

## NOTES

### Effects of Predation Risk and Foraging Return on the Diel Use of Vegetated Habitat by Two Size-Classes of Bluegills

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**Abstract.**—Little is known about nocturnal habitat selection by fishes under the risk of predation. Using a photoperiod of 15 h light : 9 h dark, we quantified the diel use of artificial macrophytes and open water by two size-classes of bluegill *Lepomis macrochirus* when the open water was empty (control), contained food, or contained both a caged predator and food. Small bluegills (6.2–7.7 cm total length) spent significantly more time in macrophytes in the predator and food treatment than in the control, followed by the food-only treatment. In addition, small bluegills spent significantly more time in macrophytes during the day than at night in all treatments. The frequency with which small bluegills were found in the same location in subsequent observations was significantly higher in the predator and food treatment during the day than in any other treatment and light combination. Large bluegills (10.2–13.0 cm total length) showed no difference in habitat use among treatments but spent significantly less time in macrophytes at night than during the day. There was no difference in the frequency with which large bluegills were found in the same location in subsequent observations among treatments or light levels. This suggests the potential for a diel littoral–pelagic habitat change by juvenile bluegills that would have important implications for the role of bluegills in lake food webs, including the possibility of nutrient translocation that could generate alternate stable states in lakes.

Predation can have strong structuring effects on communities through direct consumption of prey organisms (i.e., top-down control; Hairston et al. 1960; Carpenter et al. 1985). However, predation can also cause indirect effects by altering the behavior of prey with respect to habitat selection, diet, feeding rate, foraging location, activity level, and reproduction (see reviews by Dill 1987; Mittelbach and Chesson 1987; Sih 1987, 1994; Lima and Dill 1990). These behavioral changes, in turn, can lead to changes in competitive interactions

(Kotler and Holt 1989; Werner 1991; Abrahams 1994) and top-down control effects (Power et al. 1985; He et al. 1993), which ultimately may lead to changes in community structure. Organisms often realize reduced growth rates as a direct consequence of altering their behavior to lower predation risk (Mittelbach 1981; Gotceitas 1990a; Savino et al. 1992; Diehl and Eklov 1995).

Predation-induced habitat changes are well-documented in fish predator–prey systems, typically involving movement from open waters when predation risk is low into dense vegetated habitat when predation risk is high (e.g., He and Kitchell 1990; Diehl and Eklov 1995; Chick and McIvor 1997). Despite this wealth of research, most studies have only considered daytime habitat selection. However, many field studies suggest that some fishes forage in macrophytes during the day when predation risk is great and in open water at night when predation risk is reduced (e.g., Rodeheffer 1939; Emery 1973; Hall et al. 1979; Bohl 1980; Gaudreau and Boisclair 2000). Most of these studies used different types of sampling gear in vegetated versus open waters, making it difficult to determine whether diel differences were due to fish migration or diel variation in gear selectivity. Even studies using similar gear types in both habitats cannot rule out the possibility that there are two subpopulations, one that stays in open water and has a peak activity at one time of day, and one that stays in vegetation and has a peak activity at a different time of day. We know of only four studies in which diel effects of predation risk on fish habitat selection were examined in controlled experiments (Fraser and Cerri 1982; Schlosser 1988; Jacobsen and Berg 1998; Jacobsen and Perrow 1998), and they give conflicting results, indicating that diel habitat changes may depend on the specific predator–prey system considered.

Bluegills *Lepomis macrochirus* and largemouth bass *Micropterus salmoides* are important game fish species that are widespread across the conti-

