Experimental studies of predation by bluefish *Pomatomus saltatrix* in varying densities of seagrass and macroalgae

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ABSTRACT: We conducted ecosystem level experiments to investigate predator–prey relationships in 3 habitat types; eelgrass *Zostera marina*, macroalgae, and bare sediment. Mesocosms containing marine sediments, coastal water, and varying densities of eelgrass (75 to 1000 shoots m^{-2}) or macroalgae (50 to 1000 g wet weight m^{-2}) were used to simulate conditions found in shallow coastal lagoons of Rhode Island, USA. We used bluefish *Pomatomus saltatrix* as predators in each experiment after appropriate acclimation in each habitat type. Prey fish were provided in equally weighted rations and included silversides *Menidia menidia*, tautog *Tautoga onitis*, cunner *Tautogolabrus adspersus*, and menhaden *Brevoortia tyrranus*. Eelgrass significantly increased the survivorship of silversides, tautog and cunner at very low shoot densities. Experiments using macroalgae did not result in significantly different survival rates between bare sand and macroalgae habitat for silversides or cunner, the 2 species tested for this vegetation type. With the decline of eelgrass and increase of macroalgal cover in shallow coastal areas of Rhode Island, this information increases our understanding of the relative value of eelgrass habitat to fish stocks and should provide added incentive to protect and conserve existing eelgrass beds.

KEY WORDS: Fish habitat · Predator–prey interactions · Habitat complexity · Seagrass · Macroalgae · Bluefish

INTRODUCTION

One of the most enduring assumptions in coastal marine ecology is that meadows of seagrass provide an important habitat for numerous species of shallow water fish and invertebrates (Adams 1976, Hoss & Thayer 1993, Hughes et al. 2002). In the case of the most common temperate seagrass along the Atlantic coast, *Zostera marina* L., or eelgrass, the role of the plants as an important fish habitat was suggested almost 100 yr ago by the pioneering studies of C. G. J. Petersen and colleagues at the Danish Biological Station (Petersen 1915, 1918). Despite this long history and a large amount of anecdotal evidence, it has proven difficult to document and quantify the functional relationships between eelgrass cover and the abundance of fish and crabs at the ecosystem scale.

Common approaches taken to link eelgrass habitat with animal abundance have included field sampling for animals inside and outside of seagrass beds of varying size and/or density (Orth et al. 1984, Heck et al. 1995, Szedlmayer & Able 1996, Duffy & Baltz 1998, Scott-Denton 1999, Thayer et al. 1999), comparative sampling of animal populations in different estuaries or embayments with differing amounts of eelgrass density or coverage (Heck & Orth 1980, Deegan et al. 1997, Wyda et al. 2002), eelgrass canopy removal in the field (Connolly 1994), and experimental studies completed in a laboratory setting (Heck & Thoman 1981, Graham et al. 1998).

Habitat functionality suggested by these studies was largely inferred from high fish abundance within eelgrass habitat and led to the current paradigm of eelgrass, and seagrass meadows generally, being nursery

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habitats. In the majority of the aforementioned studies, a nursery role was defined in terms of the perceived advantages eelgrass habitat provides through sediment stability (Orth 1977), food abundance (Petersen 1918, Kikuchi 1980, Thayer et al. 1975, Valiela et al. 1992), or refuge from predation (Orth et al. 1984, Gotceitas et al. 1997). However, Able & Fahay (1998) have cautioned against the use of such abundance data in defining the nursery role of an estuarine habitat when life-history patterns and the temporal and spatial use of the habitat are unknown.

In the present study, we tested the hypothesis that eelgrass habitat may function as a refuge from predation for small prey fish. Habitat function involves some or all of a complex mix of exploitable food resources, protection from predation or physical factors, and intraspecies interactions that ensure reproductive success. In general, estuaries have lower predation rates relative to the ocean (Gunter 1961, Blaber & Blaber 1980), which may be due to the increase in structural complexity (and therefore an increase in potential refuges) in shallow water ecosystems that is provided by macrophytes such as seagrass meadows. Early work in freshwater habitats showed that as the structural complexity of a system increases, the capture rate by predators may decrease (Ivlev 1961, Ware 1972, Crow-

der & Cooper 1982, Mattila 1992). Because prey fish often select habitat where the risk of predation is lower, the potential of increased habitat complexity to shape communities is great and has been demonstrated in a number of systems (Crowley 1978, Werner et al. 1983, Turner & Mittelbach 1990).

