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The effect of vegetation density on juvenile bluegill diet and growth

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Experimental ponds (0.4 ha) were used to evaluate the effects of vegetation density on bluegill (*Lepomis macrochirus*) diet and growth in the absence of pelagic predation risk. Fish (30–50 mm, total length) were stocked at a rate of 15 kg per pond. By the end of the 3-month experiment, bluegill in the low vegetation treatment (109 g $m^{-2} \pm 21.0$ SE, $n = 4$) had grown 20% longer than the fish in the high vegetation treatment (712 g $m^{-2} \pm 54.3$ SE, $n = 4$) despite having similar mean stomach fullness. Bluegill in the high vegetation treatment ingested more gastropods and odonates and less benthic prey (chironomids) than did the fish in the low vegetation treatment. Very little pelagic zooplankton were eaten by fish in either treatment despite the lack of predation risk in the open water habitat. These results suggest that bluegill chose to forage in a vegetated habitat even in the absence of predation risk, resulting in reduced growth.

Keywords: habitat complexity; vegetation density; bluegill *Lepomis macrochirus*; habitat preference; growth; predation risk

Introduction

Many juvenile fishes select structurally complex habitats, such as submerged vegetation, in response to predation risk (Magnhagen 1988; Persson and Eklov 1995; Olson et al. 2003b; Abdel-Tawwab 2005). However, structurally complex habitats can reduce foraging return and growth rate of juvenile fishes (Persson 1991; Diehl and Eklov 1995; Shoup et al. 2003). The optimal diet for juvenile bluegill (*Lepomis macrochirus*) is often considered to be pelagic zooplankton (Mittelbach 1981). Yet juveniles often forage suboptimally in structurally complex habitats, such as dense vegetation, to avoid pelagic predation risk (Mittelbach 1981), which can be a major factor determining recruitment to age-1 (Santucci and Wahl 2003). Studies of bluegill behavior in the laboratory (Gotceitas and Colgan 1987; Savino and Stein 1989; Shoup et al. 2003) and in ponds (Werner et al. 1983a) both show that bluegill spend more time in structurally complex habitats when predators are present. Furthermore, structurally complex habitats can negatively affect foraging returns of juvenile bluegill (Mittelbach 1981; Gotceitas 1990a; Pothoven et al. 1999), and vegetation density negatively correlates with bluegill growth (Shoup et al. 2007).

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However, other studies have found that fast-growing juvenile bluegill eat mostly littoral invertebrates (Schneider 1999; Olson et al. 2003a) or that increased vegetation density either has no effect (Savino et al. 1992; Hayse and Wissing 1996) or even increases bluegill growth (Richardson et al. 1998), suggesting that foraging in vegetated habitat may not be suboptimal. The lack of growth effect may, in part, be caused by the greater biomass of prey resources that occurs as vegetation biomass increases (Gerking 1957; Gotceitas and Colgan 1990; Savino et al. 1992). All these studies were conducted in environments with different levels of predation risk, and therefore, it is difficult to determine if changes in growth were related to predator avoidance behavior or vegetation-related effects on prey choice or foraging efficiency. Therefore, the role of vegetation density in influencing juvenile bluegill diet and growth remains unclear.

Foraging by fishes can be affected in many ways by habitat, which can influence prey abundance (Gerking 1957; Savino et al. 1992; Barwick 2004), behavior patterns (Savino and Stein 1989), predator attack success (Savino and Stein 1982; Gotceitas and Colgan 1987), and ultimately prey selection (Schramm and Zale 1985; Dibble and Harrel 1997; Shoup and Wahl 2009) and competitive interactions (Abrahams 1994; Wellenreuther et al. 2007; Robertson et al. 2008). Therefore, changes in vegetation abundance could cause changes in diet and growth rate of juvenile bluegill that are independent of the effects of predation risk.

Previous studies of the role of vegetation densities in the absence of predation risk have used enclosures in lakes (Savino et al. 1992) or ponds (Crowder and Cooper 1982) that had homogeneous vegetation growth rather than the combination of littoral and pelagic habitat that exists in most natural systems. Werner et al. (1983b) conducted an unreplicated pond experiment with both littoral and pelagic habitat, but with a single density of emergent vegetation. Because of the conflicting information in the literature related to optimal foraging habitat for juvenile bluegill in natural systems and the complexity of predation risk-foraging return trade-offs, additional information is needed to quantify the effects of vegetation density independent of the influence of predation risk. In this study, replicated ponds were used to assess the effect of vegetation density on diet and growth of juvenile bluegill in the absence of predation risk.

