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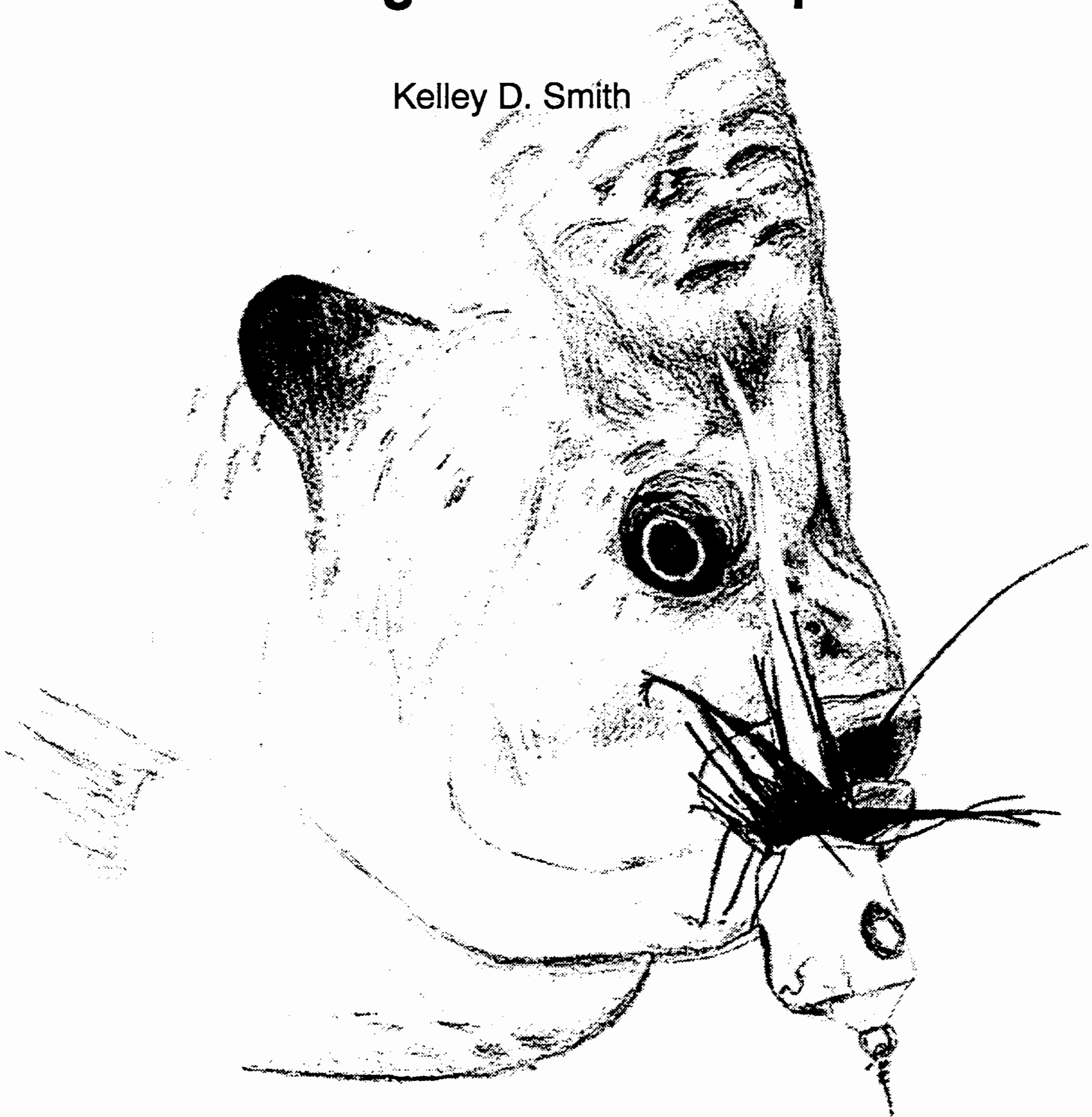

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SPORT FISH RESTORATION

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Vegetation-Open Water Interface and the Predator-Prey Interaction between Largemouth Bass and Bluegills: a Field Experiment

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Abstract.—A field experiment was designed to test effects of manipulating vegetation-open water interface (or edge) on success of largemouth bass *Micropterus salmoides* preying on bluegills *Lepomis macrochirus*. Four enclosures were placed in a natural lake, with a different level of structural complexity in each: 1) all vegetation removed (NV enclosure); 2) vegetation left untouched (CV); 3) one strip of vegetation 6-feet wide and 15-feet long removed from the middle creating 30 feet of edge (1S); and 4) two strips 3-feet wide by 15-feet long removed at 3-foot intervals creating 60 feet of edge (2S). Three sizes of bass (8, 11, and 14 inches, total length) and two size groups of bluegills (1.0-2.9 and 3.0-4.9 inches, total length) were utilized in the experiment. Predation success of all sizes of bass was much greater in 2S and NV enclosures compared to that in CV and 1S. Effects of increasing edge on predation rates were much greater than anticipated. Capture of bluegills by 8-inch bass was 5.0 times greater in the 2S enclosure than in the 1S, and by 11-inch bass it was 3.4 times greater. While 14-inch bass did not capture any bluegills in the 1S enclosure, they did consume some in the 2S. Predation rate averaged over all sizes of bass was 4.4 times greater in the 2S enclosure compared to the 1S. Effect of edge on predation rates was probably related to changes in the ability of bass to encounter bluegills in various habitats. Simple random encounter and amount of edge available for an interaction do not fully explain observed differences in predation rates. Other factors which likely influenced predation success include effects of open water width between refuges on the probability that bass detect bluegills in 2S and 1S enclosures, and changes in behavioral responses of bluegills to width of open water areas which, in turn, change relative encounter probabilities for bass. Appropriate configurations of edge for a bass-bluegill community should include knowledge of: 1) biomass and size structure of a bass population; 2) desired abundance of bluegills; 3) amount of edge needed per bass as a function of bass size and number; 4) critical size of refuges; and 5) effects of open water widths between refuges on bass and bluegill behavior.

Fishery managers are now beginning to realize the significance of predator-prey interactions in aquatic systems, which shape fish community structure (Gerking 1982). This is reflected in management plans designed to balance numbers between, and improve growth of individuals within, predator and prey populations. However, manual removal of excess predator or prey biomass, or stocking additional numbers of

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predators or their forage species, gives only temporary benefits (Parker 1958; Scidmore 1960; Snow et al. 1960). One factor which mediates success of these strategies, and which is often overlooked, is influence of structural complexity on predator-prey interactions. Structure provides refuges for prey species, and hence changes predator efficiency. This concept is particularly important because removing nuisance weeds which conflict with some recreational uses of water bodies, or adding materials to create artificial structures such as underwater reefs, are common practices in freshwater lakes. Thus, understanding effects of structure on predator-prey dynamics is not only enticing, but should help in identifying management techniques which rely on natural controls to maintain abundant and fast growing populations of predator and prey species.

The predator-prey relationship between largemouth bass *Micropterus salmoides* and bluegills *Lepomis macrochirus* has been studied extensively (Bennett 1948; Swingle 1949, 1950; Timmons et al. 1980), with emphasis on how structural complexity affects this interaction (Cooper and Crowder 1979; Crowder and Cooper 1979; Saiki and Tash 1979; Savino and Stein 1982; Gotceitas and Colgan 1987, 1990). These species have widespread geographical distributions, occur together in natural warmwater lakes (Scott and Crossman 1973; Newburg 1975), are frequently stocked in new or rehabilitated warmwater systems (Swingle 1949; Regier 1962), and provide sport fisheries of great recreational value (Newburg 1975; Becker 1976). Bass use bluegills as a source of food (Snow 1971; Bennett and Gibbons 1972), but structural complexity, usually in the form of weed beds, often provides refuges for small bluegills and protects them from predation by bass. The result can be a severe imbalance between numbers of bass and bluegill in a lake, which in turn leads to reduced growth rates and stunting problems for both species. However, it should be possible then to restore and maintain a balanced predator-prey relationship by manipulating structure in a way which enhances the ability of bass to capture bluegills. Yet, appropriate habitat changes are difficult to determine without first understanding effects of structural complexity on this predator-prey interaction.

Studies concerning influence of structure on a largemouth bass-bluegill interaction have dealt specifically with effects of vegetation density on vulnerability of prey, predators' food size preference, energy costs involved in capturing and utilizing prey, and behavioral aspects of predator and prey species (Lewis and Helms 1964; Glass 1971; Nyberg 1971; Savino and Stein 1982, 1989a). Because past experiments have been conducted under laboratory conditions and have centered around vegetation density effects, two basic problems still exist. First, relationships between laboratory results and the natural environment are not clear. Second, changing vegetation density to influence predator-prey relationships, although theoretically desirable, is not a feasible management strategy for controlling natural populations of fish. Cooper and Crowder (1979) outlined an idea for manipulating structural complexity by removing rectangular strips of vegetation from a lake. This not only increases amount of area over which biotic interactions might take place (Engel 1985), but also leaves intact refuges and feeding areas used by prey species. Cooper and Crowder hypothesized that some level of vegetation-open water interface (or edge) exists which would optimize a predator's success rate, while deviation from this level would cause predator success to decline.

Although optimizing amount of edge to maximize predator success is intriguing, there is currently no verification of a relationship between edge and numbers of bluegills captured by bass. Therefore, my objective was to determine if changes in amount of edge could significantly impact success rates of bass preying on bluegills. I hypothesized that doubling the amount of edge would double predation rates of bass feeding on bluegills. Creating edge is a very different concept than changing density of vegetation. Increasing plant density results in greater structural complexity for a predator, while maintaining a homogeneous environment. Conversely, removing strips of vegetation gives a heterogeneous environment of high structure (vegetation) and low structure areas (open water). Even though it appears to elevate structural complexity on a system-wide basis by creating a mosaic of habitat types in a lake, increasing edge may not influence, and probably decreases, a predator's perception of complexity on a microhabitat level. Thus, more edge implies lower structural complexity, and captures of bluegills by bass should increase. An experiment was designed to test this hypothesis using enclosures in a natural lake. This allowed for control and assessment of major factors that could mask edge effects on a bass-bluegill interaction, without being restricted by laboratory conditions.

