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Microhabitat use by a post-settlement stage estuarine fish: evidence from relative abundance and predation among habitats

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Abstract

Seagrass beds provide food and shelter for many fish species. However, the manner in which fishes use seagrass bed habitats often varies with life stage. Juvenile fishes can be especially dependent on seagrass beds because seagrass and associated habitats (drift macroalgae) may provide an effective tradeoff between shelter from predation and availability of prey. This study addressed aspects of habitat use by post-settlement pinfish, *Lagodon rhomboides* (Linneaus), an abundant and trophically important species in seagrass beds in the western North Atlantic and Gulf of Mexico. Abundance of post-settlement fish in seagrass beds was positively related to volume of drift macroalgae, but not to percent cover of seagrass, indicating a possible shelter advantage of the spatially complex algae. Tethering experiments indicated higher rates of predation in seagrass without drift macroalgae than in seagrass with drift macroalgae. Aquarium experiments showed lower predation with higher habitat complexity, but differences were only significant for the most extreme cases (unvegetated bottom, highest macrophyte cover). Levels of dissolved oxygen did not differ between vegetated and unvegetated habitats, indicating no physiological advantage for any habitat. Seagrass beds with drift macroalgae provide the most advantageous tradeoff between foraging and protection from predation for post-settlement *L. rhomboides*. The complex three-dimensional shelter of drift macroalgae provides an effective shelter that is embedded in the foraging habitat provided by seagrass. Drift macroalgae in seagrass beds is a beneficial habitat for post-settlement *L. rhomboides* by reducing the risk of predation, and by providing post-settlement habitat

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within the mosaic (seagrass beds) of adult habitat, thus reducing risks associated with ontogenetic habitat shifts.

Keywords: Drift macroalgae; Juvenile fish; *Lagodon rhomboides*; Microhabitat; Predation; Seagrass

1. Introduction

Seagrass beds have long been identified as an important habitat for fishes and invertebrates (Orth et al., 1984). Experimental studies investigating some of the mechanisms thought to make seagrass a preferred habitat found that food availability, refuge from predation, increased living space, and habitat richness were important (Robertson, 1980; Heck and Thoman, 1981; Lenanton et al., 1982; Leber, 1985; Sogard and Olla, 1993; Jordan et al., 1996). Furthermore, plant biomass and plant architectural configuration have been shown to be predictors of microhabitat quality in relation to fish and invertebrate abundance and diversity (Leber, 1985).

The effect of microhabitat complexity on the ability of fishes to forage and escape predation influences fish abundance and distribution (Gotceitas and Colgan, 1989; Savino and Stein, 1989). Individuals encounter a range of habitats, from those that may be too complex to allow effective foraging to habitats not providing a refuge from predation. Typically, the thresholds of habitat complexity for these juxtaposed activities are conflicting (Gotceitas and Colgan, 1989), and vary depending upon local abundances of a species' predator and prey assemblages (Stoner, 1979; Sogard and Olla, 1993; Jordan et al., 1996).

The requirements of post-settlement and juvenile fishes differ from those of sub-adults and adults (Vigliola and Harmelin-Vivien, 2001). During the early post-settlement period, fishes suffer the greatest mortality rate of the benthic portion of the life cycle, mostly via predation (Sogard, 1997). Post-settlement fishes must find habitat with sufficient refuge, yet be able to forage efficiently in order to grow to a size that is less vulnerable to predation (Sogard, 1997).

The pinfish, *Lagodon rhomboides*, is a ubiquitous species found in warm-temperate and subtropical seagrass meadows in estuaries and nearshore waters of the western North Atlantic and the Gulf of Mexico, and is among the most abundant fish species in these seagrass habitats (Muncy, 1984; Darcy, 1985). In the post-settlement and juvenile life stages, they are obligate carnivores, but are primarily herbivores as adults, and therefore impact invertebrate and macrophyte abundance through foraging (Stoner, 1980, 1982; Muncy, 1984). *L. rhomboides* are also key prey species for numerous predatory fishes (Jordan et al., 1996).

Despite the documented use of estuarine seagrass meadows by *L. rhomboides* (e.g., Nelson, 1998), an account of the species' diet (Stoner, 1980, 1982; Darcy, 1985; Luczkovich et al., 1995), and information on effects of some predators (Darcy, 1985; Jordan et al., 1996), there is limited information on microhabitat use patterns by the post-settlement life stage. Most studies of early life stage *L. rhomboides* have either grouped fishes into size categories that incorporate multiple functional life stages (e.g., Jordan et al., 1996) or have not identified microhabitat characteristics that potentially influence abundances and distributions of post-settlement stage individuals (e.g., Nelson, 1998). Furthermore, studies that concentrate on sub-adult and adult fishes are not necessarily applicable to the vulnerable early life history stages. Thus, questions concerning aspects of microhabitat use by post-settlement stage *L. rhomboides* have yet to be answered.

This study was designed to address two hypotheses concerning factors influencing distribution of post-settlement *L. rhomboides* within seagrass beds: (1) the abundance of post-settlement *L. rhomboides* is positively correlated with macrophyte cover; and (2) post-settlement *L. rhomboides* in more complex habitats would suffer lower rates of predation relative to less complex habitats.