Methods

Eight experimental 0.4-ha ponds (mean depth of 1 m) were used to evaluate the effects of habitat complexity on growth of small bluegill. The ponds were located at the Sam Parr Biological Station in Kinmundy, Illinois, USA. Vegetation was dominated by brittle naiad (*Najas minor*), with lesser amounts of *Chara* spp. and coontail (*Ceratophyllum demersum*). Sparse patches of emergent vegetation such as water primrose (*Ludwigia hexapetala*) and cattail (*Typha* spp.) were also present. The ponds, containing established vegetation, were drained and refilled with lake water from adjacent Forbes Lake (filtered to exclude fish) in mid-June to allow for colonization of zooplankton and benthic invertebrates, and to allow time to establish the vegetation treatments. After 1 month (11 July), each pond was stocked with 15 kg of young-of-year bluegills (30–50 mm, total length (TL), approximately 20,000 fish per pond) to produce a natural density for small ponds (Hackney 1979; Wahl and Stein 1988).

In order to create the two levels of vegetation complexity, grass carp (*Ctenopharyngodon idella*; ~200 mm, TL) were used to control macrophytes in four randomly selected ponds (low vegetation treatment). The four other ponds (high vegetation treatment) received four grass carp that were enclosed in a $2 \times 2 \times 1.5$-m mesh cage and fed grass clippings, so that nutrient flux into the water column from fish was similar between treatments. Grass was fed at a rate of 40% of total estimated grass carp body weight per day (Wiley and Wike 1986). Ponds had similar topography and were sufficiently deep at their deepest point that even in the high vegetation treatment approximately 20% of the pond surface area did not contain vegetation.

Plant biomass was determined by identifying and weighing (to the nearest g) the above-ground plant material contained within 1-m diameter rings (0.785 m^2) placed at 10 random locations within the littoral zone of each pond. Plant biomass was determined in this fashion every 2 weeks to verify that the treatments were maintained throughout the experiment.

Bluegill diet data were collected by dissection from up to 15 fish per pond during the last week of August and again at the end of the experiment. Stomachs were preserved in 95% ethanol until they could be analyzed in the laboratory where stomach contents were identified to the lowest possible taxonomic group (typically family). Once sorted and enumerated, up to 10 prey items of each taxa from each fish were measured using an optical micrometer ($\pm$0.04 mm). Prey lengths were converted to pre-digested dry-weight biomass using published regression equations (Dumont et al. 1975; Smock 1980; Culver et al. 1985; Sample et al. 1993; Benke et al. 1999). On the final day of the experiment (28 September), the ponds were drained and 200 bluegill from each treatment were counted and measured to the nearest mm, TL.

Because vegetation was measured over the course of the experiment, a repeated-measures ANOVA (SAS Proc GLM; SAS Institute 2004) was used to determine if the experimental design was successful in creating high and low vegetation treatments. Bluegill at the end of the experiment were measured (mm, TL) and a mean size was determined for each pond. Mean bluegill size was analyzed using an ANOVA with vegetation treatment as the main effect. Length-frequency distributions between treatments were compared with a Kolmogorov–Smirnov test. Mean stomach fullness (prey biomass divided by bluegill mass) was analyzed using a repeated-measures ANOVA with vegetation treatment and date as factors. Bluegill diet composition was analyzed using two-way MANOVA (ponds treated as subjects, vegetation density and date as treatment factors) conducted with SAS Proc mixed (Wright 1998; SAS Institute 2004). Separate MANOVA analyses were performed for percent by weight and percent by number diet metrics. Only taxa that constituted $\geq$2% of the diet were used as response variables; other taxa were pooled as 'other taxa.' Significant statistical results ($p < 0.05$) in the above tests were subsequently analyzed with a Tukey's test to compare means. Data were transformed (log or arcsine, as appropriate) to meet the assumptions of normality.

