2016

Habitat Selection Among Fishes and Shrimp in the Pelagic *Sargassum* Community: The Role of Habitat Architecture

Chelsea O. Bennice
Florida Atlantic University

W. Randy Brooks
Florida Atlantic University

Recommended Citation

Bennice, C. O. and W. Brooks. 2016. Habitat Selection Among Fishes and Shrimp in the Pelagic *Sargassum* Community: The Role of Habitat Architecture. Gulf of Mexico Science 33 (1).
Retrieved from https://aquila.usm.edu/goms/vol33/iss1/1

Habitat Selection Among Fishes and Shrimp in the Pelagic *Sargassum* Community: The Role of Habitat Architecture

Chelsea O. Bennice and W. Randy Brooks

The pelagic *Sargassum* community represents an excellent model system to advance our understanding of how a complex habitat can influence biotic interactions. This study examined the habitat architecture of pelagic *Sargassum fluitans* to determine its effects on habitat selection for one shrimp species (*Leander tenuicornis*) and two fish species (*Stephanolepis hispidus* and *Histrio histrio*). Specifically, we manipulated interthallus spacing and depth of *Sargassum* habitats independently (i.e., in separate experimental trials) to test whether spatial components of habitat architecture influence habitat selection by these animal inhabitants. Additionally, two differing habitats (*Sargassum* vs intermingled seagrass species, *Thalassia testudinum* and *Syringodium filiforme*) were tested to determine whether structural components of habitat architecture influenced habitat selection. Results showed no significant effect of habitat selections for interthallus spacing experiments for *L. tenuicornis* and *S. hispidus*. However, *H. histrio* selected habitats with medium interthallus spacing characteristics in two experiments. All three animals selected habitats with a greater depth aspect. Finally, *L. tenuicornis* and *H. histrio* selected habitats with greater structural complexity (i.e., *Sargassum* habitat). These results demonstrate that habitat architecture (i.e., spatial and structural components) of *Sargassum* influences habitat selection by the aforementioned fauna and further illustrate that this pelagic macroalga is an essential habitat for multiple species.

Introduction

Habitat architecture and complexity are important factors known to influence habitat selection of many animals (Grinnell, 1917; Gause, 1934; Crisp and Barnes, 1954; Huffaker, 1958; Connell, 1961; Emson and Faller-Fritsch, 1976; Keough and Downes, 1982; Fletcher and Underwood, 1987; Walters and Wethey, 1996; Beck, 1998; Verweij et al., 2006; Christie et al., 2007; Kerry and Bellwood, 2012; Pappal et al., 2012; Tait and Hovel, 2012). In the marine environment, structure, in general, attracts and concentrates fauna (Hunter and Mitchell, 1968; Lapointe, 1995; Ingólfsson, 1998; Roberts and Poore, 2005; Norderhaug et al., 2007; Vandendriessche et al., 2007a; Casazza and Ross, 2008; Christie et al., 2009). Specifically, objects floating in the ocean (e.g., *Sargassum* spp.) attract and concentrate fauna (Hunter and Mitchell, 1968; Kingsford, 1995; Lapointe, 1995; Ingólfsson, 1998; Casazza and Ross, 2008) by increasing the complexity of the pelagic environment (Kingsford, 1995; Ingólfsson, 1998). Generally, the fish community is more diverse and abundant below floating seaweeds than below other floating items (Dooley, 1972; Fedoryako, 1989; Lapointe, 1995; Vandendriessche et al., 2007a). Adrift alga is also important as a dispersal agent for nearshore fauna (Helmuth et al., 1994; Parker and Tunnicliffe, 1994; Ingólfsson, 1995, 1998).

Druce and Kingsford (1995) concluded that the main factor attracting fishes was the presence of objects in the pelagic environment, regardless of form or color (Ingólfsson, 1998). However, survival of the animals may depend upon habitat architecture.

Many authors have proposed mechanisms by which variations in habitat architecture may influence the composition and distribution of associated assemblages (Dean and Connell, 1987b): (1) decrease in mortality rate due to predation ("refuge effect"); (2) decrease of hydrodynamic features ("shelter effect"); and (3) collectors of species ("filter effect"), strictly related to hydrodynamic processes and the larval supply (Morse, 1992). Owing to refuge and shelter effects, some fragile species may actively select their host on the basis of its architecture instead of direct feeding preferences, taking into consideration that, generally, fauna do not feed on the host-plant tissues (Gee and Warwick, 1994).

Habitat configuration has previously been studied by examining habitat fragmentation, or habitat patch size, and habitat architecture, which includes spatial and structural components. The Roberts and Poore (2005) study on habitat configuration defined habitat fragmentation as the process that involves a reduction in size of suitable habitat patches and an increasing isolation among remnant habitat

patches. Hacker and Steneck (1990) and Hacker and Madin (1991) define structural components as the number, length, and width of fronds, branches, and vesicles measured and spatial components as the size, shape, and arrangement of spaces between fronds. Roberts and Poore (2005) also found that variation in patch size did not have an impact upon abundance of any taxonomic group except polycheate worms. This increased abundance on small, isolated patches for some fauna is inconsistent with traditional predictions, which suggest reduction of habitat should decrease species number and alter community composition (Hill and Curran, 2003). Processes affecting dispersal and mitigation of invertebrates (and vertebrates) in fragmented landscapes are no doubt complex and await further testing in the field and laboratory.

Hacker and Steneck (1990) manipulated the spatial component of algal mimics (*Ulva lactuca, Ceramium rubrum, Chondrus crispus, Corallina officinalis, Alaria esculenta,* and *Laminaria digitata*). Results showed that the more densely branched mimic "complex alga" had a greater number of amphipods, which also showed a dependence on both size-specific selections for the structural and spatial components of habitat architecture. These results have also been reported in other studies (Heck and Wetstone, 1977; Crowder and Cooper, 1982; Coull and Wells, 1983; Edgar, 1983a, 1983b, 1983d; Stoner and Lewis, 1985; Dean and Connell, 1987a, 1987b, 1987c; Hacker and Steneck, 1990). Habitat architecture should be explored not only horizontally (i.e., patch size or how densely packed the alga is arranged), but also vertically (the depth the alga covers in the water column). Algae deeper in the water column may provide or enhance the visual cues of a suitable habitat.

Marine algae, both benthic and pelagic, provide a suitable habitat for a wide range of animal species and can be deemed as biological "formers" of habitat structure (Jones and Andrew, 1992; Garcia-Charton et al., 2000; Chemello and Milazzo, 2002). Aburto-Oropeza et al. (2007) showed that the success of the leopard grouper (*Mycteroperca rosacea*) recruitment in the Gulf of California, Mexico, is affected by the availability of its preferred nursery habitat, shallow rocky bottoms with benthic *Sargassum* spp. algal beds. It is argued that complex macroalgae (such as *Sargassum* spp.) encourage a more abundant and well-diversified associated invertebrate fauna than simple and flat-thalloid algae (Heck and Orth, 1980; Gunnill, 1982; Edgar, 1983a, 1983b, 1983c; Gibbons, 1988; Gee and Warwick, 1994; Warfe and Barmuta, 2004).

The Hacker and Madin (1991) study focused on structural components of the habitat because the shrimps have a well-developed resemblance to the pelagic *Sargassum*. *Latreutes fucorum* selected *Sargassum* with fronds "only" over *Sargassum* with vesicles "only". *Latreutes fucorum* resembled the size and shape of fronds; this visual mimicry with the fronds was size dependent (i.e., small *L. fucorum* showed a preference for small fronds and large *L. fucorum* showed a preference for large fronds). Chemello and Milazzo (2002) found that molluscan assemblage in the southern Mediterranean Sea was correlated to the different attributes of algal architecture; assemblage abundance and number of species was higher on more complex algae. Clearly, structural differences in habitat can affect species richness and diversity of epifauna (Hicks, 1985; Gee and Warwick, 1994). However, there are still studies that found no effect of architecture on habitat selection by associated fauna (Schreider et al., 2003). The discrepancy of the importance of structure complexity among different habitats and the lack of investigation on both the horizontal and vertical spatial component should only encourage further investigation.