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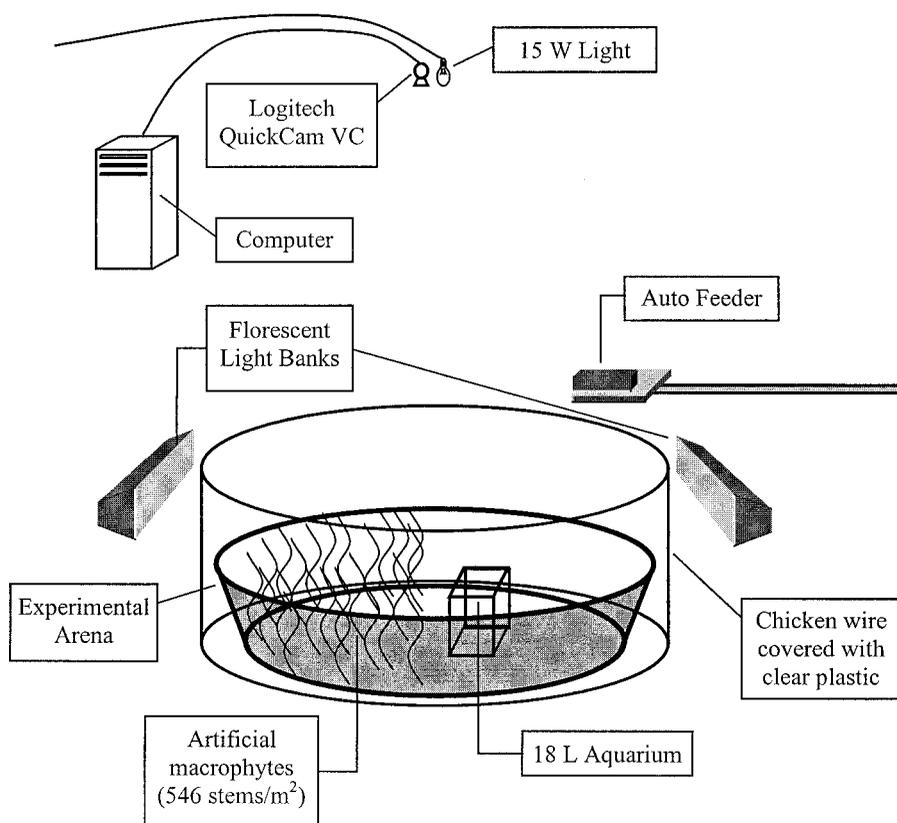


FIGURE 1.—Experimental arena used to test diel habitat preferences of bluegills under different predation risks and foraging-return conditions. A black plastic curtain surrounded the entire arena during experiments.

mental United States and are often locally very abundant. As such, the largemouth bass–bluegill predator–prey system has been extensively studied. Many studies have shown that bluegills at risk to largemouth bass predation seek out dense cover during daylight hours (e.g., Mittelbach 1981; Werner and Hall 1988; Turner and Mittelbach 1990). This habitat change by bluegills leads to foraging on less profitable prey types during the day, which would be expected to reduce bluegill growth rates (Mittelbach 1981; Gotceitas 1990a; Savino et al. 1992; but see Hayse and Wissing 1996). We are not aware of any study that has directly tested the effect of predation risk on bluegill habitat selection at night. The purpose of this study was to determine the effect of predation risk and foraging return on bluegill habitat selection (vegetated or open water) under simulated day and night conditions in a controlled laboratory environment.

#### Methods

Small (6.2–7.7 cm total length) and large (10.2–13.0 cm) bluegills were collected by seining Sandy

Lake in Portage County, Ohio. This small natural lake has a well-developed littoral zone and abundant adult largemouth bass and walleyes *Stizostedion vitreum*. All fish were first acclimated to the laboratory ( $\geq 100$  d) until they learned to readily eat crushed commercial pellets (Onarch Mistermix trout pellets 36% trout ration number 9715). Throughout the acclimation period and experiments, fish were maintained under a photoperiod of 15 h light : 9 h dark and at a water temperature of  $20 \pm 1.5^\circ\text{C}$ .

The experimental arena (Figure 1) was a 1.3-m-diameter  $\times$  25-cm-deep wading pool (filled with water to a depth of 23.5 cm) that had been painted white with latex paint. A digital video camera (parallel port Logitech Quick Cam VC) connected to a computer was suspended 2.7 m above the arena. This camera recorded 24-bit gray-scale ( $320 \times 240$  bitmap) images every 15 min during experiments. Two fluorescent light banks (two 40-W florescent lights in each bank) were placed on opposite sides of the arena. Lights were oriented facing each other (horizontally) 0.5 m above the water surface.