Results

While vegetation biomass in the low vegetation treatment was relatively constant over time (mean 109 g $m^{-2} \pm 21$ SE), biomass in the high vegetation treatment (mean 712 g $m^{-2} \pm 54$ SE) first increased and then decreased during the summer but was

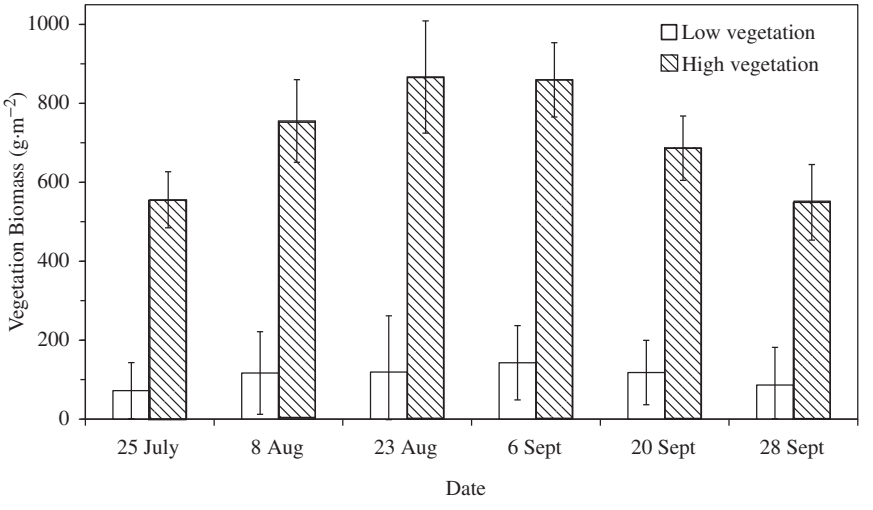

Figure 1. Mean vegetation biomass (g m^{-2} wet weight ± standard error (SE)) of high ($n = 4$; hatched bars) and low ($n = 4$; open bars) vegetation treatments in eight 0.4-ha ponds at the Sam Parr Biological Station, Kinmundy, IL, used to evaluate the effects of habitat complexity on growth of small bluegill. Mean vegetation biomass was 109 g m^{-2} ± 21.0 SE in the low vegetation treatment and 712 g m^{-2} ± 54.3 SE in the high vegetation treatment over the entire experiment.

always significantly higher than in the low vegetation treatment ($p \leq 0.01$ for all comparisons; treatment × date interaction $F_{5,30} = 5.42$, $p < 0.01$; Figure 1). The low vegetation treatment ranged from 72 to 118 g m^{-2}, with the highest values occurring during the midpoint of the experiment. Vegetation density in the high treatment was 556 g m^{-2} at the beginning of the experiment and increased to 867 g m^{-2} by mid-August before it declined to 549 g m^{-2} by the end of the experiment. Vegetation growth was relatively uniform in both treatments.

Growth of bluegill was observed in all ponds and differed between treatments (Figure 2). Pooled length-frequencies from high and low vegetation treatments at the end of the experiment were significantly different ($KS_a = 3.84$, $p < 0.01$), being skewed toward larger sizes in the low vegetation treatment. By the end of the experiment, bluegill from the low vegetation treatment were significantly longer (mean TL ± SE; 84.2 ± 2.5 mm) than bluegill from the high vegetation treatment (74.7 ± 2.4; $F_{1,6} = 7.53$, $p = 0.03$; Figure 2).

Bluegill stomach fullness (mg dry prey biomass/g wet predator biomass) was similar between vegetation treatments ($F_{1,6} = 1.48$, $p = 0.27$) and dates ($F_{1,6} = 0.00$, $p = 0.98$), and there was no treatment by date interaction ($F_{1,6} = 0.13$, $p = 0.73$; Figure 3). However, diet composition varied with treatment (Figure 4). Across all taxa, the effects of treatment varied by date (MANOVA *Wilk's* $\lambda = 0.18$, $F_{10,175} = 16.37$, $p < 0.01$); however, only the treatment effect was significant when the taxa were individually analyzed (all ANOVA interactions $F_{1,12} \leq 2.52$, $p \geq 0.14$). Small effects for some of the diet categories combined to jointly indicate significant interaction in the more powerful MANOVA analysis; in this case, the main effects from ANOVAs can still be interpreted outside of the interactive MANOVA effects (Rencher 1995). Fish from the low vegetation treatment ate a greater proportion by

