Pelagic Sargassum Mediates Predation Among Symbiotic Fishes and Shrimps

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We investigated, using microcosm experiments, predator–prey relationships of symbionts within sargassum communities. Specifically, two predatory fishes (*Stephanolepis hispidus* and *Histrio histrio*) and two shrimp species (*Latreutes fucorum* and *Leander tenuicornis*) were studied. The following research questions were addressed: 1) Do the fish predators select preferentially particular shrimp prey species? and 2) Does available habitat affect survival times of shrimp prey, or prey selection by fish predators? *Stephanolepis hispidus* showed a selection preference for *Latreutes fucorum,* as this shrimp's survival times were significantly lower than for *Leander tenuicornis* in predation trials. However, *H. histrio* did not show a preference for either shrimp species, as survival times for shrimp did not differ significantly. Differences observed in these selection patterns are likely related to 1) differences in the foraging strategies of the predators and 2) prey defenses (morphological). A comparison of survival times with and without sargassum habitat (both natural and synthetic) demonstrates clearly that both shrimp species ultimately receive some degree of protection from these fish predators by living in these morphologically complex communities.

Complex environments (biotic and abiotic) can mediate predation (Heck and Orth, 1980; Martin-Smith, 1993; Warfe and Barmuta, 2004). Pelagic sargassum communities, commonly found in the western North Atlantic and Gulf of Mexico, are highly complex morphologically and, subsequently, harbor many endemic and ephemeral symbiotic inhabitants (Weis, 1968). Although this complexity is presumed to mediate protection, research to support this hypothesis is mostly lacking for these mobile, macrophytic communities.

Many studies have focused on predator preferences for prey in aquatic systems (e.g., Werner and Hall, 1974; Stein 1977; Clements and Livingston, 1984; Main 1985; Mikheev and Wanzenböck, 1999). Habitat structure and prey accessibility can be important factors affecting foraging in these aquatic communities. Cryptic prey species that mimic patterns of their background habitat may mediate predation, presumably by increasing predator foraging time to locate prey (Endler, 1978; Clements and Livingston, 1984). Relatively few studies have looked at predator–prey interactions within mobile macrofaunal communities, especially involving sargassum.

The sargassum seaweed community, which has numerous symbiotic inhabitants living in proximity, has several examples of cryptic predators and prey. Caging experiments, excluding fishes, have addressed impacts of predation on species diversity within sargassum clumps (Edgar and Akoi, 1993; Martin-Smith, 1993), but these studies did not focus specifically on mechanisms involved in prey selection.

Therefore, in the present study, we used microcosm experiments to investigate predator–prey relationships of symbionts within sargassum communities. Specifically, two predatory fishes (*Stephanolepis hispidus* (Linnaeus) and *Histrio histrio* (Linnaeus)) and two shrimp species (*Latreutes fucorum* (Fabricius) and *Leander tenuicornis* (Say)) were studied. The following research questions were addressed: 1) Do the fish predators select preferentially particular shrimp prey species? and 2) Does available habitat affect survival times of shrimp prey, or prey selection by fish predators?