Due to the difficulties involved in carrying out predator–prey manipulations in the field, we designed manipulative experiments in specially designed lagoon mesocosms to assess predator–prey relationships in varying densities of eelgrass during the summer of 2000. A small number of studies have investigated these relationships, usually using artificial eelgrass (Heck & Thoman 1981, Gotceitas et al. 1997, Bartholomew 2002) or examining invertebrates only (Nelson 1979, Graham et al. 1998). The unique capabilities of the mesocosm facility to simulate a natural eelgrass bed provided an opportunity to test our hypothesis more realistically. We also examined predation in varying densities of macroalgae to assess the refuge value of 'nuisance' species that often replace eelgrass meadows which have been lost to nutrient enrichment or increased water temperature (Bowen & Valiela 2001, Bintz et al. 2003).

MATERIALS AND METHODS

The Mesocosm Facility. The Lagoon Mesocosm Facility is located at the University of Rhode Island Graduate School of Oceanography on the shores of Narragansett Bay (41° N, 71° W). Each of the 10 lagoon mesocosms (Fig. 1) had a surface area of 4.2 m^2 with a water depth of 1.1 m. The base of each mesocosm consisted of 2 sediment trays, each holding 30 cm of low organic (0.6% ± 0.003 weight loss on ignition) sandy sediments and associated infauna collected in nearby Block Island Sound in February of 2000. A flange surrounding the sediment trays decreased sediment surface area to 3.4 m^2. The treatments were apportioned arbitrarily among the 10 mesocosms, except that the replicates were not located on the same side or at the same end of the facility. The volume of water in each mesocosm was replaced at 10% d^{-1} with water from lower Narragansett Bay. This is roughly comparable to the rates of flushing of Ninigret Lagoon (Nixon & Lee 1981). Water column temperature and salinity were monitored every 15 min using continuously recording probes.
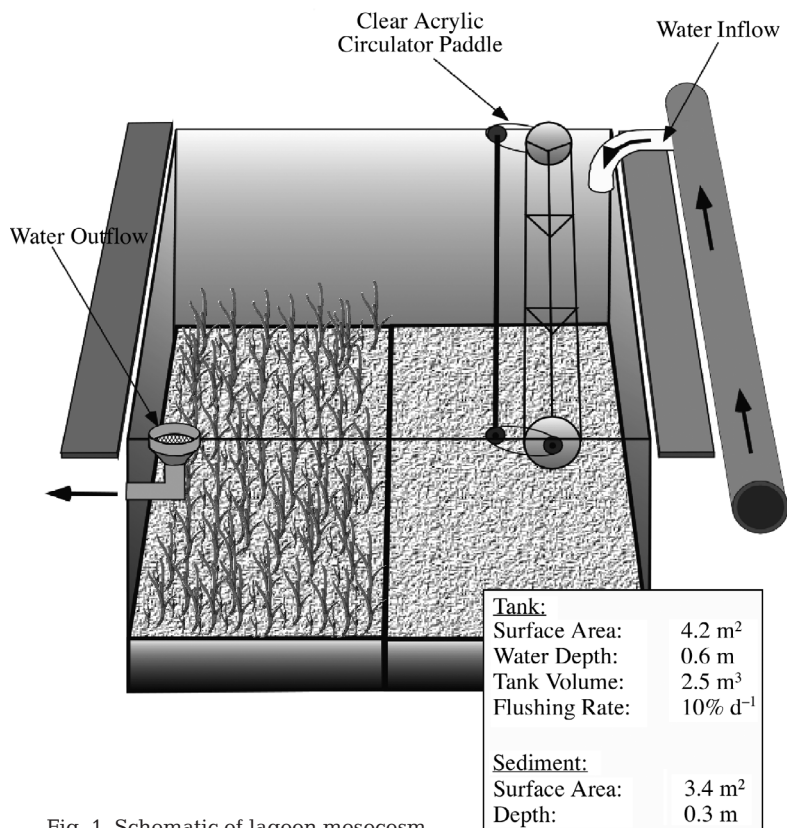