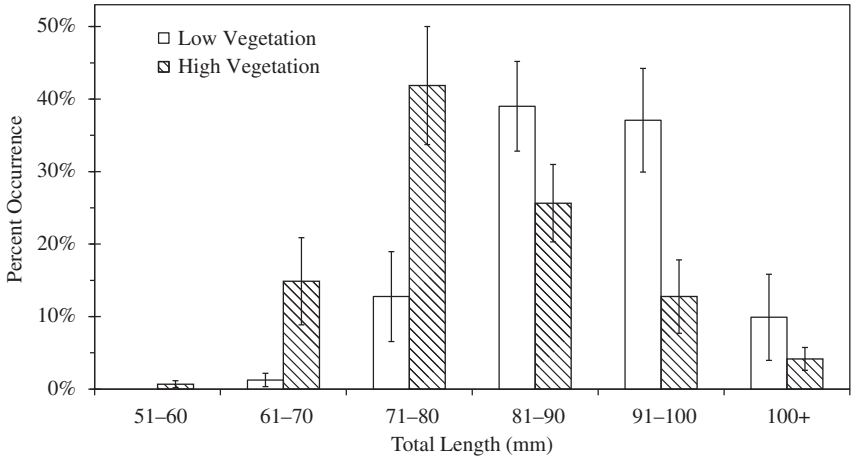

Figure 2. Bluegill length-frequency distribution at the end of a 3-month experiment conducted in eight 0.4-ha ponds. Ponds were either high ($712 \pm 54.3\,g\,m^{-2}$; hatched bars) or low ($109 \pm 21.0\,g\,m^{-2}$; open bars) vegetation biomass treatments. Bluegill were 30–50 mm in TL at the beginning of the experiment. Bars indicate 1 SE.

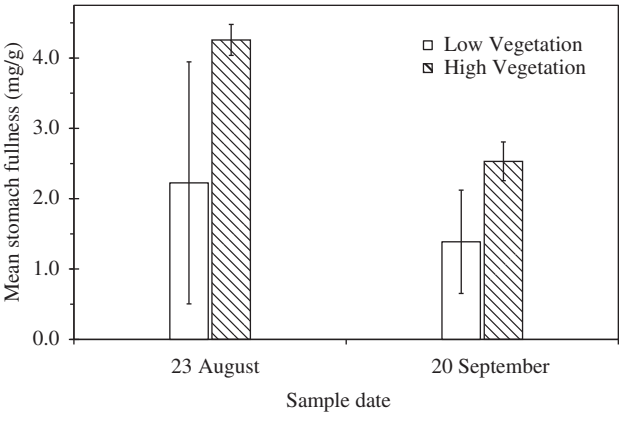

Figure 3. Mean stomach fullness (mg dry prey biomass/g wet bluegill mass) of bluegill from high ($712 \pm 54.3\,g\,m^{-2}$; hatched bars) or low ($109 \pm 21.0\,g\,m^{-2}$; open bars) vegetation treatments over a 3-month experiment conducted in 0.4-ha ponds at the Sam Parr Biological Station to test the effects of vegetation biomass on growth of juvenile bluegill. Bars indicate 1 SE.

weight of chironomids ($F_{1,12} \geq 9.28$, $p = 0.01$) and a lower proportion of gastropods ($F_{1,12} \geq 5.10$, $p = 0.04$) and odonates ($F_{1,12} \geq 5.18$, $p = 0.04$) than fish from the high vegetation treatment (Figure 4). Fish also ate more coleopterans in August than in September ($F_{1,12} \geq 14.79$, $p < 0.01$), but this difference was consistent across vegetation treatments (treatment effect $F_{1,12} \geq 0.27$, $p = 0.61$). For both treatments, zooplankton made up only 6–20% of the diet by weight (Figure 4). Excluding benthic ostracods, zooplankton consumption was $\leq 1\%$ by weight in both treatments.

