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

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Keywords: *Aplysina, Elacatinus,* mutualism, yellowline goby

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

Introduction

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

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

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

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

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

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

Methods

Study site

We conducted this study from September - October 2017 at Playa Lechi dive site (12°09'36.6"N, 68°16'55.1"W) on the leeward side of the island of Bonaire, Caribbean Netherlands. The study area is characterized by a reef slope starting at 5 m depth which 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**

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

112 Results and discussion

113 Mutualistic symbiosis

114 Pump rates of both sponge species increased when *E. horsti* were present (*A. lacunosa*:
115 $F_{1,32}$=10.56, p=0.0027, +2.35 $cm^3 s^{-1}$; *A. archeri*: $F_{1,34}$=8.39, p=0.0458, +1.78 $cm^3 s^{-1}$; Fig. 1).
116 The significantly higher pump rates of tubes with *E. horsti* supported the hypothesis of a
117 conferred feeding benefit to sponges. In nature, the symbiosis is thought to be obligatory for
118 the sponge-dwelling goby that is dependent on the sponge for both food and shelter (Colin
119 1975; Whiteman and Côté 2004a; D'Aloia et al. 2011). *Elacatinus horsti* benefit from the
120 interaction through nutrition supplied from eating parasites that feed on sponge tissue plus
121 gobies are readily attacked by predators when disturbed from their sponge tubes or held in
122 open, experimental tanks (Colin 1975). Nevertheless, it may also be that gobies choose tubes
123 with higher pump rates, a possibility that would require experimental introductions or
124 removals of gobies to test. Our results are consistent with a benefit to the sponge and,
125 therefore, a mutually beneficial symbiosis.

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

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

135 The clearing of sediment or algae from sponge tissue has also been suggested as the
136 mechanism of pump rate increases in invertebrate-sponge symbioses because the feeding
137 ability of a sponge decreases when sediment covers their collar cells (Gerrodette and Flechsig
138 1979; Burns and Bingham 2002). Decreases in pumping rate due to increased sediment has
139 been documented for *A. lacunosa* sponges (Gerrodette and Flechsig 1979). It is possible that
140 *E. horsti* movement and feeding clears sediment from sponge choanocytes in a relationship
141 similar to one seen between brittle-stars and sponges (Hendler 1984). Regardless of the
142 underlying mechanism, we found that goby presence is associated with an improved pumping
143 efficiency which likely increases the feeding ability of the host sponge. These results may
144 apply to other sponge species that host microhabitat dwellers (Tyler and Böhlke 1972;
145 Villamizar and Laughlin 1991; Bell 2008) and is likely to apply to other sponge-dwelling
146 *Elacatinus* sp. with similar biological and ecological traits.

147 **Interspecific differences**

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

156 1991). To more clearly understand the effect of tube length on pumping, other factors
157 affecting interspecific differences need to be examined.
158 *Aplysina archeri* tubes were more likely to have an *E. horsti* present than were *A.*
159 *lacunosa* tubes ($z=3.32$, $p<0.001$; Fig. 2). In other southern Caribbean reefs, Villamizar and
160 Laughlin (1991) found a lower frequency of *E. horsti* in *A. lacunosa* tubes compared to *A.*
161 *archeri* tubes. Differential settlement patterns and persistent recruitment between sponge
162 species and sizes has been recorded for another sponge-dwelling goby species, *Elacatinus*
163 *lori* (Majoris et al. 2018). The study conducted by Majoris et al. (2018) indicated that habitat
164 preferences in sponge-dwelling gobies are persistent between generations and geographical
165 area, and there is likely a genetic basis for settlement preference. Little is known about the
166 movement of sponge-dwelling gobies post-recruitment (Majoris et al. 2018). Habitat qualities
167 such as food availability and parasite density may influence the settlement of gobies;
168 however, parasite density has not been measured between sponge species or size classes
169 (D'Aloia et al. 2011). Such habitat preferences have been shown for sponge-dwelling
170 cleaning gobies that preferentially maintain territories on barrel sponges with higher parasite
171 densities (Whiteman and Côté 2004b). The movement of these gobies is critical for
172 understanding the relationships between sponges and gobies.

173 **Applications to monitoring reef health**

174 As active suspension-feeders, sponges can impact overall nutrient availability in the water
175 column and, in turn, impact reef health overall (Lesser 2006). As such, sponge health should
176 be considered when evaluating reef health and plans for monitoring reefs. With the
177 relationship between *E. horsti* and *Aplysina* sp. resulting in greater pump rate, goby presence
178 may be an indicator of sponge health. The availability of sponge microhabitat can also
179 provide insights into sponge-dwelling goby distributions and goby population health
180 (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).

Acknowledgements

We would like to thank the Council on International Educational Exchange (CIEE) Research Station Bonaire for support; CIEE station staff and students for dive support and helpful comments; and E. Siemann for statistical advice and comments on this manuscript.

