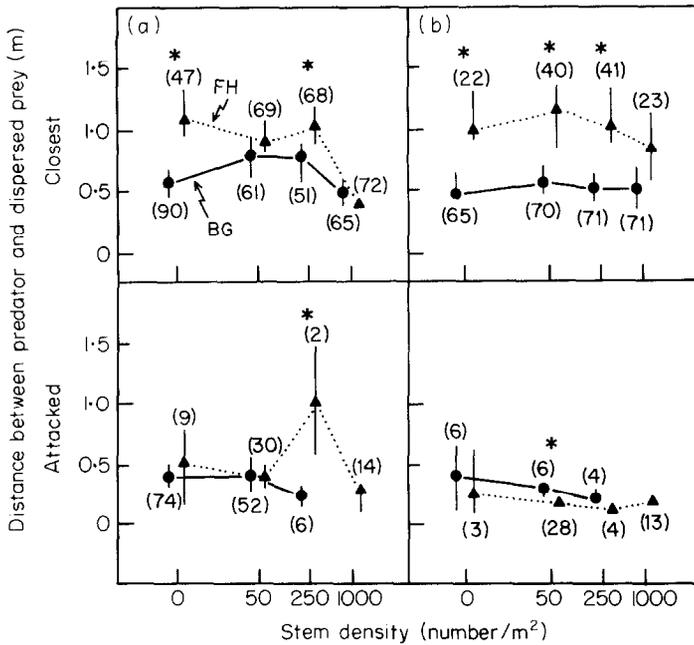


Figure 6. Distance between predator (a: largemouth bass; b: northern pike) and dispersed prey at four plant stem densities. Details and symbols as in Fig. 5.

shoaling, but 80–100% of the minnows generally stayed near the bottom of the pool, regardless of plant density or predator (Fig. 3). Minnows moved between the edge and centre of the pools, showing no clearly discernible preference.

Distances between prey and predators changed little with plant density. Shoals of bluegills and minnows generally stayed more than 1 m from the predator, regardless of plant density or predator type (Fig. 5). Because pools were 2.4 m in diameter and predators generally stayed at the edge, prey could maintain distances as great as 2.1–2.4 m. Bluegill shoals generally stayed farther (about 1.25–1.5 m) from largemouth bass than did minnows (about 1.0 m); shoals of both species stayed about 1 m from pike. Dispersed minnows generally stayed farther from predators than did bluegills (Fig. 6). As mentioned previously, few minnows were dispersed except at high plant density (see Fig. 3). Dispersed or shoaled bluegills or minnows that were attacked by bass or pike were generally closer to the predator than were fish that were not attacked, regardless of plant density. Bass generally attacked only prey that were within 0.5 m, and pike attacked only prey within 0.25 m.

DISCUSSION

Some predators adapt their foraging behaviour to changing conditions (Savino & Stein 1982; Crowder & Binkowski 1983). We used the amount of activity during a foraging bout as an indicator of the type of foraging strategy adopted by a predator. Low activity was associated with ambushing predators and high activity with searching predators. Bass captured equal numbers of minnows at all plant densities, by shifting foraging modes. Minnows seemed to be captured rather easily at zero plant density, but progressively more activity was required as plant density increased; at high plant density, bass switched to the ambushing strategy. However, even by shifting foraging modes, bass did not capture bluegills when plant densities were high. In contrast to bass, pike did not vary their foraging strategies with plant density or with prey type; they continually used the ambushing tactic. They captured more minnows than bluegills at all plant densities. Mauck & Coble (1971), using northern pike preying on bluegills and fathead minnows, also found that prey species, but not cover, determined prey vulnerability; fathead min-

nnows were more vulnerable than bluegills regardless of cover. At high plant density both predators used similar foraging strategies, but captured few bluegills. Similarly, Werner et al. (1983) found that vulnerable sizes of bluegills chose vegetated areas of ponds in response to largemouth bass and that these bass captured few bluegills, averaging only one bluegill every 4 days. Thus the adoption of different foraging strategies may not improve foraging success if prey (here, bluegills) remain in a structurally complex refuge.

Savino & Stein (1982) conducted experiments with large largemouth bass (33–37 cm long) foraging on bluegills at the four plant densities. In comparisons with the smaller largemouth bass (23–27 cm) used in this study, we found that trends in the behaviour of large largemouth bass were similar to those in small fish. Contrary to expectations expressed by Crowder & Cooper (1979), a decrease in the predator's size did not increase its ability to forage in complex environments. Possibly, the size difference involved was not large enough to alter manoeuvrability through vegetation. However, the number of prey captured by large bass was higher than the number captured by small bass, presumably because more prey were required to satiate the larger predators. Alternatively, large predators may be more experienced or may swim faster than smaller predators. Other behaviours, such as frequency of follows and attacks, reflected this increase in capture rate for large bass. As in small bass, the activity of large bass foraging on bluegills decreased as plant density increased. Little movement was required through the structure and therefore size was not a constraint in capturing prey. Manoeuvrability may not be a factor when vegetation density is high and all predators are ambushers.

Increasing structural complexity did not reduce capture success in any simple way. Rather, trends in capture success depended on types of predators and their prey. Visual contact was a good predictor of capture rate for largemouth bass; as visual contact increased, predation rate increased, even across prey species. However, visual contact of pike with their prey did not predict capture rate; even with higher visual contact, fewer bluegills were captured than minnows at all plant densities. Minello & Zimmerman (1983) found that vegetation decreased foraging success of inefficient predators that required several strikes per capture (pinfish, *Lagodon rhomboides*, and Atlantic

croaker, *Micropogonias undulatus*), but did not affect efficient predators (red drum, *Sciaenops ocellatus*, and speckled trout, *Cynoscion nebulosus*). Our results showed little difference between largemouth bass and northern pike in foraging efficiency for a given species of prey. Rather, the type of prey (bluegills, fathead minnows) as well as structural complexity, were important in determining foraging success of predators.

