1 **The influence of sponge-dwelling gobies (*Elacatinus horsti*) on the**
2 **feeding efficiency of their Caribbean tube sponge (*Aplysina* sp.)**
3 **hosts**

4 **Megan J. Siemann^{1,2,3}, Aldo Turco^{2,4}, Shannon D. Brown^{2,5}, Rita B.J. Peachey^{2,6}**

5 ¹Biosciences Department, Rice University, Houston, TX USA;

6 ²CIEE Research Station, Kralendijk, Bonaire, Caribbean Netherlands;

7 ³Department of Translational Molecular Pathology, The University of Texas MD Anderson
8 Cancer Center, Houston TX USA;

9 ⁴Golder Associates, Melbourne, Australia;

10 ⁵Red Sea Research Center, King Abdullah University of Science and Technology, Thuwal,
11 Kingdom of Saudi Arabia;

12 ⁶Institute of Sustainable Technology, Kaya Grandi #77, Kralendijk, Bonaire, Caribbean
13 Netherlands

14 **Correspondence:**

15 Megan J. Siemann

16 megan.siemann@gmail.com

17 +1-713-865-6297

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19 **Abstract** Mutualistic associations between benthic marine invertebrates and reef taxa are common.
20 Sponge-dwelling gobies benefit from protection within sponge tubes and greater food
21 availability. Sponge-dwelling gobies are hypothesized to increase sponge pump rates by
22 consuming polychaete parasites, but such increases have not yet been demonstrated. We
23 investigated the association between sponge-dwelling gobies (*Elacatinus horsti*) and two
24 species of tube sponge (*Aplysina lacunosa* and *Aplysina archeri*) in Bonaire, Caribbean
25 Netherlands. We visually assessed goby presence in sponges and used *in situ* methods with
26 fluorescein dye to measure estimate feeding rates via pump rates. *Aplysina archeri* were more
27 likely to host a goby than *A. lacunosa*. For both sponge species, pump rates of tubes with
28 gobies were higher on average than those of tubes without gobies. Our observations,
29 therefore, suggest that *E. horsti* associations with *Aplysina* are likely mutualistic relationships
30 in which sponges benefit from higher feeding rates when gobies are present.

31 **Introduction**

32 Sponges are found in most marine habitats from equatorial to Arctic waters (Bell 2008). As
 33 active suspension feeders, sponges are recognized as important planktonic feeders in coral
 34 reef food webs (Lesser 2006) with the potential to alter the environment around them.
 35 Investigating the magnitude of sponge filtration and the factors which influence their
 36 filtration ability will help clarify their influence on local ecosystems. At high biomasses,
 37 sponges reduce picoplankton availability in the water column which impacts food availability
 38 to other planktivores (Savarese et al. 1997). Oysters and brittle stars have a symbiotic
 39 relationship with sponges in which the sponge benefits from increased pump rates (Hendler
 40 1984; Burns and Bingham 2002). Here we assumed that higher pump rates enable greater
 41 feeding rates. Reviews have categorized interspecific interactions of sponges as predation,
 42 competition, or utilization of sponges as microhabitat (Wulff 2006; Bell 2008). For instance,
 43 invertebrates and fish dwell inside sponge microhabitats (Wulff 2006; Bell 2008).

44 Gobies associated with sponges include free-swimming gobies and obligate sponge-
 45 dwelling gobies, such as yellowline goby (*Elacatinus horsti*) (Tyler and Böhlke 1972; Colin
 46 1975; D'Aloia et al. 2011). Some cleaner gobies spend time in sponges but are not considered
 47 sponge-dwelling (Whiteman and Côté 2002). *Elacatinus horsti* occupy convoluted barrel
 48 sponges (*Aplysina lacunosa*) and stove-pipe sponges (*Aplysina archeri*), two species of tube
 49 sponge found in the Caribbean (Villamizar and Laughlin 1991). Both *A. archeri* and *A.*
 50 *lacunosa* grow in clumps of tubes with individual tubes reaching maximum lengths of 180
 51 cm and 90 cm, respectively (Humann and DeLoach 1992).

52 While many organisms have been documented inhabiting sponges (Tyler and Böhlke
 53 1972; Villamizar and Laughlin 1991; Meroz and Ilan 1995; Bell 2008; D'Aloia et al. 2011),
 54 little is known regarding the effects of the inhabitants on the sheltering sponge. Hendler
 55 (1984) found that sponges benefit from resident brittle stars that clear sediment from their

56 tubes. The relationship between sponge-dwelling gobies and their sponge hosts was originally
57 described as obligate commensalism with gobies benefitting from the shelter (Böhlke and
58 Robins 1969; Majoris et al. 2018). Other research has recognized sponge-dwelling
59 invertebrates as an additional benefit to *Elacatinus* goby sp.. Colin (1975) concluded that *E.*
60 *horsti* were eating parasitic polychaetes because sponge tissue was found in the gut content of
61 *E. horsti*.

