

Predictors of the distribution and abundance of a tube sponge and its resident goby

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Abstract Microhabitat specialists offer tractable systems for studying the role of habitat in determining species' distribution and abundance patterns. While factors underlying the distribution patterns of these specialists have been studied for decades, few papers have considered factors influencing both the microhabitat and the inhabitant. On the Belizean barrier reef, the obligate sponge-dwelling goby *Elacatinus lori* inhabits the yellow tube sponge *Aplysina fistularis*. We used field data and multivariate analyses to simultaneously consider factors influencing sponge and goby distributions. Sponges were non-randomly distributed across the reef with density peaking at a depth of 10–20 m. Sponge morphology also varied with depth: sponges tended to be larger and have fewer tubes with increasing depth. Knowing these patterns of sponge distribution and morphology, we considered how they influenced the distribution of two categories of gobies: residents (≥ 18 mm SL) and settlers (< 18 mm SL). Maximum tube length, number of sponge tubes, and depth were significant predictors of resident distribution. Residents were most abundant in large sponges with multiple tubes, and were virtually absent from sponges shallower than 10 m. Similarly, maximum tube length and number of sponge tubes were significant predictors of settler distribution, with settlers most abundant in large sponges with multiple tubes. The presence or absence of residents in a sponge was not a significant predictor of settler distribution. These results provide us with a clear understanding

of where sponges and gobies are found on the reef and support the hypothesis that microhabitat characteristics are good predictors of fish abundance for species that are tightly linked to microhabitat.

Keywords Distribution patterns · Microhabitat specialization · Settlement · Recruitment · *Aplysina fistularis* · *Elacatinus lori*

Introduction

Microhabitat-attached species are especially tractable systems for population studies of distribution and abundance. The phenomenon of strong attachment to sessile invertebrates is widespread throughout marine taxa. Some crustaceans exhibit microhabitat association, with shrimp inhabiting the mantle of oysters (Baeza 2008) and crabs living within the tentacles of sea anemones (Baeza et al. 2001). Several fish groups also exhibit microhabitat specialization. Pearlfishes live in the body cavities of sea cucumbers and sea stars (Lavett Smith et al. 1981; Colley et al. 2008), anemonefishes inhabit anemones (Fautin 1992; Elliott and Mariscal 2001; Buston 2002), and damselfishes and gobies often associate with corals (Sweetman 1983; Booth 1992; Kuwamura et al. 1994; Munday et al. 1997; Wilson et al. 2008) or sponges (Colin 2002, 2010). Studies that predict microhabitat and inhabitant distribution may provide initial insights into interesting ecological interactions such as microhabitat preference, the effect of microhabitat on the fitness of inhabitants, and the relationship between population density and the environment. Distribution and abundance patterns of these systems can be influenced by three broad categories of variables:

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environmental gradients, microhabitat characteristics, and conspecific interactions.

Environmental gradients have been shown to influence the distribution of both microhabitats and the fish that associate with them. Distribution and abundance patterns of invertebrate microhabitats, such as corals and sponges, may be influenced by depth (Wilkinson and Chesire 1989; Wilkinson and Evans 1989; Duckworth and Wolff 2007; Roth and Knowlton 2009), substrate (Roth and Knowlton 2009), light availability (Wilkinson and Evans 1989), turbulence (Palumbi 1984; Wilkinson and Evans 1989; Mercado-Molina and Yoshioka 2009), and food availability (Lesser 2006). Fish settlement, distribution, and abundance patterns are also influenced by environmental gradients including depth (Roberts and Ormond 1987; Srinivasan 2003; González-Sansón et al. 2009), reef zone (Tolimieri 1998; Belmaker et al. 2007), reef continuity (Levin et al. 2000; Belmaker et al. 2009), and availability of sheltered areas (Roberts and Ormond 1987). For fish living in microhabitats, the interesting question becomes, what is the effect of environmental variables on the fish over-and-above the effect of these variables on the microhabitat?

Site-attached fish may be most profoundly influenced by microhabitat distribution (Munday et al. 1997). In some systems of obligate association, there is a triangle of correlates between microhabitat size, fish size, and group size. Several hypotheses that are not mutually exclusive could explain these positive correlations. First, in cases where microhabitat size is positively related to the number and the size of fish inhabitants (Fautin 1992; Kuwamura et al. 1994; Elliott and Mariscal 2001), microhabitat size may be the driver if larger microhabitats offer more resources. Second, fish biomass may be a driver of microhabitat growth and survival (Holbrook and Schmitt 2005). For example, anemonefishes have a symbiotic relationship with their host anemones, and an experimental removal of fish resulted in anemone shrinkage, possibly because the fish protect the anemones from predation and provide them with nutrients (Porat and Chadwick-Furman 2004, 2005). Third, there could be an external driver of these correlations, such as a “site effect” where large invertebrate microhabitats and fish are simply located at favorable sites on the reef (van Noordwijk and de Jong 1986; Buston and Elith 2011).