Fig. 1. Schematic of lagoon mesocosm

Tank:
Surface Area: 4.2 m^2
Water Depth: 0.6 m
Tank Volume: 2.5 m^3
Flushing Rate: 10% d^{-1}

Sediment:
Surface Area: 3.4 m^2
Depth: 0.3 m

The water column of the mesocosms was mixed using transparent paddle wheels that rotated in alternate directions every 6 h and produced near surface and near bottom currents of 15 to 20 and 5 to 10 cm s^{-1}, respectively. Dye studies showed that water within the mesocosms was mixed uniformly within 10 to 15 min. The walls of the mesocosms were scrubbed periodically to keep attached macroalgal growth from accumulating. Material removed during cleaning remained in the tanks. The salinity of the mesocosms over the course of the summer ranged from 28.7 to 33.1 psu.

The Lagoon Mesocosm Facility has been used extensively to simulate lagoon conditions similar to those found in the coastal ponds of southern Rhode Island (eg. Taylor et al. 1995, Lin et al. 1996). Unlike previous studies that included periwinkles, shrimp, and several finfish species, the community included in our experiments was limited to benthic infauna, seagrass and associated epiphytes, zooplankton, phytoplankton, and the selected finfish described below.

Predators. Juvenile bluefish *Pomatomus saltatrix* (14.4 to 18.7 cm total length [TL]) were used as predators in all experiments. This predator is commonly found in Narragansett Bay and Rhode Island coastal lagoons or 'salt ponds', as they are called locally, from late spring to early fall (Mulkana 1966, Able & Fahay 1998). Over the course of the experiments, 53 bluefish were captured using hook-and-line and placed in flow-through aquaria for a minimum of 3 d to acclimate. Transportation from the field to the mesocosm facility involved placing the bluefish in a large insulated cooler with battery powered aerators. The aquaria were 2 m in diameter and between 1.5 and 2 m deep. Water temperatures in the holding tanks were within 1°C of mesocosm water temperatures. We define acclimation as the amount of time needed to establish regular feeding by the captive bluefish. A combination of live fish (silversides, menhaden, tautog, and cunner) and thawed squid was used to feed the bluefish between experiments. Bluefish feeding behavior in a natural setting usually includes close-knit schooling until an initial attack is made, after which the school will regroup (Pottern et al. 1989). Feeding activity is typically at a peak in early morning (Lund & Maltezos 1970, Buckel and Conover 1997). Because of this behavior, during the predation experiments we used 3 predators in each of the mesocosms and continued each experiment for 24 h. Although it was necessary to reuse some of the bluefish in multiple experiments, care was taken to allocate individuals arbitrarily among the treatments, to keep total length within a narrow range, and to establish that all fish were feeding regularly in between experiments.

Prey. Prey fish included silversides *Menidia menidia* 29 to 51 mm TL), menhaden *Brevoortia tyrranus* (45 to 65 mm TL), tautog *Tautoga onitis* (34 to 55 mm TL), and cunner *Tautogolabrus adspersus* (39 to 63 mm TL) captured using beach seines and bait traps. All species of prey are found in local eelgrass meadows (J. Temple unpubl. data); silversides and menhaden are considered transient species, while tautog and cunner show high fidelity not only to eelgrass habitat but to a local range (Able & Fahay 1998). While predation rates were determined for each species in the eelgrass treatment experiments, only cunner and silversides were used in the macroalgal experiments. All of these prey species have been found in the diet of bluefish (Hartman & Brandt 1995, Fahay et al. 1999)

Eelgrass density experiments. The first predation experiments consisted of 5 duplicate treatments of eelgrass *Zostera marina* planted at densities of 0, 75, 200, 500, and 1000 shoots m^{-2} in one half of each mesocosm tank. These densities are comparable to a range of densities measured in Rhode Island eelgrass meadows (Thorne-Miller et al. 1983). Eelgrass was collected by divers in April 2000 from Ninigret Lagoon, Rhode Island, and transplanted within 2 d to the mesocosms. Shoots averaged just under 19 cm in length. The eelgrass shoots were planted in an irregular pattern over 1 of the 2 sediment trays in each of the mesocosm tank treatments containing grass. This left 1.7 m^2 of each tank covered by plants and 1.7 m^2 of bare sediment.