62 Furthermore, it has been proposed that sponges with sponge-dwelling gobies benefit from
63 lower parasite loads (Whiteman and Côté 2002; D'Aloia et al. 2011), which may increase
64 sponge feeding efficiency. However, directly measuring a sponges' feeding efficiency *in situ*
65 is considered difficult (Yahel et al. 2005). Therefore, in numerous studies, the pump rate has
66 been considered a proxy for feeding efficiency on the assumption that the more water a
67 sponge can pump, the more food can be filtered (Gerrodette and Flechsig 1979; Hendler
68 1984; Savarese et al. 1997). The pump rate of a species is also affected by the size of sponges
69 and depth, which must be considered potential sources of variation (Lesser 2006; McMurray
70 et al. 2014), and therefore, accounted for in studies on the filtration rates of sponge.

71 In this study, we quantified the effect of *E. horsti* gobies on *Aplysina* sponges using pump
72 rate as a proxy for feeding rate. We predicted that tubes of *Aplysina lacunosa* and *Aplysina*
73 *archeri* containing *E. horsti* gobies would have a higher pump rates (i.e., greater feeding
74 efficiency).

75 **Methods**

76 **Study site**

77 We conducted this study from September - October 2017 at Playa Lechi dive site
78 (12°09'36.6"N, 68°16'55.1"W) on the leeward side of the island of Bonaire, Caribbean
79 Netherlands. The study area is characterized by a reef slope starting at 5 m depth which
80 continues until ~35 m deep where it flattens to sandy substrate. While *A. archeri* and *A.*

81 *lacunosa* are found in depths of 3-45 m (Villamizar and Laughlin 1991), on SCUBA, we
82 conducted this study between 5-15 m deep to limit depth-dependent effects on pump rate
83 (Bell 2008). Short study duration and daytime dive times were chosen to limit seasonal and
84 daily temporal cycles in sponge pump rates (Morganti et al. 2019).

85 **Investigation of sponge abundance and symbiont presence**

86 We performed 50 m transects at 10 m depth to investigate the abundance of both *Aplysina*
87 species and the frequency of *E. horsti*. Only presence and absence information was recorded
88 for the gobies. To limit the effect of the divers, a 3-min acclimation period was allotted after
89 laying the transect.

90 **Measuring pump rate**

91 *In situ methods*

92 We randomly selected *A. archeri* and *A. lacunosa* and checked tubes for *E. horsti*. At each
93 sponge, we measured tube length and pump rate on the most landward tube with *E. horsti*
94 and, where possible, the most landward tube without *E. horsti*. We measured pump rates
95 following the approach of Gerrodette and Flechsig (1979). We taped a flexible, clear tube (1
96 cm diameter) with scale marks to a hole in a 700 ml resealable, plastic bag. Then, we secured
97 the bag to the sponge osculum using rubber bands. One diver injected 2 ml of 100 mg L⁻¹
98 fluorescein dyed seawater (Yahel et al. 2005) through a hole near the base of the tube, while
99 the other stabilized the tube and filmed dye movement at 30 frames s⁻¹. For each sponge tube,
100 we released dye three times then removed the bag.

101 *Video processing*

102 We used linear regressions to calculate the velocity of the dye front on a fixed 2D plane
103 based on scale marks on the tube and frame rate (Tracker 4.11.0 software) and used the tube's
104 cross-section area to convert these to pump rates.

105 **Statistical analysis**

We performed separate repeated measures (multiple measurements per tube) ANCOVAs for each species of sponge to determine whether pump rate depended on the presence of *E. horsti* (categorical predictor) and tube length (continuous predictor). *Elacatinus horsti* presence was treated as a binary variable as only 3 of 72 tubes tested for pump rate contained more than one *E. horsti*. We used a z-test (two-tail) to test for differences between the proportions of tubes containing *E. horsti* for the two species of sponge.

Results and discussion

Mutualistic symbiosis

Pump rates of both sponge species increased when *E. horsti* were present (*A. lacunosa*: $F_{1,32}=10.56$, $p=0.0027$, $+2.35 \text{ cm}^3 \text{ s}^{-1}$; *A. archeri*: $F_{1,34}=8.39$, $p=0.0458$, $+1.78 \text{ cm}^3 \text{ s}^{-1}$; Fig. 1). The significantly higher pump rates of tubes with *E. horsti* supported the hypothesis of a conferred feeding benefit to sponges. In nature, the symbiosis is thought to be obligatory for the sponge-dwelling goby that is dependent on the sponge for both food and shelter (Colin 1975; Whiteman and Côté 2004a; D'Aloia et al. 2011). *Elacatinus horsti* benefit from the interaction through nutrition supplied from eating parasites that feed on sponge tissue plus gobies are readily attacked by predators when disturbed from their sponge tubes or held in open, experimental tanks (Colin 1975). Nevertheless, it may also be that gobies choose tubes with higher pump rates, a possibility that would require experimental introductions or removals of gobies to test. Our results are consistent with a benefit to the sponge and, therefore, a mutually beneficial symbiosis.