2. Materials and methods

2.1. Study location

Charlotte Harbor, Florida, USA, is a 700-km^2 coastal plain estuarine system bound on the seaward side by barrier islands, with tidal water exchange between the estuary and the Gulf of Mexico through Boca Grande Pass, San Carlos Bay, and four smaller inlets 5–11 m deep. Average depth of the estuary is <5 m. Considerable freshwater input (ca. 13,250 million liters per day) is received from the Peace, Myakka, and Caloosahatchee Rivers, and together, these rivers drain a basin that exceeds 12,000 km^2 (Hammet, 1990), resulting in a salinity range from 0 to 36 ppt. The climate in Charlotte Harbor is subtropical, with infrequent freezes, and seasonal mean water temperatures range from 18 to 32 °C (Nelson, 1998). Annual rainfall averages 127 cm (Stoker, 1986) and there is a fairly distinct wet and dry season that supports a variety of aquatic habitats (Taylor, 1974; Harris et al., 1983). Among the predominant habitats are seagrass flats, primarily *Thalassia testudinum* Banks ex Koenig and *Halodule wrightii* Ascherson, (262 km^2; Sargent et al., 1995) and mangrove shoreline (143 km^2; L. Kish, unpublished data).

Eight sites were sampled for patterns of microhabitat use by *L. rhomboides*, with four of these sites also used for a predation experiment. Sample sites were chosen to meet the criteria of general patterns of habitat use by young-of-year *L. rhomboides* as defined by Nelson (1998) for Charlotte Harbor: all sites were composed of seagrass beds (*T. testudinum* and *H. wrightii*) in water <1 m depth. All sampling occurred in February and March 2002, the end of the 5-month settlement season for *L. rhomboides* (Nelson, 1998). Eight study sites were chosen as a space-for-time substitution (Pickett, 1989), with sites chosen for spatial coverage of the portion of the Charlotte Harbor estuary where *L. rhomboides* are found as a substitution for sampling over time.

2.2. Patterns of microhabitat use

We used throw traps to sample eight seagrass beds in Charlotte Harbor to examine distribution patterns of post-settlement *L. rhomboides* in seagrass beds and to determine whether more post-settlement *L. rhomboides* would be found in dense seagrass or seagrass beds with drift macroalgae than in sparse seagrass or seagrass beds without drift macroalgae (Fig. 1). Each site was approximately 1 ha, and was sampled once with 20 throw traps in a single day between February and March 2002. The throw trap frame (1 m^2 with a height of 61 cm) was constructed of angle aluminum, with mesh sides (6 mm mesh), and a

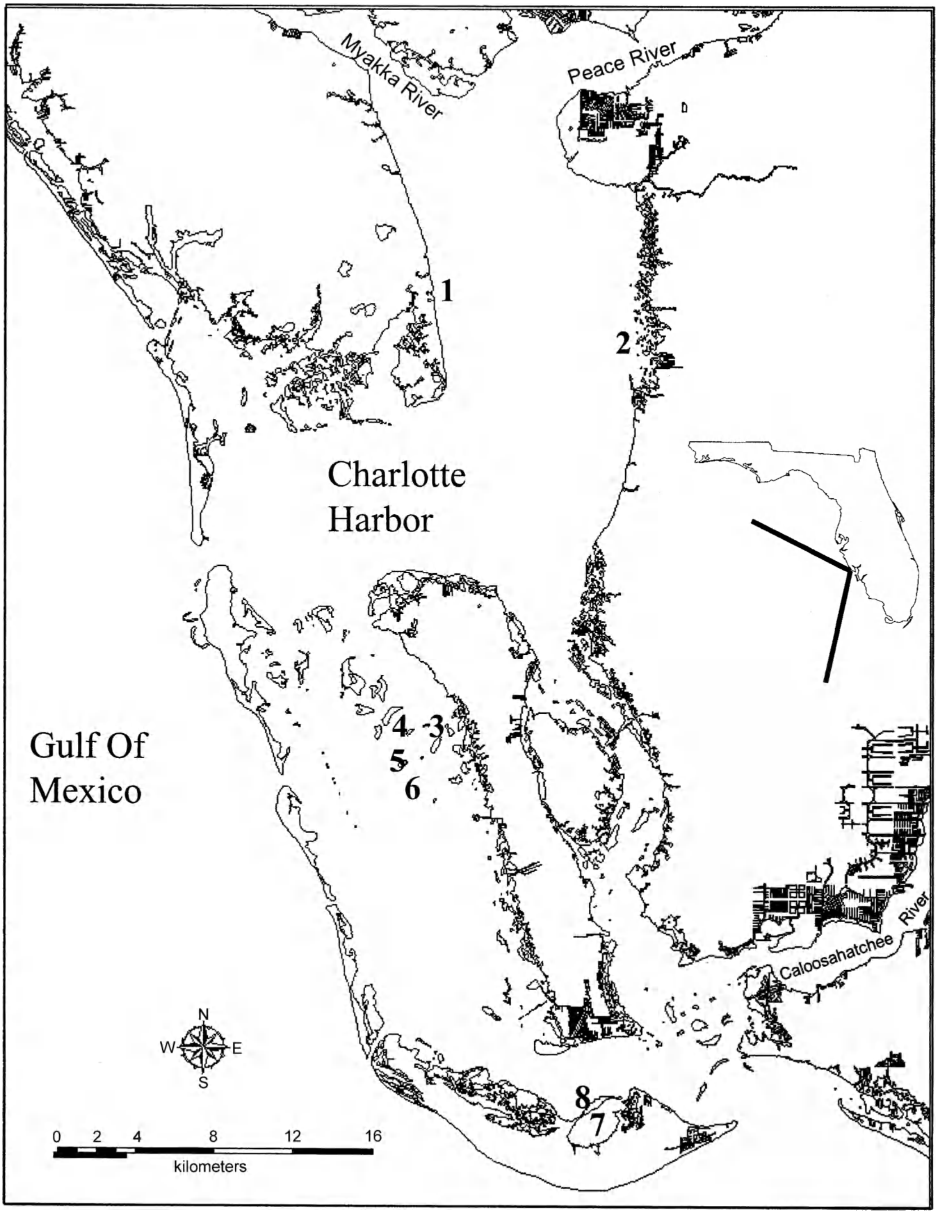

Fig. 1. Locations of eight study sites in Charlotte Harbor, Florida, USA.

