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Predator cues alter habitat use by the amphipod *Hyaella azteca* (Saussure)

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Abstract. The abundance and distribution of aquatic mesograzers may be regulated by both top-down (i.e., predator-mediated) and bottom-up (i.e., producer-mediated) effects. Under predation by fish, these herbivores may experience differential survivorship among different types of resource patches. Prey may attempt to maximize fitness by integrating information on predation risk and patch quality into foraging decisions. The freshwater amphipod *Hyaella azteca* occupies mats of the toxic cyanobacterium *Lyngbya wollei* and the green alga *Rhizoclonium hieroglyphicum* in lotic water bodies throughout the southeastern USA. We tested the hypotheses that *Lyngbya* is an effective refuge from Bluegill Sunfish (*Lepomis macrochirus*) predation and that predator cues modify habitat selection by amphipods. In no-choice assays, amphipods exposed to fish predation showed higher survivorship on *Lyngbya* than on *Rhizoclonium*. In choice assays, we observed greater proportions of amphipods on *Lyngbya* in tanks containing either predators or waterborne predator cues compared to control tanks containing only freshwater. These results suggest that *Lyngbya* is an effective refuge from predation for amphipods. Furthermore, predatory fish may indirectly influence the relative abundance of algae and cyanobacteria by reducing amphipod abundance on highly palatable species and restricting these mesograzers to less palatable species.

Key words: predator cue, refugia, trophic interactions, *Lyngbya wollei*, *Hyaella azteca*, *Lepomis macrochirus*.

Predation risk is an important factor that influences habitat selection by prey in freshwater and marine systems (Kerfoot and Sih 1987, Duffy and Hay 1994, Wellborn et al. 1996, Holomuzki et al. 2010). Under strong predation pressure, prey frequently face the dilemma of either tolerating patches with poor food quality or risking increased predation by migrating to higher-quality patches (Gilliam and Fraser 1987, Lima and Dill 1990). Habitat quality often is positively correlated with the level of predation risk, so prey that forage in high-quality patches might be more susceptible to predation than prey in low-quality patches (Křivan and Vrkoč 2000). Under such conditions, prey might increase their residence time in less-profitable patches as predation risk increases (Stephens and Krebs 1986, Lima and Dill 1990, Křivan and Vrkoč 2000). If predation risk and patch quality are variable,

selection should favor prey that can integrate predator cues when deciding to migrate between patches (Bouwma and Hazlett 2001).

The freshwater amphipod *Hyaella azteca* (Saussure) is found in nearshore aquatic habitats throughout North America and forms dense aggregations on a variety of macrophytes and detritus (Covich and Thorp 2001, Poirier et al. 2010). In the southeastern USA, *H. azteca* often occupy mats of the filamentous cyanobacterium *Lyngbya wollei* (Farlow ex Gomont) and a sympatric green alga, *Rhizoclonium hieroglyphicum* (C. Agardh) Kützing. Conspicuous fish predators of *H. azteca* include juvenile Bluegill Sunfish, *Lepomis macrochirus* (Rafinesque), which are generally restricted to littoral zones during their development and whose diet is largely composed of amphipods (Wellborn and Cothran 2004).

The high abundance of *H. azteca* on benthic mats of *L. wollei* is intriguing because this freshwater cyanobacterium produces paralytic shellfish poisons (PSPs),

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a class of potent neurotoxic alkaloids most commonly associated with toxic algal blooms and fish kills in marine ecosystems (Carmichael 1994, Yin et al. 1997). Certain freshwater invertebrates and fish can bioaccumulate PSPs in their tissues (Negri and Jones 1995, Berry and Lind 2010, da Silva et al. 2011), but the effects of PSPs on predator-prey interactions remain poorly understood. *Lyngbya wollei* cells are surrounded by a prominent extracellular polysaccharide sheath that provides mechanical defense from grazing by *H. azteca* (Camacho and Thacker 2006). *Hyalella azteca* readily consumed filaments of *R. hieroglyphicum* over *L. wollei* in laboratory feeding assays (Camacho and Thacker 2006). Given the relative unpalatability of cyanobacteria in aquatic systems (Paul et al. 2001, Camacho 2008), *L. wollei* filaments may interfere with bluegill foraging on *H. azteca* and provide a refuge for *H. azteca* from bluegill predation.