Methods

The experiment was conducted in Chilson Pond, Livingston County, Michigan (T. 1 N., R. 5 E., Sec. 33). This is a small lake of about 40 acres in surface area, with an average depth of 6 feet. The bottom consists of silt (approximately 1 to 3 inches), below which is a foundation of rock and gravel. The entire pond is densely vegetated. Floating-leaf pondweed *Potamogeton natans* and bassweed *P. amplifolius* are the dominant species, with *Chara* spp., milfoil *Myriophyllum* spp., and pondweed *P. filiformis* in some areas. Lilies *Nymphaea* spp. and cattails *Typha* spp. are found around the shoreline.

Enclosures (or pens) used in the experiment were fabricated of a 2x4 wood frame, with sides that were 15-feet long and 5-feet high. Each side was made up of a 9-foot section adjoined to a 6-foot section by hinges. This allowed for folding and easier handling. Pens were designed to be assembled in the lake using bolts to fasten the four sides together. The top and bottom were left open, and braces were used across the top of each corner for stability. Nylon netting (1/4-inch stretch mesh) was attached to the bottom, forming a skirt around the pen. This netting was held down by lead lines and effectively plugged holes between the bottom of an enclosure and the sediment, caused by uneven bottom contours. Different materials were used at various times to cover the sides, including galvanized and aluminum window screening, and nylon mesh netting (1/4-inch stretch mesh). The best seemed to be aluminum screen, but it was also the most expensive of the three materials. Each pen was anchored in the lake by driving 3/8-inch diameter black pipe approximately 4 feet into the sediment at each corner, and tying an enclosure to the stakes with rope.

Four pens were placed in 3 to 4 feet of water, and a different level of structural complexity (habitat type) was created in each. All vegetation was removed from one pen (NV enclosure), and in another it was left untouched (CV). These comprised control groups for the experiment. Vegetation was removed from remaining enclosures in strips perpendicular to the shoreline, giving heterogeneously distributed patches which were rectangular in shape, as suggested by Cooper and Crowder (1979). One strip of vegetation 6-feet wide and 15-feet long was removed from the middle of one pen (1S), creating 30 feet of edge. Two strips 3-feet wide by 15-feet long were removed at 3-foot intervals from the last enclosure (2S), creating 60 feet of edge. This design effectively doubled the amount of edge while keeping constant both enclosure size and size of areas which were vegetated versus open (Figure 1). Vegetation in the latter three enclosures reached the water surface, and was fairly uniform and very dense. Macrophyte densities in these pens ranged from 113-203 stems/m^2, and averaged 164 stems/m^2. These densities were high enough that changes in predation rates between habitat types can be attributed to effects of edge on the predator-prey interaction rather than to effects of vegetation density, based on results reported by Savino and Stein (1982).

Largemouth bass were collected from ponds at the Michigan Department of Natural Resources (MDNR) Wolf Lake Hatchery in Mattawan, Michigan, and MDNR's Saline Fisheries Research Station in Saline, Michigan. Three sizes of bass were used in the experiment, and included fish which were 8, 11, and 14 inches in total length (TL). Bluegills, which were collected from ponds at the Saline Station and from local farm ponds, were grouped into two size classes, small (1.0-2.9" TL) and large (3.0-4.9" TL). These groups represented appropriate size classes of prey which would be utilized as forage by 8- to 14-inch bass (Lawrence 1958; Wright 1970). All fish were held at the Saline Station before transport to Chilson Pond.

Prior to commencement of the experiment, rotenone was used to remove existing forage species from all pens, thus insuring that bass had only bluegills as a food source during trials. Two replicates were run for each size of bass, with individual replicates taking one week to complete. Two other treatments were also performed excluding bass to determine error rates of recovering bluegills from the four different habitat types. Predation rates observed during the experiment were adjusted based on these error levels.

A trial consisted of placing two bass of a given size, along with 38 small and 12 large bluegills, in each pen. These numbers of predators and prey gave densities inside enclosures which approximated those in an average natural lake (Carlander 1977). Size group of bass was randomly chosen such that each was used once in the first and last three weeks of the experiment, but not necessarily in the same order within these time periods. Individual bass were never reused in later trials. Bass and bluegills were separated from each other by a removable barrier, which was inserted in the middle of an enclosure parallel to shore, with bass placed in the offshore side. This gave both bass and bluegills identical views of the habitat. Fish were then allowed to adjust to their surroundings for 24 hours, at which time barriers were removed and a trial begun.

A replicate lasted 72 hours, during which daily minimum and maximum water temperatures were recorded. After a treatment, bass were immediately removed using electrofishing gear. However, this method was very inefficient in recapturing bluegills. Instead, each pen was enveloped by plastic sheets and rotenone was used to recover remaining bluegills. Rotenone was left in an enclosure for two hours and as many bluegills were removed as possible without damaging vegetation. Enclosures were then detoxified using potassium permanganate. The following day pens were searched for any remaining fish using a mask and snorkel while floating on an inner tube. This resulted in minimal damage to vegetation while allowing a thorough search for bluegills. So that conditions in pens could stabilize, the next replicate was begun two days after a final search for bluegills was completed.

Casual observations were made at various times of largemouth bass and bluegill behavior in enclosures. Both species were watched during the acclimation period before three of the replicates, once for each size of bass. Follow-up observations were made three times per day during a 72 hour trial period. Finally, bluegill behavior was again observed during the final two runs when bass were absent from enclosures.

Water temperature data were compared by single factor analysis of variance. Predation rates were compared using a three-way analysis of variance (Neter and Wasserman 1974), with main effects including habitat type (4 levels), bass size (3 levels), and bluegill size group (2 levels). The multiple comparison technique of Scheffé (1959) was employed to determine explicit differences within main effects. All tests were performed with a 0.05 level of significance.

Assumptions

Basic assumptions were required to perform this experiment in the field. First, direct manipulation of higher aquatic plants may alter a myriad of variables, including nutrient cycles, light penetration, and water chemistry. However, these effects were considered negligible because very little vegetation was removed in comparison to what exists in Chilson Pond, and each replicate was of short duration. Second, water temperature may also influence predatory interactions in lakes because it affects metabolic rates and activity levels of poikilotherms. Thus, daily minimum and maximum water temperatures were recorded during each trial, which could later be used as covariates in statistical analyses if necessary. Finally, general assumptions concerning other factors which could influence results include:

- enclosure size would not affect the predator-prey interaction;
- bass and bluegills would not escape from pens and would not be removed by other sources (e.g., bird predation);
- weekly treatments with rotenone would remove all existing forage species from enclosures before each trial; and
- plankton would repopulate pens each week thus eliminating any arbitrary changes in searching and feeding behaviors of bluegills.

Results

Methods used to recover bluegills from enclosures were very successful, based on results of replicates in which bass were absent, and observations of stomach contents of bass after each trial. Recapture of bluegills in the small size group ranged from an average of 87% in the completely vegetated pen to 98% in 2S and NV enclosures (Figure 2). Recoveries of larger bluegills were generally higher, averaging 93% in CV and 1S pens, and 100% in other habitats. Estimated numbers of bluegills consumed by bass, from each habitat type and prey size group, were adjusted for these recovery errors. When final estimates of prey consumed were added to counts of bluegills actually recovered, the resulting total was always within ±1 of the number originally placed in an enclosure at the start of a replicate. Bluegills were the only prey item ever found in bass' stomachs, and individuals from both size groups were observed after four of the six trials. Although not conclusive, inspection of bass' stomach contents did help to reconcile observed predation rates with recovery errors.

Mean water temperatures were not significantly different among replicates (ANOVA, $P > 0.05$; Figure 3). No correlation was found between number of bluegills consumed and average water temperatures for any trial ($P > 0.05$). Thus, metabolic rates and activity levels of bass should have been similar during the experiment. This result has important implications for analyses of number of bluegills consumed by both different sizes of bass in the same habitat, and the same size of bass in different enclosures. Significant changes in number of bluegills captured by bass should be related to differential effects of edge on predator behavior and efficiency in capturing prey, and prey behavior and success at eluding predators, rather than water temperatures. Also, replicates in which the same size of bass was used could be pooled for statistical analyses without relying on water temperature as a covariate.

Some significant differences between predation rates of bass (defined as bluegills consumed per bass per day) were observed for all main effects (habitat type, bass size, and bluegill size group) studied in the experiment. Predation success of all sizes of bass was much greater in 2S and NV enclosures compared to that in the other two habitats (Figure 4). However, predation rates were not significantly different between CV and 1S nor 2S and NV pens. Few prey were consumed by any size of bass in the completely vegetated enclosure (greatest structural complexity). As amount of edge increased (structural complexity decreased), more bluegills were captured by all sizes of bass with best success occurring in the enclosure with no vegetation.

Total number of prey consumed by 8- and 11-inch bass was not different, but both captured significantly more bluegills in all pens than did 14-inch bass (Figure 5). In fact, larger bass did not capture any bluegills in 1S and CV habitats during either trial in which 14-inch bass were used. Based on predictions from energetic modeling (Rice et al. 1983; Hewett and Johnson 1987; J. Breck, MDNR, personal communication), consumption of bluegills by both 8- and 11-inch bass was estimated to be close to satiation levels in 2S and NV enclosures. However, it was well below satiation for these sizes of bass in 1S and CV pens, which was also true for 14-inch bass in all habitats.

Effects of increasing edge on predation rates were much greater than anticipated. Eleven-inch bass consumed more prey in each habitat than other sizes of predators, but 8-inch bass had the greatest increase in successful capture of bluegills with an increase in edge (Figures 4 and 5). If doubling amount of edge also doubled a predator's success, then predation rates observed for bass in the 2S pen should have been twice as large as those in the 1S pen. However, capture of bluegills by 8-inch bass in the 2S habitat was 5.0 times greater than in the 1S. For 11-inch bass, success rate was 3.4 times greater in the 2S pen. While 14-inch bass did not eat any prey in the 1S enclosure, they did consume a few bluegills in the 2S habitat. Predation rate averaged over all sizes of bass was 4.4 times greater in the 2S enclosure compared to the 1S, rather than 2.0 times as originally hypothesized.