mesh collar with floats extending the height of the throw trap an additional 61 cm, resulting in an effective throw trap height of 122 cm. At each site, the trap was thrown haphazardly from a small boat and immediately pushed into the sediment. A long-handled dip net (41 × 33 cm hoop dimensions, 6 mm mesh) was used to sweep the benthos within the throw trap. Each throw trap sample was swept five times (three net passes of the bottom within the throw trap = 1 sweep). Pilot study sampling revealed >90% of post-settlement *L. rhomboides* were captured with five sweeps. Percent cover and species composition of seagrass within the 1-m^2 throw trap area were estimated by the samplers. Each sampler made independent estimates of percent cover for 10 throw trap samples and compared estimates to ensure consistency of estimates of percent cover of seagrass; sampler estimates of percent cover were identical. Volume of drift macroalgae of each throw trap sample was measured using a graduated cylinder with holes drilled in the bottom to allow water to escape (sensu Robbins and Boese, 2002). A wooden dowel was used to pack the algae in the cylinder, and the volume (in ml) was recorded. Standard length and total length were recorded for all *L. rhomboides* prior to their release.

Stepwise multiple regression (forward selection) (Sokal and Rohlf, 1995) was used to determine the extent that *L. rhomboides* abundance was a function of the drift macroalgae volume or seagrass percent cover. The relationship between volume of drift macroalgae and percent cover of seagrass was examined with a Pearson's correlation test (Sokal and Rohlf, 1995). Because our null hypothesis (H_o: the abundance of post-settlement *L. rhomboides* is not a function of drift macroalgae volume (algae) or cover (seagrass)) was applied to seagrass beds in Charlotte Harbor, and not to a particular site per se, data from all sites were pooled for analyses. The relationship between *L. rhomboides* abundance and drift macroalgal volume was examined graphically with loess smoothing (Cleveland, 1993). The loess procedure is a fitting function that graphically fits the best line to data that are not adequately fit by a parametric, linear procedure (i.e., loess is a form of nonparametric regression). The loess function assesses a moving average, accounting for any underlying pattern, accommodating for residual variation from a standard linear fit, thus allowing us to determine whether the positive relationship between *L. rhomboides* abundance and drift macroalgae volume persisted at the low and high volumes of drift macroalgae encountered in this study.

2.3. Relative predation rates: tethering in the field

Post-settlement *L. rhomboides* were tethered in each microhabitat at study sites 1, 5, 6, and 8 (Fig. 1), with one tethering experiment conducted at each site, to test the hypothesis that a more complex microhabitat (seagrass with drift macroalgae) provides more protection from predation than a less complex microhabitat (seagrass without drift macroalgae). For each tethering experiment, post-settlement *L. rhomboides* were captured from a seagrass bed immediately adjacent to the experimental bed with a 9 m. bag seine (3 mm mesh stretch mesh), and all *L. rhomboides* placed in a water-filled bucket (61 l) on the boat. Fish were sorted, and only fish between 20 and 50 mm SL ($\bar{x} = 26$ mm) were retained for use in the tethering experiment.

A sewing needle was used to pass a 30-cm-long, 6-lb test monofilament tether through the fish's body above the anal fin and below the spine. At the end of the tether was a 1-

cm piece of 20-lb test monofilament tied at its center to the 6-lb test line (i.e., a "*t*-stop"), so that the heavier monofilament laid perpendicular to the tether and thus could not be pulled through the fish's body. The tag end of each tether was then tied to a metal stake. After tethering, fish were placed in a separate bucket, and kept there until 15 fish had been successfully tethered. The tethering procedure took 5 min or less for each batch of 15 fish. Fish were released if there was any apparent damage during the tethering procedure.

Once 15 fish were tethered, they were placed at 5 m intervals by inserting the metal stake into the sediment along a 75-m transect. A second batch of fish was then tethered and placed on a transect 10 m from and parallel to the first transect: one transect in seagrass without drift macroalgae and one transect in seagrass with drift macroalgae. All drift macroalgae was removed from the seagrass without algae transect with a long-handled dipnet (3 mm mesh); drift macroalgae was added in the seagrass with algae transect if none was present naturally. In this case, approximately 600 ml of drift macroalgae was placed on the bottom and secured with the stake holding the tether. Since our hypothesis addressed the comparative refuge value of the two microhabitat types, and not the quantity of each microhabitat, percent cover of seagrass and volume of drift macroalgae were not included as factors in this experiment. Rather, an effort was made to locate transects within the study sites representing the most common microhabitat coverage.

