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The role of chemical cues in locating the host pelagic *Sargassum* spp. by the symbiotic fish *Stephanolepis hispidus*

Derek Cox[1] · W. Randy Brooks[1]

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Abstract

Pelagic *Sargassum* spp. is important in the life histories of many economically and ecologically important associated organisms, which collectively form a symbiotic community with this alga serving as the primary host. Fishes play a vital role in these communities, but it is generally unknown how they locate these floating symbiotic habitats. This study examined the role of natural chemical cues from *Sargassum* spp. patches and a synthetic chemical dimethylsulfoniopropionate (DMSP) for an associated fish, the planehead filefish (*Stephanolepis hispidus*), and a control fish species not associated with *Sargassum* spp., the masked goby (*Coryphopterus personatus*). Choice trials with a Y-maze (olfactometer) apparatus determined that *S. hispidus* responded significantly to chemical cues from *Sargassum* spp. while *C. personatus* did not. DMSP cues did not result in significant behavioral responses for either fish species. Demonstrating that *S. hispidus* can respond to chemical cues from *Sargassum* spp. helps further our understanding of this unique floating algal reef and how fishes might locate it to establish this subcomponent of the holobiont (the collective symbionts in the association).

Keywords *Sargassum* spp. · Chemical cues · Symbiosis · Holobiont · Pelagic macrofauna

1 Introduction

Sargassum sp. is a brown macroalga (Class Phaeophyceae; commonly called gulfweed) with thalli characterized by long, branching stipes with numerous blades and spherical, gas-filled bladders (pneumatocysts) that assist in floatation. Two species are holopelagic: *Sargassum fluitans* (Børgsen) and *Sargassum natans* (Linnaeus). Floating mats of *Sargassum* spp. commonly accumulate in large windrows called “weedlines” due to wind direction and Langmuir circulation (Ryther 1956; Lapointe 1995; Wells and Rooker 2004). Floating materials in the ocean, like *Sargassum* spp., can attract and concentrate fauna by providing substrate and structure for many organisms (Hunter and Mitchell 1968; Kingsford 1995; Lapointe 1995; Ingólfsson 1998; Casazza and Ross 2008), thus creating a multispecies holobiont (the collective symbionts in the association) with *Sargassum* spp. as the primary host species.

Colonization typically begins with epiphytic cyanobacteria, hydroids, and bryozoans that serve as food that subsequently attract a large variety of invertebrates (*circa* 100 species), fishes (*circa* 80 species of fish from 28 families), birds, and sea turtles (e.g., Dooley 1972, Bortone et al. 1977, Butler et al. 1983, Johnson and Atema 1986, Carr 1987, Fedoryako 1989, Manzella and Williams 1991, Wells and Rooker 2004, Casazza and Ross 2008, Witherington et al. 2012). Regarding the fishes, many are important commercially and recreationally such as billfish, jacks, and dolphin fish. Additionally, 33 of the fish species inhabiting *Sargassum* spp. patches are endemic and not found in surrounding open waters, such as the obligate symbiotic fishes *Histrio histrio* (sargassum fish) and *Syngnathus pelagicus* (sargassum pipefish) (Wells and Rooker 2004). Many of these endemic organisms (both invertebrates and vertebrates) show unique morphological and sometimes behavioral adaptations to living within *Sargassum* spp. mats.

With such a large diversity of temporary and permanent organisms utilizing these mats, pelagic *Sargassum* spp. could be called a “floating reef” as it provides benefits to inhabitants similar to benthic “reefs” (e.g., coral, oyster). Even organisms not commonly associated could find temporary shelter and protection when swept away from

✉ W. Randy Brooks
wbrooks@fau.edu

[1] Florida Atlantic University, Boca Raton, FL, USA

previous habitats by currents or storms and left stranded in open water (Lapointe 1986; Brooks et al. 2007). Additionally, these mats serve as a nursery for many juvenile fishes (Lenanton et al. 1982; Lenanton and Caputi 1989; Wells and Rooker 2004). Among known fish nursery ecosystems, the *Sargassum* spp. community has been studied the least, despite evidence that it may be critical during the larval and juvenile stages for many commercially and recreationally important fish species such as dolphin fish, tuna, ballyhoo, jacks, sailfish, swordfish, and marlin (Costen-Clements et al. 1991; Wells and Rooker 2004; Rudershausen et al. 2010). Because of this habitat's importance as host for so many symbiotic organisms, some obligate and others facultative, pelagic *Sargassum* spp. mats have been designated as Essential Fish Habitat (EFH) by the National Marine Fisheries Service (NMFS).