Materials, Methods, and Community Description

Sargassum community description.—*Sargassum* spp. are brown algae sometimes called gulfweed and consist of long branching stipes with narrow, spiny-edged fronds and spherical gas-filled bladders for floatation (Weis, 1968). Colors vary from yellow to brown to black (Hacker and Madin, 1991). Two species are common in the western North Atlantic: *Sargassum natans* (Linnaeus) and *Sargassum fluitans* Børgesen (Coston-Clements et al., 1991). Both varieties circulate between 20° and 40°N and from 30°W to the western edge of the Florida Current/Gulf Stream (Dooley, 1972; Coston-Clements et al., 1991). Gulf Stream currents and wave action break apart the sargassum and distribute it throughout the North Atlantic Ocean and into the Gulf of Mexico, forming floating clumps and windrows, which provide shelter, food, and substrate to numerous organisms (Weis, 1968; Dooley, 1972; Stoner and Greening, 1984; Coston-Clements et
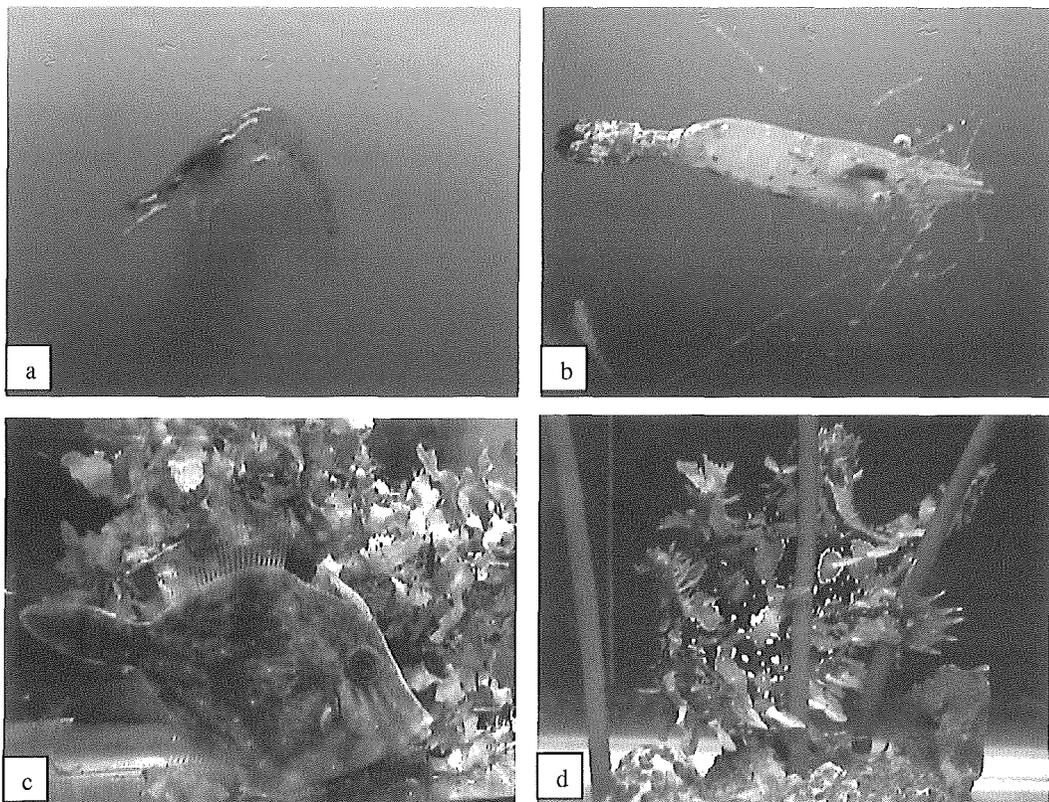
Fig. 1.   Sargassum animals used in this study: a) *Latreutes fucorum* (10 mm), b) *Leander tenuicornis* (30 mm), c) *Stephanolepis hispidus* (54 mm), d) *Histrio histrio* (91 mm).

al., 1991; Moser et al., 1998; Wells and Rooker, 2004).

One abundant shrimp species in this community is *Latreutes fucorum* (Fig. 1a), which occurs in various tints and color patterns with stripes and bars (Brown, 1939; Hacker and Madin, 1991). A second highly abundant, endemic shrimp species, *Leander tenuicornis* (Fig. 1b), also occurs in various color patterns with spots. This latter shrimp species, although common in sargassum, is less abundant than *Latreutes fucorum* (Stoner and Greening, 1984).

Many fishes also inhabit the sargassum community. We chose two species: the planehead filefish *S. hispidus* (Family: Monacanthidae) (Fig. 1c), and the sargassum fish *H. histrio* (Family: Antennariidae) (Fig. 1d). *Stephanolepis hispidus* was used because it is one of the most abundant predatory fishes found within this community, especially as juveniles (Fine, 1970; Dooley, 1972; Bortone et al., 1977; Stoner and Greening, 1984; Fedoryako, 1989). These filefish feed mainly on hydroids (Stachowicz and Lindquist, 1997) and encrusting bryozoans, secondarily feeding on sargassum shrimps (Dooley, 1972).