The four separate experiments ran for 4, 2, 2 and 1 h. Since the measure of interest was the relative predation rate at each habitat, not an absolute measure of predation, data (number of fish missing and number of fish remaining at the end of the experiment) were pooled for all experiments and examined with a 2 × 2 contingency table and chi-square test (Sokal and Rohlf, 1995). Data (number fish missing per time) were also expressed graphically. Three of the sixty tethers in seagrass without drift macroalgae treatment, and two tethers in the Seagrass With Drift macroalgae failed, so these fish were discarded prior to analysis, resulting in sample sizes of $N=57$ and $N=58$, respectively.

2.4. Relative predation rates: aquarium experiments

Four experimental trials were conducted in the laboratory to measure relative predation rates among four discrete habitats along a continuum of habitat complexity under controlled conditions,. A large aquarium (4 m length, 80 cm width, 90 cm height) was divided into five chambers of equal size (80 cm length, 80 cm width, 90 cm height) using 5 mm nylon mesh netting. The mesh netting was secured to the sides of the aquarium with PVC fasteners and foam inserts were installed between the mesh netting and sides of the aquarium to ensure that *L. rhomboides* were not able to escape from individual chambers during the course of experiments. Black shower curtains with small observation ports cut into each were hung over the face of the aquarium to reduce stress of the fish and to promote acclimation of fish to laboratory conditions. Water used in all experiments was pumped directly from Tarpon Bay (a side bay within Charlotte Harbor, see Site 7, Fig. 1) and was sand-filtered prior to entering the aquarium. The system was closed, internal circulation during all experiments, with water filtration achieved with an in-line sand filter and an ultraviolet filter.

All experimental chambers had a sand bottom, and each a different habitat: Chamber 1 contained 50% cover of artificial seagrass made of polyolefin plastic imitating *T. testudinum*; Chamber 3 contained 600 ml of drift macroalgae (primarily *Hypnea* spp, *Gracilaria* spp, and *Spyrida* spp); Chamber 4 was unvegetated sand bottom; and Chamber 5 contained 50% cover of artificial seagrass and 600 ml of drift macroalgae. Chamber 2 was used to store captured post-settlement *L. rhomboides* for use in subsequent experiments. This experimental setup provided habitat complexity levels of low (unvegetated), intermediate (seagrass only and drift macroalgae only), and high (seagrass + drift macroalgae).

Ladyfish, *Elops saurus* (Linnaeus), a known predator of *L. rhomboides* in seagrass beds (Jordan et al., 1996), were captured with barbless hook and line and placed in the experimental tank—one fish ($\bar{x} = 299$ mm TL, ± 16.5 mm) per experimental chamber. Predators were starved for 2 days, and on the third day were given post-settlement *L. rhomboides* as prey. The acclimation period was complete when the predators began feeding—2 weeks from time of introduction to the aquarium. The first of four experimental trials began after completion of the acclimation period. Due to the long acclimation time for *E. saurus*, the same four individuals were used for all trials and were rotated among treatments so that each individual was placed in each treatment once, so any predator “learning trajectory” was applied equally across treatments.

Prior to each trial, post-settlement *L. rhomboides* were captured with a 30-in. bag seine (3 mm mesh) or a minnow trap (5 mm mesh), placed in a livewell, and sorted. Only fish < 50 mm were retained for use in the experimental trials. Prior to each trial, *E. saurus* predators were removed from the chambers and placed in a separate livewell while seven post-settlement *L. rhomboides* individuals were placed into each chamber. (Seven *L. rhomboides* were used per each trial because this was the average number of individuals eaten by *E. saurus* predators during the acclimation period.) The seven *L. rhomboides* were allowed 5 min to acclimate to their surroundings before the reintroduction of the *E. saurus* (rotation of individuals to a new treatment chamber). The four experimental trials lasted 3, 4, 4, and 4 days, which was adequate time for the number of *L. rhomboides* remaining in one or more chambers to decline to zero.

The number of post-settlement *L. rhomboides* remaining in each habitat at the end of each trial was used to rank habitats to determine whether predation of post-settlement *L. rhomboides* differed among habitat types. Ranks were examined with Kendall’s coefficient of concordance (Sokal and Rohlf, 1995). Concordance was used because of lack of independence of the repeated measures for both predators (the same individuals were used for all experiments) and habitat chambers (the same chambers were used repeatedly for all trials) precluded the use of parametric statistics. Since all predators were exposed to all habitat chambers, it was assumed that biases were equal across treatments. Moreover, since Kendall’s coefficient is, in itself, a measure of independence of measures (Sokal and Rohlf, 1995), if biases (e.g., a “learning trajectory” of predators) were influential, low or no concordance would result. In addition, concordance is an appropriate tool for discerning pattern from experimental data that otherwise might be too variable to provide conclusive results (Underwood, 1997). Bonferroni post hoc comparisons (experiment-wise error rate, $p < 0.05$) of treatment means (Sokal and Rohlf, 1995) were used to determine which treatments differed from one another based on the concordance results. Since all *E.*

saurus predators were exposed to each habitat type once, and any bias from the predators "learning trajectory" was equal across treatments, the individual predator was not considered as a factor.

3. Results

The seagrass beds sampled at each of the eight sites were primarily *T. testudinum*, with occasional sparse *H. wrightii* mixed in. Mean estimated percent cover of seagrass was 34% (S.E. = 1.66%) (Table 1). Drift algae at the eight sites was primarily *Hypnea* spp., *Gracilaria* spp., and *Spyrida* spp., and averaged 352 ml/m^2 (S.E. = 46.41).