Although macrophytes as habitats and producers have received increased research interest recently (cf. Christie et al., 2009), the majority of these habitat complexity studies have been on benthic macrophytes (Bell and Westoby, 1986; Hacker and Steneck, 1990; Chemello and Milazzo, 2002; Levin and Hay, 2002; Roberts and Poore, 2005; Verweij et al., 2006; Canion and Heck, 2009; Christie et al., 2009; Tait and Hovel, 2012), which are arguably less complex structurally than pelagic *Sargassum* spp. (Chemello and Milazzo, 2002; Levin and Hay, 2002).

Additionally, very few algal studies have examined both spatial and structural components (cf. Hacker and Steneck, 1990) and focused on the habitat architecture of pelagic *Sargassum* spp. (cf. Hacker and Madin, 1991). Pelagic *Sargassum* spp., in general, represent excellent systems for testing both spatial and structural effects of habitat architecture on habitat selection by associated fauna. A number of these associated fauna have an obligatory facultative association and rely on the habitat to mediate predation and provide a food resource (Dooley, 1972; Smith, 1973; Hacker and Madin, 1991; Wells and Rooker, 2004; Brooks et al., 2007).

The objective of this research was to investigate the role of habitat architecture by examining the effects of spatial and structural components on the habitat selection using the pelagic species *Sargassum fluitans* (Bøgesen, 1914) and three common fauna (i.e., *Histrio histrio* (Linnaeus, 1758), *Stephanolepis hispidus* (Linnaeus, 1766),

and *Leander tenuicornis* (Say, 1818)). Preparing habitat patches of *Sargassum* spp. for experimental trials can be problematic, since using algal biomass alone can be deceptive because patches of similar biomass can differ spatially (i.e., differing distances between neighboring thalli within a patch and differing vertical depth in the water column). Therefore, we focused on an approach where the effect on host selection by fishes and shrimp was examined by varying characteristics of patches in two specific ways for the spatial component of habitat architecture: (1) varying distances between algal thalli within given patches (i.e., interthallus spacing) and (2) varying patch depth of two patches in the water column. Additionally, some habitat patches collected consisted mostly or entirely of seagrasses (pers. obs.). Structural complexity of patches can be important factors affecting habitat selection. Thus, we attempted to examine the structural component of habitat architecture by having fishes and shrimp select between a patch of *Sargassum* only vs a habitat comprised of two species of seagrass in aquaria set up in the laboratory.

METHODS

Community description.—*Sargassum* spp. is a brown alga referred to as gulfweed and consists of long branching stipes with fronds and spherical gas-filled bladders for flotation (Weis, 1968; Brooks et al., 2007). Species vary depending on the texture and size of frond(s) and air bladder(s). Colors vary from yellow, to brown, to black (Hacker and Madin, 1991; Brooks et al., 2007). Spatial distribution within the water column and quantity of *Sargassum* is highly variable. *Sargassum* distribution along the East Coast of the United States depends on the Florida Current and the Gulf Stream, which entrain pelagic *Sargassum* from the Sargasso Sea (Wells and Rooker, 2004; Casazza and Ross, 2008). There are two holopelagic species primarily found in the Sargasso Sea within the North Atlantic Central Gyre: *Sargassum natans* (Linnaeus) and *Sargassum fluitans* (Børgesen). The term patch is used to describe the aggregation of seaweed to form a three-dimensional structure in the water column. *Sargassum* patches often accumulate in large windrows, thereby forming productive "weed-lines" in oligotrophic waters as a result of Langmuir circulation aligning the *Sargassum* parallel with the wind direction (Ryther, 1956; Lapointe, 1995; Wells and Rooker, 2004).

The endemic fish *Histro histro* (Linnaeus) (Family: Antennariidae) receives its common name, the *Sargassum* fish, from being found in *Sargassum* communities circumtropically and from its highly intricate morphology that mimics *Sargassum* weed with patterns of yellow, brown, and olive (Adams, 1960; DeLoach and Humann, 1990; Brooks et al., 2007). Gut analyses confirm that this fish has a diet that consists of invertebrates (*Sargassum* crustaceans) frequently found inhabiting the *Sargassum* (Dooley, 1972; Smith, 1973; Hacker and Madin, 1991; Brooks et al., 2007) and will also eat fish (conspecifics included) of a similar or smaller size (pers. obs.)

Stephanolepis hispidus (Linnaeus) (Family: Monacanthidae), the planehead filefish, is another highly abundant inhabitant in the *Sargassum* community, especially as juveniles (Dooley, 1972; Bortone et al., 1977; Stoner and Greening, 1984; Fedoryako, 1989; Brooks et al., 2007). This fish has an adaptive coloration allowing it to "blend" with the floating reef (Dooley, 1972). In contrast to *H. histrio*, more mobile species (e.g., filefish) have developed a facultative association using the pelagic habitat for a portion of their early life. These filefish feed mainly on hydroids (Stachowicz and Lindquist, 1997; Brooks et al., 2007) and encrusting bryozoans, secondarily feeding on *Sargassum* shrimp (Dooley, 1972; Brooks et al., 2007).

One of the most common invertebrates found in *Sargassum* is the *Sargassum* shrimp *Leander tenuicornis*. Although this species has been observed within seagrass habitats (Bauer, 1985; Leber, 1985; Jobe and Brooks, 2009), this shrimp is highly specialized for life within the *Sargassum* patches and is commonly referred to as the gulf-weed shrimp. This shrimp has elongate slender chelae on the second legs, which are used for feeding (bryozoans and hydroids) and grooming behavior (Geiselman, in Butler et al., 1983; Johnson and Atema, 1986).

Field collections and behavioral observations.—Typically, floating algae aggregates in larger habitat patches (e.g., many meters across) farther off-shore, which usually means a larger number of animals inhabiting these patches compared with inshore patches that are usually smaller due to wind and wave action, which leads to fragmentation. However, this does not mean smaller patches close to shore are unimportant to invertebrates and vertebrates. Both invertebrates and vertebrates inhabit small, nearshore patches. Lenanton et al. (1982) found that drift algae in the surf zone of sandy beaches in Western Australia support high densities of young fish that are usually restricted to nursery areas within estuaries in other parts of Australia.

Similarly, we collected small patches of *Sargassum* using a dip net (i.e., <20 g total biomass) near the coast and in the surf zone with

numerous fishes (including juveniles and adults) (pers. obs.), illustrating the importance of these habitat patches across a wide range of sizes. *Sargassum* patches off the southeast coast of Florida vary in size temporally, from those with a surface diameter of 2–10 m in prevalent months to <1 m in other months (Brooks et al., 2007; Jobe and Brooks, 2009). Floating clumps of *S. fluitans* were collected using a dip net via boat 1.5–3.5 km directly offshore from Boca Raton Inlet from May to December 2010– 12 when they were typically more prevalent (Wells and Rooker, 2004; Jobe and Brooks, 2009). Field observations were made by snorkeling around or within patches and from the boating platform. Using a dip net to collect patches resulted in fragmentation of the patch and separation of animals from the patch, which allowed for behavioral habitat selection observations. The small clumps of *Sargassum* and all associated organisms were placed into a cooler aerated by a portable air pump until we reached the laboratory at Florida Atlantic University, Boca Raton. Once in the laboratory, *Sargassum* spp., fishes, and shrimp were maintained in separate aquaria prior to use in trials.

Sargassum fluitans, two fish species (*S. hispidus* and *H. histrio*) and one shrimp species (*L. tenuicornis*) were collected using a fine-mesh dip net and brought back to the laboratory for experiments. Two species of seagrass (*Thalassia testudinum* and *Syringodium filiforme*) were also observed in the field within the floating *Sargassum* clumps. These seagrass species were collected for use in the habitat structural complexity experiments. Structural complexity has been defined in this study as the structural components such as the number, length, and width of fronds, branches, and air bladders measured as well as the degree of texture. These species of seagrass have a simple structural morphology of a flat or circular blade, whereas *S. fluitans* thalli are comprised of multiple rigid fronds and air bladders, making this alga more structurally complex. The fronds and air bladders may also add a degree of texture for the animals to cling to, thereby adding another degree of structural complexity.