There was also a pattern in size of prey consumed as a function of predator size (Figure 6). Bass captured significantly higher numbers of small bluegills than large in all habitat types. However, a greater percentage of bluegills from the larger size group were observed in the diet as bass size increased. Eight-inch bass did not consume any bluegills from the larger size group in CV, 1S, and 2S habitats, and only 6% of those preyed upon in the enclosure with no vegetation were 3.0" or larger. In comparison, 21% of bluegills captured by 11-inch bass in all pens were from the larger size group, ranging from a low of 0% in the CV to 40% in the 1S habitat. Fourteen-inch bass consumed so few bluegills that no conclusions could be reached concerning their selection of prey by size. These results indicate that predator size was important in determining size of bluegills attacked and captured by bass.

No attacks on, or captures of, individual prey were ever witnessed during times when bass and bluegill behavior was observed in enclosures. It was nearly impossible to watch fish in the completely vegetated enclosure, and both species were wary and would immediately attempt to hide from an observer who did not approach the other three pens carefully. Although observations could not be quantified, it was apparent that bass and bluegills did adjust to their surroundings during the 24 hour separation time at the start of a replicate.

In general, largemouth bass stayed on the bottom in areas which were shaded by either a side of a pen or the vegetation-open water interface. Individual bass always remained widely separated except when they could not see each other due to vegetation. In the 1S enclosure, bass usually remained in the single open water area, along opposite edges of vegetation. Bass were usually found in different open water areas in the 2S habitat. Occasionally, one would move across the middle strip of vegetation resulting in both bass occupying the same open water area, but they would rarely be together for any length of time. When spooked, bass would move into vegetation or, in the NV habitat, to the darkest side of the enclosure. They were never seen actively searching for prey in any enclosure, although observations were made only during daylight hours.

Bluegills were rarely observed near bottom, and were usually suspended a foot or more up in the water column. During the acclimation period, they formed a large group and stayed along edges of the pen with no vegetation. In other pens, they scattered and hid in vegetation. Although bluegills showed a tendency to remain in or near vegetation if it was available, they eventually began moving about either individually or in groups depending on habitat type. Bluegills of all sizes were often observed feeding on plankton in open water areas of pens during both the acclimation period and trial runs.

Once the middle barrier was removed, bluegills in the NV enclosure continued to school and swim slowly around the perimeter of the enclosure. Smaller groups of 3 to 5 bluegills were observed moving about in the 1S pen, but they usually remained close to vegetation and rarely crossed the 6-foot open water area. Group size was further reduced in the 2S enclosure, and movements were more dramatic. Bluegills often traversed open water from one strip of vegetation to another, either individually or in groups which rarely exceeded 3 fish in size. They also stayed in open areas for longer periods feeding on plankton.

Discussion

Predation rates for largemouth bass preying on bluegills were improved by increasing the amount of edge, which was consistent with the hypothesis tested. Since successful attacks by predators depend on probabilities of encountering a prey organism and capturing that individual after it has been detected, this result suggests that edge influenced one or both of these probabilities. However, capture probabilities were most likely not affected by amount of edge in a given habitat type. There is no reason to assume that the ability of bass to capture bluegills was different between 2S and 1S enclosures since interactions most likely occurred along an edge or outside of vegetation in open water areas. First, there are no obstructions to affect capture probabilities, in contrast to studies of vegetation density effects on predator-prey interactions where physical interference from vegetation can result in an unsuccessful capture (Glass 1971; Savino and Stein 1982). Second, the probability of capturing a specific prey species is generally constant for a given predator species, assuming an interaction occurs in an area with little or no structural complexity. For example, Nyberg (1971) suggested that coordination of bass during the attack stage led to a constant rate of failed attempts to capture prey. This failure rate was similar to that observed for other predators, including squid and mantids. Weihs and Webb (1984), Webb (1986), and Wahl and Stein (1988) also reported that various piscivores had constant capture probabilities. Using experimentation and models, they concluded that success of predators in capturing prey was controlled by innate morphological and behavioral characteristics specific to a given prey species, which decreased chances of a chase or caused predators to either forego an initial strike or end an attack prematurely.

Effect of edge on predation rates was most likely related to changes in the ability of bass to encounter bluegills in various habitat types. Since the interaction depends on visual acuity of bass to locate bluegills, and occurs near the vegetation-open water interface, area available for an encounter is twice as great per bass when edge is doubled. In addition, the geometrical configuration of edge used in this study allowed a bass to search two edges in the 2S enclosure in the same amount of time it would take a bass to search one edge in the 1S pen, assuming bass could detect prey across the full width of an open water area in the 2S habitat. This implies that captures of bluegills by all sizes of bass should have been twice as large in the 2S habitat compared to the 1S, assuming random encounter of prey. Although results for 14-inch bass were inconclusive, predation rates of 8- and 11-inch bass in the 2S pen averaged 5.0 and 3.4 times greater, respectively, than in the 1S. Thus, simple random encounter of bluegills and amount of edge available for an interaction do not fully explain observed differences in predation rates. Another factor which could have significantly influenced predation success was the effect of open water width between refuges on the probability that bass would encounter bluegills in 2S and 1S enclosures.

Width of open water most likely had a stronger negative effect on the ability of 8-inch bass to encounter bluegills in the 1S enclosure than on 11-inch bass. This is one possible explanation for why 8-inch bass had a greater change in predation success with increasing edge than did 11-inch bass. All sizes of bass remained along edges of vegetation in 2S and 1S enclosures, based on observations made during the experiment. Similar behavior by bass has been reported in other experimental (Savino and Stein 1989b) and field (Engel 1985, 1987; Butler 1988) studies, and is usually attributed to the fact that prey species are found in and near vegetation. Predators may also enhance their success by associating with structure through indirect benefits resulting from physical shading (Helfman 1979) and background camouflaging (Endler 1986). Given this behavior, and estimated distances at which bass react to bluegills (Howick and O'Brien 1983), bass could not watch both edges during a search for bluegills in the 1S habitat because of the wide open area between refuges in this enclosure. Conversely, bass could simultaneously see two edges while searching in the 2S habitat because of the relatively narrow widths of open water. However, distance at which bass react to bluegills increases with bass and bluegill size, implying that open water width in the 1S pen should have a greater negative effect on the ability of 8-inch bass to encounter bluegills than it does on 11-inch bass. Thus, creating additional edge with narrower open water widths between refuges would increase predation success of smaller bass, assuming a constant density of predator and prey. Further analyses of relationships between reaction distances of different sized bass and width of open water areas between refuges are required to test this hypothesis.

Predation rates in 2S and 1S enclosures were probably also affected by changes in behavioral responses of bluegills to width of open water areas which, in turn, change relative encounter probabilities for bass. Bluegills were observed out in, and crossing, open water more frequently in the 2S pen compared to the 1S, probably because they perceived a decrease in predator density and a closer proximity of refuges to each other. Since bass remained in separate open water strips in the 2S enclosure, density of predators would appear lower and bluegills might modify behaviors associated with reduced predation risk. This would result in bluegills moving into open water areas more frequently and at greater distances from vegetation than they would in the 1S habitat. Bluegills may also have responded positively to close proximity of another refuge in the 2S pen, since distance between vegetated plots was only half as far as that in the 1S enclosure. Again, this would result in increased travel into and across open water areas from one vegetated strip to another. Thus, the probability of bass encountering bluegills in the 2S habitat would be greater than in the 1S.

Animals sample their environment to determine foraging possibilities in different habitats (Krebs 1978; Gilliam 1982), and risks associated with utilizing a specific habitat (Fraser and Huntingford 1986; Gilliam and Fraser 1987). Predator density and/or distance between refuges can modify such assessments, which then alter behavioral responses exhibited by prey species in their attempt to reduce predation risk. Bluegills also verify foraging opportunities and risk of predation in open water habitats by moving short distances from refuges (Werner and Hall 1988). Distance traveled from a refuge appears to be size-related, with larger individuals moving further into open water. Bluegills seem to estimate risk in open water as a function of how often predators are encountered and proximity of available refuge (Werner and Hall 1988). If macrophyte beds are available which afford sufficient protection from predators, bluegills move closer to and inside of vegetated plots as either encounters with predators or distance between refuges increases (Gotceitas and Colgan 1987; Werner and Hall 1988). Their reaction to associate closely with structure occurs even though such behavior causes lost foraging opportunities, in return for reduced risk of predation (Werner et al. 1983; Ehlinger 1986).

Appropriate configurations of edge may increase time spent foraging by bluegills in open water and distances traveled between refuges, both of which lead to a greater probability that they will be detected by bass. Werner et al. (1983) suggested that variation in use of open water versus vegetated habitats by small bluegills on any given day was due to the closeness of these habitats to each other in small experimental ponds. Bluegills could feed in open water or sediments while remaining close to refuges. Werner et al. concluded that because large open water areas usually exist between macrophyte beds in natural lakes, such foraging bouts, and probably travel between plots, should be severely curtailed depending on the density of bass near refuges. However, a fundamental result of creating edge is the establishment of heterogeneous habitat types on a small scale (i.e., within individual macrophyte beds) which are close together. Open water areas remaining after removal of vegetation may negate effects of large distances between refuges on bluegill behavior. The resulting increase in movements by bluegills would raise their probability of detection, and thus improve predation success of bass.

The relationship between edge and predation success of 8- and 11-inch bass, assuming constant predator and prey densities, can be described by a sigmoid function. This implies that a critical level of edge exists at which the ability of bass to capture bluegills changes quickly from one of disadvantage to one of greatly improved success. In contrast, Crowder and Cooper (1979; in particular see Figure 1A) hypothesized that increasing structural complexity should cause a monotonic decline in successful captures of prey by predators. However, responses similar to the one between edge and predation rate have also been reported for experiments dealing with effects of vegetation density on predator-prey interactions. Savino and Stein (1982) showed that captures of bluegills by bass during a one hour period decreased sigmoidally with increasing vegetation density, although results after twenty four hours showed a monotonic decline in captures. Savino and Stein (1989a) again demonstrated a sigmoid relationship between vegetation density and successful captures of bluegills by bass after a one hour foraging experiment and, in contrast to their earlier results, this same response was observed after a period of 24 hours. However, they also reported that prey captures did not decline in a sigmoid fashion with increasing vegetation density, regardless of time allowed for foraging, when fathead minnows *Pimephales promelas* were offered as prey to bass or when northern pike *Esox lucius* were used as predator with either prey species.