3.1. Patterns of microhabitat use

Two hundred sixty-four post-settlement *L. rhomboides* were captured, measured, and released (mean standard length = 25.78 mm, min = 13 mm, max = 42 mm) in 160 throw trap samples ($n = 20$ samples/site) (Table 1). The mean number of *L. rhomboides* per throw trap was 1.66 (S.E. = 0.176). The abundance of post-settlement *L. rhomboides* was weakly but significantly dependent upon volume of drift macroalgae (Table 2), with percent cover of seagrass entering the model at $p = 0.15$ but contributing little to the explanation of variation in *L. rhomboides* abundance. Loess smoothing indicated the positive relationship held for the most common volumes of drift macroalgae and for the samples with large volumes of drift macroalgae (Fig. 2).

The correlation between volume of drift macroalgae and percent cover of seagrass was weak, negative, and significant (Pearson = − 0.187, Bartlett chi-square = 5.108, $p < 0.05$, $df = 1$). High volumes of drift macroalgae only occurred in samples with low percent cover of seagrass (Fig. 3). Seagrass cover and drift macroalgae volume were similar at all but one site (Site 7, see Fig. 1). The apparent association between high drift macroalgae volume and low seagrass cover is similar to preliminary findings from an ongoing study of patchy vs. continuous seagrass beds in Charlotte Harbor in which patchy seagrass beds (seagrass

Table 1
Results of throw trap samples for the eight study sites (20 throw traps per site) in Charlotte Harbor, Florida, USA

Site	Total number of *L. rhomboides*	Standard length (mm) of *L. rhomboides*		Volume (ml/m^2) of drift macroalgae				Percent cover of seagrass			
	Captured	Mean	S.E.	Mean	S.E.	Min	Max	Mean	S.E.	Min	Max
1	26	25.5	0.81	129.5	46.95	0	770	43.3	4.11	10	80
2	29	29.1	0.97	226.3	44.16	0	760	18.5	1.59	5	30
3	17	23.5	0.81	276	34.61	0	590	19.6	2.77	5	50
4	44	26.8	0.57	260.5	39.46	50	680	58.1	5.15	15	90
5	24	20.9	0.79	201.8	52.55	0	740	26.7	2.5	12	55
6	14	27.6	1.76	773	148.65	170	1480	50.5	2.73	35	60
7	23	26.5	0.45	74.7	28.88	0	3610	41.5	2.86	5	65
8	69	25.2	0.42	1063	259.76	0	500	26.5	4.17	25	70
Total	246	29.1	0.97	352.8	46.41	–	–	34.1	1.66	–	–

Refer to Fig. 1 for site locations.

Table 2

Results of the forward stepwise regression to examine the log($x+1$)-transformed post-settlement *L. rhomboides* abundance as a function of drift algae volume (ml) and percent seagrass cover

$R^2=0.30$					
Factor	Coefficient		*t*		*p*
Drift algae volume	0.558		7.833		<0.001
Percent cover seagrass	0.131		1.834		0.069
Source	SS	*df*	MS	*F*	*p*
Regression	3.833	2	1.916	30.75	<0.001
Residual	8.912	143	0.062		

Variables entered and exited the model at $p=0.15$, tolerance = 0.1.

with patches of open bottom) contain significantly more drift macroalgae than continuous seagrass beds (Robbins and Adams, unpublished data).

Anecdotally, observations by mask and snorkel suggested that post-settlement *L. rhomboides* utilized gaps within seagrass beds and edges between seagrass and open bottom habitats. These areas often contain substantial volumes of drift macroalgae. Upon approach by the observer, post-settlement *L. rhomboides* would swim into a clump of drift macroalgae or flee first over and then among seagrass blades. Escape routes were generally short - cover was sought quickly to avoid the observer. Due to the short distance of apparent travel of post-settlement *L. rhomboides*, and the space (≥ 7 m) between throw trap samples, it was assumed that there was minimal recapture of individuals in samples. Even if some individuals were recaptured, given the high abundance of small *L. rhomboides* in seagrass beds (Nelson, 1998; this study), their influence on the findings is likely minimal.

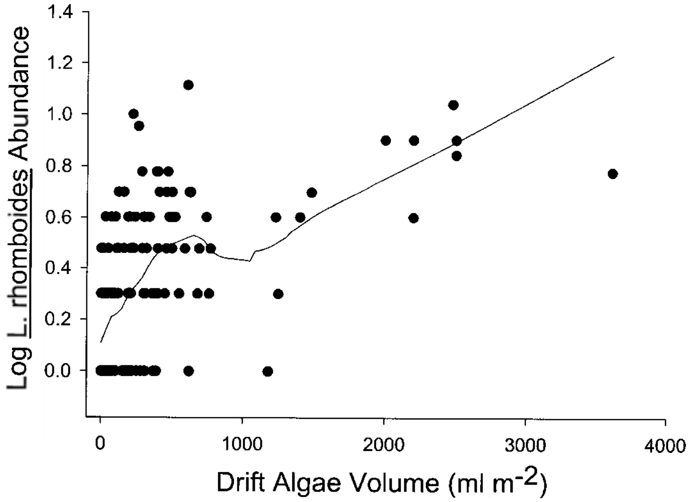

Fig. 2. Abundance of *L. rhomboides* on a log scale, as a function of the volume of drift algae sampled in throw traps. Line represents loess smoothing (tension = 0.5).