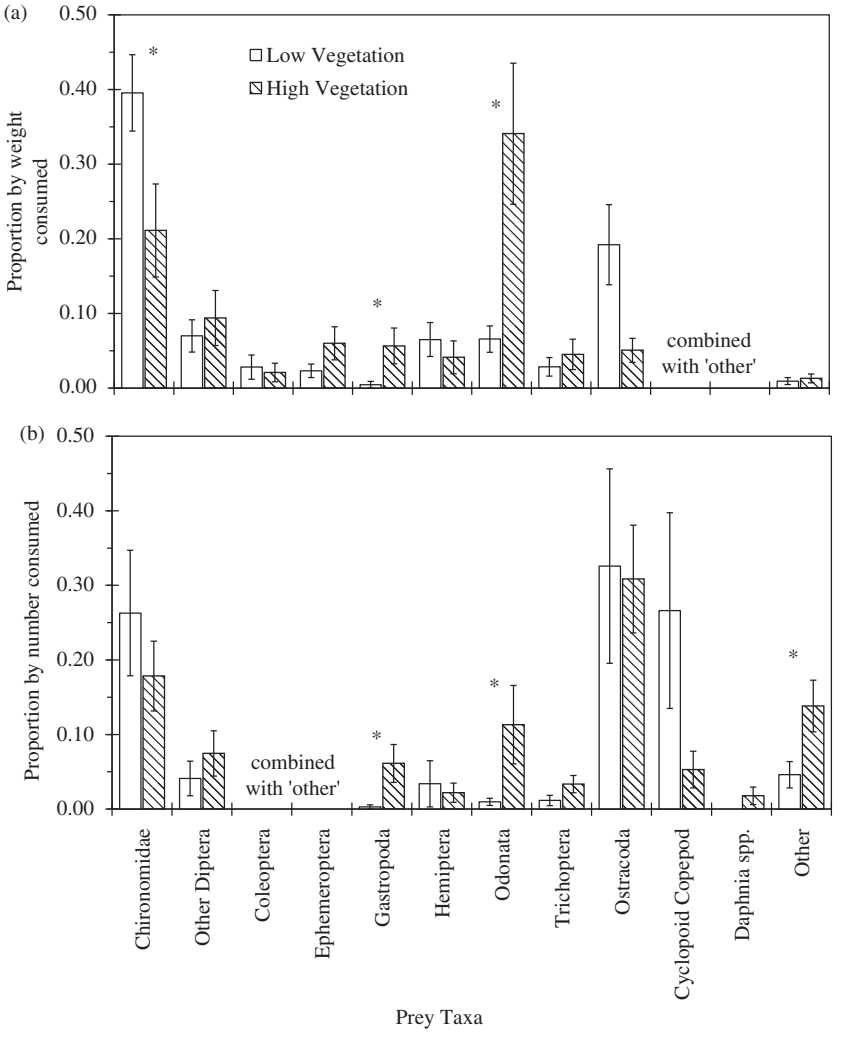

Figure 4. Proportion by weight and number of different prey taxa consumed by juvenile bluegill during a 3-month experiment conducted in 0.4-ha ponds to test the effects of vegetation biomass on growth of bluegill. Ponds were high ($n = 4$; $712 \pm 54.3\,g\,m^{-2}$; hatched bars) or low ($n = 4$; $109 \pm 21.0\,g\,m^{-2}$; open bars) vegetation biomass treatments. Taxa that always had proportion by weight or number $<2\%$ of the total were pooled with unidentifiable taxa as 'other'. Taxa marked 'NA' were grouped as 'other' for the analysis. Bars indicate 1 SE.

Diets expressed as percent by number also varied between treatments (*Wilk's* $\lambda = 0.075$, treatment effect $F_{10,125} = 6.25$, $p = 0.03$). Bluegill from the low vegetation treatment ate fewer gastropods ($F_{1,12} = 4.43$, $p = 0.03$), odonates ($F_{1,12} = 6.40$, $p = 0.03$) and 'other' taxa ($F_{1,12} = 5.81$, $p = 0.03$) than the fish in the high vegetation treatment (Figure 4). Despite their small size, zooplankton still accounted for only 38–59% of fish diets by number (Figure 4). If benthic ostracods are excluded, zooplankton consumption was only 7–27% by number.

Discussion

There is much disagreement in the literature about how vegetation density affects foraging return and growth of juvenile bluegill. Several studies have found reduced foraging return for bluegill when they forage in structurally complex habitats (Mittelbach 1981; Gotceitas 1990a; Pothoven et al. 1999), whereas others have found that bluegill growth was unaffected or even increased when foraging in complex environments (Savino et al. 1992; Hayse and Wissing 1996; Richardson et al. 1998). Much of this is confounded by differing levels of pelagic predation risk; so, it has been difficult to determine if changes in growth were related to predator avoidance behavior or vegetation-related effects on prey choice or foraging efficiency. Our study is the first to examine the effect of vegetation density on diet and growth of bluegill in the absence of predation risk outside of the laboratory environment. Increased vegetation led to a greater use of macrophyte-dwelling insect prey (gastropods and odonates) and reduced use of benthic prey (chironomids). These changes in prey consumption likely caused the observed decrease in growth rate of juvenile bluegill in high vegetation environments.