For each experiment, predators were chosen arbitrarily from the aquaria holding tank and placed at random in the experimental mesocosms, where they were allowed to acclimate for 24 h before prey were added. The prey were introduced to the mesocosms through a clear, open-ended PVC tube held flush with the sediment and extending above the water surface. After an acclimation period of 5 min, the tube was pulled out of the mesocosm, releasing the prey for the 24 h experiment. We measured survival rates for each of the prey species separately. Six experiments were completed using silversides as prey and 4 experiments were performed for each of the 3 remaining prey species: cunner, tautog, and menhaden. At the completion of each experiment, approximately 300 to 325 g (2.9 to 3.4 mol) sodium bisulfite was added to each of the mesocosms to lower oxygen concentrations to about 0.2 g ml^{-1}. Oxygen levels were monitored during these additions using a YSI Model 600XL rapid pulse polargraphic probe. The predators and surviving prey were then easily netted from the mesocosms, and survival rates were calculated from the remaining prey fish.

Macroalgae experiments. Following the completion of the eelgrass experiments, the eelgrass was removed and replaced with a mixture of *Ulva lactuca* and *Gracillaria* spp. in amounts equivalent to 0, 50, 250, 500, and 1000 g wet weight m^{-2}. As with the eelgrass density experiments, the 10 mesocosm tanks were

used to create 2 replicates of each treatment. This range of biomass is comparable to macroalgal levels found in Rhode Island (Thorne-Miller et al. 1983).

The protocol for adding and removing predators and prey proceeded as described for the eelgrass density experiments. However, only 2 species of prey were tested, cunner and silversides. Four experiments were completed for each of these species. All data were analyzed using ANOVA and multiple comparisons tests.

Calculation of experimental prey densities. Because the mesocosms restricted the feeding range of the predators, it was important to avoid offering prey fish in densities so high that the bluefish could potentially feed to satiation and then stop pursuing and capturing prey (Bartholomew et al. 2000). This potential feeding cessation could complicate survival rates estimated from remaining prey in the mesocosms, as the prey may have survived simply because the predators were no longer feeding. To account for this possibility, we calculated a maximum consumption rate (C_{max} g wet weight) using a species specific allometric relationship provided by Harman & Brandt (1995) for Age 0 through Age 2 bluefish:

$$C_{max} = CA \times W^{CB} \times f(T)$$

where CA is an empirically determined intercept, CB is an empirically determined coefficient of C_{max} versus weight (W), and $f(T)$ describes the temperature dependency of the consumption rate as modeled by Thornton & Lessem (1978). Values of CA and CB were taken from Hartman & Brandt (1995). We estimated a prey ration of 27 g wet weight to offer the 3 bluefish placed

in each experimental mesocosm in order to satisfy 100% of C_{max}. By calculating a regression of total length to weight for each prey species, we were able to select the number and targeted lengths of prey fish to include in each of the mesocosm treatments. Table 1 lists the mean weight, mean total length, and number of each prey species used in the predator–prey experiments. This procedure eliminated weighing all prey fish and the associated stress on the prey prior to each experiment.

RESULTS

While most predation occurred during dawn and dusk hours, the bluefish were also observed chasing and occasionally capturing prey at other times. In general, the 3 bluefish displayed schooling behavior while swimming around the tank. When the tanks were planted with eelgrass, most of this swimming occurred at the edges of the planted areas with only occasional forays into the plants. Menhaden and silversides also swam in a schooling pattern, often near the surface of the tank and diving into the eelgrass when the bluefish would attack. Once the tautog and cunner were placed in the tanks, they swam into the eelgrass plants and were difficult to see.