Obligate symbionts include the sargassum fish, *H. histrio*, with its unique adaptations in coloration and patterns to mimic the algae and provide camouflage. A facultative symbiont includes the planehead filefish, *Stephanolepis hispidus* (Family Monacanthidae), which is extremely abundant as juveniles (Casazza and Ross 2008) feeding mainly on hydroids (Stachowicz and Lindquist 1997; Brooks et al. 2007) and secondarily on other small invertebrates such as sargassum shrimps (*Latreutes fucorum* and *Leander tenuicornis*)(Dooley 1972, Brooks et al. 2007). Like *H. histrio*, the coloration of *S. hispidus* is also adapted to blend in with these macroalgae; however, this filefish is a much more mobile species, preferring to swim underneath the mat unless threatened, when it then moves up into the algal fronds (Dooley 1972). Once juvenile filefish reach between 5.0 and 10.0 cm in length, they begin migrating away from mats to benthic, coral reef habitats (Berry and Vogele 1961).

Currents, gyres, winds, and storms cause high variability in the distribution and abundance of *Sargassum* spp. along coastal waters (Dooley 1972; Wells and Rooker 2004). Along with these mats constantly drifting, Stoner (1983) also showed seasonal variability in the patch size and abundance. Massive drifting blooms have increased in abundance in recent years, including a current accumulation in the tropical Atlantic and Caribbean (Barnes et al. 2023). The factors discussed above, along with wave action, large predators, and occasional storms breaking up *Sargassum* spp. mats, can potentially cause mat inhabitants to be separated from their patch and may result in difficulty relocating the mat or finding a replacement.

The need to locate these mats, either for temporary or permanent residence, requires detecting environmental cues. Specifically, chemical cues could be critical for these organisms to locate *Sargassum* spp. patches, especially when visual cues are limited or unavailable. Visibility in the open ocean and nearshore environments is highly variable and dependent on many factors, including levels of dissolved organic matter, wave action, phytoplankton abundance, and sediment runoff. Low visibility during storms or at night and the potential to be separated by relatively large distances from *Sargassum* spp. mats could result in a shift to relying more on chemical rather than visual cues to locate these patches.

Fishes can detect a variety of specific compounds, many of which could potentially be used to locate *Sargassum* spp. patches including amino acids, amines, nucleotides, bile acids, aminosterols, sex steroids, and prostaglandins (Derby & Sorenson 2008). Secondary metabolites from *Sargassum* spp. and its epiphytes contain amino acids and fatty acids that could potentially be detected by fishes within the marine environment (Wong and Cheung 2001; Turner and Rooker 2006).

Dimethylsulfoniopropionate (DMSP) is also a common chemical cue detected by some marine organisms (Debose et al. 2008, Nevitt 1995, Kowalewsky et al. 2006). DMSP is excreted by marine algae such as the dinoflagellate *Prorocentrum micans* when it is damaged during attacks by zooplankton or other predators (Dacey and Wakeham 1986; Hill and Dacey 2006). This chemical release has the potential secondary effect of attracting organisms that prey on the zooplankton, which could lessen the grazing impact on the phytoplankton patch (Hay 1996). DMSP can have cascading effects throughout the food chain, including being utilized by reef fishes (DeBose et al. 2008), sea birds (Nevitt et al. 1995), harbor seals (Kowalewsky et al. 2006), and potentially whale sharks (Martin 2007). High DMSP concentrations have been recorded in mats in the Sargasso Sea (order of magnitude of 10^{-9} Vila-Costa et al. 2014). Some jack species (*Caranx hippos* and *C. melampygus*), which are facultatively associated with *Sargassum* spp. mats, showed significant behavioral responses to DMSP (Debose et al. 2010) suggesting that jacks (and possibly other fishes) could potentially use DMSP to locate areas with *Sargassum* spp.