This arrangement minimized light glare in the bitmap images. Florescent lights were connected to a timer to control photoperiod. Chicken wire with clear plastic taped to it was wrapped around the arena to diffuse light, thus minimizing differences in illumination in different parts of the arena. This also prevented fish from jumping out of the arena. A 15-W incandescent light controlled by a rheostat and suspended from the ceiling was used to simulate "night" light levels; light intensity was adjusted to approximately half that of the full moon and stars on a clear night. Light intensity at 11 locations in the arena was measured with a Gossen Luna Pro light meter between replicate fish to ensure similar lighting among fish. Day (florescent lights on) and night (only incandescent light on) light levels at the 11 locations in the arena averaged  $509 \pm 98$  and  $1.1 \pm 0.05$  lx. Light readings were always symmetrical on the two sides of the arena.

One-half of the arena contained artificial macrophyte stems constructed from 23-cm-long pieces of 0.3-cm-diameter yellow polypropylene rope attached to 0.64-cm, 23-gauge galvanized steel hardware cloth that was cut to fit into half the bottom of the arena. The edge of the artificial macrophytes was oriented to be parallel to the two light banks. Stem density, at 546 stems/m<sup>2</sup>, was slightly above the threshold level (516 stems/m<sup>2</sup>) at which juvenile bluegills choose a plot of vegetation as a refuge from largemouth bass (Gotceitas and Colgan 1989). This density also nearly eliminates the ability of largemouth bass and northern pike *Esox lucius* to capture bluegills (Savino and Stein 1982, 1989). The other half of the arena contained an 18.9-L glass aquarium centered in the arena approximately 4 cm from the edge of the artificial macrophytes. Three different treatments were administered sequentially on this side of the arena. The first treatment was the control treatment, which had only the aquarium. A second treatment was the food-only treatment, which had the aquarium and an automatic feeder (Fish Mate model F14) suspended 1.6 m above the water surface. Food cells in the feeder were subdivided so that two crushed food pellets (approximately 6 mg for small and 12 mg for large fish) were delivered during a 2-h interval four times each day. The third treatment was the predator + food treatment, which had the automatic feeder as in the second treatment and a 23.2-cm (total length) largemouth bass placed in the aquarium. Putting the bass in the aquarium provided a visual stimulus but no olfactory cue and no actual risk of injury to the

bluegills. The same individual bass was used in all trials. The side of the arena on which the artificial macrophytes were placed was randomized between replicate fish. The treatments were always administered in random order to the side without macrophytes. Preliminary tests indicated that there was no significant difference in the amount of time spent on the two sides of the arena by bluegills when both sides were empty (no macrophytes, aquarium, or treatments). Arcsine-transformed data were tested by means of a one-sample, two-tailed *t*-test using a hypothesized population mean equal to 50% of the observations on side A and a significance level of 0.05 ( $t = 2.76$ ,  $df = 3$ ,  $P = 0.07$  for day;  $t = 2.76$ ,  $df = 3$ ,  $P = 0.32$  for night).

Six small and three large bluegills were used in the experiment. Lawrence (1958) and Hambricht (1991) found that largemouth bass could eat fish with a maximum body depth equal to or slightly larger than their mouth width. The bass used in the predator and food treatment had a 22-mm mouth width. Small fish had a maximum body depth of 15–22 mm and would therefore be vulnerable to a bass of this size. Large fish had a maximum body depth of 30–39 mm and would not have been vulnerable to this size of bass.

The order in which each bluegill received the three treatments was randomized. To begin a trial, the experimental arena was filled with aged tap water and the first treatment to be administered to the bluegill was set up. An individual bluegill was then added to the center of the arena, and a black plastic blind around the arena was lowered. The bluegill was allowed to acclimate at least 7 h before data were collected. Preliminary data indicated fish habitat selection and activity levels always stabilized within 6 h, regardless of treatment. Data collection always began at the night period (florescent lights off). Pictures were taken every 15 min for 57 h (two day period and three night periods). This typically produced 120 day pictures and 108 night pictures. At the end of this treatment, the blind was raised and the next treatment was set up. The fish was again given at least 7 h to acclimate after the blind was lowered before data were collected. This procedure was repeated until the fish had received all three treatments. The arena was drained, rinsed and refilled before the next bluegill was tested.