When the mesocosm tanks contained macroalgae, the bluefish used schooling behavior in all areas of the tank. Rather than using the vegetation during a bluefish attack, the silversides would scatter from their schooling pattern. The cunner swam within the macroalgae cover and were difficult to see because of their coloring.
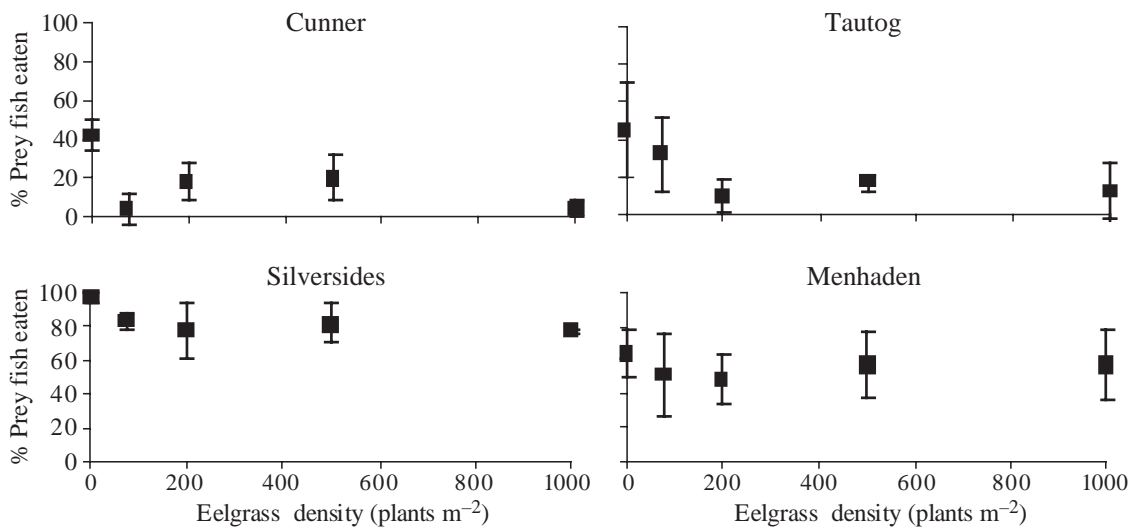

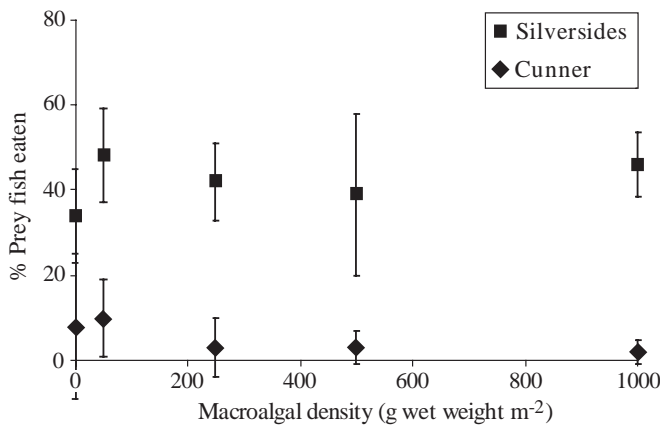Fig. 2. Mean predation rates (±1 SD) in varying eelgrass densities with 4 prey species

Fig. 3. Mean predation rates (±1 SD) in varying macroalgal densities for 2 prey species

In no case were all the prey fish consumed at the completion of an experiment. Tautog, cunner, and silversides were eaten significantly more frequently ($p < 0.05$, 1-way ANOVA) in bare sediment habitat versus eelgrass (Fig. 2). No significant differences between eelgrass treatments were seen for the menhaden. In contrast, there was no difference between the bare sediment and the macroalgal habitat at any density tested for silverside and cunner survivorship ($p > 0.05$, 1-way ANOVA) (Fig. 3).

No significant variation in predation rates among the 4 different eelgrass densities was detected for cunner or silversides using Tukey's multiple comparisons test (Table 2). However, a significant decrease in predation rates for tautog was first noticeable at densities of 200 shoots m^{-2} and above (Table 2).

DISCUSSION

Results from the present eelgrass experiments firmly establish that eelgrass beds, even those of modest density, increase the survivorship of tautog, cun-

ner, and silversides, but do not affect predation by bluefish on menhaden. These findings confirm the hypothesis that eelgrass habitats serve a functional role as refuges from predation for some prey fish. The difference between species may be due to the diversity of life history strategies in the prey selected for experiments. Able & Fahay (1998) insist that experiments such as those completed for this study must be interpreted and applied to the natural system in the context of thorough data describing habitat use on temporal and spatial timescales. Tagging studies have indicated that menhaden follow a widespread migration route over a diversity of habitat types from open ocean areas to estuaries (Nicholson 1978). Adaptation to the use of a complexly structured habitat may be less evident in menhaden than in resident fish such as tautog and cunner. For example, cryptic coloration of tautog has been documented in eelgrass meadows, where the fish are tinted a dark green color (Sogard et al. 1992). Both tautog and cunner appear to prefer eelgrass habitat and to exhibit very short ranging distances (Able & Fahay 1998).