Intraspecific interactions may also influence fish distribution and abundance patterns. Many studies have shown that conspecific interactions affect spatial patterns of settlement and recruitment. Conspecific presence may have a positive (Sweatman 1983, 1985, 1988; Booth 1992, 1995; Öhman et al. 1998), negative (Elliot et al. 1995; Öhman et al. 1998; Buston 2003), or insignificant correlation (Öhman et al. 1998) with settlement and recruitment

depending on the ecology of the species. Adult conspecific attraction (Gardiner and Jones 2010) and density-dependent survival of juveniles and adults due to intraspecific competition have also been shown to influence distribution and abundance (Holbrook and Schmitt 2002; Hixon and Jones 2005; Wilson 2005).

The yellow tube sponge *Aplysina fistularis* (Class: Demospongiae) is a common species of the Caribbean reef community. It is a keratose tube sponge with a distinct yellow-green coloration. This sponge exhibits a high level of morphological variation that may be strongly influenced by its environment (Neigel and Schmahl 1984). Sponges exist as single tubes or clusters of tubes and show wide variation in tube length. Sponges also tend to be bigger and have a faster growth rate with increasing depth, up to 30 m, as a result of greater food availability (Lesser 2006). *A. fistularis* provides habitat to a number of marine organisms including the sponge-dwelling goby *Elacatinus lori*. The sponge may benefit from hosting *E. lori* if the goby consumes the sponge’s polychaete parasite *Haplosyllis spongicola* (López et al. 2001), as has been documented for other sponge-associated *Elacatinus* species (Smith and Tyler 1972; Colin 1975; Whiteman and Coté 2002).

Elacatinus lori (Family: Gobiidae) is one of at least 25 neon goby species in the tropical western North Atlantic (Colin 2010). Distributed throughout the Gulf of Honduras, *E. lori* is distinguished from sympatric *Elacatinus* species (*E. colini*, *E. lobeli*, and *E. louisae*) by having a thin, white stripe running laterally along the body length and a white stripe on the snout (Colin 2002). Like most coral reef fishes, *E. lori* has a bipartite life cycle with a dispersing larval phase and a relatively sedentary reef resident phase. At the end of the pelagic phase, larvae settle to the reef and attempt to recruit to the resident population (Williams and Sale 1981; Buston 2003). For this system, we distinguish between settlement and recruitment, with settlement defined as the point when a late-stage larva settles near or outside the microhabitat and recruitment defined as the transition when a settler joins the group inside of the microhabitat. As residents, *E. lori* are obligate sponge dwellers (Colin 1975, 2002, 2010) found almost exclusively in *A. fistularis*. Beyond this, little is known about the distribution, abundance and group structure of this goby in yellow tube sponges. *E. lori* is strongly attached to the sponge, making it a good system to test the relationship between microhabitat distribution and fish distribution.

The purpose of this study is to evaluate the influence of environmental variables (e.g., depth), microhabitat characteristics and intraspecific interactions on the distribution of two reef species at Carrie Bow Cay, Belize: the yellow tube sponge *A. fistularis* and its neon goby inhabitant *E. lori*. We simultaneously consider sponge and goby distribution and specifically address the following questions:

1. How are sponges distributed across the reef and does sponge morphology change with an environmental variable (depth)?
2. What variables (depth and microhabitat characteristics) influence resident distribution and abundance?
3. What variables (depth, microhabitat characteristics, and conspecific interactions) influence settler distribution and abundance?

Methods

Study site

The Belize barrier reef complex is the largest contiguous reef in the Northern hemisphere (Rützler and Feller 1999), extending nearly 250 km along the coast of Belize from the Yucatán Peninsula to the Guatemalan border. Carrie Bow Cay (16°48′10″ N 88°05′45″ W) sits on the main barrier reef and is bordered by two channels: South Water Cut to the north and Curlew Cut to the south. Here, the barrier reef has several distinct reef zones, defined by Rützler and Macintyre (1982): reef crest, inner fore reef (high spur and groove, low spur and groove), outer fore reef (inner reef slope, sand trough, outer ridge, and fore reef slope). Our study area was haphazardly chosen among barrier reef sites off Carrie Bow Cay. We sampled across all reef zones and had no prior data on the distribution of sponges and gobies. We expect the sponge and goby distribution patterns found at this study site to be representative of other locations across the barrier reef.