These results demonstrate three important points about effects of structure on predator success. First, the conceptual model of Crowder and Cooper (1979) does not generally apply to edge or vegetation density effects on predator success for the above mentioned species. Second, foraging experiments of short duration may mask true relationships between structural complexity and predation rates. Finally, types of structure available along with diversity and abundance of predator and prey species will change the distribution because of differences in either search strategy of predators or behavioral responses of prey to their environment. For example, the sigmoid function relating edge and predation success occurs because the probability that bass will encounter bluegills changes in the different habitat types. These changes are regulated by effects of both amount of edge and open water width between vegetated areas on distances at which bass react to bluegills, and behavioral responses of bluegills to habitat type. Since edge and resulting widths of open water are interdependent, it is not possible in this study to determine which factor is more important in generating the sigmoid relationship. Thus, a better description of how and why predation rates are affected by structural complexity is needed given different types of structure, and various combinations and densities of predator and prey species found in natural lakes.

The assumption that vegetation density in enclosures should not confound effects of edge on predation rates was warranted. Average predation rate for 8- and 11-inch bass combined was very low (0.15 bluegills consumed per bass per day) in the CV habitat. This result is comparable to findings of other researchers who used a similar habitat type in laboratory (Savino and Stein 1982) and field (Werner et al. 1983; Werner and Hall 1988) experiments. Savino and Stein (1982) reported that 33-37 cm bass (TL) consumed approximately 1.0 bluegill per day in a pool that contained 1,000 stems/m^2 of artificial vegetation. In a pond with mixed habitat types that included a wide band of vegetation around the perimeter and open water with no structure in the center, Werner et al. (1983) estimated a predation rate of 0.26 for bass averaging 198.8 mm standard length (SL). Werner and Hall (1988) reported a rate of 0.17 for smaller-sized bass (165-245 mm SL) in vegetated habitats. These similarities suggest that effect of edge on predation success in my enclosures was not biased by influence of vegetation density.

Enclosure size also did not appear to have any significant affect on the predatory interaction. First, given ambient water temperatures existing during my field experiment, estimated consumption rates of 8- and 11-inch bass in the NV habitat were very close to predicted satiation levels. Second, diet compositions of bass were not different from what has been reported previously. Davies et al. (1982) found that bluegills captured by 2- to 12-inch largemouth bass in West Point Reservoir were 40% to 30% of the length of bass which consumed them. Thus, 8-inch bass would select bluegills smaller than 3 inches while 11-inch bass could handle bluegills as large as 4.5 inches, which is consistent with my results as well as predictions by Lawrence (1958) and Wright (1970). Finally, predation rate for 8- and 11-inch bass combined in the NV enclosure averaged 1.5 bluegills consumed per day. This estimate is well below the range of 7.8-9.0 bluegills consumed by bass per day in other experiments which included unvegetated habitats (Savino and Stein 1982; Werner and Hall 1988). However, de Lafontaine and Leggett (1987) studied effects of container size on predation mortality of postemergent capelin *Mallotus villosus* by jellyfish *Aurelia aurita*, and concluded that use of small containers resulted in serious overestimates of predation mortality when compared to in situ observations. Thus, variation in predation rate estimates between studies is related to differences in enclosure size, ambient water temperature, initial density and size structure of predator and prey populations, and methods to determine numbers of prey consumed, used in a given experiment. Predation success of bass in the NV enclosure seems low compared to results from other studies but it appears to be accurate since satiation levels were reached and diet compositions were reasonable, which suggests that enclosure size did not significantly bias edge effects.

Other factors that might also mask results of increasing edge on the bass-bluegill interaction include social facilitation and interference. Both can have significant ramifications on dynamics of predator-prey and parasite-host interactions (Hassell and May 1973; Beddington 1975). Social facilitation per se probably did not affect predation rates in either enclosure containing edge, but it is possible that one bass did in fact aid another, albeit unknowingly, in capturing bluegills in the 2S habitat. Since the middle strip of vegetation in this enclosure was only 36" wide, either attack lunges into vegetation or failed capture attempts by bass could have caused bluegills to flee through the refuge into open water on the other side. This would then make bluegills vulnerable to attack by the second bass, especially in light of my observations that bass in the 2S pen were rarely in the same open strip together. Since I never witnessed any attacks during my experiment and other studies performed in the laboratory have not used more than one bass at a time, the likelihood of this dynamic interaction is unknown. However, Gotceitas and Colgan (1987) observed bass in pools making attack-like lunges into cover plots with 1,000 stems/m^2 in an attempt to drive prey from this refuge. They reported that such behavior was usually successful in chasing prey out of heavy cover plots and into more vulnerable positions in open water. These results imply that refuge size is important because it affects the probability that bluegills might flee beyond protection of vegetation when attacked, thus changing encounter probabilities for bass. Therefore, pseudo-facilitation may have biased effects of edge on the bass-bluegill interaction in the 2S enclosure if the middle strip of vegetation was not sufficiently wide to afford protection to fleeing bluegills.

Direct and indirect interference probably had much greater influence on predator success, especially in the 1S enclosure, than pseudo-facilitation. Both bass occupied the single open water area in the 1S habitat along opposite edges of vegetation. This may have resulted in direct interference between bass, which would reduce their search efficiency because of time wasted in intraspecific aggression (Beddington 1975). Indirect interference could also have biased my results since bass were probably spotted more often in the 1S habitat, causing bluegills to increase their association with vegetation. This would greatly reduce the probability of bass encountering bluegills in the 1S enclosure compared to the 2S, and might result in predation rates similar to those I observed regardless of amount of edge. It is known that predator density alters prey behavior. As encounters with predators increase, prey become more wary because of a greater possibility of attack, and respond by moving closer to, and spending more time in, a refuge (Gilliam and Fraser 1987; Werner and Hall 1988). Prey may also learn to avoid predators after either a personal encounter with a predator or as a result of reacting to an attack on a nearby individual (Snyder 1967; Charnov et al. 1976). Thus, exposure to predators, which significantly contributes to overall prey predation risk (Ware 1973; Savino and Stein 1989a), is diminished because of behavioral responses of prey species to predator density. However, the relative impacts of direct interference between bass versus behavioral responses of bluegills in different habitat types on capture success of bass could not be determined in this study.

There is no empirical evidence which explains why the largest sized bass performed so poorly in my field experiment. Various factors which could have negatively affected 14-inch bass include possibilities that enclosure size was too small, or acclimation (starvation) period prior to a replicate was not long enough. However, I suspect that conditions existing in ponds at the Saline Station, where bass were held prior to the experiment, contributed to the lack of performance. Eight- and 11-inch bass were held together in a pond which was completely vegetated and had a high abundance of minnows. A separate pond was used to hold 14-inch bass, which contained no vegetation or minnows but did have a large population of crayfish. I observed pieces of crayfish in the transportation tank, which had been regurgitated by 14-inch bass during travel from Saline to Chilson Pond. A plausible explanation then is that larger bass had formed expectancies and search images for crayfish (a benthic organism) and found it difficult to switch to piscivory in only 3 days. Effects of learning and search image formation on predator success are well documented (see e.g., Murdoch and Oaten 1975). For example, Anderson (1984) observed that bass exhibited specific behaviors while foraging in reaction to types of habitat available and structure of prey communities. He suggested that bass learned to capture different prey species in various habitat types through a process of trial and error. Ehlinger (1986) found that bluegills, which had fed regularly on prey from one habitat type, were 50% less efficient in capturing that prey once they began switching to prey from another habitat type. Although these studies do not imply cause and effect, the results do support my hypothesis about why large bass did not capture bluegills in this experiment.

The relationship between edge and predator abundance should be similar to that hypothesized by Crowder and Cooper (1979), who used vegetation density to define structural complexity. Since bass search along edges of weed beds in their search for prey (Engel 1987), some level of edge will exist for a given predator biomass which maximizes predation rate. Although the level would be mediated to some extent by refuge carrying capacity and prey density, it is also highly dependent upon size structure of the predator population, and how much edge is required by an individual bass to fulfill its energy requirements. Only a finite amount of edge can be created in a lake. Therefore, as predator biomass increases, amount of profitable edge per bass will become limiting and success rates of bass will decline. The opposite situation will occur when predator density is low relative to available edge. In this instance, creating profuse amounts of edge will have little overall affect on predator and prey communities since bass have already maximized their forage return, and maximum mortality from predators has already been incurred by a prey population. Thus, density and size structure of predator populations will significantly influence estimates of how much edge is required to maximize predatory effects on prey species. These factors are poorly understood and need clarification, but especially important is the question: how much edge does an individual bass of a given size need to maximize its capture of prey?

The association between edge and prey density should also be similar to that described by Crowder and Cooper (1979, in particular see Figure 1B). Yet, operative mechanisms are probably not the same since predator and prey species appear to react somewhat differently to edge than they do to vegetation density. Given a constant amount of edge, more individuals will be forced from refuges as prey density increases, resulting in greater numbers of prey attacked by predators (Figure 7). This is a result of creating edge, which limits refuge habitat area relative to high prey densities. Thus, predation success for bass will be limited by satiation given optimal amounts of edge, and will decrease slightly as amount of edge is decreased because of reduced encounters with prey. As prey abundance decreases, refuge space relative to prey density increases and encounter of prey by predators will drop more significantly depending on amount of edge. In this situation, predation rates will be very low as hypothesized by Crowder and Cooper for effects of vegetation density. However, these hypothetical relationships have not been explicitly tested, and more research is needed to determine functional responses of fish predators given concurrent influences of structural complexity and prey density.

It is interesting to note that the interaction between edge and vegetation density is complex. As amount of edge is increased, which leads to a system with no vegetation, or decreased, which leads to complete vegetation, there will be a point at which vegetation density effects may become more important than edge effects. This can also occur at intermediate levels of edge if open water areas between refuges become very large. Finally, edge will have much less impact on predation rates if vegetation density is low or growth forms of vegetation occurring in a lake do not provide sufficient refuge (Dionne and Folt 1991). Thus, effects of edge can be limited and confused by these factors, and the conceptual model of Crowder and Cooper (1979) may appear to apply without exception in many instances.