General experimental procedures.—Three different habitat selection experiments were conducted in this study (two for spatial and one for structural components of habitat architecture). We chose to establish initial, baseline studies using single-factor experiments, which can potentially serve as a basis for future orthogonal-based studies. Specifically, each experiment had two different habitat options for habitat selection. The exper-
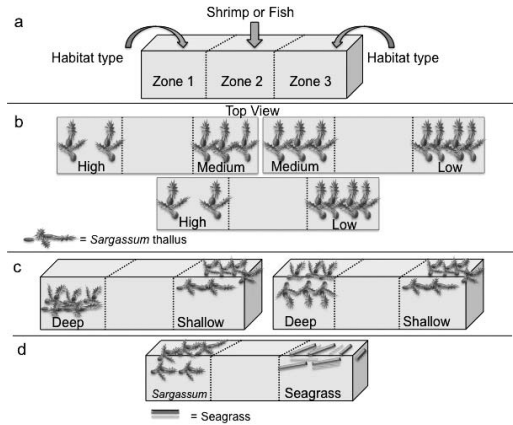

Fig. 1. (a) Experimental aquarium setup. Aquarium dimensions (cm): 40.64 × 20.32 × 25.40. (b) Differing interthallus spacing experimental setup (top view of aquaria) for three different treatments: high vs medium, medium vs low, and high vs low interthallus spacing. (c) Differing depth experiments: A—deep (with completely submerged surface) vs shallow and B—deep (with floating surface) vs shallow. (d) Structural component experimental setup. Comparing patches of *Sargassum* vs seagrass mixture. Biomass of each habitat = 20 g ± 0.5 g except the differing depth experiment habitats = 30 g ± 0.5 g.

imental aquaria were divided into three equal zones (Fig. 1a). Previous studies have used aquaria/zones of similar dimensions (Hacker and Madin, 1991; Jobe and Brooks, 2009). Zones 1 and 3 both had a specific habitat type. Zone 2 was always designated as an "open water/no habitat" zone.

Habitat types (e.g., algal or seagrass patches) were placed in zones 1 and 3 prior to the experiment. Previous algal studies have used patch sizes ranging from a single algal thallus to greater than 100 g (Roberts and Poore, 2005; Christie et al., 2007; Vandendriessche et al., 2007a; Christie et al., 2009; Jobe and Brooks, 2009). Habitat sizes of either 20 g ± 0.5 g or 30 g ± 0.5 g were used for habitat selection experiments. Either a single shrimp or a fish (one of the two species) was placed initially in zone 2 "open water area/no habitat" (Fig. 1a). In preliminary observations, shrimp showed increased nocturnal activity (swimming). Thus, to ensure that shrimp had adequate opportunities for selection, shrimp experiments ranged from 15 to 24 hr, so that both diurnal and nocturnal activity periods were included. Once the shrimp was in a patch at the end of the trial, the patch selected was recorded. If the shrimp was still in zone 2, "no selection" was recorded.

For the fish experiments, individual fishes were allowed 1 hr to acclimate in the experi-

mental aquaria. If the fish did not acclimate during this time (i.e., showed erratic swimming or other aberrant behaviors), it was placed back in the holding tank and used at another time. As soon as the fish acclimated, but not sooner than 5 min, the trial began. Trials ran for 30 min with continuous observation. Total time spent in each zone/habitat, and behavioral observations (i.e., location in or around patch and whether fish was swimming or stationary) were recorded.

Sample size for each animal species was 20 unless stated otherwise.

Spatial components of habitat architecture experiments.—In the first set of experiments, interthallus is defined as the empty space or space occupied by water between the *Sargassum* thalli. The thallus is referred to as the entire part of *Sargassum* including its stipe, air bladders, and fronds. Only interthallus spacing was manipulated by arranging the thalli differently within equal dimensions of each patch (i.e., diameter, as most patches are circular/oval in shape when viewed from above and depth) while using the same biomass (biological material derived from living or recently living organisms) for each patch. For the second set of experiments, the depth at which the *Sargassum* thalli were placed was manipulated, while keeping the algal biomass and surface diameter of each patch constant. The specific experiments were as follows:

Differing interthallus spacing experiment: There were three treatment levels for interthallus spacing experiments (hereafter referred to as high, medium, and low) (Fig. 1a). Patches had the same algal biomass of 20 g $\pm$ 0.5 g and were alternated consecutively between zones 1 and 3 between trials. The 20 g of algal biomass were divided into high, medium, or low treatments to examine differences in interthallus spacing without changing the biomass of the patches. The "open water area/no habitat choice" always occurred in zone 2. Pieces of *Sargassum* thalli used to construct patches ranged from 6 to 10 cm. *Sargassum* thalli were tied together using string to reach an average distance of 12.2 cm across the width of the tank. To ensure patches did not deviate significantly in density (determined by visual comparison) and thalli did not shift positions, strings were used to affix thalli of *Sargassum* to the sides of the aquarium.

Twenty photographic images of each treatment setup were chosen at random to calculate the interthallus spacing using *Image J* software. Specifically, average distances between thalli of *Sargassum* within patch treatments were as follows: 4.2 cm $\pm$ 0.5 cm for "high," 2.1 cm $\pm$ 0.2 cm for "medium," and 1.2 cm $\pm$ 0.2 cm for "low." Interthallus spacing between the three treatment levels was tested to ensure there were significant differences in spacing using a Kruskal–Wallis test (normality was not met for parametric test) and a Dunn's method for pairwise comparisons. Each treatment was significantly different in spacing from the others (Kruskal–Wallis $P < 0.001$, Dunn's $P < 0.05$). Sample sizes for this experiment were as follows: *L. tenuicornis,* n = 28; *S. hispidus,* n = 20; and *H. histrio,* n = 28.

Differing depth experiment A: The objective of this experiment was to vary the vertical depth spatial component of habitat architecture to determine the effects of habitat selection among fishes and shrimp. Specifically, one patch was left to float at the water surface while the surface of the other patch was completely submerged (Fig. 1c). Depths of *Sargassum* in the field, as measured by the deepest point of the patch, typically ranged from 3–4 cm minimally to a depth of 10–12 cm, with some patches occasionally observed descending to more than 30 cm into the water column (Lapointe, pers. obs.) Thus, a shallow depth of 3–4 cm and deep depth of 10–12 cm were used. Both patch choices consisted of equal algal biomass of 30 g $\pm$ 0.5 g. Strings affixed to pieces of *Sargassum* within each patch and weighted netting (both roughly the same brown color as the *Sargassum* collected) were placed over the surface of each patch to ensure position did not shift vertically or horizontally in aquaria. Shallow and deep depth patches were alternated consecutively between zones 1 and 3 between trials. The "open water area/no habitat choice" always occurred in zone 2.

Differing depth experiment B: The objective of this experiment was to construct a more natural scenario of habitats varying in depth, while the top portions of both patches remained floating at the surface (Fig. 1c). However, because of the need to place some *Sargassum* thalli vertically in these trials to achieve a deeper depth aspect and simultaneously keep biomass constant between the two habitat choices, the confounding factor of differing interthallus distances/spacing was introduced. This factor is addressed in the interthallus trials in the first set of experiments. Thus, this version of "differing depth" experiments should be compared directly with the Differing Depth Experiment A in which *Sargassum* habitat types were used with only depth aspect as the varying factor. The same biomass and depths as the previous depth experiment

were used for these trials. The deep depth habitat was structurally supplemented by the use of wires, which were bent to manipulate and maintain vertical positions of thalli in the aquaria. To control for a wire effect, both *Sargassum* habitat types within each trial were wrapped with the same amount of wire. The shallow depth *Sargassum* habitat had wire applied that was unbent, which allowed these patches to float so that the primary axis of the stipe of each *Sargassum* strand maintained a horizontal aspect in the water column. Shallow and deep depth habitat types were alternated consecutively between zones 1 and 3 between trials. The "open water area/no habitat choice" always occurred in zone 2.

Structural component of habitat architecture experiment.—The objective of this experiment was to test whether differences in structural complexity between habitat types of two seagrass species vs *Sargassum* influenced habitat selection of shrimp and fishes. Patches consisted of the same biomass (20 g $\pm$ 0.5 g) and were of similar surface dimensions, depth, and density (Fig. 1d).