In this study, we examined the potential of two fish species to chemically detect *Sargassum* spp. and DMSP. We chose *Stephanolepis hispidus* as it is a common facultative symbiont as juveniles in *Sargassum* spp. patches. As a control, a marine fish not found in *Sargassum* spp. patches, the masked goby, *Coryphopterus personatus* (Family Gobiidae), was also tested. This latter fish species is common in the Caribbean and off the coast of South Florida but is benthic and usually found associated with coral reefs. *C. personatus* is similar in size to juvenile *S. hispidus* allowing it to be used in the same experimental setup. Although specimens used of this control species would likely be adults rather than juveniles, it is less likely they would respond to *Sargassum* spp. cues at any life history stage compared to potential *S. hispidus* responses.

The following specific questions were addressed:

1. Do *S. hispidus* and *C. personatus* respond to chemical cues from *Sargassum* spp. patches?
2. Do *S. hispidus* and *C. personatus* respond to dimethylsulfoniopropionate (DMSP) in seawater?
3. Does *S. hispidus* show a shift in response to chemical cues from *Sargassum* spp. patches or DMSP in the size ranges commonly found inhabiting *Sargassum* spp.?

2 Materials and methods

2.1 Collection and maintenance of specimens

All specimens were collected using a fine mesh dip net over the side of a boat from 1 to 12 km offshore from the Boca Raton Inlet in southeast Florida. The net was placed fully in the water while the boat slowly drifted by the floating *Sargassum* spp. mat to collect *S. hispidus* and *Sargassum* spp. Collected samples were then gently shaken from the net, rinsed in natural seawater, and visually inspected afterwards to ensure all possible macroscopic organisms had been removed and sorted quickly by hand. Animals not being used for experimentation were released back into the *in-situ* patches. Fish and algae to be used for trials were transferred into insulated plastic coolers containing natural seawater with portable aerators until they could be transported back to the laboratory in the Biological Sciences building at Florida Atlantic University, Boca Raton, FL.

Synthetic seawater using Instant Ocean Sea Salt^{tm} was mixed to a specific gravity matching natural seawater (1.023–1.025) for all laboratory holding aquaria and experiments. All filefish were placed using a fish net (which was rinsed with synthetic sea water between uses throughout the trials) into 75 L aquaria. Larger fish were kept separated from smaller ones to minimize cannibalism or aggressive behaviors. Tanks were exposed to a 12 L:12D photoperiod with aeration systems and water filters to maintain appropriate living conditions for the organisms. Water level and parameters were checked daily including pH, salinity, ammonia, and nitrate. Visual checks and feeding of frozen brine shrimp or flakes also took place each day. Fishes were given 24 h, or until their color and behavior returned to normal, whichever came second, to acclimate to their laboratory environment prior to being used in a trial.

For the *Sargassum* spp. chemical cue treatment, 1 kg of *Sargassum* spp. was collected and thoroughly rinsed prior to being placed in 37 L of synthetic seawater for 48 h to allow chemical compounds to be released. This duration was chosen as *Sargassum* spp. shows rapid deterioration in aquaria around 72 h after collection (Jobe and Brooks 2009). *Sargassum* spp. composition can vary greatly throughout the year due to many factors such as age, amount of epibiotic growth, species present, and seasonal conditions. To ensure that there was no chemical composition variability in *Sargassum* spp. effluent between trials, 45 ml aliquots were taken from one batch and then frozen for subsequent use throughout experimentation.