The affinity of fishes to congregate around and use artificial and natural structure is well documented (e.g., see Johnson and Stein 1979 for a review). Yet, carrying capacity of structure is limited by physical space available for individuals (Johnson et al. 1988; Lynch and Johnson 1989) and food resources accessible to fishes within a structure (Wiley et al. 1984). Creation of edge is intrinsically linked to these components because it results in removal of structure from a system. Thus, the concept of a critical refuge size, which I define in terms of the ability of a refuge to afford prey species protection from predators, has important consequences for predator-prey dynamics.

Physical size of a refuge, beyond effects of carrying capacity, is an important determinant of how well prey species are protected from predators. Both the possibility of attacked individuals fleeing through a refuge into areas of high vulnerability, and behavior of predators to lunge into, then circle, a refuge in hopes prey flee from cover, illustrate this point. Refuge size is also significant because selective forces exerted by predators over time cause ontogenetic shifts in habitat and resource use by prey species, and confine small fish to protective structures. Removal of vegetation, then, can only intensify size-class interactions within and between species, which already have profound impacts on organization of fish communities (Mittelbach 1986; Mittelbach and Chesson 1987). For example, both intra- and interspecific aggression can force individuals from cover and make them more vulnerable to encounter and capture by predators. Helfman (1981) observed high levels of territorial aggression in juvenile bluegills protecting their nocturnal resting areas, especially during twilight periods when predators like bass were most active. Coen et al. (1981) concluded that losers of competitive interactions between two species of shrimp suffered far more predatory mortality because they were forced from a refuge offered by seagrass. Thus, cognizance of the critical refuge concept and a better understanding of the interplay between structure and system production are mandatory if managers wish to manipulate edge with a goal of balancing ecosystem dynamics and improving growth of predator and prey species. Further research is required to better describe physical attributes of a critical refuge in terms of carrying capacity (space and food available to fish), and size and geometry of a refuge necessary to ensure effective safety from predation.

Creation of edge can have measurable effects on predation success of bass. These effects are most likely related to behavioral responses of bluegills to edge and effects of open water widths on distances at which bass react to bluegills, which in turn determine encounter rates for bass. Distance between refuges and proximity of refuges to open water habitats with highly profitable forage also influence bluegill behavior. Along with bass density and relative size, these factors mediate reactions of individual bluegills to risk of predation in terms of distances they are willing to travel from a refuge. Density and type of vegetation present in a lake can also change results anticipated for programs which are aimed at improving bass and bluegill populations by establishing edge. Finally, the concept of a critical refuge size is important. Edge is created by removing portions of macrophyte beds, which reduces the size and amount of refuge available to small bluegills. Therefore, a reasonable estimate of an appropriate configuration of edge for a bass-bluegill community must include knowledge of: 1) biomass and size structure of a bass population; 2) desired abundance of bluegills; 3) amount of edge needed per bass as a function of bass size and number; 4) critical size of refuges; and 5) effects of open water widths between refuges on bass and bluegill behavior. Actually, estimates for the first three components and either 4) or 5) will constrain the problem and give a solution, since 4) and 5) are interdependent. However, careful consideration of both refuge size and width of open water areas is appropriate. Manipulating macrophytes based on one of these factors will significantly change physical dimensions of the other, leading to different effects on predator and prey species and, in turn, on structure of fish communities in lakes. Thus, increasing amounts of edge may not always result in improving predator success, and other criteria will need to be assessed before adopting this strategy in an overall management plan.

Management Implications

Creation of edge can have measurable impacts on the predator-prey interaction between largemouth bass and bluegills. Effects of edge are related to widths of open water areas between refuges which, in turn, alter behaviors exhibited by bluegills and distances at which bass and bluegills react to each other. Interactions between these factors may either increase or decrease numbers of bluegills encountered by bass, and thus predation rates of bass. It is now clear that size and shape of macrophyte beds, their abundance in a lake, their proximity to each other and open water habitats, and density and morphology of vegetation within beds all have significant effects on abundance, growth potential, and behavior of predator and prey species. Creation and destruction of structure in aquatic systems can have serious impacts on the outcome of short- and long-term interactions between species, and thus fish community stability in natural lakes. Therefore, fishery managers must become more cognizant of these consequences when determining merits of proposals aimed at dramatically changing the type and abundance of physical structure in a lake.

Coupling my experimental work with empirical observations from the field (Engel 1985 and 1987), it is apparent that creating edge in lakes with abundant bass and bluegill populations and large amounts of dense vegetation can enhance growth of both species, which leads to evident benefits for sport anglers. In addition, channels through macrophyte beds attract bass which cruise along them in search of prey (Engel 1987). Such openings and the resulting increase in concentration of bass in these areas can also lead to indirect benefits for anglers, including easier access into previously unfishable areas and greater capture rates of bass (Paxton and Stevenson 1979; Wege and Anderson 1979).

Creation of edge is a feasible management tool (see Engel 1985 and 1987 for examples). Weeds can be harvested in a variety of ways, from something as simple as pulling a rake or an old box spring along the bottom of a lake to more sophisticated methods which employ underwater weed harvesters. Edge can be maintained by repeated harvesting of macrophytes or by placing removable screens on a lake bottom (Engel 1987). Thus, many configurations can be explored easily and cost-effectively in the field for a variety of conditions encompassing macrophyte densities and abundance, and different mixes of predator and prey species.

Creating edge may not always result in positive benefits, and individual weed removal projects will need to consider other factors before adopting this strategy as part of an overall management plan. Although I have shown that edge can have considerable impact on the interaction between bass and bluegills, such logic does not automatically apply if other prey species are available or if the major predator is a species other than bass. For example, bass may use very different foraging strategies when preying on fathead minnows (Savino and Stein 1989a and 1989b) and this prey species may react differently to edge than do bluegills. Hence, edge may be ineffective in this predator-prey interaction. On the other hand, northern pike are strictly ambush predators which remain in, or on an edge of, weed beds. Current evidence has shown that edge does not appear to have an impact on pike capture rates of bluegills or fathead minnows in laboratory experiments (Savino and Stein 1989b), but if it did in natural settings, operative mechanisms would surely be different than those described for bass. Also, behavioral responses of prey species to edge is not clearly understood. Consequences of both open water distances between refuges and proximity of refuges to open water habitats with highly profitable forage are of particular importance. This is especially true if these factors, along with predator density and relative size, mediate reactions of individual prey to predation risk in terms of distances they are willing to travel from a refuge. More research is needed to determine influences of edge on other predator and prey species.

Effects of creating edge on predator success can also be mediated by the morphology and density of vegetation present in a lake (Savino and Stein 1982; Dionne and Folt 1991). Both factors are important determinants of predator success in structured environments and thus could negate the influence of edge. However, wise use of macrophytes and alterations to vegetation which incorporate the concept of edge will be very important in many freshwater lakes which are literally choked with vegetation. Macrophyte management policies should begin to embrace the concept of creating edge, rather than complete annihilation of weed beds, because resulting effects can include both enhanced growth rates of predator and prey species and increased balance and stability in aquatic communities.

Clarification of relationships between open water strip widths and bass reaction distances to bluegills are needed to determine suitable geometric configurations of edge. Given average sizes of bass which will be involved in a predatory interaction in a lake, it is possible to estimate open strip widths which maximize the potential for bass to encounter bluegills. However, foraging strategies of bass must be utilized in such calculations (i.e., active search during day or at twilight) because light intensity has significant impacts on reaction distances of bass and bluegills to each other (Howick and O'Brien 1983), and thus on appropriate widths for open water areas. Finally, subtle changes in behavior of bluegills reacting to bass density and relative bass size can significantly modify estimates of open strip size needed to maximize numbers of bluegills encountered by bass. Bluegill behavioral responses to edge are poorly understood and more research is necessary to determine their effects on encounter rates for bass. Regardless, it is now possible to predict appropriate open water widths which should come close to maximizing encounter rates for bass, and hence their level of predation on bluegills.

Fishery managers should not be dissuaded by complexities involved in determining an appropriate use for, and design of, edge as part of a management plan for any lake. Although many factors will need to be assessed to determine possible consequences of edge on an aquatic system and communities therein, short- and long-term benefits can be real and very positive. The inherent ease and flexibility of employing the concept of edge in lake management plans also suggests that a framework of adaptive management is probably appropriate in studying edge effects. A methodical approach using an adaptive management process will permit identification and testing of competing, multiple hypotheses, any one of which may be important in ascertaining effects of edge on various systems and predator-prey communities. Through this process, establishment of general criteria to determine optimal configurations for edge may be feasible in a relatively short time, given specific constraints operating in an aquatic system (e.g., types of predator and prey species inhabiting a lake, and species, density, and abundance of macrophytes present). Hence, it might be possible to identify simple rules-of-thumb which allow managers to determine if creating edge would help attain specific goals outlined for a given lake. This would be a major step toward accepting, and giving deserved recognition to, importance of structure in maintaining stable and healthy aquatic communities.

Although macrophytes conflict with many recreational water uses and are often considered a great nuisance, managers need to find ways of arbitrating weed removal programs such that they benefit a variety of users while maintaining or enhancing stability and performance of species within an ecosystem. Successful use of edge in managing aquatic systems is attainable and desirable. It can be cost-effective as a management tool, especially since it could diminish the necessity for other human intervention (e.g., poisoning and/or stocking of predator and prey species). This benefit is a direct consequence of a greater reliance upon, and wiser use of, predatory and competitive interactions between species which occur naturally in lakes, and which can be very effective in maintaining stability within aquatic systems. Knowledgeable management of macrophytes will surely be a challenge in future management of lakes and streams.

Future Research

There are two pathways which may be taken in future study of edge effects on predator and prey species in aquatic systems. They are complementary in nature and could be utilized simultaneously, depending on logistical constraints which confront implementation of any research project. The first step is to utilize an adaptive management approach in field studies as outlined in the previous section. The second course of action would include more rigorous testing of specific hypotheses either in laboratory or field experiments as deemed appropriate.