The location of the bluegill in each bitmap image was recorded using a macro program that recorded in a spreadsheet the *x*- and *y*-coordinates of the fish. The picture resolution and camera position allowed for discrimination of fish locations

as close as 0.6 cm. Because there were a different number of pictures analyzed from day and night periods, and because some replicates had fewer than normal pictures due to occasional computer glitches, we measured the percent of observations where the bluegill was on the macrophyte side of the arena instead of the actual number of occurrences. Percentage data are typically binomial rather than normally distributed (Zar 1984). Although the analysis of variance (ANOVA; Zar 1984) and Tukey test (Keselman 1976) procedures are quite robust with respect to violations of the normality assumption, we performed an arcsine-transformation using Freeman and Tukey's modification (Zar 1984) to normalize the data before analysis. A two-factor (treatment  $\times$  light level) repeated-measures (subjects) ANOVA was used to test for differences in the proportion of time spent in the macrophytes among treatments and light conditions.

Savino and Stein (1982) found that bluegills under the threat of predation remained motionless for long periods. To assess this behavior in our experiment, we calculated the percent of observations where the bluegill was observed in the same location as the previous observation. A two-factor (treatment  $\times$  light level) repeated-measures (subjects) ANOVA was used to test for differences in the percent of observations where the bluegill was observed in the same  $x$ - and  $y$ -coordinates as the previous observation among treatments and light conditions. The data were arcsine transformed using Freeman and Tukey's modification (Zar 1984) before analysis.

Small and large fish were expected to have different predation risks. Therefore, the treatments probably provided a different stimulus for the different size-classes. Because of this, data from the two size-classes were analyzed using separate ANOVAs. When ANOVA procedures detected significant differences ( $\alpha = 0.05$ ), a Tukey test was used to determine which levels of the factors differed.

### Results

The amount of time small fish spent in the macrophytes differed significantly among treatments ( $F_{2,10} = 30.7$ ;  $P < 0.01$ ) and light levels ( $F_{1,5} = 29.5$ ;  $P < 0.01$ ; Figure 2). Small fish spent the most time in macrophytes in the predator + food treatment (Tukey  $P < 0.01$ ), followed by the control (Tukey  $P < 0.01$ ) and food only (Tukey  $P < 0.01$ ) treatments. Small bluegills always ate all available food pellets during the food-only treat-

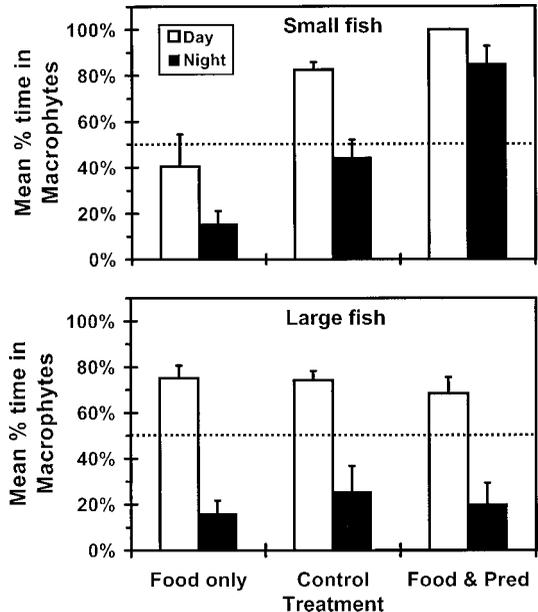


FIGURE 2.—Mean percent of observations in which small (6.2–7.7 cm total length) and large (10.2–13.0 cm) bluegills were in artificial macrophytes (one-half of tank area) under three treatment conditions: no treatment (control), food only, or predator (pred) and food. Food was presented on the side of the tank without macrophytes. The photoperiod consisted of 15 h light:9 h dark. Bars indicate SEs.

ment but always left some food uneaten in the predator + food treatment. Small fish spent significantly more time in macrophytes in the day than in the night period (Tukey  $P < 0.01$ ). There was no significant treatment  $\times$  light level interaction ( $F_{2,10} = 0.5$ ;  $P = 0.60$ ), indicating that the pattern of habitat selection across treatments was the same under both light conditions.