Histrio histrio was used because it is an endemic species in sargassum communities circumtropically (Adams, 1960), and is best known for its intricate mimicry, resembling sargassum weed with patterns of yellow, brown, and olive (De Loach and Humann, 1999). *Histrio histrio* is a highly sedentary, lie-in-wait predator spending most of its time clinging to sargassum fronds and has poor swimming abilities (Pietsch and Grobecker, 1990). Distinguishing features include a large mouth and fleshy tabs or appendages on the body that have a weedlike appearance (Adams, 1960; De Loach and Humann, 1999). Facilitated by a large mouth and distensible stomach, *H. histrio* is a voracious predator, and gut analyses confirm that sargassum shrimps are among prey types consumed frequently (Dooley, 1972; Smith, 1973).

Collection and maintenance of specimens.—Floating mats (approximately 0.3–4.0 m in diameter, with the smaller clumps usually located proximally to the coast) of *Sargassum natans* and *Sargassum fluitans* were collected via boat 1.5–3.5 km off the southeast coast of Florida using a fine-mesh dip net. Fishes and shrimps were

removed by shaking the seaweed clumps over a cooler supplied with a portable air pump. Small clumps of *S. natans* or *S. fluitans* were placed in the container to provide a temporary refuge for fishes and shrimp while in transport. Animals were kept in laboratory aquaria (38–75 liters in size) at Florida Atlantic University.

Total length of fish was measured (to nearest millimeter) from snout tip to end of caudal fin tip. *Stephanolepis hispidus* ranged in size from 26 to 105 mm; *H. histrio* ranged in size from 22 to 91 mm. Fish were then placed in aquaria, keeping both species separate. Shrimp were separated by species and measured (to nearest millimeter) from rostrum tip to end of telson, then segregated in aquaria (without sargassum) by the following size classes: 10 ± 5, 20 ± 5, and 30 ± 5 mm. General predation observations were made with all shrimp and fish size class combinations. However, only shrimp of 10 ± 5 mm were used in the specific predation trials, as this size class was the most abundant collected and potentially the most abundant prey size available to fishes in situ. Fish and shrimp were acclimated to the laboratory environment for at least 2 d before use in experiments. Fish and shrimp were fed commercial flake food and live brine shrimp, respectively, three times per week. Animals were maintained in aquaria using natural seawater (32–35 ppt) from Gumbo Limbo Environmental Complex. All animals were exposed to a 12 light:12 dark photoperiod.

General experimental predation trial procedures.— Before experimentation, all fishes were starved for 36 hr. The experimental unit consisted of an individual fish added to a 9.5-liter aquarium in which 10 min before, 10 shrimp of both species (20 shrimp total, all 10 ± 5 mm in size) were added. Once introduced into the aquarium, the fish were allowed to feed on the shrimp for 30 min before being removed. Survival times of the shrimp were recorded. Because survival times of the 20 shrimp with an individual fish were linked, statistical comparisons were made between average survival times for each shrimp species and between independent replicates with new fish.

To minimize possible observer distractions, we used a cardboard blind attached to the front of the experimental aquarium, making continuous observations of experiments through a small cutout viewing port (4 × 15 cm). Additionally, specific predator–prey behaviors were observed in all of the predation trials. Fish and shrimp were used only once in any of the predation trials. Fish and shrimp were added to 38-liter experimental aquaria using a small dip net.

Predator size can potentially influence prey response (Dall et al., 1990). As such, we attempted to maintain predator/prey size ratios that avoided extremes (i.e., a very large fish with very small prey likely has a simpler predation strategy than with larger prey). Thus, fishes were grouped into two size categories: large (48–105 mm for *S. hispidus* and 46–91 mm for *H. histrio*) and small (26–44 mm for *S. hispidus* and 22–36 mm for *H. histrio*). Additionally, the maximum ratios of fish/shrimp size in any of the trials (described below) were 21/1 and 18/1 for *S. hispidus* and *H. histrio*, respectively.

All statistical analyses were done using SigmaStat® (Version 3.2).