Field work should be designed to study effects of edge on a variety of different predator-prey interactions (i.e., different species of predator and prey). Hypotheses concerning effects of open strip widths, macrophyte abundance and density, and carrying capacity of various sizes of vegetation beds in relation to prey species abundance could be tested together given a proper design. A priori information should include estimates of biomass and size structure of a predator population; predator and prey diet composition; both age- and size-specific growth rates of predator and prey species (see Osenberg et al. 1988); age and size at which recruitment to the fishery occurs; and size at which ontogenetic habitat switches occur for prey species confined to vegetation by predators (Werner et al. 1983; Werner and Hall 1988). Effects of edge can then be determined by monitoring possible changes in one or more of these factors. For example, ontogenetic habitat switches would still occur at the same size for a given prey species. However, in relation to time (age), they may occur more quickly if growth of a prey species is improved. Increases in growth rates of prey could be due to either reduced abundance because of mortality from predators (i.e., lower density of prey, therefore more resources available per individual), or because individuals may now be able to successfully forage in more profitable habitats outside, but very near to, refuges. My intent here is to illuminate only broad concerns which are appropriate in determining edge effects on structure of aquatic communities. Specific direct and indirect impacts of predation on juveniles and adults, interactions between these two groups and between species, and effects of changes in available resources on juvenile and adult performance have been discussed in great detail elsewhere (e.g., see Gilliam 1982; Werner et al. 1983; Mittelbach and Chesson 1987; Osenberg et al. 1988; Werner and Hall 1988).

The approach outlined above would lead to general realizations about how edge affects predator and prey species, and resulting consequences for community structure. Yet, more detailed laboratory and field experiments will also be required to identify and understand specific operative mechanisms which control a predator-prey interaction, in relation to edge, if general rules-of-thumb are to be useful. Future research should aim at answering the following six questions, all of which are critical to a successful use of edge in fishery management.

1) What is the interaction between effects of edge and vegetation density on a bass-bluegill, predator-prey interaction? If intermediate levels of vegetation density give optimal predation rates in a homogeneous environment, can channelizing large macrophyte beds, which would create heterogeneity within a system, further elevate predation rates in these habitats? Also, at what levels of vegetation density (both high and low) does the importance of edge become insignificant, or will creating channels of appropriate widths in vegetation always impact a predator-prey interaction regardless of density?
2) What is the effect of varying width of open water strips (i.e., distances between refuges) on behavioral responses of bluegills to their environment? Does distance between refuges significantly change behavior of bluegills reacting to predation risk by altering their willingness to travel away from a refuge into open water? And how is such behavior mediated by changes in density and relative size of bass?

3) If responses of bluegills to predation risk on a diel scale can be described in terms of distances they are willing to travel from a refuge, are these distances a function of individual bluegill size? Or do bluegills of all sizes, which have been confined to a specific habitat type during their ontogeny to escape predation mortality, react similarly in these smaller habitats on a daily basis?
4) Is creation of edge effective in altering a predator-prey interaction between bass and prey species other than bluegills? What are the results if more than one prey species is available? What are the effects of edge on predator species other than bass under similar conditions (i.e., bluegills as prey, other prey species, and more than one available prey species)?
5) What are the implications of the concept of critical refuge size to edge, and a predator-prey interaction in general? What constitutes a critical refuge in terms of protection afforded prey during an attack? How does carrying capacity of a refuge (both physical space and food resources) adjudicate effects of edge on a predator-prey interaction?
6) How do bass (and other predators) react to edge? What foraging strategy do they prefer? Are foraging strategies affected by width of open water between refuges or number of open water areas within a certain proximity? Where are predators located if they do in fact forage in these open water channels?

Like most research projects, I have finished with more questions than I started with. The above list may appear imposing. Yet, these questions need to be answered if managers are to successfully use the concept of edge, and other manipulations of habitat and structure, to cost-effectively maintain and enhance aquatic communities in the future.

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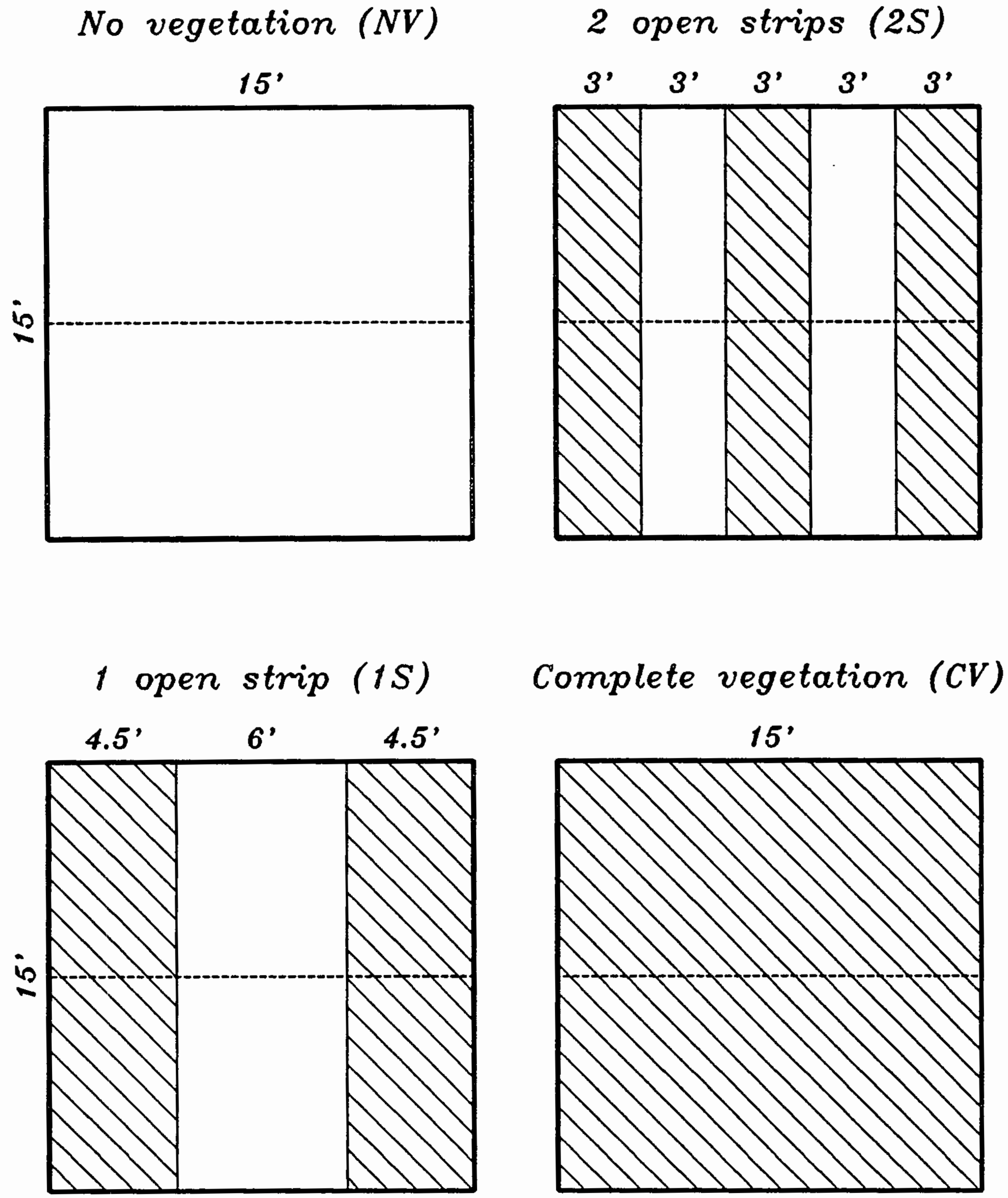

Figure 1.—Dimensions and habitat configurations for each pen type. Cross hatching designates vegetated areas and barrier placement is shown by dashed lines.

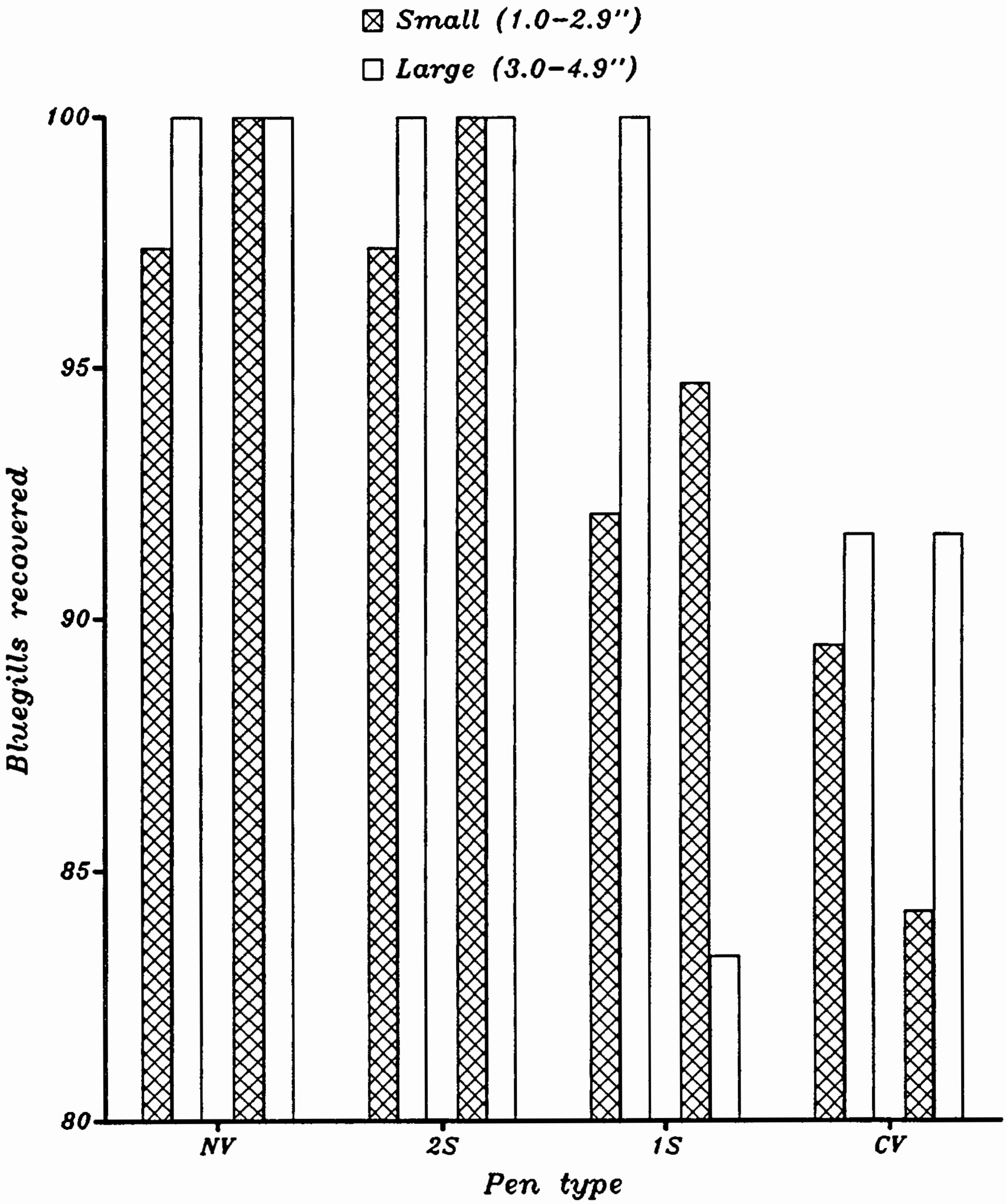

Figure 2.—Percent of small and large bluegills recovered from each pen type in two replicates which excluded bass.