2.2 Experimental procedure

Chemoreception trials took place in laboratories at the Florida Atlantic University Boca Raton Campus. Prior to trials, standard lengths and wet-body weights for *S. hispidus* were recorded. Size data for the control species *C. personatus* were not recorded because all individuals were of nearly identical size (2.0 ± 0.1 cm) and presumably adults. The test apparatus consisted of a modified Y-maze or sometimes called a Y-tube olfactometer (e.g., Frahm and Brooks 2021) made from clear acrylic, and measuring 10 cm in depth, 10 cm wide, and two 28 cm long arms (Fig. 1). The Y-maze was composed of three regions, A, B, and C (no actual markings were made on the apparatus). Before trials started, the Y-maze was filled with 6 L of synthetic seawater. During trials, each arm (A and B) received a constant flow of synthetic seawater at 60 ml/min via two 5 mm diameter tubes connected to two source water buckets. This flow of water from the two source buckets eventually caused water to exit the tank via an overflow tube at the base of region C, thereby maintaining a constant depth and flow rate in the aquarium throughout the experiment. Black plastic surrounded (sides and top) the Y-maze to minimize the use of any extraneous visual cues throughout the trials, but minimal light was still available for recording fish behaviors. Control tests without fish were run with colored dyes from both sources to confirm that the cues were not crossing over between regions A and B (Fig. 1). Source cues for A and B were decided randomly prior to each trial by coin toss.

Preliminary control trials were done to confirm whether the behaviors of these fishes in the Y-maze would be suitable and observable. These consisted of observing several individuals of each fish species to unaltered synthetic seawater from both sources flowing into regions A and B. Individuals of both fish species swam out of area C once the perforated partition was lifted and investigated each arm at some point.

Each fish was placed and contained (by a perforated divider) in the home base region C to acclimate for 10 min. or until they appeared calm, whichever came first. After acclimation, flow of water from each source was initiated through the tank simultaneously for 5 min, exposing the fish to potential chemical cues prior to its release from the contained area in region C. As water from each source continued to flow into each arm, the perforated divider was