Predators may also indirectly influence the abundance of amphipods among different patches through waterborne cues emitted by the predator or injured prey. For example, Åbjörnsson et al. (2000) reported that the freshwater amphipod *Gammarus pulex* decreased locomotor activity in response to waterborne fish cues. *Gammarus minus* reduced its movements and stayed longer in leaf packs when exposed to Green Sunfish (*Lepomis cyanellus*) cues than in the absence of cues in laboratory treatments (Holomuzki and Hoyle 1990). These responses may effectively enhance amphipod survivorship by reducing the probability of an encounter with fish (Wudkevich et al. 1997, Wooster 1998) and may indirectly influence ecosystem processes, such as litter decomposition and breakdown (Åbjörnsson et al. 2000).

We investigated the feeding preferences of bluegills on *H. azteca* that were raised on either *L. wollei* or *R. hieroglyphicum*. We then tested the hypotheses that: 1) *L. wollei* is an effective refuge from predation for *H. azteca*, and 2) predator cues modify habitat use by *H. azteca* on *Lyngbya* and *Rhizoclonium* mats.

Methods

We collected bluegills, amphipods, green algae, and cyanobacteria by hand from nearshore habitats in freshwater lakes and ponds in northern Alabama. We held *Lyngbya* and *Rhizoclonium* in 40-L aquaria with filtered lake water at 75°F under a 12:12 light:dark photoperiod (with fluorescent lighting providing an average of 10 $\mu\text{mol quanta s}^{-1} \text{m}^{-2}$) and constant aeration.

We used a feeding-preference test to examine whether bluegills preferentially consumed *H. azteca* raised on filaments of the green alga *R. hieroglyphicum*

over amphipods raised upon the toxic cyanobacterium *L. wollei*. In a previous study, amphipods consumed filaments of both *Lyngbya* and *Rhizoclonium*, but consumption rates were lower for *Lyngbya* (Camacho and Thacker 2006). We held ~200 amphipods on live *Lyngbya* filaments and, in a separate aquarium, an additional 200 amphipods on *Rhizoclonium* filaments. We allowed each group of amphipods to graze on the mats for 2 wk before isolating and then sacrificing them by holding them for 5 min at -20°C . We placed 10 amphipods from each group on opposite ends of a 7-cm-long strip of fiberglass window screening. We placed a square mold ($\sim 3.36 \text{ cm}^2$) around each group of amphipods and poured a thin layer of heated agar mixture (0.45 g agar in 20 mL water; cooled to 60°C) into the mold over the amphipods and the screen. When the agar had solidified, we removed the molds. The result was a single strip of screen with 2 thin raised squares of agar each containing 10 amphipods. We marked the agar square that contained *Lyngbya*-fed amphipods by a small cut on the screen next to the agar to distinguish between the 2 amphipod groups on each strip. We formed 10 strips of screen, each with paired agar blocks with amphipods. We presented individual bluegill ($n = 10$) with a single strip and allowed the fish to feed on the amphipods for 2 h, or until $\geq \frac{1}{2}$ of the amphipods on 1 side of the strip had been consumed. We also placed 3 strips in individual aquaria lacking fish to assess the potential for amphipods to be lost from the agar because of effects other than fish consumption. At the end of the assay, we counted the number of amphipods consumed from each group for each strip. We compared differences in fish consumption of amphipods raised on *Lyngbya* vs *Rhizoclonium* with a paired *t*-test.

We used a no-choice assay to evaluate the effectiveness of *Lyngbya* and *Rhizoclonium* mats as refuges from predation in the absence of alternative habitats. We offered individual bluegills a 0.5-g mat of either *Lyngbya* or *Rhizoclonium* that contained 10 live amphipods. Before presenting a mat to a fish, we allowed amphipods to acclimate on the mat for ~2 h. During this acclimation period, we fed the fish frozen brine shrimp until satiated. Each fish ($n = 10$) was allowed to prey upon amphipods in a mat for 2 h, after which we recovered the mat and counted the number of remaining amphipods. The experiment was then repeated with the same fish, but with a different mat type than was used in the previous trial. After each trial, we counted the surviving amphipods on the mat. We never observed amphipods away from the refuge of a mat, so we assumed that missing amphipods were consumed by fish. Data were

TABLE 1. Results of a repeated measures analysis of variance testing the effects of subjects (individual fish, $n = 10$), trial, and mat type (*Lyngbya* or *Rhizoclonium*) on the number of amphipods surviving a no-choice assay after exposure to fish predation.