Fish prey species selection without habitat cover.—In these trials, predation by fishes on shrimps was tested in a bare aquarium (i.e., without any habitat cover). This was intended to mimic field conditions where we observed that natural perturbations (e.g., wind, waves, and feeding frenzies by large, pelagic, predatory fishes) could break up algal mats, disassociating shrimp, and other inhabitants from the sargassum habitat. Sometimes distance between algal mats was over 30 m, and these perturbations could disperse and diminish mats to merely individual algal strands. Thus, re-establishment by the shrimps (and other inhabitants) of adequately sized patches could be spatially and temporally challenging. Although placing fish and shrimp in a bare aquarium confines both animals (i.e., spatially limiting escape ability compared with open water), it removes any effect of refuge from structured habitat. Thus, information about predation success could be compared with equally confined conditions in which habitat cover was present.

Both species of fish were tested in separate trials. We used both shrimp species simultaneously to determine any preferences by the fishes. The experiment was replicated nine times for each fish species using different individual fish each time. Species selection experiments were analyzed using a Mann–Whitney rank sum test, as assumptions of normality were not met.

Fish prey species selection with habitat cover.— Because *Sargassum fluitans* was collected much more frequently than *S. natans*, only the former alga was used in these trials. Additionally, a plastic mimic of *S. fluitans* was available commercially (manufactured by SeaGardens), which was preferable in several ways to natural sargassum because: 1) the latter was difficult to maintain in laboratory conditions for more than several days,

and 2) it was basically impossible to remove all epibionts (which could potentially affect experimental results) from the algal fronds. This artificial algae was available in two distinct colors. Although natural *S. fluitans* does not vary in color as did these artificial forms, the availability of these two artificial color variants allowed us to tests for possible effects of prey contrast with background habitat on predation by the fish predators.

Both species of fish were tested in separate trials using the following protocol. Ten individuals of both species of shrimp, each the same size (10 ± 5 mm), were placed in a 9.5-liter aquarium containing one of the following habitats: experiment 1, natural *S. fluitans* plant light brown in color; experiment 2, artificial *S. fluitans* plant red in color; experiment 3, artificial *S. fluitans* plant light green in color. After shrimp were in the tank for 10 min, an individual fish was placed into the tank. The fish was allowed to feed for 30 min before being removed. The experiment was replicated four times for each fish species using different individual fish each time. The same protocol was followed using the two additional habitat choices. Additionally, we repeated the experiments above, this time allowing *H. histrio* to acclimate first in the aquarium for 10 min instead of the shrimp. *Histrio histrio* is an ambush predator and may be more likely to consume prey after it has established a position in the habitat.

Habitat cover experiments were analyzed using ANOVA. Tukey post hoc multiple comparisons test was used to analyze overall treatment effects.

RESULTS

General behavior of fishes and shrimp during predation.—The two fishes used markedly different approaches to attacking shrimp, and in some cases there was variation depending upon whether habitat cover was present.

Stephanolepis hispidus attacked the smallest shrimp (10-mm size range) from the side and attempted to bite the abdomen until the shrimp stopped moving, subsequently consuming the entire shrimp. In general, *S. hispidus* would initially approach the head of the larger shrimp (20- and 30-mm size range) and subsequently maneuver to pull off the shrimp's chelae and rostrum before attempting to take bites out of the abdomen. When removed, the rostrum was often discarded by the fish before consuming the rest of the shrimp within minutes.

Histrio histrio was a typical lie-in-wait predator, waiting motionless for shrimp to pass nearby before attacking. Sometimes larger fish (>60 mm) appeared to use their dorsal spines as lures to attract shrimp. Occasionally, fish appeared to pursue shrimp either by slowly swimming toward the prey (especially during trials where there was no habitat cover or when there was cover in which the fish had established itself before shrimp were introduced) or crawling through the algal fronds. Unlike *S. hispidus*, which has a relatively small mouth, the relatively large gape of *H. histrio* allowed it to ingest and swallow whole shrimp most of the time.

Smaller shrimp individuals of both species (10-mm size range) would try to flee backward from the predatory fishes in a typical caridoid escape response (cf. Main, 1985). At times these smaller shrimp appeared to hide beside larger shrimp. The 20-mm shrimp would either try to flee or snap their chelae when approached by a fish. There were a few instances where the shrimp clung to the attacking fish with its chelae. Subsequently, the fish either tried to remove the shrimp or it kept looking for other prey. The 30-mm shrimp remained motionless until the fish had obviously detected them, then the shrimp snapped their chelae at the fish. During an attack, these larger shrimp occasionally spread their lateral rostrum before attempting to swim away.