The difference in growth rates of bluegill in low and high vegetation density could be caused by several mechanisms. First, the high vegetation treatment may have had lower prey abundance, and bluegill were unable to find sufficient food. Prey abundance data were not collected during the experiment; however, this hypothesis does not appear likely as fish in both treatments appeared to find and ingest ample food resources. Mean stomach fullness (1.4–4.3 mg dry prey/g wet predator) was higher than those reported by Booth (1990) for bluegill feeding in Lake Opinicon (0–1.4 mg dry prey/g wet bluegill, depending on the time of the day). Stomach fullness was also similar to fish fed a 2.2% daily ration (g wet prey/g wet bluegill; Gerking 1955), the midpoint of the range of daily rations (1–4%) reported for this species (Gerking 1954; Windell 1966; Keast and Welsh 1968; Whitledge and Hayward 2000). Further, invertebrate abundance typically increases with increased vegetation density (Gerking 1957; Savino et al. 1992; Gotceitas and Colgan 1990), suggesting that insufficient food is not the primary mechanism.

Second, differences in energetic value or digestibility of the prey types eaten by fish in the two treatments may have differed. Bluegill in the high vegetation treatment ingested more gastropods and odonates and less chironomids than did the fish in low vegetation biomass treatment. However, all the commonly eaten prey types have similar energy densities (Cummins and Wuycheck 1971). No published information exists on the digestibility of these prey types to bluegill, but rainbow trout are able to assimilate similar amounts of energy from all three prey types (Groot 1995). Therefore, it seems unlikely that energetic or digestibility differences among prey types could account for the difference in growth rate of bluegill between treatments.

Finally, difference in search efficiency or handling costs could account for the differences in growth rates between treatments. Bluegill that forage in vegetation expend more energy searching for prey (Gotceitas 1990a, 1990b). Reduced search and handling efficiency has also been demonstrated by laboratory studies for roach (*Rutilusrutilus*; Persson 1991) and largemouth bass (*Micropterus salmoides*; Anderson 1984) feeding in dense vegetation. Additionally, gastropods (a prey type heavily used by fish in the high vegetation treatment) require longer handling times than other prey such as chironomids (Mittelbach 1984; Osenberg et al. 1992).

Therefore, while fish from both treatments had similar stomach fullness (suggesting similar consumption rates), it is likely that bluegill in the high vegetation treatment expended more energy to ingest their food, leading to reduced growth. Regardless of the mechanism, our results demonstrate that increased vegetation densities reduced bluegill growth rates even in the absence of pelagic predation risk.

Diets of bluegill indicated that they fed mostly in littoral or benthic habitats. Percent of pelagic zooplankton in the diet, excluding benthic ostracods, was <1% by weight in both treatments. Although pelagic zooplankton are often considered the optimal prey type for bluegill, several studies have demonstrated that bluegill eat a high proportion of invertebrates (Mittelbach 1981; Schneider 1999; Olson et al. 2003a), presumably because they use littoral habitat to avoid predation risk associated with pelagic habitat (Mittelbach 1981; Ostrand et al. 2004). Similar predator-mediated habitat and diet shifts have been found for other fish species (Diehl and Eklov 1995; Persson and Eklov 1995). Because piscivorous fish were not present in the ponds, it was surprising that bluegill foraged so heavily in the vegetated habitat. Shoup et al. (2003) found that bluegill in the laboratory spent 40–80% of their time in artificial macrophytes even in the absence of a predator and when food was only available in the open water. Either bluegill cannot accurately assess predation risk or some other mechanism causes bluegill to forage in vegetated habitat. The propensity of bluegill to forage in vegetated habitat could be genetically linked (Lister and Neff 2006) or related to phenotype (Layzer and Clady 1987; Ehlinger and Wilson 1988; Chipps et al. 2004). In both cases, fish would not be expected to alter their habitat use in response to the absence of predators over short time scales. Bluegill may also select habitat due to temperature preference rather than foraging return (Wildhaber 2001), highlighting the potential for mechanisms other than predation risk. Previous laboratory (Persson 1991) and enclosure (Diehl and Eklov 1995) studies have found that Eurasian perch (*Perca fluviatilis*) and roach occasionally chose to feed in vegetation rather than open water even when no predator was present. Additional research is needed to determine the pervasiveness of these behaviors and the underlying mechanisms.

Interactions among structural complexity, fish habitat selection and predator–prey interactions are complex, making recommendations about habitat management for optimizing fish densities and size structure difficult. By separating the role of each of these factors, it is possible to better understand the importance of each in the overall system response. Our results demonstrate that bluegill chose to forage in littoral habitat even in the absence of open-water predation risk, leading to reduced growth rate at higher vegetation densities. Managing for moderate vegetation density or cutting deep channels through vegetation (Olson et al. 1998) may be useful for maximizing bluegill growth, even when piscivore biomass is not high enough to constitute a significant predation risk.

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