Source	df	SS	MS	F	p
Mat type	1	21.677	21.677	101.770	<0.001
Subjects	9	4.401	0.489	2.296	0.116
Residual	9	1.913	0.213		

$\sqrt{(x + 0.5)}$ -transformed to meet the assumptions of analysis of variance (ANOVA). We then compared differences in fish consumption of amphipods among the 2 mat types with a repeated measures ANOVA, where fish were treated as subjects and mat type was treated as a fixed effect (Zar 2010).

We used a choice assay to examine amphipod habitat selection and survivorship when mats of *Rhizoclonium* and *Lyngbya* were simultaneously available for amphipods to colonize. We conducted the choice assay in 3 separate trials with 5 aquaria per treatment per trial. We placed individual mats (~0.5 g each) of either *Lyngbya* or *Rhizoclonium* in individual beakers, each containing 10 amphipods, and allowed the amphipods to acclimate to the mats. We set up 40-L aquaria and assigned each to 1 of 3 treatments: 1) fish present; 2) fish absent, but with waterborne fish cues; and 3) control tanks with freshwater only because other freshwater amphipod species respond to waterborne predator cues and injured conspecifics (Holomuzki and Hoyle 1990, Wudkevich et al. 1997, Wisenden et al. 1999). We added individual bluegills to the aquaria designated to receive predators or predator cues. We fed bluegills frozen amphipods ad libitum for 2 h. At the end of that period, we removed fish from the aquaria that were to be used for the waterborne predator cue treatments and filtered the water from those aquaria through 55- μ m mesh to remove any fecal particles or amphipod remains before returning the water to each tank. We did not remove fish from tanks designated for the predator treatment, and we did not filter the water in the predator or control aquaria. Last, we added pairs of *Lyngbya* and *Rhizoclonium* mats and their associated amphipods to each aquarium. Thus, each aquarium received each type of mat each with an initial abundance of 10 amphipods. After 2 h, we removed both mats simultaneously from tanks with fine-mesh nets and counted the number of amphipods remaining on each mat. For each replicate, the proportion of amphipods remaining on *Lyngbya* relative to the total number of amphipods remaining on both mats was calculated as $L/(L + R)$, where L was the number of

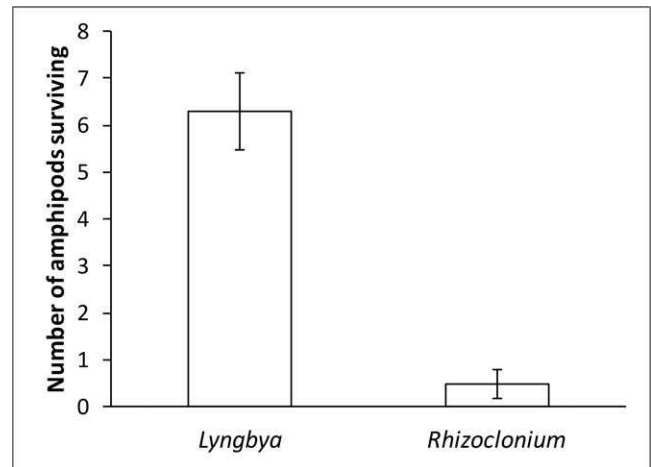


FIG. 1. Mean (± 1 SE, $n = 10$) number of amphipods surviving a no-choice assay, in which bluegills consumed amphipods occupying a mat of either the cyanobacterium *Lyngbya wollei* or the green alga *Rhizoclonium hieroglyphicum*. Amphipod survivorship was significantly higher on *Lyngbya*.

amphipods recovered from a *Lyngbya* mat and R was the number of amphipods recovered from the *Rhizoclonium* mat from the same aquarium. We compared mean proportions among the treatments with a 2-way, fixed effects ANOVA in which trial and treatment were independent effects. In the absence of a significant trial \times treatment interaction, we ran simultaneous post hoc comparisons of treatment means (Tukey's Honestly Significant Difference; Zar 2010).

Results

In the feeding-preference test, fish did not discriminate between *Hyaella* that had been fed *Lyngbya* or *Rhizoclonium* (*Lyngbya*: 6.1 ± 0.59 amphipods/fish [mean ± 1 SE]; *Rhizoclonium*: 6.1 ± 0.63 amphipods/fish; $n = 10$, $t = 0.000$, $p = 1.000$). During visual monitoring of foraging fish, we observed no rejection responses (e.g., spitting or regurgitating) after a fish removed an amphipod from the screens. No *Hyaella* were lost from the screens placed in tanks without fish.