Sponge population

Initial surveying of all tube sponges on the reef revealed that *E. lori* was found almost exclusively in *A. fistularis*; *A. fistularis* was the only sponge species that harbored more *E. lori* than expected by chance, assuming an equal abundance of fish in all tube sponges (Chi-Square: $\chi^2 = 54.52$; $df = 4$; $P < 0.001$). Given this, we exclusively mapped *A. fistularis* sponges. We surveyed a 100 m wide \times 300 m long transect of reef around Carrie Bow Cay by SCUBA to map the distribution of the *A. fistularis* population. The transect extended due east from the reef crest and included each reef zone out to the outer ridge of the outer fore reef (maximum depth 30 m). Three divers swam along sub-transects, approximately 3 m apart, until the entire area was surveyed. Sponge “waypoints” ($n = 509$), defined as the x and y coordinates of each sponge, were recorded using the Garmin GPSMAP® 76Cx in an underwater housing produced by Sound Ocean Systems. We mapped every *A. fistularis* regardless of whether

any *E. lori* were present. At each sponge, we recorded the following data: depth at base of sponge (m), number of tubes, length (nearest cm), and width (nearest cm) of each tube. We focused on the role of the environmental parameter “depth” which has been shown to be correlated with food availability and growth rates for *A. fistularis* (Lesser 2006). We measured depth not because we believe that depth alone offers a biological explanation of distribution patterns, but because depth is a proxy for several other environmental gradients, including light availability, wave exposure, and reef zone.

Fish population

To map the distribution and abundance of the *E. lori* population, we recorded the number of fish at each tube, and assigned them into two size-based categories: residents or settlers. Based on the logic of previous investigators (Williams and Sale 1981; Buston 2003), residents were defined as being 18 mm standard length (SL) or greater, while settlers were defined as being less than 18 mm (SL). To test this size cut-off for *E. lori*, we collected a sub-set of residents and settlers using hand-nets and slurp guns, and measured the SL of each individual with calipers to confirm that all of the fish we classified as settlers visually were < 18 mm SL and all of the fish we classified as residents visually were ≥ 18 mm SL. This cut-off between residents and settlers coincided with an apparent shift in life history: in general, large fish (residents) lived inside sponge tubes while small fish (settlers) lived on the outside of tubes.

Data analysis

We analyzed sponge distribution by looking at the relationship between the independent variable “depth” and the dependent variable “number of sponges”. The observed number of sponges at each depth was determined from raw data, with depth categorized into four zones: (1) 0–10 m; (2) 10.1–15 m; (3) 15.1–20 m; and (4) 20.1–30 m. These categories with unequal bin sizes were chosen to balance the data set and did not affect the results. The expected number of sponges at each depth was estimated by assuming that, if sponges were randomly distributed with respect to depth, the density of sponges (number sponges m^{-2}) would be the same at each depth. To generate the expected number of sponges in each zone, we multiplied the proportion of total reef area in each depth zone by the total number of sponges. We calculated the reef area in each zone by plotting the depth of each sponge against its position on the transect (Fig. 1), and fitting a smoothing spline through the data (JMP 8.0.1). From the fitted curve, we estimated the horizontal distance encompassed by each depth zone and then estimated the surface area in each