Statistical analyses.—Results for shrimp experiments were recorded as dichotomous data (habitat selection for one of the given two habitat choices) and analyzed using the binomial (Z) test. Time (recorded in minutes) fishes spent in each habitat type was analyzed by using the nonparametric Mann–Whitney U-test since normality was not met for a parametric test. Additionally, experimental data for each animal species were separated into two groups based on size (i.e., small and large size class) for post hoc analysis for potential size effects (after Brooks et al., 2007; Jobe and Brooks, 2009). The size range for *L. tenuicornis* was 15–33 mm, with small and large groups of <25 mm and ≥25 mm, respectively. *Stephanolepis hispidus* ranged from 10 to 90 mm, with small and large groups of <40 mm and ≥40 mm, respectively. *Histrio histrio* ranged from 12 to 87 mm, with small and large groups of <40 mm and ≥40 mm, respectively. A chi square test (X^2) or Fisher's Exact test (when n ≤ 5) for shrimp data and a Kruskal–Wallis with Dunn's method (for all pairwise comparisons) for fishes were performed. When separated into size classes, the sample sizes for small and large *L. tenuicornis* and *H. histrio* were n = 14 for both size classes. Sample size for size classes for *S. hispidus* varied between each interthallus treatment: high vs medium small and large *S. hispidus*, n = 15, n = 5, respectively; medium vs low, n = 12, n = 8, respectively; and high vs low, n = 13, n = 7, respectively.
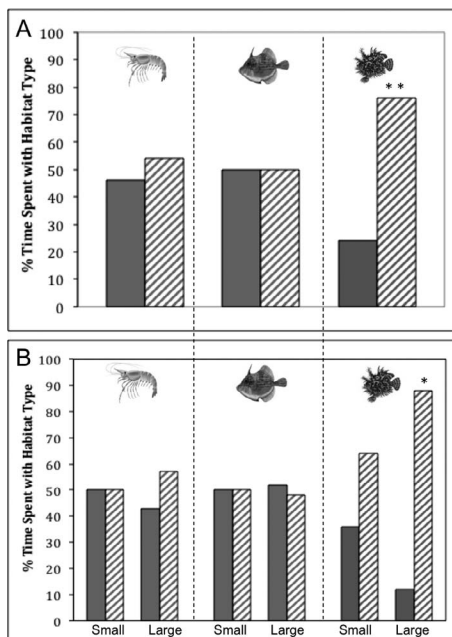

Fig. 2.   (A) Habitat selection based on differing interthallus spacing: high (solid) vs medium (striped). *Leander tenuicornis*, n = 28; *S. hispidus*, n = 20; and *H. histrio*, n = 28. (B) Data were separated into small and large size categories; *L. tenuicornis* and *H. histrio* were n = 14 for both size classes, and small and large *S. hispidus* were n = 15 and n = 5, respectively. * = significance of $P \leq 0.05$ and ** = significance of $P \leq 0.001$.

RESULTS

Differing interthallus spacing experiment: High vs medium.—One out of the three species showed significant results for habitat selection (i.e., *H. histrio*, Fig. 2). *Leander tenuicornis* spent 46% (13 out of 28 shrimp) in high and 54% (15 out of 28 shrimp) in the medium patches (Z = 0.54; P = 0.74). *Stephanolepis hispidus* spent 50% of time in both the high (average time 15.0 out of 30 min) and medium patches (average time 15.1 out of 30 min) (P = 0.81). *Histrio histrio* spent 24% (average time 7.2 out of 30 min) in high and 76% (average time 23.0 out of 30 min) in medium patches (P ≤ 0.001). Post hoc analyses for size effects showed no significant differences for small and large size classes for *L. tenuicornis* ($X^2 = 0$, P = 1.00) or for small and large *S. hispidus* (P = 0.50). However, *H. histrio* did show a size effect (P ≤ 0.001), having only large *H. histrio* significantly select medium (average time 26.4 out of 30 min) more often than high (3.6 out of 30 min) patches (P ≤ 0.05).

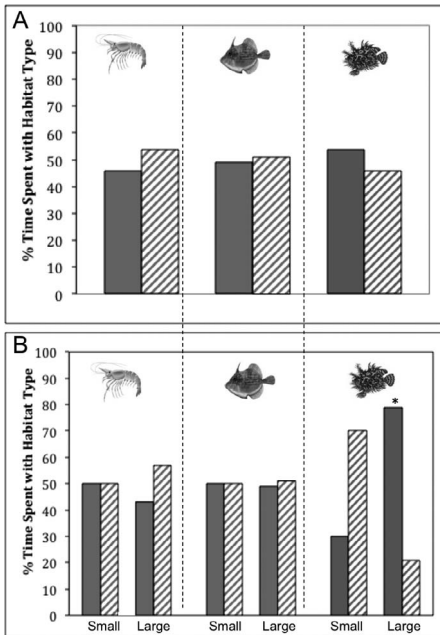*Differing interthallus spacing experiment: Medium vs low.*—One out of the three species showed

Fig. 3. (A) Habitat selection based on differing interthallus spacing: medium (solid) vs low (striped). *Leander tenuicornis,* n = 28; *S. hispidus,* n = 20; and *H. histrio,* n = 28. (B) Data were separated into small and large size categories; *L. tenuicornis* and *H. histrio* were n = 14 for both size classes, and small and large *S. hispidus* were n = 12 and n = 8, respectively. * = significance of $P \leq 0.05$ and ** = significance of $P \leq 0.001$.

Fig. 4. (A) Habitat selection based on differing interthallus spacing: high (solid) vs low (striped). *Leander tenuicornis,* n = 28; *S. hispidus,* n = 20; and *H. histrio,* n = 28. (B) Data were separated into small and large size categories; *L. tenuicornis* and *H. histrio* were n = 14 for both size classes, and small and large *S. hispidus* were n = 13 and n= 7, respectively. * = significance of $P \leq 0.05$ and ** = significance of $P \leq 0.001$.

significant results for habitat selection (i.e., *H. histrio,* Fig. 3). *Leander tenuicornis* spent 57% (16 out of 28 shrimp) in medium and 43% (12 out of 28 shrimp) in low patches (Z = 0.78; $P = 0.44$). *Stephanolepis hispidus* spent 52% (average time 15.6 out of 30 min) in medium and 48% (average time 14.4 out of 30 min) in low patches ($P = 0.92$). Again, *H. histrio* showed a significant difference with 70% (average time 20.9 out of 30 min) time spent in medium and 30% (average time 9.1 out of 30 min) time spent in low patches ($P \leq 0.01$). Post hoc analyses for size effects showed no significant differences for small and large size classes for *L. tenuicornis* ($X^2 = 1.31$, $P = 0.25$), for small and large *S. hispidus* ($P = 0.97$). Although results for *H. histrio* were statistically significant ($P \leq 0.05$), multiple comparisons (Dunn's method) revealed data were size skewed. The larger size class of *H. histrio* selected medium patches (average time 21.7 out of 30 min) over low (average time 8.3 out of 30 min), but not in a statistically significant pattern.

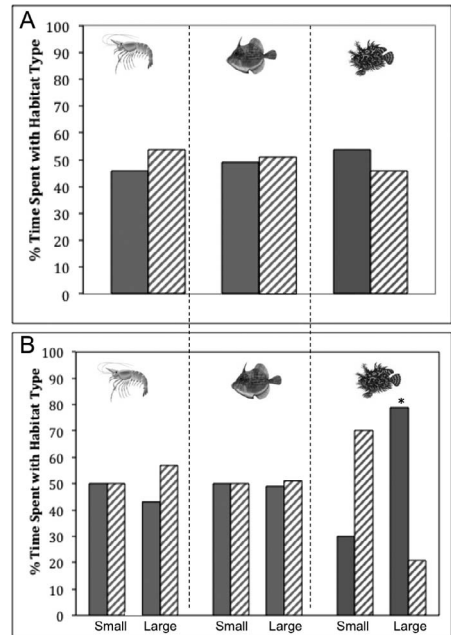*Differing interthallus spacing experiment: High vs low.*—None of the three species tested for this habitat selection treatment trial showed significant preference, except when separated into size classes (i.e., *H. histrio,* Fig. 4). *Leander tenuicornis* spent 46% (13 out of 28 shrimp) in high and 54% (15 out of 28 shrimp) in low patches (Z = 0.33, $P = 0.74$); *S. hispidus* spent 49% (average time 14.8 out of 30 min) in high and 51% (average time 15.2 out of 30 min) in low patches ($P = 0.97$); and *H. histrio* spent 54% (average time 16.3 out of 30 min) in high and 46% (average time 13.8 out of 30 min) in low patches ($P = 0.43$). Post hoc analyses for size effects showed no significant differences for small and large size classes for *L. tenuicornis* ($X^2 = 0$, $P = 1.00$) and for small and large *S. hispidus* ($P = 1.000$). *Histrio histrio* did show a size effect ($P \leq 0.05$), having only large *H. histrio* significantly select the high (79%, average time 23.6 out of 30 min) more often than the low (21%, average time 6.4 out of 30 min) patches ($P \leq 0.05$).