Fish prey species selection without habitat cover.—*Leander tenuicornis* survived significantly longer than *Latreutes fucorum* with the fish predator *S. hispidus* (P = 0.002, Mann–Whitney rank sum test; Fig. 2). However, survival times of both shrimp species did not differ with the fish predator *H. histrio* (P = 0.656, Mann–Whitney rank sum test; Fig. 2).

Fish prey species selection with habitat cover.—Overall, habitat type did not significantly affect survival times of the two shrimp species when shrimp were allowed to acclimate 10 min before the addition of either fish predator. However, when the fish *H. histrio* was allowed to acclimate for 10 min before shrimp were added, habitat type did significantly influence survival of one shrimp species. Specifically, average survival times of *Leander tenuicornis* were greater in the artificial green and artificial red habitats than in the natural sargassum habitat (P < 0.05, Tukey post hoc multiple comparison; Fig. 3a). Survival times in both artificial habitats were statistically similar.

Only the artificial green habitat was associated with differential survival of shrimp species, with *L. tenuicornis* having greater survival times than
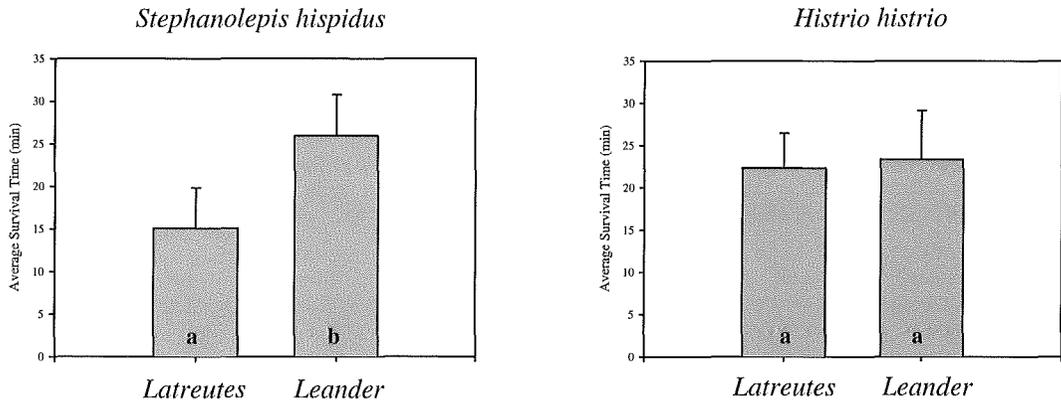
Stephanolepis hispidus   Histrio histrio

Fig. 2.   Shrimp species prey selection by the fish predators *Stephanolepis hispidus* and *Histrio histrio* without habitat cover. *Leander tenuicornis* survived significantly longer than *Latreutes fucorum* with the fish *S. hispidus* ($P <$ 0.05, Mann–Whitney rank sum test). No difference in survival times of shrimp existed with the fish *H. histrio* ($P =$ 0.656, Mann–Whitney rank sum test) (letters on histograms indicate statistical groupings; bars indicate standard deviations).

Latreutes fucorum with the fish *H. histrio* ($P < 0.05$, Tukey post hoc multiple comparison; Fig. 3b).

Habitat cover effectiveness summary.—Data were pooled from previous trials to estimate the overall effect of habitat cover vs no cover on predation of shrimp by both fish predators. Specifically, survival times for both species of shrimp with and without habitat were compared. Overall, shrimp survived significantly longer when habitat was available with the fishes *S. hispidus* ($P < 0.001$, Mann–Whitney rank sum test) and *H. histrio* ($P = 0.009$, Mann–Whitney rank sum test; Fig. 4).