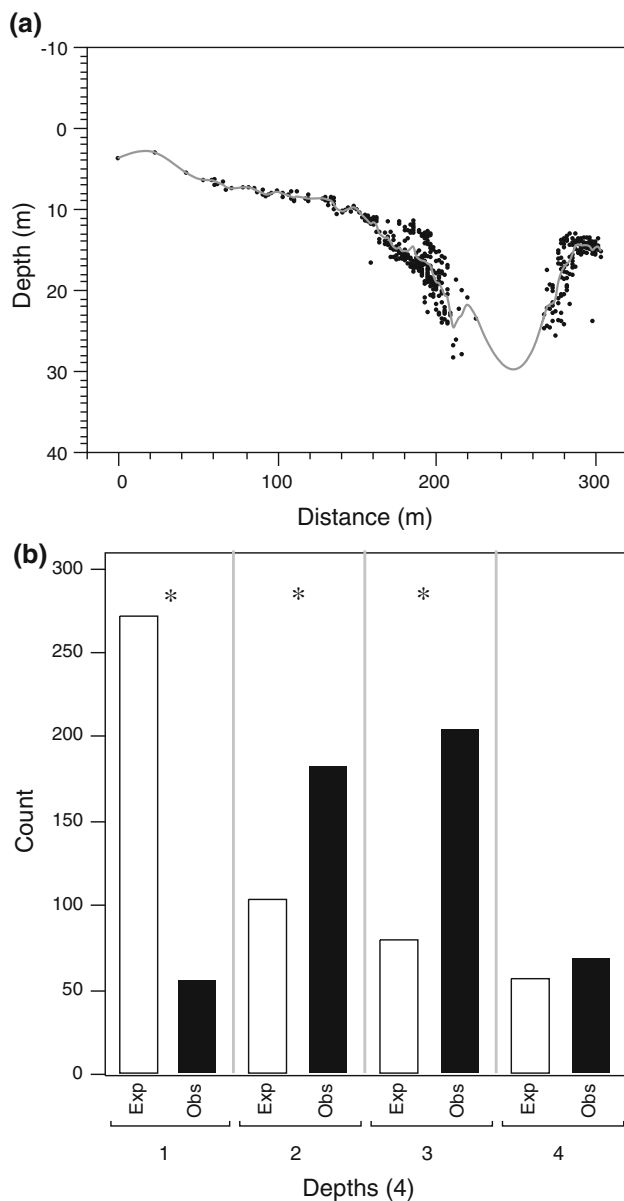


Fig. 1 **a** Distribution of sponges along the transect at Carrie Bow Cay, Belize. *Dots* represent individual sponges ($n = 509$), with a smoothing spline best fit line. Each sponge is shown at its location along the West-East transect relative to the first sponge of the transect ($x = 0$ m). **b** Expected (*white*) and observed (*black*) sponge distribution at each depth zone, with *representing a significant difference within each zone. Depth zones are divided into the following depth categories: (1) 0–10 m, (2) 10.1–15 m, (3) 15.1–20 m, (4) 20.1–30 m

depth zone using Pythagoras' theorem. We then compared the observed distribution of sponges at each depth zone to the expected distribution of sponges at each depth zone using a chi-square test for multiple classes with subsequent subdivision of the chi-square analysis (Zar 1984).

Next, we assessed the variables that influenced sponge size and morphology using analysis of variance (JMP 8.0.1). First, treating sponges as individual entities, we

used “maximum tube length” per sponge as a metric of sponge size and investigated the relationship between “depth” and “maximum tube length”. Second, using “number of tubes” as a metric of sponge morphology, we investigated the relationship between “depth” and “number of tubes”. Finally, treating tubes as individual entities, we tested the relationship between “depth” and “tube length” to know if, and how, tube size changed. In this latter analysis, “Sponge ID” was entered as a random effect to account for the lack of independence among tubes from the same sponge. Tukey–Kramer tests were used for all post-hoc comparisons (JMP 8.0.1).

Having determined sponge distribution, we tested which variables could be used to explain resident distribution and abundance patterns using a two-step approach. First, we investigated the probability of a resident occupying a sponge using logistic regression (JMP 8.0.1). Considering whole sponges as entities, we investigated the effect of the independent variables “depth”, “number of sponge tubes”, “maximum tube length” and their interactions on the dependent variable “probability of occupancy by resident(s)”. Variables were removed in a backward stepwise fashion if they did not have a significant effect ($P > 0.05$). Second, considering only the sponges occupied by residents, we investigated the predictors of the abundance of residents using analysis of covariance (JMP 8.0.1). Again, we investigated the relationship between “depth”, “number of sponge tubes”, “maximum tube length”, and their interactions on the number of residents per sponge. We used this two-step approach for two reasons: (1) to deal with the large number of zeros in our dataset; and (2) because distinct biological processes might drive presence and abundance when present. We completed similar analyses to investigate settler distribution and abundance, with the independent variable “presence or absence of residents” included as an additional predictor.

Results

Sponge distribution and morphology

The observed distribution of sponges at each depth was significantly different from the expected distribution (Chi-square test: $\chi^2 = 434$, $df = 3$, $P < 0.001$) (Fig. 1). The expected density across all zones was 0.02 sponges m^{-2} . Subsequent subdivision of the chi-square revealed that sponges were observed less often than expected by chance from 0 to 10 m (0.004 sponges m^{-2} ; $\chi^2 = 172$, $df = 1$, $P < 0.001$), more often than expected by chance from 10.1 to 15 m (0.03 sponges m^{-2} ; $\chi^2 = 61$, $df = 1$, $P < 0.001$) and 15.1–20 m (0.05 sponges m^{-2} ; $\chi^2 = 198$, $df = 1$, $P < 0.001$), and no different than expected by

chance from 20.1 to 30 m (0.02 sponges m^{-2} ; $\chi^2 = 2.57$, $df = 1$, $P > 0.05$).