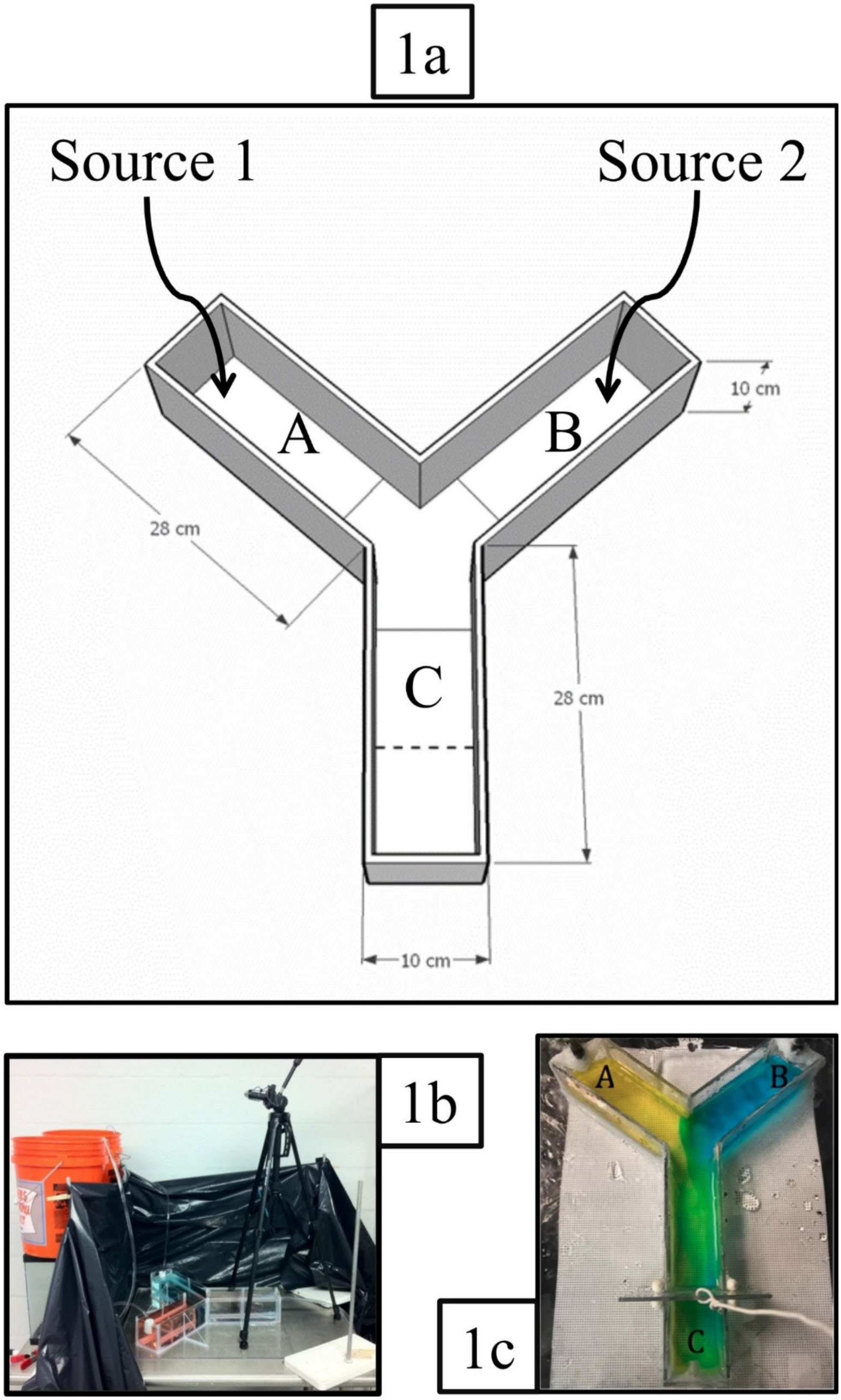

Fig. 1 (**a**) Y-maze schematic showing chemical cues potentially coming in from either region A or B. Region C is where the fish began the experiment. The area below the dotted line in region C indicates the perforated divider which was lifted after acclimation of the fish. Dark arrows represent flow of water through the apparatus, starting at each end of regions A and B and exiting at the base of region C (no actual markings were made on the apparatus). (**b**) Shows actual experimental setup with Y-maze. Black plastic was used to block fish's view of observer who was positioned behind plastic (to the left in the picture) while the camera (attached to tripod) recorded fish behavior and movement for the 10 min trials. Prior to experimental trials, two different dyes were allowed to run from source A and B, respectively, to ensure the seawater flow moved unidirectionally from the sources (A and B) with minimal mixing until they joined at area C and flowed out of the system. (**c**) Similar Y-maze showing dye movement confirming flow integrity in such apparatuses (Image used with permission from Frahm and Brooks 2021; Published by MDPI under the terms of the Creative Commons Attribution License)

then removed to allow the fish access to the entire tank for 10 min. while water continued to flow for the duration of the trial. Each trial was recorded using a digital camera to allow for review of behavior (by D. Cox) and time spent by the fish in each region of the tank.

Trials consisted of treatments that had unaltered synthetic seawater flowing into the apparatus from one source, and from the other synthetic seawater that had a 45 ml aliquot addition of *Sargassum* spp. effluent seawater. This treatment examined whether chemical cues from *Sargassum* spp. were being detected and altering behavior of the fish. The next treatment used synthetic seawater from one source and synthetic seawater containing DMSP, which was obtained as dimethyl sulfide from Sigma-Aldrich in an anhydrous liquid form > = 99.0%. It was diluted in seawater at a concentration found commonly in situ of 10^{-9} M (from Vila-Costa et al. 2014 and Debose et al. 2010) and stored in between uses at 1.0 ° C.

At the end of each trial, the Y-maze and water sources were emptied and cleaned by rinsing with tap water then synthetic seawater to remove any residual chemical cues before beginning the next trial. 25 replicates were performed for each experiment and species, while each fish was used only once.

2.3 Statistical analysis

Analysis of the fish response consisted of several variables including the first region occupied, A or B, the total number of visits to regions A or B, and the total time spent in each region A or B. The fish was only considered to have left or entered a region A or B once the entire body of the fish had crossed into or out of the region. Results were analyzed in "R" using:

1) Binomial test of significance for region first occupied between A and B,
2) T-tests for number of visits to each region, A or B, and total time spent in each of these regions,
3) Logistic regression to analyze the effect of length and mass of *S. hispidus* on first region (either A or B) entered,
4) Linear regression to determine mass and length effect on time spent in regions A and B and number of times each of these regions was visited.