Differing depth experiments: Experiment A: Shallow vs deep with completely submerged patch surface.—One out of the three species showed significant results selecting for deep depth patches (i.e.,
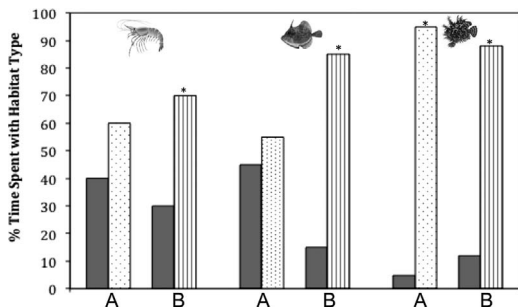
Fig. 5. Differing depth experiments. Experiment A: animals were given a choice between shallow (solid) vs deep (completely submerged surface) (dotted). Experiment B: animals were given a choice between shallow (solid) vs deep (with floating surface) (striped). * = significance of $P \leq 0.05$ and ** = significance of $P \leq 0.001$.

Fig. 6. Structural component experiment. Animals were given a choice between seagrass (solid) vs Sargassum (dashed) habitats. * = significance of $P \leq 0.05$ and ** = significance of $P \leq 0.001$.

H. histrio, Fig. 5). *Leander tenuicornis* spent 60% (12 out of 20 shrimp) in deep and 40% (8 out of 20 shrimp) in shallow patches (Z = 0.95, $P = 0.34$). *Stephanolepis hispidus* spent 55% (average time 16.4 out of 30 min) in deep and 45% (average time 13.6 out of 30 min) in shallow patches ($P = 0.50$). *Histrio histrio* spent 95% (average time 28.5 out of 30 min) in deep and 5% (average time 1.5 out of 30 min) in shallow patches ($P \leq 0.001$). Post hoc analyses for size effects showed no significant differences for *L. tenuicornis* and *S. hispidus* ($P = 1.00$, $P = 0.83$, respectively). *Histrio histrio* did show a size effect ($P \leq 0.001$) for both small and large size categories selecting the deep depth patch (both $P \leq 0.05$). Small *H. histrio* spent 93% (28 out of 30 min) in deep patches, and large *H. histrio* spent 100% (30 out of 30 min) in deep patches.

Differing depth experiments: Experiment B: Shallow vs deep with floating patch surface.—All three species spent significantly more time in deep patches, which maintained a floating aspect (Fig. 5). *Leander tenuicornis* spent 70% (14 out of 20 shrimp) and 30% (6 out of 20 shrimp) of their time in deep vs shallow patches, respectively (Z = 2.21, $P \leq 0.05$). *Stephanolepis hispidus* spent 85% (average time 25.4 out of 30 min) and 15% (average time 4.6 out of 30 min) in deep vs shallow patches, respectively ($P \leq 0.001$). *Histrio histrio* spent 88% (average time 26.4 out of 30 min) and 12% (average time 3.6 min out of 30 min) in deep vs shallow patches, respectively ($P \leq 0.001$). Post hoc analyses for size effects showed no significant differences for *L. tenuicornis* ($P = 1.000$), but significance for *S. hispidus* and *H. histrio* (both $P \leq 0.001$).
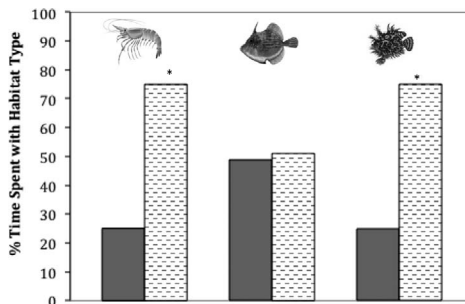
For *S. hispidus*, the small size class selected the deep depth patches (78%, average time 23.4 out of 30 min) significantly more than the shallow (22%, average time 6.6 out of 30 min) ($P \leq 0.05$), and both small and large size classes of *H. histrio* selected the deep patches (both $P \leq 0.05$) significantly more often. Small size class *H. histrio* class selected deep patches 82% of the time (average time 24.7 out of 30 min) and selected the shallow patches 18% of the time (average time 5.3 out of 30 min). Large size class *H. histrio* selected deep patches 95% of the time (average time 28.5 out of 30 min) and the shallow patches 5% (average time 1.5 out of 30 min) of the time.

Structural component for habitat selection experiment: Seagrass vs Sargassum patches.—Two of the three species showed significant preference for *Sargassum* patches (i.e., *L. tenuicornis* and *H. histrio*, Fig. 6). There was no significant selection for *S. hispidus*, which spent essentially the same portion of time in the *Sargassum* patches (51%, average time 15.3 out of 30 min) as the seagrass patches (49%, average time 14.7 out of 30 min) ($P = 0.99$). However, both *L. tenuicornis* and *H. histrio* did exhibit significant responses. Specifically, both *L. tenuicornis* and *H. histrio* spent a greater portion of time in the *Sargassum* patches (both 75%, 15 out of 20 shrimp and average time 22.5 out of 30 min for *H. histrio*) than the seagrass patches (both 25%, 5 out of 20 shrimp and average time 7.5 out of 30 min for *H. histrio*) (Z = 2.85, $P \leq 0.01$ for *L. tenuicornis*, and $P \leq 0.001$ for *H. histrio*). Post hoc analyses for size effects showed no significant difference for any of the three animals.

Behavioral observations associated with habitat.—Certain behavioral trends were observed over the course of this research for each of the three
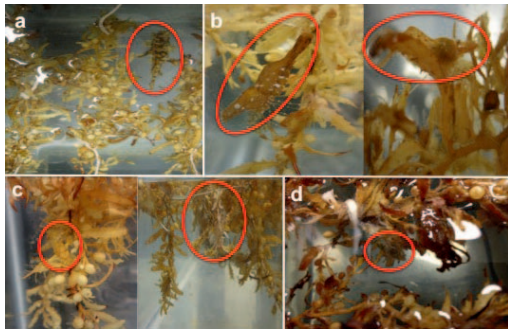
Fig. 7. Behavioral observations associated with laboratory habitat selection experiments: (a) *H. histrio,* (b) *L. tenuicornis,* (c) *H. histrio,* (d) *S. hispidus.* Animals outlined by circle.

species. In laboratory trials, *L. tenuicornis* was eventually always found associated with a habitat and the majority of the time clinging to *Sargassum* thalli. The shrimp's body was positioned in a parallel orientation and direction to the fronds or entire thallus (Fig. 7b). This positioning was also observed in the field.

Stephanolepis hispidus was always found swimming directly below the habitat (laboratory and field observation). For the deep vs shallow habitat selection in experiment B, *S. hispidus* remained swimming between the vertical *Sargassum* thalli (Fig. 7d).

Similar to the previous two species, *H. histrio* also selected a habitat. Unlike *S. hispidus, H. histrio* would select a spot in the habitat and remain there for the entire duration of the trial or slowly move short distances across the habitat with its modified pectoral fins clinging to the *Sargassum* thalli. For the interthallus space experiments, *H. histrio* would wedge itself between two *Sargassum* thalli (Fig. 7a). This was also observed for experiment B (shallow vs deep habitat selection). *Histrio histrio* used its pectoral fins to grasp the vertically dispersed *Sargassum* thalli (Fig. 7c). It was difficult to observe *H. histrio* in the field due to its highly adaptive morphology and effective camouflage. However, if a patch of *Sargassum* was collected using a dip net and *H. histrio* was left without a habitat; it would quickly swim to the closest area of *Sargassum.*

Discussion

The use of three different species allowed for a comparison of how each species uses the *Sargassum* as a habitat, and which components of habitat architecture (i.e., spatial, structural, or both) are important to each species.

Results for the spatial component (interthallus spacing) experiment differed from a previous study also involving crustaceans. Hacker and Steneck (1990) found a correlation between both small (<4.0 mm) and medium sized (4.0–10.0 mm) amphipods and the spatial component of habitat architecture. The body sizes of *L. tenuicornis* used in our study were larger than 10 mm (size range 15–33 mm) and may account for the lack of significant results for the interthallus experiment. However, Hacker and Steneck (1990) also did not find any significant results for large amphipods (>10 mm) and the spatial component of habitat architecture. It should be noted that their methods for measuring interthallus/interstitial spacing differed from this study, and different types of algae were used, which may contribute to a different interstitial spacing.