At the scale of the sponge, the mean “maximum tube length” was 21.19 cm \pm 14.38 (mean \pm S.D.). “Maximum tube length” of the sponge was also related to “depth” ($r^2 = 0.08$; ANOVA: $F = 16.11$, $df = 3$, $P < 0.0001$), with sponges at greater depths generally having longer maximum tube lengths than sponges at shallower depths (Fig. 2a). Specifically, a post-hoc Tukey–Kramer test revealed that sponges at depths greater than 15 m had longer maximum tube lengths than sponges shallower than 15 m, and sponges at 10–15 m had longer maximum tube lengths than sponges at 0–10 m ($P < 0.05$).

The mean number of tubes per sponge was 1.66 ± 1.05 (mean \pm S.D.). The variable “number of tubes per sponge” was related to “depth” ($r^2 = 0.06$; ANOVA:

$F = 11.51$, $df = 3$, $P < 0.0001$), with sponges at greater depths having fewer tubes than sponges at shallower depths (Fig. 2b). A post-hoc Tukey–Kramer test showed that sponges at 0–10 m have significantly more tubes than sponges in all other depth categories ($P < 0.05$).

At the scale of the tube, the mean tube length was 18.43 cm \pm 13.94 (mean \pm S.D.). We found that “tube length” was positively related to “depth” (Fixed Effect Test: $F = 22.04$, $df = 3$, $P < 0.0001$). Consistent with the sponge-level analysis, a post-hoc Tukey HSD test revealed that individual tubes at depths greater than 15 m were significantly longer than tubes at 15 m or shallower, and tubes from 10.1 to 15 m were longer than tubes from 0 to 10 m. This model provided the strongest explanation for variation in sponge morphology ($r^2 = 0.67$). A reduced model without the random effect explained 8% of the variation in tube length, consistent with analyses at the scale of the sponge. This indicates that the majority of variation was accounted for by the random effect “Sponge ID”.

Resident distribution

The mean probability of one or more residents occupying a sponge was 0.32. The probability of occupancy was related to “depth”, “number of sponge tubes”, “maximum tube length” and the interaction between “depth” and “maximum tube length” ($r^2 = 0.36$) (Fig. 3; Table 1). The interaction indicates that the relationship between the probability of occupancy and maximum tube length varies with depth (Fig. 3a). Specifically, the initial rate of increase in the probability of occupancy with maximum tube length was much lower at depths less than 10 m than at all other depths. In addition to the interacting effects of depth and maximum tube length, the probability of resident occupancy increased with the number of sponge tubes (Fig. 3b).

Considering only occupied sponges, the mean number of residents per sponge was 1.27 ± 0.60 (mean \pm S.D.). The number of residents per sponge was related to “number of sponge tubes” ($df = 1$; $F = 59.26$; $P < 0.0001$), “maximum tube length” ($df = 1$; $F = 8.47$; $P = 0.004$), and the interaction between “number of sponge tubes” and “maximum tube length” ($df = 1$; $F = 17.48$; $P < 0.0001$) (ANCOVA: $r^2 = 0.41$). The interaction between the number of tubes and maximum tube length indicates that the effect of one sponge metric on the number of residents varies with the other sponge metric. Specifically, the effect of maximum tube length on the number of residents is small when the number of tubes is small, and vice versa. In other words, the number of residents was highest in sponges with many, large tubes.

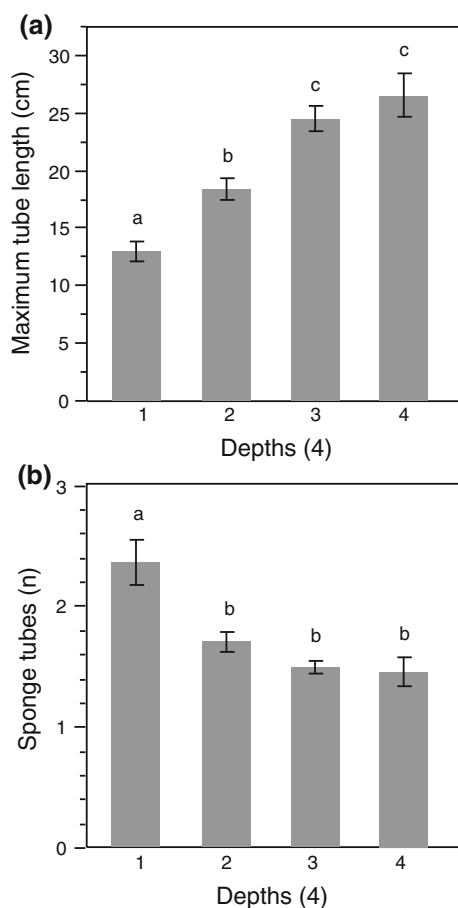


Fig. 2 Sponge size and morphology versus depth. Depth zones are divided into the following depth categories: (1) 0–10 m, (2) 10.1–15 m, (3) 15.1–20 m, (4) 20.1–30 m. Zones not connected by letters are significantly different in both panels. Gray bars represent the least squares mean estimate in each zone and vertical bars represent the standard error (S.E.) of the mean. **a** Maximum tube length per sponge at four depth categories; **b** Number of tubes per sponge at four depth categories

