

ORIGINAL ARTICLE

Collaboration among sponge species increases sponge diversity and abundance in a seagrass meadow

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Abstract

Caribbean sponge species typical of coral reefs are generally inhibited from living in seagrass meadows by their vulnerability to predation by the large starfish *Oreaster reticulatus* (Linnaeus 1758). Although readily consumed by *Oreaster*, the conspicuous coral reef sponge species *Lissodendoryx colombiensis* Zea & van Soest, 1986 has expanded its habitat distribution to include a seagrass (*Thalassia testudinum* Banks ex König, 1805) meadow in Belize, where individuals grow to volumes of nearly 7 l. By simple observation, *L. colombiensis* appears to be an inferior competitor in this system, because portions of many individuals are overgrown by seagrass sponge species. However, experimentally clustering seagrass sponges around *L. colombiensis* individuals deterred starfish from feeding on them, suggesting an advantage to being overgrown. Sizes of individual *L. colombiensis* can fluctuate widely over short time intervals, reflecting both a relatively fast growth rate and the high rate at which starfish consume this species. At the population level these fluctuations are not evident, as losses of *L. colombiensis* due to *Oreaster* are balanced by a combination of efficient recruitment, rapid regeneration and growth, and protection of portions of many individuals by the overgrowth of seagrass sponge species that are unpalatable to *Oreaster*. In turn, the seagrass sponges acquire stable perches on *L. colombiensis* individuals in this sediment-dominated habitat. Community ecology theory relating to diversity patterns in sessile organisms has focused on competition between space-requiring neighbors as the underlying process that inevitably decreases diversity unless curtailed. Sponges, with their propensity for engaging in beneficial interactions with neighbors, demand expansion of the theory to acknowledge how collaboration can increase abundance and species diversity within a community.

Problem

Sponges stand out among sessile marine animals in the great variety of collaborative associations in which they participate. When intimately associated organisms represent taxa with very different characteristics, the ways in which they might benefit each other are readily apparent. For example, non-sponge partners can provide mobility (e.g. decorator crabs, Stachowicz & Hay 2000), solid stable substratum (e.g. clams, Marin & Belluga 2005; man-

grove roots, Ellison *et al.* 1996), skeletal reinforcement (e.g. macroalgae, Rützler 1990; Carballo & Ávila 2004), or food (e.g. zooxanthellae, Rosell & Uriz 1992) for sponges, while the unusual chemistry and flexible morphology of sponges enable them to provide protective coverings or homes (review in Wulff 2006b). How an intimate association can be mutually beneficial is less clear when both participants are sponges. In particular, associations that involve overgrowth of one sponge by another, blocking water intake surfaces of these efficient filter feeders, seem

as if they should have negative consequences. Still, many sponges thrive when overgrown by heterospecific sponges, and it has long been known (Rützler 1970; Sarà 1970) that overgrowth may not indicate competitive dominance when observed among sponges. Although in a few cases (e.g. Rützler 1965; Sutherland 1980; Thacker *et al.* 1998; Wulff 2005), sponges have been shown to eliminate heterospecific sponge neighbors by overgrowing them, in the majority of reports of intimate associations of sponges, mutual benefit has been suggested or demonstrated by stability of associations, lack of evidence of harm to overgrown sponges, and increases in growth and survival of participating sponges (e.g. Rützler 1970; Sarà 1970; Sim 1997; Wulff 1997a; Wilcox *et al.* 2002).

The possibility that collaborative associations among neighbors may be important in space-limited systems has not been integrated into the theory of community ecology (e.g. Agrawal *et al.* 2007). Underlying many key theories aiming to explain diversity patterns is the demonstration that unchecked competition among space-requiring neighbors can decrease diversity, whereas predators or disturbances that prevent competitively superior species from dominating can increase diversity (e.g. Tansley & Adamson 1925; Paine 1966). Suggestions that beneficial interactions may be particularly important in stressful or marginal habitats (e.g. Bertness & Callaway 1994) still cast competition as the default interaction. Although sponges are often neglected because they are difficult to study, they can be the most diverse and abundant space-occupying organisms in many marine solid substratum habitats, and play many key functional roles (e.g. Diaz & Rützler 2001; Wulff 2001; Rützler 2004). Their propensity for collaborating with neighbors suggests that the potentially very different consequences for community structure and dynamics of collaborative, rather than competitive, associations should be taken seriously in a comprehensive theory of community ecology.