DISCUSSION

We investigated predator–prey relationships of symbionts within sargassum communities, using microcosm experiments. Two predatory fishes (*S. hispidus* and *H. histrio*) and two shrimp species (*L. fucorum* and *Leander tenuicornis*) were studied. In general, these fishes used disparate feeding strategies. *Stephanolepis hispidus* had a relatively small mouth compared with the extremely large mouth of *H. histrio*. These morphological differences are likely major factors in differences observed in predation patterns during trials. In bare aquaria, *L. tenuicornis* survived significantly longer than *Latreutes fucorum* from predation by *S. hispidus* in bare aquaria. However, survival times of *Leander tenuicornis* and *Latreutes fucorum* did not differ significantly when exposed to *H. histrio* under the same experimental conditions. Prey selectivity by fringed filefishes has been suggested to be influenced by prey pigmentation patterns (Clements and Livingston, 1984). The filefish preferred to feed on a species of

amphipod with a barring pattern over two other amphipod species that lacked bars. It is not clear whether color pattern differences between *L. fucorum* and *Leander tenuicornis* were distinct enough to account for differences in predation by *S. hispidus*. Additionally, these potential color pattern differences apparently had no effect on detection and predation by *H. histrio*.

An alternative explanation for the selection of *Latreutes fucorum* over *Leander tenuicornis* by *S. hispidus* may be related to shrimp morphology. *Leander tenuicornis* has a rostrum that is highly serrated both dorsally and laterally, which may be effective, along with snapping their chelae (as seen with other crustaceans, e.g., crayfish; see Stein, 1976; Stein and Magnuson, 1976), in partially deterring predation—especially in larger shrimp, which generally took longer for *S. hispidus*, with its small gape, to handle and consume. *Latreutes fucorum* does not possess a rostrum with such extensive morphological modifications. Both shrimp attempted unsuccessfully to use their chelae for defense, as observed in other crustaceans (e.g., crayfish; see Stein and Magnuson, 1976).

Histrio histrio may not have a preference for species because of its ambush predation strategy and relatively large mouth (cf. Pietsch and Grobecker, 1990). Ambush predators encounter prey at unpredictable rates and can procure a wide range of prey species (Hughes, 1980). Because *H. histrio* typically waited for prey to pass through its visual field, discriminating prey species from their background may be less important in its foraging strategy. However, occasionally *H. histrio* swam in pursuit of prey (either shrimp species, nonpreferentially) in our experiments. James and Heck (1994) observed a