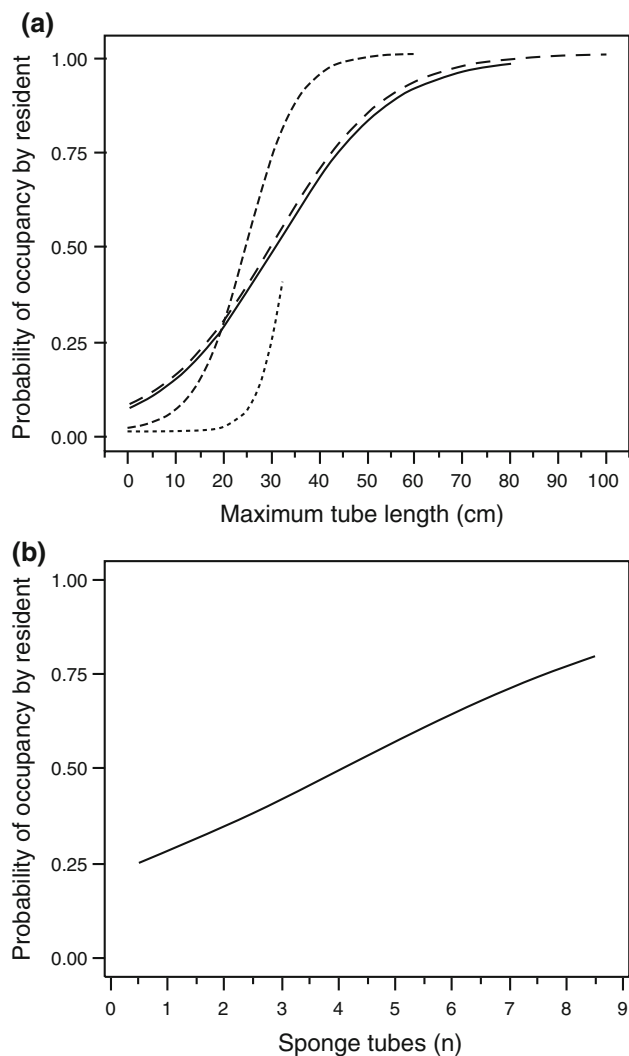


Fig. 3 Probability of residents occupying a sponge as predicted by three variables. **a** Probability of occupancy by resident is related to the interaction between maximum tube length and depth. There are four depth zones: (1) 0–10 m, *short dashed line*, (2) 10.1–15 m, *medium dashed line*, (3) 15.1–20 m, *long dashed line*, (4) 20.1–30 m, *solid line*. **b** Probability of occupancy by resident is related to the number of sponge tubes. In both **a** and **b**, *lines* represent the relationship between the probability of occupancy and independent variables estimated from the parameters of the logistic model (Table 1)

Table 1 Logistic regression of predictors of the probability of a resident occupying a sponge

Variable	df	χ^2	<i>P</i>
Depth	3	16.75	0.0008
Number of sponge tubes	1	4.53	0.003
Maximum tube length	1	16.35	<0.0001
Maximum tube length * Depth	3	13.18	0.004

Settler distribution

The mean probability of one or more settlers occurring at a sponge was 0.06. Their occurrence was related to the “number of sponge tubes” and “maximum tube length” ($r^2 = 0.45$) (Fig. 4), but not the presence or absence of residents (Table 2). The main effects indicate that the probability of settlers occurring at a sponge increased with both the number of sponge tubes and maximum tube length, with maximum tube length being a stronger predictor. Considering only settler-occupied sponges, the mean number of settlers per sponge was 1.26 ± 0.44 (mean \pm S.D.). The “number of settlers” was related to “maximum tube length”, with the number of settlers increasing with maximum tube length ($r^2 = 0.18$; ANCOVA: $df = 1$; $F = 6.32$; $P = 0.018$).