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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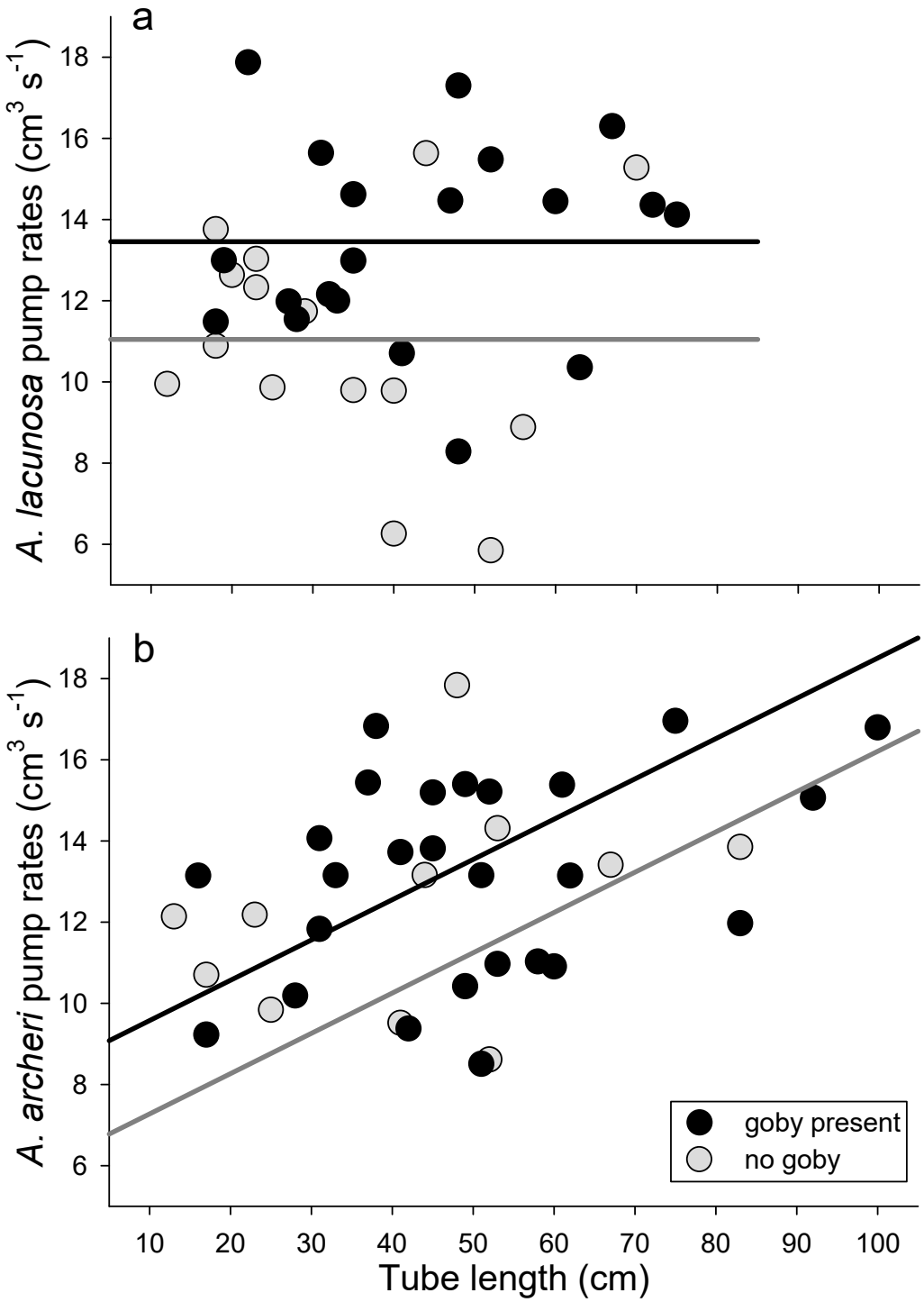
Figure legends

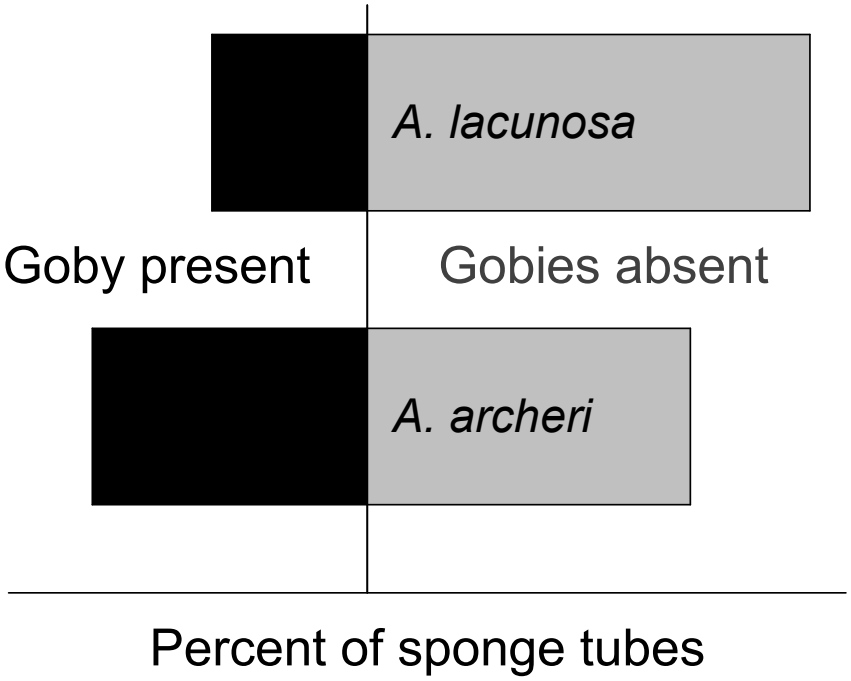
Fig. 1 The dependence of average pump rate on tube length and goby presence for a) *Aplysina lacunosa* and b) *Aplysina archeri*. Black symbols and lines indicate a sponge tube with a *Elacatinus horsti* . Gray symbols and lines indicate a sponge tube with no *E. horsti*.

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).


a
A. lacunosa pump rates (cm3 s-1)
18
16
14
12
10
8
6
b
A. archeri pump rates (cm3 s-1)
18
16
14
12
10
8
6
goby present
no goby
10
20
30
40
50
60
70
80
90
100
Tube length (cm)

261

262


A. lacunosa
Goby present
Gobies absent
A. archeri
Percent of sponge tubes

263