The percentages of observations in which small fish were observed in the same location as in the previous observation differed significantly among treatments ( $F_{2,10} = 5.8$ ;  $P = 0.02$ ) and light levels ( $F_{1,5} = 19.8$ ;  $P < 0.01$ ; Figure 3). There was also a significant interaction ( $F_{2,10} = 9.1$ ;  $P < 0.01$ ), indicating that the effect of treatments was different when light levels were different. Significantly more fish remained in the same location as previously observed in the predator + food treatment under day light conditions than in any other treatment and light combination (Tukey  $P < 0.01$ ; Figure 3), none of which differed significantly.

In contrast to small fish, large fish showed no significant difference in the time spent in macrophytes among treatments ( $F_{2,4} = 0.2$ ;  $P = 0.85$ ;

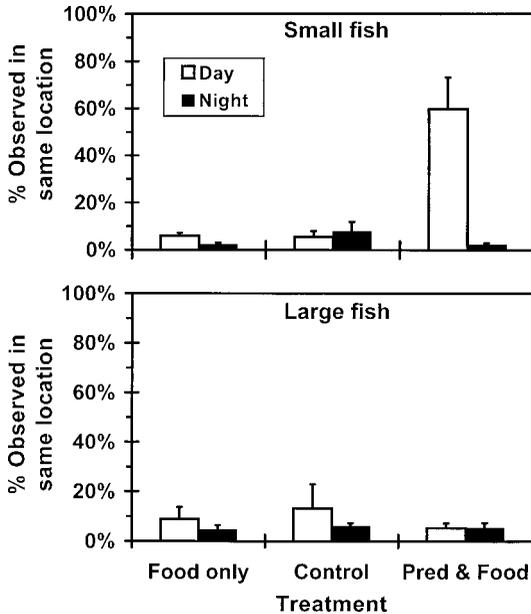


FIGURE 3.—Mean percent of observations in which a tested bluegill was found in same position as in the previous observation. Results compare small (6.2–7.7 cm) and large (10.2–13.0 cm) bluegills under three treatment conditions: no treatment (control), food only, or predator (pred) and food. The photoperiod consisted of 15 h light: 9 h dark. Bars indicate SEs.

Figure 2). All large fish ate all available food pellets in both the food-only and the predator + food treatments. However, as with small fish, large fish showed a significant difference in the time spent in macrophytes in day versus night periods ( $F_{1,2} = 48.8$ ;  $P = 0.02$ ), more time being spent in macrophytes during the day period (Tukey  $P = 0.02$ ). There was no significant treatment  $\times$  light level interaction ( $F_{2,4} = 0.5$ ;  $P = 0.64$ ). The percentages of observations where large fish were observed in the same location as in the previous observation did not differ across treatments ( $F_{2,4} = 0.6$ ;  $P = 0.61$ ) or light levels ( $F_{1,2} = 0.6$ ;  $P = 0.53$ ), nor was there a significant treatment  $\times$  light level interaction ( $F_{2,4} = 0.3$ ;  $P = 0.75$ ; Figure 3).

### Discussion

Bluegills spend 1–2 months after hatching eating zooplankton in the pelagic habitat, then shift to littoral habitat to avoid predation until they are 51–83 mm (total length), when they again return to the pelagic zone to feed on zooplankton (Werner 1969; Werner et al. 1977, 1983; Werner and Hall 1988). Our results for 62–77 mm bluegills are consistent with these and other studies that have dem-

onstrated that juvenile bluegills seek dense cover to avoid largemouth bass predation risk during daylight (e.g., Mittelbach 1981; Gotceitas and Colgan 1987; Werner and Hall 1988; Turner and Mittelbach 1990; Hayse and Wissing 1996). Foraging in the littoral zone often is less profitable for these intermediate-sized bluegills, which can lead to slower growth rates (Mittelbach 1981; Gotceitas 1990a; Savino et al. 1992; but see Hayse and Wissing 1996). Our results show that these intermediate-sized fish may not spend all their time in the littoral zone but may move to open-water areas to forage on zooplankton at night and therefore might not suffer as large a decrease in growth as previously thought. Several other studies have shown similar diel changes in habitat use by other fishes under the risk of predation (Fraser and Cerri 1982; Schlosser 1988; Jacobsen and Berg 1998; Jacobsen and Perrow 1998).