Discussion

In this study, we simultaneously consider factors influencing sponge and goby distribution on the reef around Carrie Bow Cay, Belize using a large empirical data set and multivariate analyses. Given that the goby, *E. lori*, is an obligate sponge-dweller, we also use sponge characteristics to predict fish distribution and abundance. We found the sponge *A. fistularis* to be distributed non-randomly across the reef, with sponge density peaking at intermediate depths (10–20 m). Sponge morphology also varied across the reef, and sponges tended to have fewer, but longer tubes with increasing depth. Considering only *A. fistularis* as fish habitat, fish presence also increased with depth, and fish were more common in bigger sponges with multiple tubes. There was no significant effect of conspecific fish interactions on settler distribution patterns.

Given our results, we can consider why sponge distribution and morphology might vary with depth. We found that sponges were sparsely distributed above 10 m, and sponges at these shallow depths were significantly shorter than sponges at greater depths. It is possible that this morphology, and the low density of sponges at shallow depths, can be attributed to close proximity to strong surface currents (Palumbi 1984; Wilkinson and Evans 1989; Mercado-Molina and Yoshioka 2009). Sponges were densely distributed along the reef at depths of 10–20 m. This pattern of sponge distribution, with fewer sponges shallower than 10 m and a density peak at intermediate depths, is consistent with previous research (Wilkinson and Chesire 1989; Wilkinson and Evans 1989). *A. fistularis* is usually not found below 40 m, though it has been shown to survive at up to 100 m in transplantation experiments (Maldonado and Young 1998). Sponge size also increased with depth, a pattern that has been observed in several

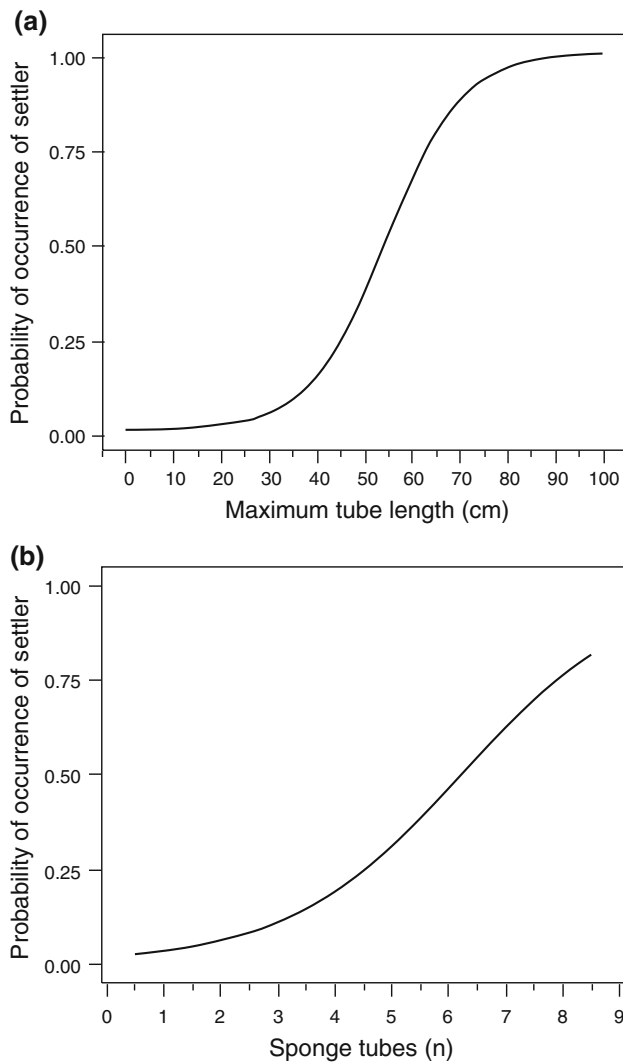


Fig. 4 Probability of settlers occurring at a sponge as predicted by two variables. **a** Probability of occurrence is related to maximum tube length, **b** Probability of occurrence is related to the number of sponge tubes. In both **a** and **b**, lines represent the relationship between the probability of occurrence and independent variables estimated from the parameters of the logistic model (Table 2)

Table 2 Logistic regression of predictors of the probability of a settler occurring at a sponge

Variable	df	χ^2	<i>P</i>
Number of sponge tubes	1	16.08	<0.0001
Maximum tube length	1	79.86	< 0.0001

species of tube sponges. Lesser (2006) found that *A. fistularis* and other tube sponges are bigger and grow faster with increasing depth up to 30 m because their primary food source, picoplankton, is more abundant. If food is more abundant at 10–20 m, and sponges are protected from near-surface turbulence, sponges may simply live longer

and grow more at these depths, which could explain the patterns we observe.