We did not explicitly test parasite reduction as a potential mechanism driving the difference in pump rates. But other studies have shown that parasitic polychaetes, which live inside sponge tissue and consume choanocytes, have a negative impact on the sponge (Magnino and Gaino 1998). Colin (1975) found that *E. horsti* consume *Haplosyllis* sp., but this conclusion was based on gut content analysis of a small number of fish. In addition, the

relationship between *Haplosyllis* sp. and the pump rate of a sponge remains poorly understood (Lattig and Martin 2011). To fully understand the interaction among gobies, sponges, and polychaetes, it is important to examine the relationship between parasite loads and the pump rate of sponges.

The clearing of sediment or algae from sponge tissue has also been suggested as the mechanism of pump rate increases in invertebrate-sponge symbioses because the feeding ability of a sponge decreases when sediment covers their collar cells (Gerrodette and Flechsig 1979; Burns and Bingham 2002). Decreases in pumping rate due to increased sediment has been documented for *A. lacunosa* sponges (Gerrodette and Flechsig 1979). It is possible that *E. horsti* movement and feeding clears sediment from sponge choanocytes in a relationship similar to one seen between brittle-stars and sponges (Hendler 1984). Regardless of the underlying mechanism, we found that goby presence is associated with an improved pumping efficiency which likely increases the feeding ability of the host sponge. These results may apply to other sponge species that host microhabitat dwellers (Tyler and Böhlke 1972; Villamizar and Laughlin 1991; Bell 2008) and is likely to apply to other sponge-dwelling *Elacatinus* sp. with similar biological and ecological traits.

Interspecific differences

We found that pump rates increased with tube length for *A. archeri* ($F_{1,34}=24.26$, $p<0.0001$, slope: $0.097 \text{ cm}^2 \text{ s}^{-1}$) but did not depend on tube length for *A. lacunosa* ($F_{1,32}=0.09$, $p=0.7664$; Fig 1). Other studies have shown that the pump rates of sponges are higher for longer tubes (Lesser 2006). The pump rates we found here are comparable to those reported previously for sponges of similar size (Gerrodette and Flechsig 1979; Morganti et al. 2019). The underlying differences between the sponge species, such as the bumpy outer surface seen in *A. lacunosa* versus the smoother textured *A. archeri* tube, may be the cause of our observed lack of correlation between tube lengths and pump rate in *A. lacunosa* (Villamizar and Laughlin

1991). To more clearly understand the effect of tube length on pumping, other factors affecting interspecific differences need to be examined.

Aplysina archeri tubes were more likely to have an *E. horsti* present than were *A. lacunosa* tubes ($z=3.32$, $p<0.001$; Fig. 2). In other southern Caribbean reefs, Villamizar and Laughlin (1991) found a lower frequency of *E. horsti* in *A. lacunosa* tubes compared to *A. archeri* tubes. Differential settlement patterns and persistent recruitment between sponge species and sizes has been recorded for another sponge-dwelling goby species, *Elacatinus lori* (Majoris et al. 2018). The study conducted by Majoris et al. (2018) indicated that habitat preferences in sponge-dwelling gobies are persistent between generations and geographical area, and there is likely a genetic basis for settlement preference. Little is known about the movement of sponge-dwelling gobies post-recruitment (Majoris et al. 2018). Habitat qualities such as food availability and parasite density may influence the settlement of gobies; however, parasite density has not been measured between sponge species or size classes (D'Aloia et al. 2011). Such habitat preferences have been shown for sponge-dwelling cleaning gobies that preferentially maintain territories on barrel sponges with higher parasite densities (Whiteman and Côté 2004b). The movement of these gobies is critical for understanding the relationships between sponges and gobies.

Applications to monitoring reef health

As active suspension-feeders, sponges can impact overall nutrient availability in the water column and, in turn, impact reef health overall (Lesser 2006). As such, sponge health should be considered when evaluating reef health and plans for monitoring reefs. With the relationship between *E. horsti* and *Aplysina* sp. resulting in greater pump rate, goby presence may be an indicator of sponge health. The availability of sponge microhabitat can also provide insights into sponge-dwelling goby distributions and goby population health (D'Aloia et al. 2011; Majoris et al. 2018). Taking into account these interspecific

relationships can help to make reef monitoring more comprehensive (Bell et al. 2017). With current climate trends, accounting for factors that may impact the competitive relationship between corals and sponges may also help scientists to understand and predict future shifts towards or away from sponge-dominated reefs (Bell et al. 2017, 2018).

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Data availability

All data are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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Figure legends

- Fig. 1** The dependence of average pump rate on tube length and goby presence for a) *Aplysina lacunosa* and b) *Aplysina archeri*. Black symbols and lines indicate a sponge tube with a *Elacatinus horsti*. Gray symbols and lines indicate a sponge tube with no *E. horsti*.
- Fig. 2** The percent of *Aplysina lacunosa* (n = 226) and *Aplysina archeri* (n = 85) sponge tubes with *Elacatinus horsti* (black bar) or no *E. horsti* (gray bar).

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