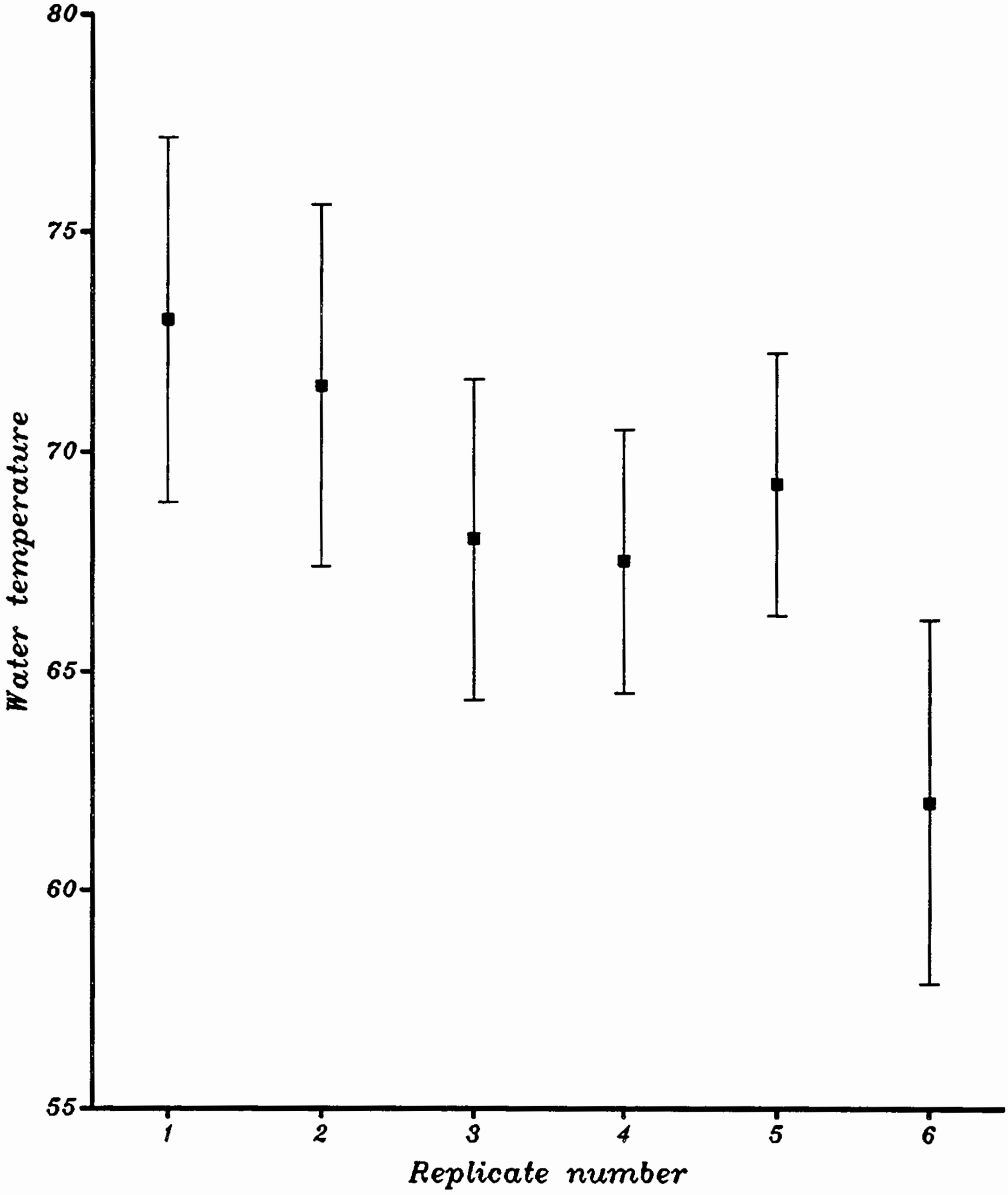

Figure 3.—Average water temperature (°F) during each three-day replicate. Vertical bars represent two standard errors.

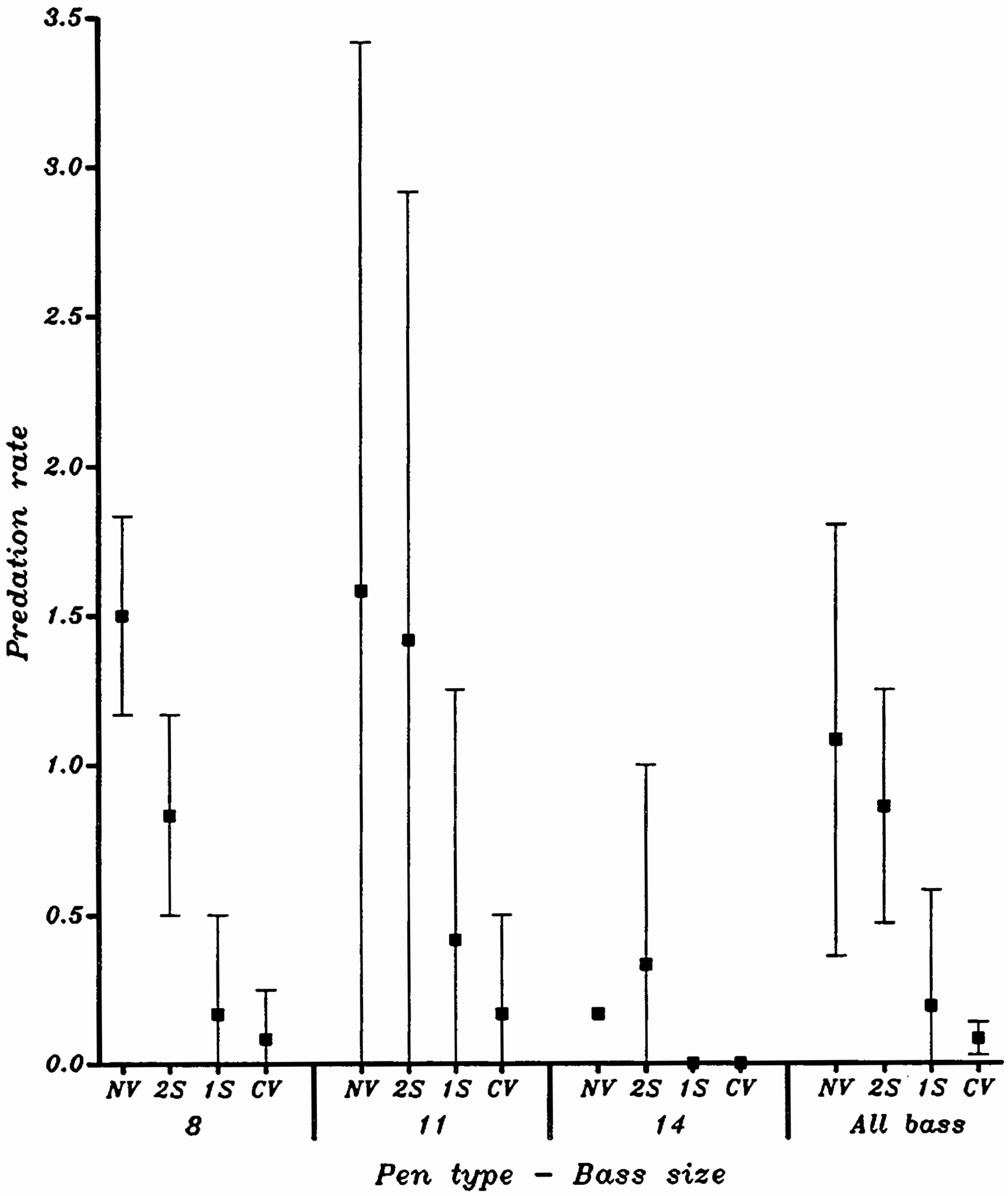

Figure 4.—Average rate of predation on both size groups of bluegills by 8-, 11-, 14-inch, and all sizes of bass combined, for each pen type. Vertical bars represent two standard errors.