Very high regional diversity of tropical marine sponges reflects the combined species diversity of distinctive sponge faunas within each of a variety of habitats (e.g. Alcolado 1994; Zea 1994, 2001; Reed & Pomponi 1997; Hooper *et al.* 2002). Full understanding thus depends on our identifying processes influencing species diversity within each habitat, as well as processes enforcing low overlap in species among habitats. Low overlap between the sets of sponge species that live on Caribbean coral reefs and those that live in adjacent seagrass meadows is maintained, at least in part, by the ability of the large starfish *Oreaster reticulatus* (Linnaeus 1758) to consume typical reef sponges (Wulff 1995). *Oreaster* are generally confined to seagrass meadows, where the typical sponge inhabitants are well defended against them (11/14 seagrass and rubble bed sponge species rejected in

experiments, *versus* only 3/20 coral reef sponge species rejected; Wulff 1995). Thus typical coral reef sponges are inhibited from extending their habitat distributions into seagrass meadows by their vulnerability to *Oreaster*, which can quickly eliminate them if they are washed into seagrass meadows in a storm or placed there by a curious biologist (Wulff 1995).

In a seagrass (*Thalassia testudinum* Banks ex König, 1805) meadow in Belize, several sponge species live in clusters, often associated with small patches of hard substrata that frequently also include the scleractinian coral *Porites furcata* Lamarck, 1816. Closer inspection of these clusters reveals that in many cases the sponge species *Lissodendoryx colombiensis* Zea & van Soest, 1986 is overgrown by all the others (Fig. 1). *Lissodendoryx colombiensis*, which has a massive, and exceptionally cavernous, overall morphology, is also distinguished by being the only sponge species in the studied seagrass meadow that is not typically a member of the seagrass associated fauna. It was described from Colombian coral reefs (Zea & van Soest 1986) and its habitat was described as 'Patch reef and lagoonal environments in waters with less than 6-m depth...It grows in sand and coral rubble, on dead lateral parts of massive corals, and between branches of ramose and foliose corals'. *Lissodendoryx colombiensis* can also be found on mangrove prop roots at sites where mangroves are closely associated with reefs in Bocas del Toro, Panama, and in the Pelican Cays, Belize (J. L. Wulff, personal observation; Rützler *et al.* 2000).

One possible explanation of the apparently anomalous distribution of *L. colombiensis* in a seagrass meadow is that the specimens from there are members of a different species that is not palatable to *Oreaster*. Sponges in this same seagrass meadow that appeared to be *Tedania ignis* (Duchassaing & Michelotti, 1864), a mangrove root-inhabiting sponge that is readily consumed by *Oreaster*, turned out instead to represent a previously undescribed *Oreaster*-resistant species, *Tedania klausii* (Wulff, 2006). Another possibility is that the *L. colombiensis* population inhabiting this seagrass meadow is ephemeral, perhaps established during a low ebb in the starfish population and now being eliminated by predation. Overgrowth of many *L. colombiensis* individuals by more typical seagrass sponge species could reflect its position at the bottom of a competitive hierarchy, with other sponges harming it as they use it to perch themselves above the sediment. Alternatively, the net result of overgrowth by species that are not palatable to starfish could be beneficial to *L. colombiensis*. I used a combination of (i) manipulative experiments investigating predator consumption and sediment burial as mortality agents; (ii) measurements of growth, recruitment and mortality; and (iii) monitoring population structure and dynamics by repeat censusing, to



Fig. 1. *Lissodendoryx colombiensis* at Twin Cays, Belize, partially overgrown by the seagrass meadow sponges A: *Clathria schoenus*, B: *Chondrilla caribensis* forma *caribensis*, with only 'snorkels' of the *L. colombiensis* exposed, C: *Clathria* sp. (saturated dark orange/red), D: *Chondrilla caribensis* forma *caribensis*, E: *Tedania klausii*; F: *Amphimedon erina*; G: The starfish *Oreaster reticulatus* attempting to consume *L. colombiensis* that is protected inside a mesh cage; H: a healed feeding scar, 5 days after an *Oreaster* consumed this portion of the sponge; I: denuded skeleton, directly after an *Oreaster* meal; J: *Oreaster* in the midst of feeding.

distinguish among possible explanations of this apparent habitat distribution puzzle.