Several field studies have suggested that bluegills migrate between littoral and pelagic habitats on a diel basis (Baumann and Kitchell 1974; Werner et al. 1977; Helfman 1981). These studies proposed that bluegills were in pelagic habitat during day and littoral habitat at night, which is opposite to the pattern we observed in the laboratory. This disparity could be explained by differences between conditions in the field and the laboratory (e.g., turbidity, higher day light levels, different predator densities or food abundance levels between habitats). Baumann and Kitchell (1974) and Helfman (1981) suggested the diel changes in habitat they observed were the result of diel changes in prey availability of the two habitats. In our experiment, the relative foraging potential of the two habitats was constant. However, the predation risk associated with open water would be lower at night than during day because largemouth bass are not as effective at foraging on bluegills at the low light levels used in the night period of our experiment (Howick and O'Brien 1983; McMahan and Holanov 1995). Therefore, the results of our experiment indicate that bluegills can be induced to change habitats on a diel basis, even when no change in foraging return between habitats occurs.

Ultimately, habitat selection by bluegills would be expected to follow a pattern that minimizes the ratio of mortality risk to feeding rate ( $\mu/f$ ; Gilliam and Fraser 1987; Gotceitas 1990b). Therefore, bluegills would be most likely to use pelagic habitat at night in those lakes where large-bodied zooplankton are more abundant at night due to vertical migration (Wetzel 1983) or lakes where the dominant piscivores are not efficient nighttime foragers

(e.g., largemouth bass; Howick and O'Brien 1983; McMahon and Holanov 1995).

We also found that small bluegills were found in the same location in our behavior arena on subsequent observations significantly more often in the predator + food treatment during the day period than in any other treatment and light-level combination. It was common to find the bluegills in the same position at the edge of the tank farthest from the predator in successive pictures covering several hours. When these bluegills were eventually found in a different position, it often was only a few centimeters from the original location, and these fish usually were found in the new position in successive pictures for several more hours. This is consistent with the results of Savino and Stein (1989) who found that when bluegills observed a foraging bass, they moved out of predation range and remained motionless. Although this reduced activity by bluegills appears to reduce the reactive distance for largemouth bass preying on bluegills (Howick and O'Brien 1983), it probably comes at the cost of reduced food consumption (Fraser and Gilliam 1987; Lima and Dill 1990).

Large bluegills did not differ in their habitat use among treatments. Because these fish were too large to be vulnerable to the predator we used, we did not expect a significant difference between the food-only and the predator + food treatment. However, it is not clear why these fish did not use the open water more in the treatments with food than in the control treatment. When presented with a choice between habitat patches with different prey densities, bluegills accurately choose the patch with the highest foraging profitability (Wildhaber and Crowder 1991), regardless of predation risk or stem density of the patch (Gotceitas and Colgan 1990). Bluegills also use foraging return as the criteria for deciding when to leave a patch of vegetation (DeVries et al. 1989; Wildhaber and Crowder 1991). Therefore, it would be hypothesized that our large bluegill would spend more time on the side where food was presented. Further research is needed to identify the mechanism underlying this result.

Both length-classes spent significantly more time in the open water at night than during the day across all treatments. This indicates the potential for a diel littoral–pelagic habitat change by juvenile bluegills. If this behavior occurs in the field, it would have several important biological implications. First, it could lead to failed biomanipulation efforts, where piscivores are stocked to create a trophic cascade (i.e., piscivores are added to

the system to reduce planktivore biomass, which in turn releases zooplankton from predation control and allows zooplankton to decrease phytoplankton biomass through direct consumption). If bluegills are the planktivore of the system and they refuge in vegetation during the day and feed on zooplankton in the open water at night (when piscivores are not effective at capturing them), then the addition of piscivores will have no effect on phytoplankton biomass. Second, it would also produce a spatially subsidized food web (Polis et al. 1997) that could lead to larger bluegill populations than would be possible if bluegills stayed only in the littoral habitat, where food quality is reduced, or in the pelagic habitat, where heavy predation mortality would occur. And third, it could generate a net flux of nutrients between the littoral and pelagic habitats that could regulate productivity of the two habitats (Kitchell 1980; Carpenter et al. 1992; Schindler et al. 1996; Vanni 1996; Shoup 2001), potentially providing a stabilizing mechanism for the alternate stable states observed in some lakes (Hosper and Jagtman 1990; Scheffer 1990; Scheffer et al. 1993).

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