A

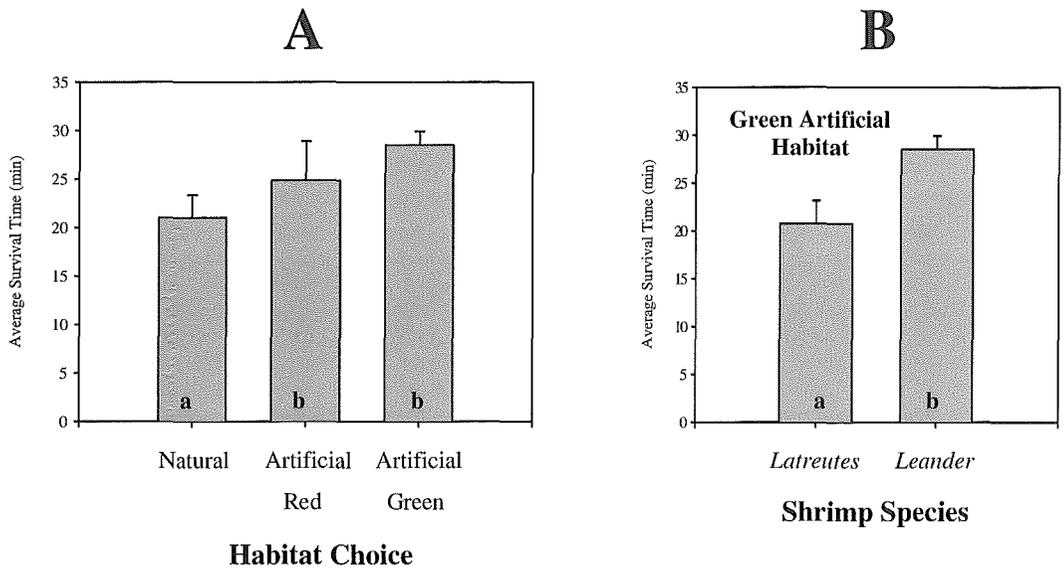

Habitat Choice

B

Shrimp Species

Fig. 3. a) Shrimp (*Leander tenuicornis*) prey selection by the fish *Histrio histrio* in three sargassum habitat types (one natural, two artificial) when the fish was first acclimated in the aquarium before introduction of shrimp. Under these circumstances, artificial habitats provided significantly better protection for shrimp than did sargassum (natural) habitat ($P < 0.05$, Tukey post hoc multiple comparison) (letters on histograms indicate statistical groupings; bars indicate standard deviations). b) Shrimp species prey selection by the fish *H. histrio* in green artificial habitat. *Leander tenuicornis* survived significantly longer than *Latreutes fucorum* in this habitat ($P < 0.05$, Tukey post hoc multiple comparison) (letters on histograms indicate statistical groupings; bars indicate standard deviations).

similar situation with the seahorse *Hippocampus erectus*, wherein it would abandon the "sit and wait" foraging strategy in the absence of habitat structure. With the element of mimicry of the sargassum patch no longer an advantage, *Histrio histrio* modified its foraging strategy as well. However, pursuing shrimp was, in general, less efficient (a chase would involve greater energy output) than waiting for an ambush strike. Overall, shrimp defenses, even with larger animals, had little effect on predation success by *H. histrio* with the size classes of animals used in this study. This might not be the case always, as very large adult shrimp could potentially defend themselves against very small juveniles of either fish species.

Camouflage is defined as an organism resembling in color pattern the mosaic of patches or spots of varying sizes, shapes, colors, and brightness levels of its habitat such that the predator does not perceive the prey against the background (Endler, 1978; Hacker and Madin, 1991). We hypothesized that camouflage by the shrimp might be effective in deterring predation by *S. hispidus* and *H. histrio*. Furthermore, the effectiveness of the shrimp's camouflage might vary if the habitat type and color were varied, as many shallow-water fishes have excellent visual

acuity, including color vision (cf. Douglas and Hawryshyn, 1990).

With *S. hispidus*, there were no significant differences in survival times in species selection trials of either shrimp species in artificial red, artificial green, or natural sargassum habitats. Essentially, this fish actively searched and preyed upon the shrimp with equal effectiveness in all habitats presented. With *H. histrio*, there were some significant differences but only when artificial habitats were involved. For example, when *H. histrio* was allowed to acclimate for 10 min before the addition of both shrimp species, *Leander tenuicornis* survived significantly longer than *Latreutes fucorum* in the artificial green habitat. Additionally, *Leander tenuicornis* survived significantly longer with this fish predator in both artificial habitats compared with the natural seaweed. Because these habits were not natural sargassum, the most that can be stated is that predation by *H. histrio* on these shrimp may be influenced in novel habitats. Both presentation sequences are reasonable scenarios for mimicking natural conditions (i.e., which may occur as fish and shrimp are commonly disassociated from algal fronds by natural perturbations—see discussion below). Allowing *H. histrio* to establish itself first in the habitat cover is