The models describing the relationship between depth and sponge metrics explained low levels of variation in our data. This was particularly true for the whole sponge-level analyses. Depth explained only 6% of the variation in number of tubes per sponge, and 8% of the variation in maximum tube length. Interestingly, the tube-level analysis was a better model in terms of explaining variance: the model explained 67% of the variation in tube length. However, most of that variation was explained by the random effect “Sponge ID”. This result is indicative of a site effect, where tubes from a single sponge were generally more similar to each other in comparison to tubes at other sponges. Tubes from a single sponge live in the same small-scale microhabitat on the reef and are likely to be close in age. They may, therefore, have a shared history of exposure to biotic and abiotic parameters such as predation and wave action (none of which we measured). Site effects may be particularly influential for long-lived organisms such as sponges and sea anemones.

Given the resident distribution results, we can hypothesize why *E. lori* have high occupancy rates and are most abundant in large, multi-tubed sponges at depths greater than 10 m. Residents were less likely to occur in sponges at depths shallower than 10 m than in sponges at all other depths. However, a closer look at the statistical interaction between depth and maximum tube length indicates that depth per se may not be limiting resident distribution. Within this shallow depth zone, the slope of the relationship between maximum tube length and the probability of resident occupancy initially increases slowly, but sharply increases when maximum tube length reaches 30 cm (Fig. 3). This suggests that it may be the lack of large sponges above 10 m (Figs. 1, 2) that explains why there are few residents found there.

Large sponges could offer fitness advantages to the fish by influencing survival and reproductive success. First, resident survival rates may be higher in large sponges if their deep oscula offer enhanced protection from predation. Second, larger tubes may offer more nutrients to *E. lori*, influencing both survival and reproductive success. Food can be a limiting resource to fish even within suitable habitat (Jones 1986; Wong et al. 2008). Larger tubes may offer more nutrients if they harbor more *H. spongicola* polychaetes, and if *E. lori* eats these polychaetes. Stomach content analyses will be needed to test this hypothesis, but analyses of closely related *Elacatinus* spp. have shown *H. spongicola* to constitute a high percentage of the gut contents (Smith and Tyler 1972; Colin 1975; Whiteman and Coté 2002). Another plausible hypothesis is that being associated with a large microhabitat enables the residents to grow large, an effect seen in other

microhabitat-associated species (Fautin 1992; Elliott and Mariscal 2001; Buston 2002). In such species, female body size can be positively correlated with the number of eggs hatched by breeding pairs (Buston and Elith 2011). If these ecological processes lead to differential survival and reproductive success, then they will lead to natural selection for pre-settlement, post-settlement, or post-recruitment preferences for large sponges.

For *E. lori*, our data suggest that settlers were most abundant on the same sponge archetype as residents (long sponges with multiple tubes). However, there was no significant relationship between the presence of residents and the distribution of settlers. Even though there is no significant effect of conspecifics on settlement, preliminary behavioral observations indicate that there may be a negative effect on recruitment into the sponge. Residents evicted settlers that were pushed into tubes, and settlers only recruited into tubes when residents were absent. Resident fish of several fish species have been documented to push settlers and/or juveniles to the edges of their microhabitat, and this has been shown to have a negative effect on recruitment (Holbrook and Schmitt 2002; Almany 2003, 2004; Buston 2003; Wong et al. 2007; Ben-Tzvi et al. 2008). Taken together, these observations suggest that although conspecific interactions might influence recruitment, they are not a strong predictor of *E. lori* settler distribution and abundance patterns.

One interesting aspect of this study system, in contrast to other systems (e.g., anemonefishes), is that the sponge habitat is not totally saturated by fish. This is all the more remarkable given that settlers remain on the outside of resident-occupied sponges, presumably exposed to predators, while there are nearby sponges with no residents. Settlers may stay at occupied sponges because the benefits of staying outweigh the costs of leaving (Emlen 1982, 1991). In this case, the chance of inheriting the tube or becoming the resident's mate outweighs the energy cost or risk of predation in searching for another suitable sponge (Buston 2004; Wong et al. 2007; Wong 2010). It has also been shown in other fishes that settlers remaining close to residents may gain protection from predators because of resident aggression toward predators (Sandin and Pacala 2005; White and Warner 2007), though the observation that residents rarely leave their tubes makes this hypothesis less plausible in *E. lori*.

Overall, these results provide a framework for understanding how different ecological factors may influence the distribution and abundance of two interacting reef species. All reef species are interconnected with members of their community, and this system provides an excellent opportunity to explore the relationship between two tightly linked reef species—a sponge goby and the tube sponge it associates with. Given the fish's strong site-attachment, this

could be a good system for marine ecological studies. Future studies will benefit from the natural history framework that this study provides, and will focus on the behavioral ecology and population ecology of these fish.

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