Prey sightings did not necessarily lead to captures, especially if prey were able to evade predators or perhaps to stay beyond striking range. Bluegills adapted to changing conditions by changing their behavioural patterns. Shoaling is a common response to predation (Radakov 1973; Treisman 1975; Keenleyside 1979). The reaction of one fish that sights a predator transmits this information to other members in the shoal, causing the shoal to swim in tighter formation (Radakov 1973) or to disperse into areas with cover (Keenleyside 1979). Because northern pike were mainly stationary predators, bluegills did not modify their shoaling behaviour or location, other than simply to observe predators and to stay beyond their attack range. In contrast, bluegill reactions were modified most when bass were predators. Fish were shoaled at the edges at low plant densities and dispersed in the centre at high plant densities. Bass were also less successful than pike in capturing the prey attacked. Because bass were more active predators and attacked prey from greater distances, their movements probably initiated anti-predatory responses in bluegills. Upon observing a foraging predator, bluegills react and move out of attack range or 'freeze' and wait until the predator moves away, behaviour similar to that observed by Reist (1983) for brook sticklebacks, *Culaea inconstans*, in avoiding northern pike predation.

Fathead minnows had a rather inflexible behavioural response to predators; shoaling was reduced at high plant density, but trends did not differ in relation to the presence or type of a predator. Inasmuch as visual contact is an essential factor (though not the only one) involved in maintaining shoals (Radakov 1973), minnows may not have been able to maintain shoals when visual barriers exceeded some threshold. Shoaling was not always an effective defence against predators; shoaled prey can be successfully attacked by ambushing predators (Grobeck 1983). Fathead minnows, which formed loose aggregates (rather than the tighter shoals of bluegills), provided

individuals that could be singled out and attacked. Minnows reacted little to predators, moving away from them only after a chase had begun. Though we did not quantify the degree of prey activity, we noted that most dispersed bluegills close to predators were motionless whereas minnows at the same distance from predators were seldom motionless. Because prey activity seemingly attracts predator attention and increases the likelihood of attack (Howick & O'Brien 1983), one may infer that prey close to the predator may escape detection by remaining motionless. Awareness of the presence of pike also may have been greater in bluegills than in minnows. Indeed, bluegills in other studies with another esocid predator, the tiger muskellunge (F1 hybrid of female muskellunge, *Esox masquinongy*, and male northern pike), were less susceptible than fathead minnows to predation (Tomcko 1982; Moody et al. 1983). Compared with minnows, bluegills oriented to tiger muskellunge more often and were startled at a greater distance from the predator (Tomcko 1982). Such behaviour is similar to the predator inspection visits used by another minnow, *Phoxinus phoxinus*, in response to northern pike (Magurran & Pitcher 1987). Hence, bluegills actively avoided predators, but fathead minnows did not.

We believe we have begun to explain the presence of predators in areas of high structural complexity. Bluegills and fathead minnows differ in body form, behavioural reactions and susceptibility to predation. Minnow behaviour changed with habitat but less with a predator. Hence, the more flexible reactions of bluegills, as compared with those of minnows, may account for the reduced susceptibility to predation of bluegills but not of minnows at high plant density. If suitable prey (here, fathead minnows) were present, piscivores expended little activity in dense vegetation to capture prey, thereby reducing energy demands. In addition, ambushing close prey increases capture success and reduces the probability of alerting other nearby prey (Grobeck 1983), possibly increasing daily capture rates. Hence, predator growth rate, the summation of energy gains and losses, may be enhanced in vegetated areas, if appropriate, vulnerable prey (here, fathead minnows) are present.

A strictly behavioural approach in the laboratory can be extremely useful in interpreting species associations in the field. Lack of appropriate anti-predator responses could explain the absence of fathead minnows where predators are abundant. In

surveys of northern lakes, cyprinids other than golden shiners, *Notemigonus crysoleucas*, did not coexist with centrarchid predators (Tonn & Magnuson 1982; Rahel 1984). Presumably, the golden shiner was the only cyprinid that could grow large enough to avoid predators (Rahel 1984). Our work and that of others (Mauck & Coble 1971; Moody et al. 1983; Tomcko et al. 1984) demonstrate that fathead minnows are vulnerable. Hence, it is not surprising that fathead minnows often do not persist in lakes (Johnson & Anderson 1972) or ponds (Ball & Ford 1953) stocked with largemouth bass. In contrast to fathead minnows, bluegills had successful anti-predator responses. In addition, the dorsal and anal spines of bluegills increase handling time and apparent size of bluegills over minnows (Moody et al. 1983). Bluegills, unlike minnows, can grow beyond edible size of piscivores, creating a size refuge (Lawrence 1958; Helfman 1981; Werner et al. 1983). Differences in prey response to predators and the ability of the prey to hide effectively no doubt result in differences in their persistence in lakes. Bluegills show considerable behavioural flexibility when plant densities or predators change whereas fathead minnows do not. Consequently, bluegills avoid predation and coexist in ponds and lakes with predators but fathead minnows cannot. Understanding how prey avoid predation under changing conditions aids in predicting species assemblages in natural lakes.

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