Stephanolepis hispidus
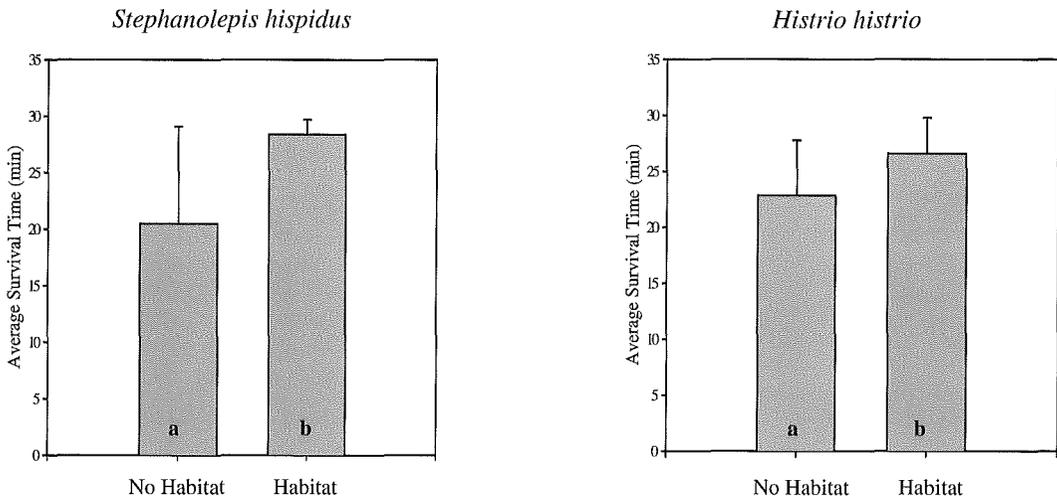
Histrio histrio

Fig. 4. Effect of habitat cover on survival of shrimp species with fish predators. Pooled data from previous trials showed that shrimp (both species) survival times increased significantly with habitat with the fishes *Stephanolepis hispidus* ($P < 0.001$, Mann–Whitney rank sum test) and *Histrio histrio* ($P = 0.009$, Mann–Whitney rank sum test) (letters on histograms indicate statistical groupings; bars indicate standard deviations).

probably reflective of typical predation patterns in undisturbed sargassum patches.

CONCLUSIONS

Clearly the complexity of the sargassum habitat contributes significantly to the abundance and diversity of the associated fauna (Martin-Smith, 1993). Predation, however, is also a very important component of the dynamics within this community. Habitat complexity and vegetation density have been demonstrated to affect predation success in seagrass, mangrove, and freshwater vegatation communities (Heck and Thoman, 1981; Kenyon et al., 1995; Primavera, 1997; Savino and Stein, 1989; Warfe and Barmuta, 2004). Our study demonstrates that the sargassum habitat can also affect predation.

Pooled data from the present study demonstrate that the sargassum habitat can also affect predation, with both shrimp species more vulnerable when isolated. Fish and shrimp in situ are periodically separated from sargassum habitat cover in several situations. For example, sargassum clumps are subjected to abiotic natural perturbations such as wave actions, currents, and substrate interactions (such as when clumps are driven near shore). Additionally, biotic perturbations can also disrupt clump size and structure. Feeding frenzies by schools of fish (e.g., dolphin fish, *Coryphaena* sp.) can scatter a mat of sargassum several meters in diameter into dozens of smaller clumps within minutes (pers. obs.). Subsequently, fauna are

disturbed and temporarily separated from the sargassum fronds. We have also observed *H. histrio* in the surf zone (within 3–4 m of the shoreline) completely disassociated from sargassum patches, apparently swimming away from algal clumps that subsequently washed up on beaches at high tide.

The fate of "isolated" fish and shrimps in the field is unknown. However, both species of shrimp are also found in other habitats, such as seagrass communities (Leber, 1985; Delgado, 2004). Thus, potentially, displaced sargassum shrimp could relocate to benthic communities. Our experiments involving bare aquaria demonstrate that shrimp without habitat cover are more vulnerable to predation. Our data showing that *Leander tenuicornis* survived longer than *Latreutes fucorum* in some situations (including without habitat cover) indicate the possibility that this shrimp would be more successful against some potential predators and in relocating algal clumps or benthic seagrass beds.

The complexity of the predator–prey interactions in the sargassum community does not involve only the animals chosen in this study. This complex community of symbiotic organisms is an important part of the food chain in the open ocean, as shrimp are eaten by the predatory fishes used in this study, which are in turn fed upon by larger game fishes (Dooley, 1972). Ultimately, humans consume some of these game fishes. Thus, the dynamics of fish predation on these shrimp in the sargassum community are significant. Several recent studies

have focused on the effects of simultaneous multiple predators on prey in complex habitats (Warfe and Barmuta, 2004; Griffen and Byers, 2006; Van Son and Thiel, 2006). The sargassum community, in general, represents an excellent model system for future studies on the effects of multiple predators and habitat patch size.

Observations of *S. hispidus* and *H. histrio* in this study illustrate important factors influencing preferences for prey. These fish predators use different foraging strategies for these shrimp prey, and, in the case of *H. histrio*, can even switch behavioral feeding strategies. Differences observed in these selection patterns are also related to shrimp prey defenses (morphological). Finally, experiments comparing survival times of shrimps with and without sargassum habitat (both natural and synthetic) demonstrate clearly that both shrimp species ultimately receive some degree of protection from these fish predators by living in these morphologically complex, symbiotic communities.

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