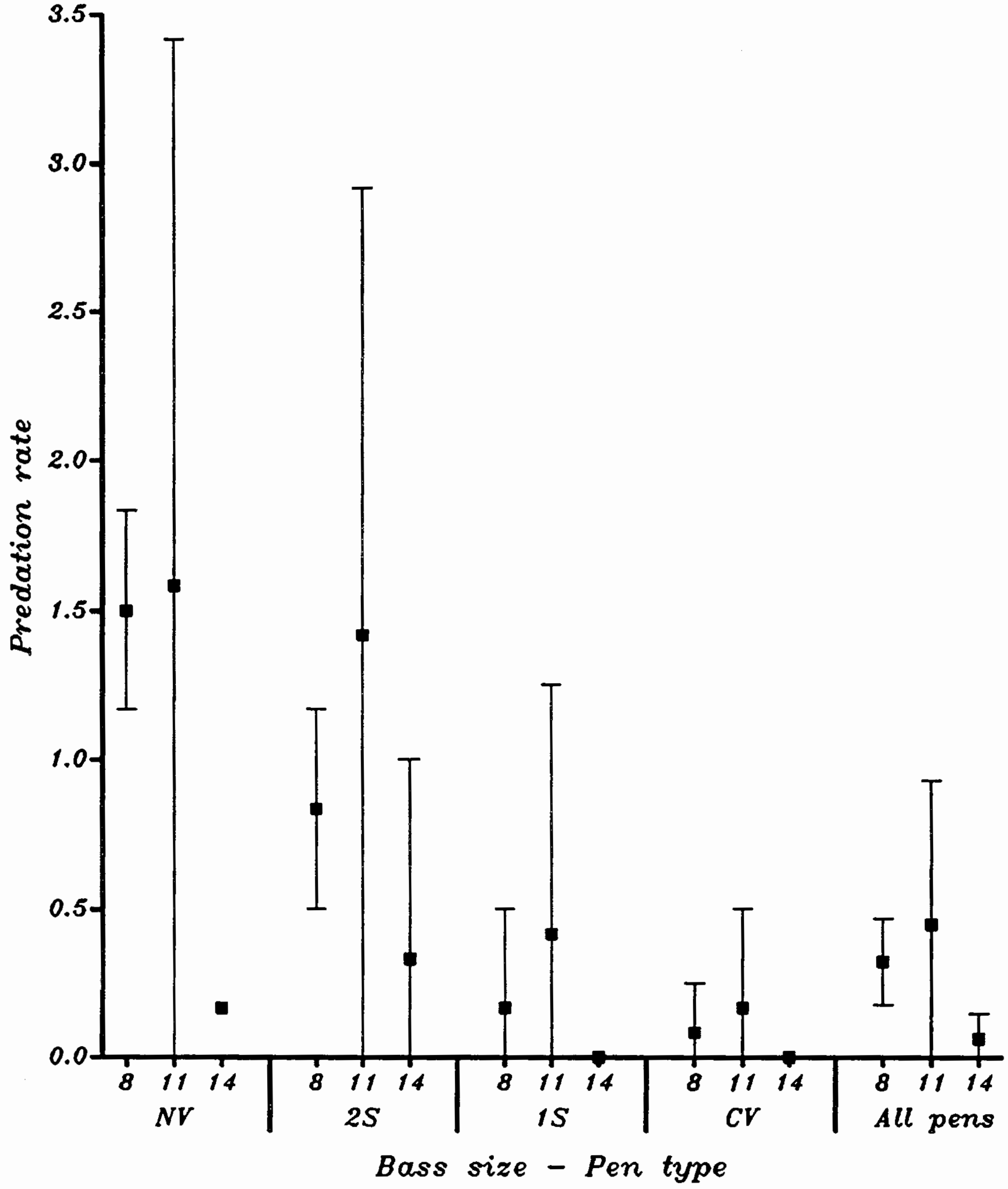

Figure 5.—Average rate of predation on both size groups of bluegills by 8-, 11-, and 14-inch bass, for each pen type and all pens combined. Vertical bars represent two standard errors.

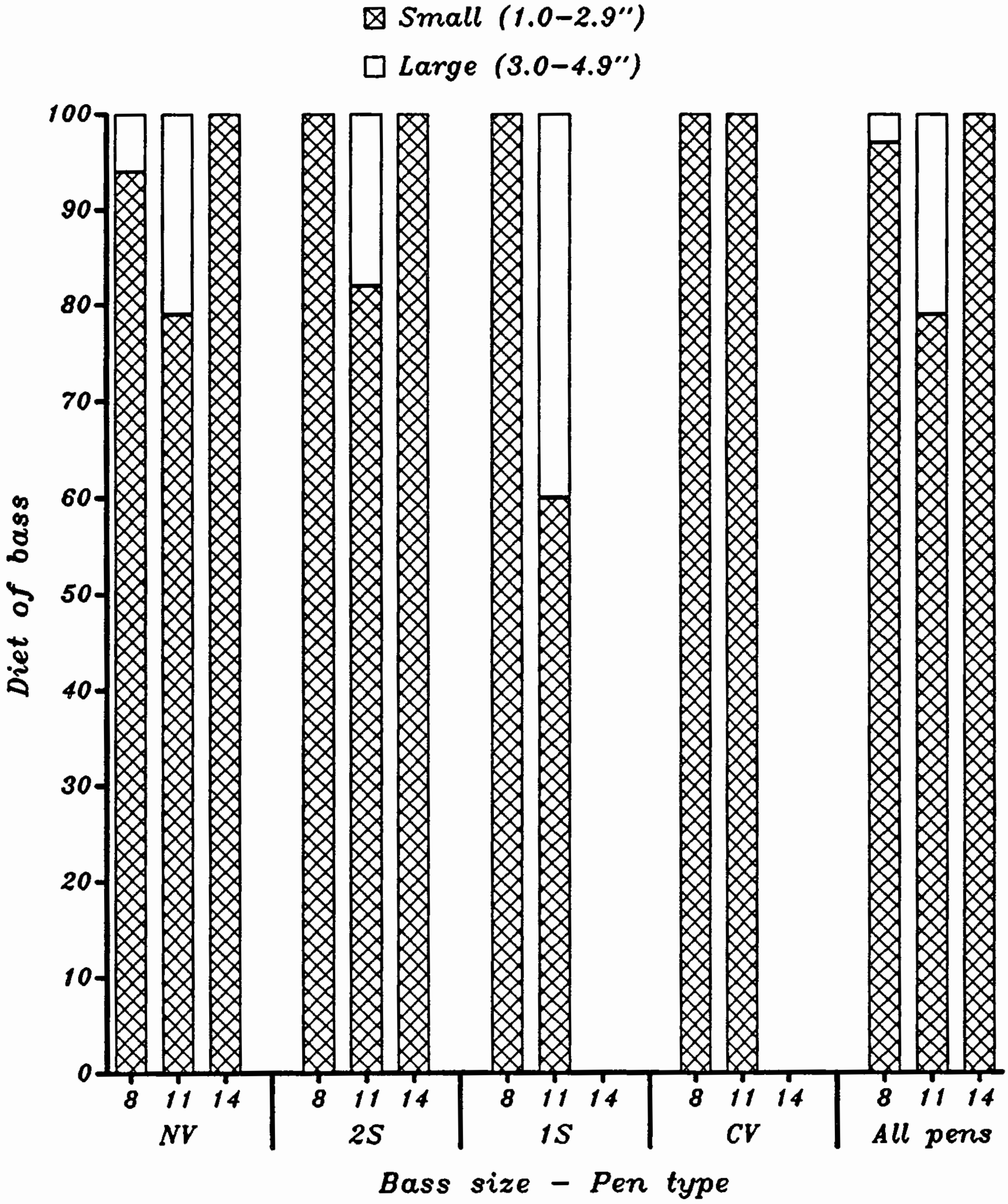

Figure 6.—Percent of small and large bluegills in the diet of 8-, 11-, and 14-inch bass over all replicates, for each pen type and all pens combined.

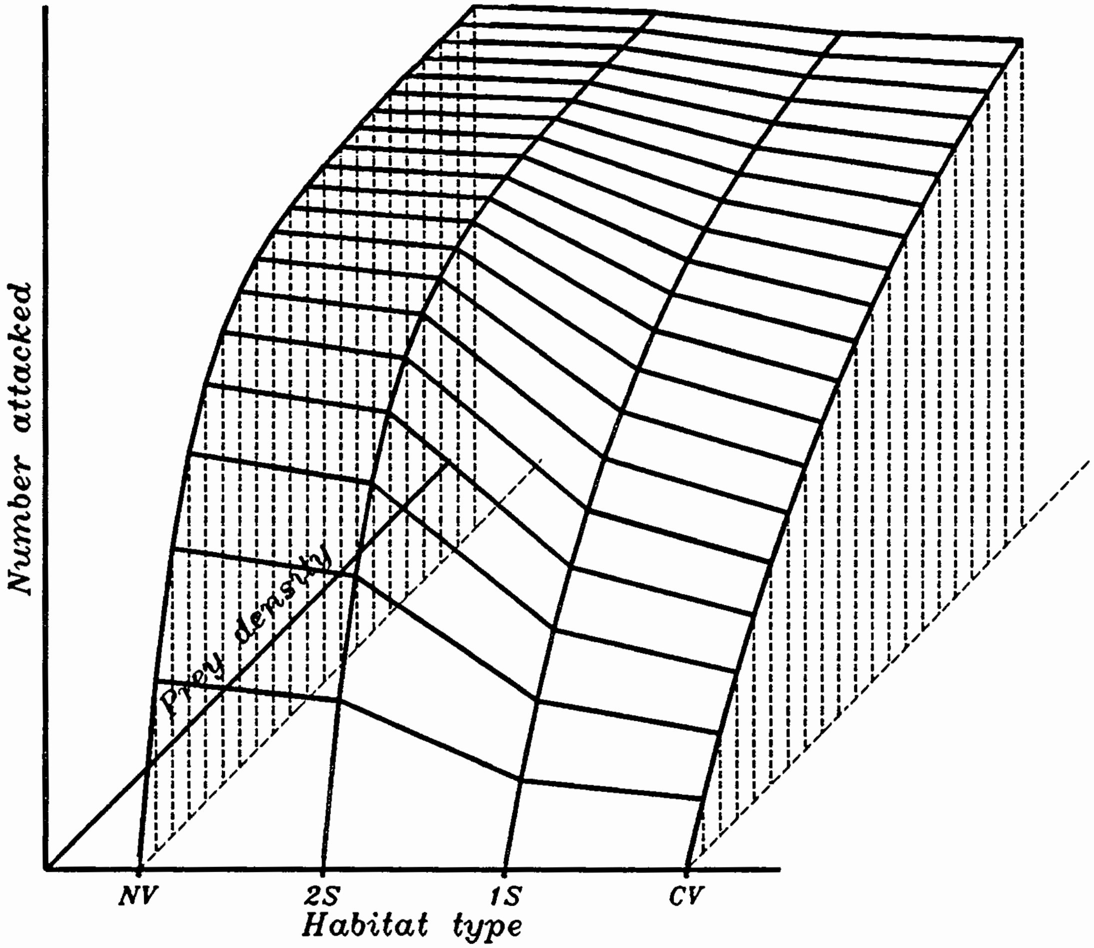

Figure 7.—Hypothetical effects of increasing prey density and amount of edge on numbers of prey attacked, showing a Type II functional response to prey density and a sigmoid response to habitat type.

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