In the no-choice assay, significantly more *Hyaella* survived on *Lyngbya* than on *Rhizoclonium* ($p < 0.001$; Table 1, Fig. 1). Fish foraged actively among both mats. They aggressively pulled filaments away from the mat with their mouths while foraging on *Rhizoclonium*, a behavior they did not display when foraging on *Lyngbya* mats.

In the choice assay, the treatment effect was highly significant, and the trial \times treatment interaction was

TABLE 2. Results of a 2-way analysis of variance testing the effects of trial and treatment on the distribution of amphipods between mats of *Lyngbya wollei* and *Rhizoclonium hieroglyphicum*. Treatments exposed amphipods to fish predation, predator cues, or freshwater only.

Source	df	SS	MS	F	p
Trial	2	0.109	0.054	2.758	0.077
Treatment	2	2.161	1.081	54.832	<0.001
Trial × treatment	4	0.137	0.034	1.732	0.164
Error	36	0.710	0.020		

not significant (Table 2). The mean proportions of amphipods on *Lyngbya* differed among all treatments (Tukey's HSD, $p < 0.001$ for all comparisons; Fig. 2). The proportion of amphipods recovered from mats of *Lyngbya* was highest in aquaria containing bluegill and lowest in control aquaria (Fig. 2). In aquaria containing fish, total survivorship on mats was ~31%, and >86% of those amphipods were recovered from *Lyngbya* mats. In aquaria containing waterborne predator cues, approximately equal numbers of amphipods were recovered from each mat. In the control tanks, several amphipods were not recovered from either mat at the end of the assay and were found elsewhere in the aquaria.

Discussion

Predators can influence prey abundance directly via consumption or by modifying patterns of prey habitat use via indirect physical or chemical cues. We examined whether *H. azteca* experienced greater survivorship in mats of a toxic cyanobacterium (*L. wollei*) compared to a chemically undefended green alga (*R. hieroglyphicum*). In a choice assay, the proportion of amphipods recovered from *Lyngbya* in tanks containing predatory fish was higher than in control tanks containing freshwater only. Higher survivorship also was observed for *Hyalella* on *Lyngbya* in the no-choice assay. These results support the hypothesis that amphipods have a stronger survival advantage on *Lyngbya* filaments than on *Rhizoclonium* in the presence of predatory fish. Our results agree with those of Duffy and Hay (1994) who found that chemically defended seaweed were effective refugia for amphipods from fish predators. Several aquatic taxa, including zooplankton (Burks et al. 2001), fish (Chipps et al. 2004), and gastropods (Nyström and Pérez 1998, Turner et al. 2000), incur lower fish predation rates when among aquatic vegetation than when exposed in the water column or on sediments. Nevertheless, our study is one of the

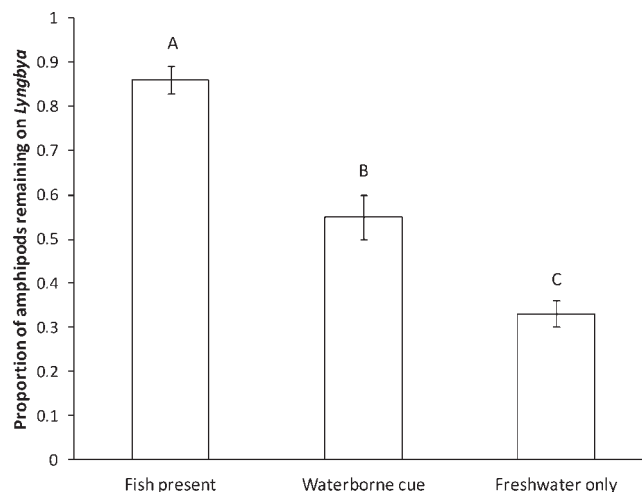


FIG. 2. Mean (± 1 SE, $n = 15$) proportion of amphipods recovered from mats of *Lyngbya* following exposure to bluegills, waterborne bluegill cues, or freshwater only. Bars with different letters are significantly different (Tukey's Honestly Significant Difference, $p < 0.001$ for all pairwise comparisons).

first to demonstrate increased prey survival through association with a cyanobacterial mat. Larvae of *Cricotopus* sp. (Chironomidae) use the interior of *Nostoc* cells for shelter and larval development in a purported mutualism (Brock 1960), although the actual nature of the relationship remains uncertain. Rejmánková et al. (1996) observed a greater abundance of *Anopheles albimanus* mosquito larvae among mats of *Leptolyngbya* than at sites lacking this cyanobacterium and demonstrated that female mosquitoes oviposited preferentially in those mats. In surveys of macroinvertebrate assemblages on various primary producers in a Canadian lake, Poirier et al. (2010) speculated that the higher densities of mobile invertebrates, particularly amphipods, occupying *L. wollei* mats may have been a result of lower predation rates by fish among those mats. Our study provides evidence that such a mechanism is plausible.