Unlike the more mobile fish species (*S. hispidus*) used in our study, *H. histrio* typically stayed within the fronds of *Sargassum* and swam only once separated from the patch. Therefore, it is possible that interthallus spacing may have a more important role in habitat selection for *H. histrio* than *S. hispidus.* Large *H. histrio* selected medium interthallus spacing 88% of the time over high; low interthallus spacing 79% of the time over high; and medium interthallus spacing 72% of the time over low. Large sized *H. histrio* were observed clinging onto thalli while positioning themselves in the interthallus spaces (i.e., open spaces between thalli). Size dependent trends were not significant, but this may have been due to a small sample size. These results may suggest that an optimum interthallus spacing exists for *H. histrio* to maximize its camouflage (from both prey and predators) while allowing enough space to maneuver for its "lie in wait" predatory strategy (Pietsch and Grobecker, 1990; Brooks et al., 2007).

Only *H. histrio* (small and large size classes) significantly selected the deep depth habitat type with the completely submerged patch surface, while all three species significantly selected the deep depth habitat type with the floating patch surface. By having these two different experimental designs for shallow vs deep depth habitats, the importance of a surface coverage of *Sargassum* with thalli descending vertically in the water column was demonstrated. This may create a more complex habitat where animals of both small (*S. hispidus* and *H. histrio*) and large size classes (*H. histrio*) are (1) protected from predators below and above the *Sargassum* patch (i.e., fish and aerial predators such as species of seabirds (Vandendriessche et al., 2007b; Moser and Lee, 2012) and (2) have a greater opportunity

for visual detection of a habitat due to thalli hanging deeper in water column (i.e., patches with greater depth aspects should have a larger visual profile in the water column than shallower patches). Many studies have shown that animals use visual cues to select habitats (cf., Myrberg and Fuiman, 2002; Montgomery et al., 2006; Huijbers et al., 2008; Simpson et al., 2008; Huijbers et al., 2011; Igulu et al., 2011).

We show that structural complexity plays an important role in habitat selection for both *L. tenuicornis* and *H. histrio* (i.e., they significantly selected *Sargassum* over seagrass patches). *Leander tenuicornis* was frequently positioned on or around fronds and parallel with the adjacent fronds. A similar species of shrimp, *L. fucorum*, also uses *Sargassum* as its habitat and was shown to have the same algal-part mimicry or camouflage (i.e., morphology that resembles *Sargassum* fronds and/or air bladders) with *Sargassum* (Hacker and Madin, 1991; Brooks et al., 2007). Therefore, the shrimp may be influenced only by the structural component and not the spatial component of its habitat (Hacker and Steneck, 1990). *Leander tenuicornis* may also be exhibiting algal-part mimicry to avoid predators (Brooks et al., 2007). Color of seaweed has also been known to attract animals to a habitat (Hacker and Madin, 1991). Both *Sargassum* and seagrass can vary in color from a light yellow-green to green, to a dark brown color depending on nutrient load and the alga's or seagrass's stage of vitality. Fresh *Sargassum* and seagrasses were always used during experiments, which ranged in color from yellow-green to green, to minimize this issue.

The predatory fish *H. histro* is well camouflaged within *Sargassum* and has morphological adaptations (fins that can grasp alga thalli), which are likely the reason for the selection of *Sargassum* over seagrass patches. Most fish predators do not have such highly adapted morphological features to habitats because they are proficient at swimming and can typically chase down prey with relative success. However, the *Sargassum* fish's characteristics allow it to operate effectively as a "lie in wait" or ambush predator in *Sargassum* patches. Specifically, small *H. histrio* may resemble an air bladder or frond, while a large *H. histrio* may resemble an entire thallus.

Stephanolepis hispidus did not select the structurally more complex *Sargassum*. This may be due to this species being relatively more mobile and swimming primarily underneath patches instead of spaces within the patch. Highly mobile fishes, such as *S. hispidus,* typically use the *Sargassum* as a temporary refuge when they are juveniles (Wells and Rooker, 2004; Casazza and

Ross, 2008). Therefore, complex habitat architecture may not be as important as it is to other species that are either endemic or spend a majority of their life in *Sargassum* (i.e., *H. histrio* and *L. tenuicornis*, respectively). However, if this habitat did not persist in the open ocean, *S. hispidus* would likely have a lesser chance of survival to its adult stage (Rogers et al., 2001). Juvenile fish species that are associated with floating seaweed are typically larger than those not associated (i.e., inhabit neuston waters) (Vandendriessche et al., 2007a). Additionally, *S. hispidus* is commonly found in different habitats, including seagrass beds. Prado and Heck (2011) found *S. hispidus* to be one of the most abundant omnivorous fishes to inhabit seagrass communities, suggesting that this animal may use whichever habitat is readily available.

This study examined one component of habitat architecture per experiment to first determine which component was significant for each species. Future studies should incorporate orthogonal combinations of factors (e.g., deep vs shallow and interthallus spacing) to develop a richer understanding of the dynamics in these floating habitats.

Pelagic *Sargassum* can be regarded as an autogenic engineer by altering the otherwise depauperate marine, pelagic environment by providing physical structure for the attraction of fauna (Jones et al., 1994). *Sargassum* is an excellent three-dimensional habitat where interthalli spaces vary among different, fragmented patches, and structural units vary in complexity with other habitats (e.g., seagrasses). These results clearly demonstrate that habitat architecture (i.e., spatial and structural components) of *Sargassum* influences habitat selection by the aforementioned fauna. Larger fish predators (e.g., yellowfin tuna, dolphinfish) also use *Sargassum* for a refuge and for prey items, making *Sargassum* ecologically important for the food web and economically important for the fisheries (Oxenford and Hunte, 1999; Logan et al., 2013; Farrell et al., 2014). Dolphinfish have been reported in a high percentage to be associated with pelagic *Sargassum* (Farrell et al., 2014). Also, gut analyses show most prey items of the dolphinfish are associated with *Sargassum,* indicating dolphinfish congregate underneath *Sargassum* patches (Dooly, 1972; Oxenford and Hunte, 1999). Furthermore, these results illustrate that this pelagic macroalga is an essential habitat for multiple species, providing a habitat for symbiotic species, a nursery for juvenile reef and sport fishes, and prey for ocean systems including sustainable fisheries (Rosenberg et al., 2000; Wells and Rooker, 2004).

Literature Cited

Aburto-Oropeza, O., E. Sala, G. Paredes, A. Mendoza, and E. Ballesteros. 2007. Predictability of reef fish recruitment in a highly variable nursery habitat. Ecology 88:2220–2228.

Adams, J. A. 1960. A contribution to the biology and postlarval development of the *Sargassum* fish *Histrio histrio* (Linneaeus), with a discussion of the *Sargassum* complex. Bull. Mar. Sci. Gulf Carib. 10:55–82.

Bauer, R. T. 1985. Diel and seasonal variation in species composition and abundance of caridean shrimps (crustacea, decopoda) from seagrass meadows on the north coast of Puerto Rico. Bull. Mar. Sci. 36:150–162.

Beck, M. W. 1998. Comparison of the measurement and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. Mar. Ecol. Prog. Ser. 169:165–178.

Bell, J. D., and M. Westoby. 1986. Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. Oceologia 68:205–209.

Bortone, S. A., P. A. Hastings, and S. B. Collard. 1977. The pelagic *Sargassum* ichthyofauna of the eastern Gulf of Mexico. Northeast Gulf Sci. 1:60–67.

Brooks, W. R., K. A. Hutchinson, and M. G. Tolbert. 2007. Pelagic *Sargassum* mediates predation among symbiotic fishes and shrimps. Gulf Mexico Sci. 2:144–152.

Butler, J. N., B. F. Morris, J. Cadwallader, and A. W. Stoner. 1983. Studies of *Sargassum* and the *Sargassum* community. Bermuda Biological Station Special Publ. No. 22., 307 pp.

Canion, C. R., and K. L. Heck Jr. 2009. Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. Mar. Ecol. Prog. Ser. 393:37–46.

Casazza, T. L., and S. W. Ross. 2008. Fishes associated with pelagic *Sargassum* and open water lacking *Sargassum* in the Gulf Stream off North Carolina. Fish. Bull. 106:348–363.