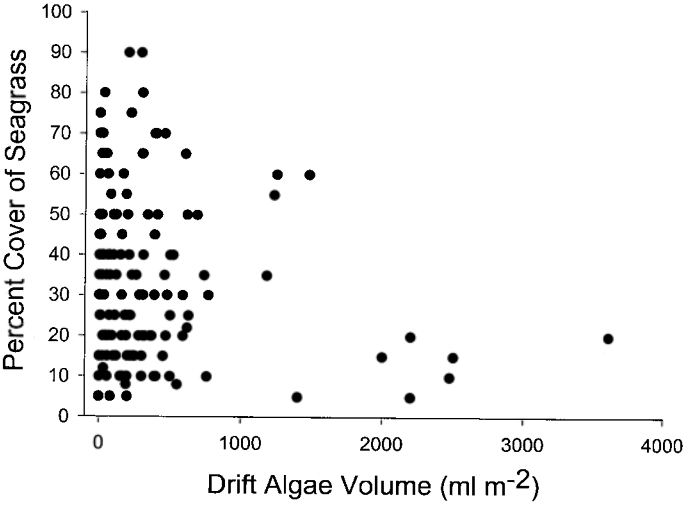

Fig. 3. Relationship between percent cover of seagrass and volume of drift algae as sampled in throw traps.

3.2. Relative predation rates: tethering in the field

Four tethering trials were completed, with tethers remaining intact during all trials. More post-settlement *L. rhomboides* were missing in treatments of seagrass without algae

Table 3

Results of tethering experiments to examine the relative predation rate of post-settlement *L. rhomboides* tethered in seagrass beds with drift algae and in seagrass beds without drift algae

(A) Two-way contingency table showing results of the tethering experiment

Treatment	Number remaining		Number missing		Σ
	Actual	Expected	Actual	Expected	
Without drift algae	14	19.3	43	37.7	57[a]
With drift algae	25	19.7	33	38.3	58[a]
Σ	39		76		115

(B) Proportion of tethered *L. rhomboides* remaining at the end of each trial. Refer to Fig. 1 for site locations

Location	Trial duration (h)	Percentage of tethered fish missing at end of trial	
		Seagrass with algae	Seagrass without algae
4	4	60	79
7	2	80	93
1	2	27	77
6	1	57	53

$\chi^2 = 4.40999$; $p < 0.05$.

Data pooled across all four sites.

[a] Three of the sixty tethers in the Seagrass without drift algae treatment, and two tethers in the Seagrass with drift algae failed, so these fish were discarded prior to analysis, resulting in sample sizes of $N = 57$ and $N = 58$, respectively.

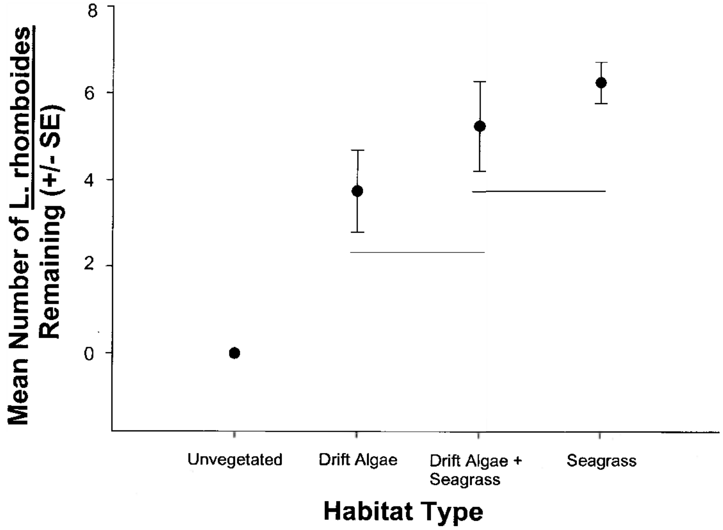

Fig. 4. Number of *L. rhomboides* remaining per habitat type in the aquarium predation experiment. Habitats that share an underline were not significantly different (Bonferroni post hoc comparisons, experiment-wise error rate, $p < 0.05$). $n = 4$ trials per habitat.

than in seagrass with algae. The number of post-settlement fish missing from seagrass without algae treatments was less than expected by chance, and the number of fish remaining in seagrass with algae treatments was greater than expected by chance, indicating a higher level of predation in seagrass without drift macroalgae (Table 3A). When data were examined by site and trial duration, predation was higher in treatments without algae for all trials except the trial of shortest duration (Table 3B).

3.3. Relative predation rates: aquarium experiments

Number of fish remaining in each habitat was ranked consistently among treatments (Kendall coefficient of concordance = 0.89, $W = 10.658$, $p < 0.05$, $df = 3$). Since Kendalls' coefficient of concordance was significant, the mean number of fish remaining in each habitat was examined with a post hoc pairwise comparison; the Bonferroni test revealed predation was greatest in the unvegetated habitat, where all post-settlement *L. rhomboides* were eaten (Fig. 4). Among vegetated treatments, predation was higher in drift macroalgae on open bottom and lower in seagrass.

4. Discussion

The findings of these experiments provide evidence that seagrass and drift macroalgae within seagrass beds are both important microhabitats for post-settlement *L. rhomboides*. The results of these experiments indicate higher utilization of mixed-vegetation habitats with high structural complexity (drift macroalgae within seagrass beds) by post-settlement

L. rhomboides than seagrass alone, and a greater rate of predation in low complexity habitats (open bottom, drift macroalgae on open bottom), reflecting a likely tradeoff between foraging and refuge from predation.