We also investigated whether waterborne cues from bluegills could modify the habitat use patterns of *Hyalella* in ways that reduced predation risk and maximized fitness for the amphipod. In the choice assay, significantly higher proportions of *Hyalella* were recovered from *Lyngbya* mats when exposed to predator cues than when in freshwater only. We were unable to measure rates of amphipod movement between mats in our experiment, but our results support the hypothesis that *Hyalella* preferentially forage among mats of the more palatable *Rhizoclonium* in the absence of predators, but modify their habitat use patterns and restrict their movements in the

presence of bluegill cues. Such predator-mediated patterns of patch use may be common among amphipods. For example, the freshwater amphipod *Gammarus minus* reduced swimming activity when exposed to waterborne cues from Green Sunfish in laboratory manipulations (Holomuzki and Hoyle 1990). *Gammarus minus* also exhibited positive geotaxis and reduced movement in response to water containing cues from injured conspecifics (Wisenden et al. 1999).

A fundamental assumption of our study was that bluegill predation was not influenced by long-term amphipod feeding on the different mat types. Such a bias could occur if fish perceive differences in amphipod nutritional quality resulting from differences in the nutritional content of the 2 mat types. Fish also might avoid *Lyngbya*-reared amphipods as a result of bioaccumulation of paralytic shellfish poisons (PSPs) in amphipod tissue. However, the lack of preference by bluegill for amphipods fed on either mat species indicates that prey diet did not influence predator choice and that higher amphipod survival in *Lyngbya* probably was a result of physical or chemical properties of the *Lyngbya* mats that reduced the foraging efficiency of the bluegill. These results contrast with those of Rowell and Blinn (2003), who found that insect predators avoided consuming *H. azteca* that were fed roots of the aquatic macrophyte *Berula erecta*.

Several traits may make *Lyngbya* an effective refuge from fish predation for invertebrate mesograzers, such as amphipods. The extracellular polysaccharide sheath may prevent fish from tearing filaments away from the mat and exposing amphipods. The sheath may also be robust enough to resist the mechanical force of fish bites. The PSPs in *Lyngbya* cells might deter fish from foraging among *Lyngbya* mats, but it is unclear whether bluegill can discern the presence of PSPs. Last, the generally darker color of *Lyngbya* than *Rhizoclonium* may have made it difficult for bluegill to locate prey items among the mats. However, Dorn et al. (2001) noted that bluegill were able to extract lepidopteran larvae from cases made of leaf fragments with no incidental consumption of plant tissue, a result suggesting that bluegill are capable of discriminatory feeding. Thus, in future studies, investigators should address the mechanisms underlying the reduced foraging success by bluegill on *Hyalella* in patches of *Lyngbya*.

Our results suggest that predators, such as bluegill, may indirectly promote coexistence between aquatic algae and cyanobacteria by reducing amphipod abundance on palatable species and by restricting herbivores to species of poorer food quality. Marine

amphipods shifted the abundance of algae in mesocosms from brown algae to red algae when released from fish predation (Duffy and Hay 2000). McCollum et al. (1998) found that predator cues from Redear Sunfish (*Lepomis microlophus*) depressed the grazing rates of physid snails on periphyton, including cyanobacteria. Similarly, waterborne stimuli from Pumpkinseed Sunfish (*Lepomis gibbosus*) led to increased shelter use by the snail *Physa integra* and increased periphyton cover in near-surface habitats (Bernot and Turner 2001). We did not measure changes in mat mass in these choice assays, but *Hyalella* has been reported to consume *Rhizoclonium* preferentially over *Lyngbya* filaments in the absence of fish cues (Camacho and Thacker 2006). Thus, predator cues from bluegill may influence cyanobacterial and algal biomass in nearshore aquatic communities through trait-mediated indirect effects on amphipods (Werner and Peacor 2003).

In conclusion, *L. wollei* may be an effective spatial refuge from predation by bluegill for *H. azteca*. Furthermore, waterborne predator cues can modify habitat use by *Hyalella*, and in the absence of such cues, amphipods may exploit more profitable algal patches. These trophic interactions may allow palatable algae to persist among less palatable species by influencing patch use by invertebrate mesograzers.

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