Chemello, R., and M. Milazzo. 2002. Effect of algal architecture on associated fauna: some evidence from phytal molluscs. Mar. Biol. 140:981–990.

Christie, H., N. M. Jørgensen, and K. M. Norderhaug. 2007. Bushy or smooth, high or low; importance of habitat architecture and vertical position for distribution on kelp. J. Sea Res. 58:198–208.

⸺, K. M. Norderhaug, and S. Fredriksen. 2009. Macrophytes as a habitat for fauna. Mar. Ecol. Prog. Ser. 396:221–233.

Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on the distribution of the barnacle *Balanus balanoides*. Ecol. Monogr. 31:61–104.

Coull, B. C., and J. B. J. Wells. 1983. Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. Ecology 64:1599–1609.

Crisp, D. J., and H. Barnes. 1954. The orientation and distribution of barnacles at settlement with particular reference to surface contour. J. Anim. Ecol. 23:142–162.

Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1802–1813.

Dean, R. L., and J. H. Connell. 1987a. Marine invertebrates in algal succession. I. Variations in abundance and diversity with succession. J. Exp. Mar. Biol. Ecol. 109:195–215.

⸺, and ⸺. 1987b. Marine invertebrates in an algal succession. Marine invertebrates in an algal succession. II. Tests of hypotheses to explain changes in diversity with succession. J. Exp. Mar. Biol. Ecol. 109:217–247.

⸺, and ⸺. 1987c. Marine invertebrates in an algal succession. III. Mechanisms linking habitat complexity with diversity. J. Exp. Mar. Biol. Ecol. 109:249–273.

DeLoach, N., and P. Humann. 1990. Reef Fish identification: Florida-Caribbean-Bahamas. New World Publications, Jacksonville, Florida.

Dooley, J. K. 1972. Fishes associated with the pelagic *Sargassum* complex, with a discussion on the *Sargassum* community. Contrib. Mar. Sci. 16:1–32.

Druce, B. E., and M. J. Kingsford. 1995. An experimental investigation on the fishes associated with drifting objects in coastal waters of temperate Australia. Bull. Mar. Sci. 57:378–392.

Edgar, G. J. 1983a. The ecology of south-east Tasmanian phytal animal communities. I. Spatial ogranisation at a local scale. J. Exp. Mar. Biol. Ecol. 70:129–157.

⸺. 1983b. The ecology of south-east Tasmanian phytal animal communities. II. Seasonal change in plant and animal populations. J. Exp. Mar. Biol. Ecol. 70:159–179.

⸺. 1983c. The ecology of south-east Tasmanian phytal animal communities. III. Patterns of species diversity. J. Exp. Mar. Biol. Ecol. 70:181–203.

⸺. 1983d. The ecology of the south-east Tasmanian phytal animal communities. IV. Factors affecting the distribution of ampithoid amphipods among algae. J. Exp. Mar. Biol. Ecol. 70:205–225.

Emson, R. H., and R. J. Faller-Fritsch. 1976. An experimental investigation into the effect of crevice availability on abundance and size-selection in

a population of *Littornia rudis* (Maton): Gastropoda: Prosobranchia. J. Exp. Mar. Biol. Ecol. 23:285–297.

FARRELL, E. F., A. M. BOUSTANY, P. N. HALPIN, AND D. L. HAMMOND. 2014. Dolphinfish (*Coryphaena hippurus*) distribution in relation to biophysical ocean conditions in the northwest Atlantic. Fish. Res. 151:177–190.

FEDORYAKO, B. I. 1989. A comparative characteristic of the oceanic fish assemblage associated with floating debris. J. Icthyol. 29:128–137.

FLETCHER, W. J., AND A. J. UNDERWOOD. 1987. Interspecific competition among subtidal limpets: effects of substratum heterogeneity. Ecology 68:387–400.

GARCIA-CHARTON, J. A., I. WILLIAMS, A. PÉREZ-RUZAFA, M. MILAZZO, R. CHEMELLO, C. MARCOS, M. S. KITSOS, A. KOUKOURAS, AND S. RIGGIO. 2000. Evaluating the ecological effects of Mediterranean marine reserves: habitat, scale and the natural variability of ecosystems. Environ. Conserv. 27:179–199.

GAUSE, G. F. (ED.) 1934. The struggle for existence. Hafner Publishing, New York.

GEE, J. J., AND R. M. WARWICK. 1994. Metazoan community structure in relation to the fractal dimension of marine macroalgae. Mar. Ecol. Prog. Ser. 103:141–150.

GIBBONS, M. J. 1988. The impact of sediment accumulation, relative habitat complexity and elevation on rocky shore meiofauna. J. Exp. Mar. Biol. Ecol. 12:225–241.

GRINNELL, J. 1917. The niche-relationship of the California thrasher. Auk 34:427–433.

GUNNILL, F. C. 1982. Effects of plant size and distribution on the numbers of invertebrate species and individuals inhabiting the brown alga *Pelvetia fastigiata*. Mar. Biol. 69:263–280.

HACKER, S. D., AND L. P. MADIN. 1991. Why habitat architecture and color are important to shrimps living in pelagic *Sargassum*: use of camouflage and plant-part mimicry. Mar. Ecol. Prog. Ser. 70:143–155.

———, AND R. S. STENECK. 1990. Habitat architecture and the abundance and body-size dependent habitat selection of a phytal amphipod. Ecology 71:2269–2285.

HECK, K. L. J., AND R. J. ORTH. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages, p. 449–464. *In:* Estuarine perspective. V. S. Kennedy (ed.). Academic Press, London.

———, AND G. S. WETSTONE. 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. J. Biogeogr. 4:135–142.

HELMUTH, B., R. R. VEIT, AND R. HOLBERTON. 1994. Long-distance dispersal of a subantarctic brooding bivalve (*Gaimardia trapesina*) by kelp-rafting. Mar. Biol. 120:421–426.

HICKS, G. F. G. 1985. Meiofauna associated with rocky shore algae, p. 36–56. *In:* The ecology of rocky coasts. P. G. Moore and R. Seed (eds.). Hodder and Stoughton, London.

HILL, J. L., AND P. J. CURRAN. 2003. Area, shape, and isolation of tropical fragments: effects on tree species diversity and implications for conservation. J. Biogeogr. 30:1391–1403.

HUFFAKER, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27:343–383.

HUIJBERS, C. M., E. M. MOLLEE, AND I. NAGELKERKEN. 2008. Post-larval French grunts (*Haemulon flavolineatum*) distinguish between seagrass, mangrove, and coral reef water: implications for recognition of potential nursery habitats. J. Exp. Mar. Biol. Ecol. 357:134–139.

———, I. NAGELKERKEN, L. L. GOVERS, M. VAN DE KERK, J. J. OLDENBURGER, AND J. H. F. DEBROUWER. 2011. Habitat type and schooling interactively determine refuge-seeking behavior in a coral reef fish throughout ontogeny. Mar. Ecol. Prog. Ser. 436:241–251.

HUNTER, J. R. AND C. T. MITCHELL. 1968. Field experiments on the attraction of pelagic fish to floating objects. J. Cons. Int. Explor. Mer. 31:427–434.

IGULU, M. M., I. NAGELKERKEN, R. FRAAIJE, R. VAN HINTUM, H. LIGTENBER, AND Y. D. MGAYA. 2011. The potential role of visual cues for microhabitat selection during the early life phase of a coral reef fish (*Lutjanus fulviflamma*). J. Exp. Mar. Biol. Ecol. 401:118–125.

INGÓLFSSON, A. 1995. Floating clumps of seaweed around Iceland: natural microcosms and a means of dispersal for shore fauna. Mar. Biol. 122:13–21.

———. 1998. Dynamics of macrofaunal communities of floating seaweed clumps off western Iceland: a study of patches on the surface of the sea. J. Exp. Mar. Biol. Ecol. 231:119–137.

JOBE, C. F., AND W. R. BROOKS. 2009. Habitat selection and host location by symbiotic shrimps associated with *Sargassum* communities: the role of chemical and visual cues. Symbiosis 49:77–85.

JOHNSON, B. R., AND J. ATEMA. 1986. Chemical stimulants for a component of feeding behavior in the common gulf-weed shrimp *Leander tenuicornis* (Say). Biol. Bull. 170:1–10.