The abundance of post-settlement *L. rhomboides* increased in relation to the amount of macrophyte cover. While this might be interpreted as being a simple function of an increase in macrophyte biomass (seagrass and drift macroalgae), the positive relationship was due mostly to drift macroalgae volume. Given that drift macroalgae is a microhabitat that occurs within seagrass beds and that drift macroalgae and seagrass are highly intermixed habitats, that a relationship was detectable and significant indicates that the relationship is likely valid. Moreover, the loess smoothing procedure (Fig. 2) suggests a positive relationship between abundance of post-settlement *L. rhomboides* and drift macroalgae volume is valid at both low and high levels of algae volume encountered in this study, although the slope of the relationship differs at low and high drift macroalgae volume.

One possible explanation for the findings of this study is that post-settlement *L. rhomboides* are simply using the habitats available during their settlement season. The abundance of drift macroalgae in Florida is greatest in winter months (Virnstein and Carbonara, 1985), which is when the bulk of *L. rhomboides* settlement occurs (Darcy, 1985; Nelson, 1998). Moreover, the dominant seagrasses—*T. testudinum* and *H. wrightii*—become dormant or experience blade mortality in winter in this region (Robbins, unpublished data), resulting in lower above ground biomass and less available habitat. Thus, post-settlement *L. rhomboides* may merely be using drift macroalgae because it is the most abundant habitat. However, if this parsimonious explanation (more habitat = higher post-settler abundance) is valid, one would also expect a significant and positive relationship between post-settler abundance and percent cover of seagrass, which was not the case in this study. A more likely explanation is that a combination of habitat selection, foraging, and different rates of predation among habitats resulted in the observed distribution of post-settlement *L. rhomboides*.

The importance of drift macroalgae microhabitat to post-settlement *L. rhomboides* may be, in part, a function of diet. Early stage juveniles are obligate carnivores (Stoner, 1980; Luczkovich et al., 1995), and shift to an increasingly herbivorous diet as they grow (Montgomery and Targett, 1992). The major prey items in the diet of post-settlement *L. rhomboides* are amphipods and isopods (Stoner, 1980), which are in high abundance in both drift macroalgae and seagrass (Brooks and Bell, 2001). Moreover, epifaunal abundance and biomass (dominated by amphipods and isopods) was higher on drift macroalgae than on seagrass in Tampa Bay, Florida (Knowles and Bell, 1998).

Species that are preyed upon by post-settlement *L. rhomboides* are also present on grass blades, but the structural complexity of *T. testudinum* and *H. wrightii* may not provide post-settlement *L. rhomboides* as much protection from predation as drift macroalgae. Given the high abundance and diversity of amphipods and other prey species in both drift macroalgae and on seagrass blades (Stoner, 1980), refuge from predation is most likely the greatest advantage provided to post-settlement *L. rhomboides* by drift macroalgae. The prey selection by juvenile *L. rhomboides* is different for fish foraging in drift macroalgae than for fish foraging in seagrass (Stoner, 1979, 1982): the structural complexity of drift macroalgae makes it more difficult for juvenile *L. rhomboides* to locate and eat prey, so they are less selective when foraging. In contrast, seagrass blades provide less complex shelter for amphipods and other prey species (Knowles and Bell, 1998), and juvenile *L. rhomboides* became more selective in their diets. Thus, when viewed from a strictly foraging perspective, seagrass blades may provide a more desired prey base for juvenile *L. rhomboides* than drift macroalgae.

Experimental evidence provides insight into the importance of shelter as a refuge from predation. When prey species are placed in aquaria without a predator and are allowed to choose among different habitats, individuals use both complex and simple habitats (Savino and Stein, 1989; Jordan et al., 1996), or are more abundant in simple (i.e., open) habitats (Sogard and Olla, 1993). When predators are introduced, most prey seek refuge within the more complex habitat (Savino and Stein, 1989; Sogard and Olla, 1993; Jordan et al., 1996). In field studies of reef fishes, for example, predation rates of juvenile fishes are greater on reefs with more holes large enough to be used by predators than on reefs with fewer small holes that can be used by juveniles (Hixon and Beets, 1993), again indicating the importance of microhabitat complexity to small fishes. Moreover, direct comparisons of predation rates of juvenile spiny lobster in algae and seagrass indicated algae provided better shelter from predation (Lipcius et al., 1998). In this study, *L. rhomboides* in the experimental aquarium chambers were distributed equally prior to the introduction of the *E. saurus* predators. Upon introduction of the predators, the *L. rhomboides* immediately sought shelter deep within the drift macroalgae and against the base of seagrass blades. In the unvegetated chamber, the post-settlement *L. rhomboides* sought shelter in the corners or low against the sides of the chamber.