Data collected from otter trawls taken over a range of substrate types indicated high abundances of silversides over eelgrass and sand (Szedlmayer & Able 1996). These density data, combined with the results from our experiments, may provide insight into the balance between foraging and refuge opportunities in

Table 1. Calculations of prey rations for each predator–prey experiment

Prey species	Allometric relationship[a]	Mean weight (g)	Predicted length[b] (mm)	Number[c]
Silversides	$L = 38.8 \times W + 22.6$	0.35	36	75
Menhaden	$L = 6.47 \times W + 32.5$	0.90	38	30
Tautog	$L = 12.6 \times W + 27.4$	1.80	50	15
Cunner	$L = 4.8 \times W + 40.8$	1.80	50	15

[a]Length (L) to fresh weight (W)
[b]Prey used in experiments were within 5 mm of this targeted length
[c]Number of prey fish necessary to meet 27 g ration prey/3 bluefish/24 h experiment

Table 2. Survival rates of 4 species in eelgrass experiments. Tukey-grouping delineates significantly different means, $p < 0.05$ (Tukey's multiple comparisons test). Densities sharing the same letter are not significantly different

Eelgrass density (shoots m^{-2})	Mean percent predation of prey fish							
	Cunner	Tukey-grouping	Tautog	Tukey-grouping	Silversides	Tukey-grouping	Menhaden	T-Group
0	42 %	B	45 %	B	97 %	B	63 %	A
75	4 %	A	32 %	B A	83 %	A	51 %	A
200	18 %	A	10 %	A	77 %	A	48 %	A
500	20 %	A	17 %	A	82 %	A	57 %	A
1000	4 %	A	12 %	A	77 %	A	57 %	A

different habitat types. Silversides appear to be opportunistic feeders that must travel to tidal marsh systems in order to spawn in the summer months (Cadigan & Fell 1985). Their use of another structurally complex habitat, *Spartina* marshes, for vulnerable spawning and larval/post-larval stages (Fay et al. 1983) may indicate a generalized use of habitat complexity as refuge from predators by silversides.

Studies investigating complexity in a variety of habitat types often report a linear decrease in predation rates with an increase in structural complexity (Ware 1972, Crowder & Cooper 1979, Savino & Stein 1982, Nelson & Bonsdorff 1990). Alternatively, Nelson (1979) proposed a 'complexity threshold' which must be reached before a significant decrease in predation is evident.

The results from the eelgrass experiments suggest that if such a 'threshold' is present, it must lie at a relatively low density of ≤ 75 shoots m^{-2} for cunner and silversides and 200 shoots m^{-2} for tautog. Similarly, if there is a linear decrease in predation with increasing complexity, it must be limited to the lower range of eelgrass density. Our results for bluefish and the 4 prey species tested showed that the refuge from predation function is more appropriately modeled as an asymptotic function of plant density that is saturated at low levels of plant cover. Nelson & Bonsdorff (1990) have criticized complexity threshold findings as an artifact of experimental design. It would obviously be interesting to pursue additional studies in the future, incorporating density treatments that fall between 0 and the 75 shoots m^{-2}.

Because loss of eelgrass habitat has occurred in temperate ecosystems worldwide, it is particularly timely to compare predator–prey results from eelgrass substrate types to the macroalgae that most commonly replace eelgrass meadows (e.g. Hauxwell et al. 2003). Lenanton et al. (1982) completed a study in Australia that found an increase in 0+ year classes of 4 species of economically important fish in nearshore macroalgae collections and hypothesized that the macroalgae conferred added protection from predators to the young fish. As in Rhode Island, these macroalgae assemblages are typically detached from the benthos and form floating mats in shallow areas. Using silversides and cunner, we were unable to detect a difference in predation over bare sand or in mesocosms filled with varying weights of macroalgae. These results provide better insight into the different habitat value of eelgrass meadows versus macroalgal mats. Our findings support a continuation of efforts to protect and manage eelgrass meadows effectively. For 3 of the 4 prey species studied, it appears that even low densities of eelgrass provide a functional role as refuge from predators where a similar advantage is not observed in macroalgal mats.

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