JONES, C. G., J. H. LAWTON, AND M. SHACHAK. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

JONES, G. P., AND N. L. ANDREW. 1992. Temperate reefs and the scope of seascape ecology, p. 63–76. *In:* Proceedings of the 2nd International Temperate Reef Symposium. C. N. Battershill, D. R. Schiel, G. P. Jones, R. G. Creese, and A. B. Macdiarmid (eds.). NIWA Marine Publication, Wellington, New Zealand.

KEOUGH, M. J., AND B. J. DOWNES. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia (Berl.) 54:348–352.

KERRY, J. T., AND D. R. BELLWOOD. 2012. The effect of coral morphology on shelter selection by coral reef fishes. Coral Reefs 31:415–424.

KINGSFORD, M. J. 1995. Drift algae: a contribution to near-shore habitat complexity in the pelagic environment and an attractant for fish. Mar. Ecol. Prog. Ser. 116:297–301.

LAPOINTE, B. E. 1995. A comparison of nutrient-limited productivity in *Sargassum natans* from neritic vs. oceanic waters of the western North Atlantic Ocean. Limnol. Oceanogr. 4:625–633.

LEBER, K. M. 1985. The influence of predatory decopods, refuge, and microhabitat selection on seagrass communities. Ecology 66:1951–1964.

LENANTON, R. C. J., A. I. ROBERTSON, AND J. A. HANSEN. 1982. Nearshore accumulations of detached macrophytes as nursery areas for fish. Mar. Ecol. Prog. Ser. 9:51–57.

LEVIN, P. S., AND M. E. HAY. 2002. Fish-seaweed association on temperate reefs: do small-scale experiments predict large-scale patterns? Mar. Ecol. Prog. Ser. 232:239–246.

LOGAN, J. M., R. TOPPIN, S. SMITH, B. GALUARDI, J. PORTER, AND M. LUTCAVAGE. 2013. Contribution of cephalopod prey to the diet of large pelagic fish predators in the central North Atlantic Ocean. Deep-Sea Res. II 95:74–82.

MONTGOMERY, J. C., A. JEFFS, S. D. SIMPSON, M. MEEKAN, AND C. TINDLE. 2006. Sound as an orientation cue for the pelagic larvae of reef fishes and decapod crustaceans. Advances in Marine Biology 51:143–196.

MORSE, A. N. C. 1992. Role of algae in the recruitment of marine invertebrate larvae, p. 385–403. *In:* Plant-animal interaction in the marine benthos. D. M. John, S. J. Hawkins, and J. H. Price (eds.). Clarendon, Oxford, UK.

MOSER, M. L., AND D. S. LEE. 2012. Foraging over *Sargassum* by Western North Atlantic Seabirds. Wilson J. Ornithol. 124:66–72.

MYRBERG, J. A. A., AND L. A. FUIMAN. 2002. The sensory world of coral reef fishes, p. 123–148. *In:* Coral reef fishes. Dynamics and diversity in a complex ecosystem. P. F. Sale (ed.). Academic Press, San Diego.

NORDERHAUG, K. M., H. CHRISTIE, AND S. FREDRIKSEN. 2007. Is habitat size an important factor for faunal abundances on kelp (*Laminaria hyperborea*)? J. Sea Res. 58:120–124.

OXENFORD, H. A., AND W. HUNTE. 1999. Feeing habits of the dolphinfish (*Coryphaena hippurus*) in the eastern Caribbean. Sci. Mar. 63:303–315.

PAPPAL, A. L., R. A. ROUNTREE, AND D. G. MACDONALD. 2012. Relationship between body size and habitat complexity preference in age-0 and -1 year winter flounder *Pseudopleuronectes americanus.* J. Fish Biol. 81:220–229.

PARKER, T., AND V. TUNNICLIFFE. 1994. Dispersal strategies of the biota on an oceanic seamount: implications for ecology and biogeography. Biol. Bull. 187:336–345.

PIETSCH, T. W., AND D. B. GROBECKER. 1990. Frogfishes. Sci. Am. 262:96–103.

PRADO, P., AND K. L. HECK JR. 2011. Seagrass selection by omnivorous and herbivorous consumers: determining factors. Mar. Ecol. Prog. Ser. 429:45–55.

ROBERTS, D. A., AND A. B. G. POORE. 2005. Habitat configuration affects colonization of epifauna in a marine algal bed. Biol. Conserv. 127:18–26.

ROGERS, J. S., J. A. HARE, AND D. G. LINDQUIST. 2001. Otolith record of age, growth, and ontogeny in larval and pelagic juvenile *Stephanolepis hispidus* (Pisces: Monacanthidae). Mar. Biol. 138:945–953.

ROSENBERG, A., T. E. BIGFORD, S. LEATHERY, R. L. HILL, AND K. BICKERS. 2000. Ecosystem approaches to fishery management through essential fish habitat. Bull. Mar. Sci. 39:535–542.

RYTHER, J. H. 1956. The Sargasso Sea. Sci. Am. 194: 98–104.

SCHRIEDER, M. J., T. M. GLASBY, AND A. J. UNDERWOOD. 2003. Effects of height on the shore and complexity of habitat on abundances of amphipods on rocky shores in New South Wales, Australia. J. Exp. Mar. Biol. Ecol. 293:57–71.

SIMPSON, S. D., M. G. MEEKAN, A. JEFFS, J. C. MONTGOMERY, AND R. D. MCCAULEY. 2008. Settlement-stage coral reef fish prefer the high-frequency invertebrate-generated audible component of reef noise. Anim. Behav. 75:1861–1868.

SMITH, K. L., JR. 1973. Energy transformations by the Sargassum fish, *Histro histro.* J. Exp. Mar. Biol. Ecol. 12:219–227.

STACHOWICZ, J. J., AND N. LINDQUIST. 1997. Chemical defense among hydroids on pelagic *Sargassum*: predator deterrence and absorption of solar UV radiation by secondary metabolites. Mar. Ecol. Prog. Ser. 155:115–126.

STONER, A. W., AND H. S. GREENING. 1984. Geographic variation in the macrofaunal associates of pelagic *Sargassum* and some biogeographic implications. Mar. Ecol. Prog. Ser. 20:185–192.

———, AND F. G. I. LEWIS. 1985. The influence of quantitative and qualitative aspects of habitat complexity in tropical seagrass meadows. J. Exp. Mar. Biol. Ecol. 94:49–40.

TAIT, K. J., AND K. A. HOVEL. 2012. Do predation risk and food availability modify prey and mesopredator microhabitat delection in eelgrass (*Zostera marina*) habitat? J. Exp. Mar. Biol. Ecol. 426–427:60–67.

VANDENDRIESSCHE, S., M. MESSIAEN, S. O'FLYNN, M. VINCX, AND S. DEGRAER. 2007a. Hiding and feeding in floating seaweed: floating seaweed clumps as possible refuges or feeding grounds for fishes. Estuar. Coast. Shelf Sci. 71:691–703.

———, E. W. M. STIENEN, M. VINCX, AND S. DEGRAER. 2007b. Seabirds foraging at floating seaweeds in the Northeast Atlantic. Ardea 95:289–298.

VERWEIJ, M. C., I. NAGELKERKEN, D. DE GRAAFF, M. PEETERS, E. J. BAKKER, AND G. VAN DER VELDE. 2006. Structure, food and shade attract juvenile coral reef fish to mangrove and seagrass habitats: a field experiment. Mar. Ecol. Prog. Ser. 306:257–268.

WALTERS, J. H., AND D. S. WETHEY. 1996. Settlement and early post settlement survival of sessile marine invertebrate on topographically complex surfaces: the importance of refuge dimensions and adult morphology. Mar. Ecol. Prog. Ser. 137:161–171.

WARFE, D. M., AND L. A. BARMUTA. 2004. Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia 141:171–178.

WEIS, J. S. 1968. Fauna associated with pelagic *Sargassum* in the Gulf Stream. Am. Midl. Nat. 80:554–558.

WELLS, D. R. J., AND J. R. ROOKER. 2004. Spatial and temporal patterns of habitat use by fishes associated with *Sargassum* mats in the northwestern Gulf of Mexico. Bull. Mar. Sci. 74:81–99.

DEPARTMENT OF BIOLOGICAL SCIENCES, FLORIDA ATLANTIC UNIVERSITY, 777 GLADES ROAD, BUILDING 1, ROOM 136, BOCA RATON, FLORIDA 33431. Send reprint requests to COB. Date accepted: April 16, 2015