In this study, both field and laboratory experiments were conducted to address predation as a factor influencing habitat use patterns by post-settlement *L. rhomboides*. Although there are numerous potential problems with using tethering to measure predation rates (Peterson and Black, 1994), tethering can provide useful results. One potential problem with tethering mobile prey is entanglement of the tether, and subsequently higher than normal vulnerability to predators (Adams et al., in press). This is especially problematic when tethers are used to estimate relative predation rates in structurally different habitats (e.g., vegetated vs. unvegetated) (Micheli, 1996; Adams et al., in press), where artifacts associated with tethering might vary by habitat. In this study, tether entanglement was similar in both drift macroalgae and seagrass habitats (Adams, personal observation), so tethering artifacts were not thought to be a factor in among habitat comparisons. While it is possible that tethered fishes in this study were susceptible to predators that are not a threat under normal circumstances, the results only confirm the importance of habitat structural complexity as a refuge from predation: tethered fishes in structurally complex drift macroalgae were less vulnerable relative to fish tethered in seagrass, regardless of possible predators. Moreover, field observations of post-settlement *L. rhomboides* behavior support the findings of the tethering study. When post-settlement *L. rhomboides* use drift macroalgae as a refuge from predation, they burrow into the drift macroalgae and remain, motionless, until the predation threat is over. In contrast, post-settlement *L. rhomboides* pursued in seagrass flee above and among the seagrass blades before diving into the seagrass.

The results from the field and aquarium experiments suggest an interaction of predation, prey, and habitat. Seeking shelter at the base of seagrass blades, or even burrowing into the sediment, may provide post-settlement *L. rhomboides* better refuge from predation than drift macroalgae that is unattached to the bottom, or even resting on seagrass blades. This may be especially true with a fast, mid-water predator, such as *E. saurus*. Drift macroalgae that is not attached to open bottom does not allow this close association with the benthos, and does not provide the additional vertical shelter as does seagrass. Thus, it may be that the structural complexity of the finely branched drift macroalgae is too compact, or small-scale, to provide adequate protection from predators (Deegan et al., 2002).

Since post-settlement *L. rhomboides* are both predators and prey (Stoner, 1982; Darcy, 1985; Jordan et al., 1996), they are faced with a tradeoff between habitats that are best for foraging and habitats that provide sufficient refuge from predation. Foraging efficiency and the efficacy of a habitat as a refuge from predation change with habitat complexity, and the tradeoff between these factors varies with prey availability and predator presence (Gotceitas and Colgan, 1989; Savino and Stein, 1989; Jordan et al., 1996). Nelson (1998) suggested that more young-of-year *L. rhomboides* were found in patchy seagrass beds because the combination of seagrass and open bottom habitats resulted in a positive tradeoff between refuge and foraging opportunities, respectively. Moreover, *L. rhomboides* forage more efficiently in low density seagrass but are better able to avoid predation in higher density seagrass (Jordan et al., 1996). That predation rates of benthic invertebrates may be higher along the interface between seagrass and unvegetated bottom (Peterson et al., 2001) further supports this hypothesis.

The results of this study suggest a more complete explanation. In a separate, ongoing study, we have found the volume of drift macroalgae is greater in patchy seagrass beds than in continuous seagrass beds. Given the positive relationship between abundance of post-settlement *L. rhomboides* and volume of drift macroalgae, and the apparent refuge and forage value of drift macroalgae, we argue that patchy seagrass beds with drift macroalgae constitute a structurally complex habitat mosaic that provides refuge (drift macroalgae in seagrass) in close proximity to lower complexity (sparse seagrass, open bottom) foraging habitats. Furthermore, amphipod abundance was higher in drift macroalgae that moved through seagrass beds than in drift macroalgae that remained within seagrass and drift macroalgae that remained on open bottom (Brooks and Bell, 2001). Thus, drift macroalgae passing through seagrass into open bottom provide both foraging and shelter attributes.

The findings of this study contrast with recent research in a north temperate estuary (Deegan et al., 2002), which found a negative relationship between macroalgal biomass and fish abundance, fish species richness, and fish biomass. Part of the explanation for these differences may be the study species. *L. rhomboides* settlement occurs in late winter, which is when abundance of drift macroalgae in Florida is greatest (Virnstein and Carbonara, 1985), and seagrasses are naturally dormant. In the north temperate estuary, the negative influence of high macroalgae biomass on fish abundance, species richness, and biomass was a community level effect, while in this study we examined only the abundance of the post-settlement stage of a single species that may have a positive relationship with drift macroalgae (cf. Deegan et al., 2002 and references within). Moreover, Deegan et al. (2002) studied the north temperate estuary in summer, a time of maximum production, while our experiments took place in winter. A second partial explanation might be the amount and types of macroalgae studied. Only in a few samples did the amount of macroalgae in this study reach the high biomass treatment of Deegan et al. (2002), and while those high abundances of macroalgae do occur in the Charlotte Harbor estuary, they were not examined in this study. Clearly, more study is needed to determine if there is a threshold of macroalgal abundance that benefits post-settlement *L. rhomboides*.

In summary, the conclusion of this study—that drift macroalgae is an important microhabitat for post-settlement *L. rhomboides* in seagrass beds—is not surprising, and suggests the settlement of *L. rhomboides* in seagrass beds during the season of peak drift macroalgae abundance provides an adaptive advantage. Drift macroalgae is a three-dimensional, structurally complex habitat that provides appropriately sized shelter for these small fishes and provides suitable prey. Although each microhabitat habitat alone provides benefits for post-settlement *L. rhomboides*, seagrass beds that contain drift macroalgae offer the advantage of providing refuge (drift macroalgae in seagrass) intermixed with a widespread habitat (seagrass intermixed with open bottom) that contains a more available source of food for post-settlement fishes, and furnishes characteristics necessary for subsequent life stages (Montgomery and Targett, 1992). Future studies might focus on formulating a habitat index that incorporates the microhabitat characteristics of seagrass beds and drift macroalgae as a predictive tool for *L. rhomboides* abundance.

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