There were no significant differences in responses (all p > 0.050) within the size ranges for *S. hispidus* (Length: Range = 2.1–6.9 cm, Avg = 3.7 cm, SD = 9.4 cm; Weight: Range, 0.3–9.3 g, Avg = 1.9 g, SD = 1.4 g) of fish collected for this study. All filefish collected and sampled were presumed juveniles as they still inhabited and were collected directly from *Sargassum* spp. patches. Transition to adults generally occurs after leaving the algal mats at around 1 year of age and maturing around 2 years and at a typical length of 13.9 and 14.9 cm for both sexes (Mancera-Rodriguez and Castro-Hernandez 2015).

3 Results

3.1 Sargassum spp. *cue trials*

S. hispidus showed no significant preference for the region containing *Sargassum* spp. chemical cues based upon choice of region first entered (11 visited cue side first, 11 visited control side first, 3 remained in area C; Binomial test, df = 1, p = 1.000) or by average number of visits to that region (3.4 visits to cue side, 3.2 visits to control side; T-test, t = 0.173, df = 46, p = 0.863) with both metrics being statistically equal. However, *S. hispidus* did show a significant response towards the *Sargassum* spp. cues in the total amount of time spent in each region, spending an average of almost twice the amount of time in the region containing the algal effluent (166 s) as the region without (87 s) (T-test, t = 2.067, df = 41, p = 0.045) (Fig. 2). Neither fish mass nor length had a significant effect on their response for any of the three previously mentioned variables (all p > 0.050).

C. personatus also showed no significant response to the region containing *Sargassum* spp. cues in the first two measured behaviors including initial region entered (7 visited cue side first, 5 visited control side first, 13 remained in area C; Binomial test, df = 1, p = 0.564) and average number of visits (0.7 visits to cue side, 0.7 visits to control side; T-test, t = 0, df = 42, p = 1.000). Results from the trials regarding total time spent by the masked gobies in each region also were insignificant (T-test, t = -1.778, df = 35, p = 0.084) (Fig. 2).

3.2 DMSP cue trials

During the trials using DMSP cues, *S. hispidus* and *C. personatus* showed no significant preference for regions containing DMSP concentrations in either the first region entered (*S. hispidus* – 9 visited cue side first, 4 visited control side first, 12 remained in area C, Binomial test, df = 1, p = 0.166; *C. personatus* – 6 visited cue side first, 7 visited control side first, Binomial test, df = 1, p = 0.782) or average number of visits to each region (*S. hispidus* – 1.2 visits to cue side; 0.9 visits to control side, T-test, t = 0.643, df = 47, p = 0.523; *C. personatus* – 0.3 visits to cue side; 0.5 visits to control side; T-test, t = -1.086, df = 34, p = 0.285, or time spent in either region (*S. hispidus* – 138 s in cue side, 46 s in control side, p = 0.066; *C. personatus* – 106 s in cue side, 63 s in control side, T-test, t = 0.891, df = 43, p = 0.378).

Size of the filefish also did not have a significant impact on any preference variables for DMSP cues (all p > 0.05).

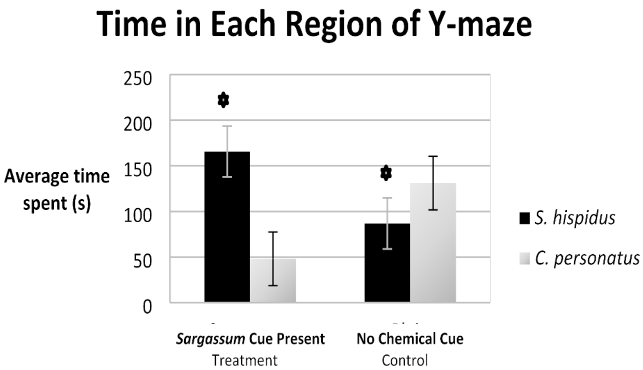

Fig. 2 Time spent in each region (**A** or **B**) of the Y-maze by fishes during *Sargassum* chemical cue trials (t-test; *S. hispidus* p = 0.045, *C. personatus* p = 0.084; n = 25 for each fish species; * Significant difference between treatment and control groups)

4 Discussion

The significant finding in this study was the planehead filefish *S. hispidus* detected chemical cues from *Sargassum* spp., averaging nearly twice the amount of time in the *Sargassum* spp. region of the Y-maze than in the plain (control) seawater region (Fig. 2). In initial studies by Jobe and Brooks (2009), sargassum shrimps *Leander tenuicornis* and *L. fucorum* responded significantly to *Sargassum* spp. chemical cues only when visual cues were present simultaneously. Subsequent studies, with modifications of experimental procedures and increased sample sizes, showed that chemical reception by these two shrimp species was employed exclusively for potential location of *Sargassum* spp. (Frahm and Brooks 2021). The current study results, based on similar experimental methods, show that *S. hispidus* could also potentially use *Sargassum* spp. chemical cues either primarily or secondarily for host location.

Like many fishes, a variety of cues may be employed simultaneously or sequentially, depending on the environmental circumstances that may have separated the fish from the mats. Locating mats during the day in clear water may involve a different set of responses than doing so at night or in turbid waters. Visual cues were kept to a minimum in this study, but lights were used so that fish positions and behavior could be monitored and evaluated. Future studies should consider the option of eliminating visual cues completely by performing trials in darkness and utilizing infrared cameras to see if responses differ when forced to rely on olfactory cues alone. Such experimental scenarios limiting light availability might more accurately represent nighttime or crepuscular periods in situ.

We also chose to use smaller (likely juveniles) *S. hispidus* in the current study as this cohort is more likely to associate symbiotically with these mats. In fact, all *S. hispidus* were collected directly from these algal mats. Future studies may show as *S. hispidus* reaches larger stages (mostly adults) an ontogenetic shift in response from *Sargassum* spp. chemical cues – possibly to using benthic habits ques - may occur. Such shifts have been observed in reef fishes (Lecchini et al. 2007).

Significant responses to dimethylsulfoniopropionate (DMSP) were not observed for either *S. hispidus* or *C. personatus*. This was predicted for the latter species because it served as a control fish naturally inhabiting coral reefs and not found in *Sargassum* spp. patches. However, some reef fishes associated with *Sargassum* spp. patches as juveniles, such as jacks, do respond to DMSP (Debose et al. 2010).

5 Conclusions

We referred earlier in this paper to *Sargassum* spp. and its associated organisms as "floating reefs." Coral reefs have a plethora of both microscopic and macroscopic organisms associated that are both facultative and obligate "symbionts" (cf., Zilber-Rosenberg and Rosenberg 2008). Thus, coral reefs and *Sargassum* spp. communities are examples of significant symbiotic holobionts; i.e., both possessing symbionts that contribute to the ecological balance of the entire superstructure.

In this study we focused on one of the most abundant fish species - *S. hispidus* - in this symbiosis and how it could potentially use chemoreception to locate the *Sargassum* spp. host, which functions as the base for this biological habitat. The ability to locate these mats quickly through any sensory input available is an important factor for many fishes as they are typically more vulnerable to predation when isolated from this protective habitat. Not only is this important for fish survival, but this symbiotic relationship may be not only commensalistic but approaching mutualism in some situations. That is, *Sargassum* spp. mats are typically located in oligotrophic waters and rely on large numbers of fishes for nutrient input (from their waste in the forms of nitrogen and phosphorous) (Lapointe et al. 2014), especially the planehead filefish which comprise the most common and abundant fish associated with these patches (Wells and Rooker 2004).

Finding that *S. hispidus* can detect chemical cues from *Sargassum* spp. mats and potentially utilize them to locate this essential habitat increases the likelihood that additional fish species and other pelagic macrofauna (e.g., hatchling sea turtles; Mansfield et al. 2021) found in these weedlines can do so, too. This information is especially important for the management and conservation of habitats that are not stationary and house many species.

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Declarations

• The authors have no relevant financial or non-financial interests to disclose.
• No funding was received for conducting this study.
• All handling and experiments with fishes were approved by the Florida Atlantic University Institutional Animal Care and Use Committee (IACUC), established in accordance with the Animal Welfare Act and Public Health Service Policy on the Humane Care and Use of Animals.

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