Methods

Lissodendoryx colombiensis population dynamics, growth, recruitment, mortality

Abundance of *Lissodendoryx colombiensis* in a seagrass (*Thalassia testudinum*) meadow on the east side of the mouth of the main channel at Twin Cays, Belize, was evaluated within a representative 10 × 10 m area, 2.5 m deep, in June 2005. The exact location was chosen

primarily to make use of underwater landmarks that could be used to accurately re-establish boundaries of the censused area in case corner markers and transect lines were removed. All *L. colombiensis* individuals were measured by snorkeling. Volume was chosen as the most meaningful measure of size, and external linear measurements were made for later conversion into volume estimates using appropriate conglomerations of geometric solids. The degree to which sponges of other species, as well as other organisms, were growing over individuals of *L. colombiensis* was recorded as percent of the surface covered or perimeter surrounded for all individuals inside and within 3 m of the outside perimeter of the censused

area. The census was repeated 21 months later (March 2007). Shorter term population dynamics were evaluated by repeating the census once more in June 2007. Individual sponges were mapped to allow calculation of increases or decreases in their volumes that occurred during these monitoring periods.

Small pieces (5–19 cm³) of *L. colombiensis* were cut and protected in cages until cut edges healed, and then affixed to pieces of clean coral rubble that were stabilized using stainless steel wires (details in Wulff 1991). These individuals were either placed inside small cages (n = 12) or adjacent to the cages but exposed (n = 17). Survival and growth were evaluated at intervals of 2–6 months for 1 year. Cages provided protection only from predators larger than the meshes of the caging material, which were 1 × 1.3 cm.

Recruitment was assessed by deploying five small mounds of sun-dried coral rubble in the seagrass meadow. Rubble pieces were held together by narrow (1 mm) beaded cable ties, resulting in mounds approximately 20 × 20 cm in footprint and 12 cm high, which were each anchored in the sediment with a single 20-cm-long stainless steel wire stake.

Scars on *L. colombiensis* individuals resulting from recent feeding by *Oreaster reticulatus* (i.e. spicule skeleton from which tissue had been digested) were measured in three dimensions to roughly estimate the volume of tissue consumed using formulas for appropriate geometric solids, in most cases a spherical segment [$V = \pi h^2 (r - h/3)$]. Feeding scars were monitored daily to determine how quickly evidence of feeding was effaced by sloughing of dead areas and surface regeneration.

Comparisons of tolerance to burial in sediment were made among the seven most common large-bodied sponge species in this seagrass meadow: *L. colombiensis*, *Tedania klausii* Wulff, 2006, *Clathria schoenus* (de Laubenfels, 1936), *Clathria* sp. (saturated dark orange/red), *Hyrtilios proteus* Duchassaing & Michelotti, 1864, *Amphimedon erina* (de Laubenfels, 1936) and *Chondrilla caribensis* forma *caribensis* Rützler *et al.*, 2007. A total of eight small (12–40 cm³) pieces of each species were cut and attached to clean pieces of dead coral rubble (*Porites furcata*) with narrow cable ties. Each sponge was placed in a small depression made in the sediment, with the rubble on top. Their condition was evaluated after 24 and 48 h, and then they were left uncovered with the sponge on top of the rubble for 48 h in an attempt to mimic natural cycles of burial and unburial caused by bioturbation.

Oreaster reticulatus abundance, unmanipulated feeding, prey choice experiments

Within the 100 m² area in which *L. colombiensis* was censused, all *O. reticulatus* were measured (mean of two radii,

i.e. center of mouth to arm tips) on 28 census days scattered over 4.5 years. During most of the censuses, the food being ingested by any starfish individual with its stomach everted was recorded. All feeding observations fit into one of the following categories: filamentous algae on sediment or solid carbonate, filamentous algae on seagrass or macroalgae, *L. colombiensis* tissues, other sponge tissues.

In the field, individual *O. reticulatus* were enclosed in cages (30 × 35 × 15 cm high, with meshes 5 × 7 cm) with pieces of sponges affixed to the plastic bottom with small cable ties (method details in Wulff 1995). Sponge pieces (generally 10–20 cm³) were allowed to heal for 2 days before they were used in trials, in order for cut surfaces to reconstitute themselves. Although *L. colombiensis* from a coral reef had been previously tested (Wulff 1995), seagrass specimens were tested because of the possibility that they represented a different species or subspecies that is starfish-resistant. Three seagrass sponge species that were not previously tested were included: *Hyrtilios proteus*, *Clathria* sp., and *Tedania klausii*. For each 24-h trial, live pieces of sponges of five different species (including species from other habitats) were used. Starfish can consume all five sponge pieces within 24 h if all represent palatable species (Wulff 1995), and thus sponges remaining alive are not unconsumed due to lack of time for feeding or to starfish satiation.

To determine whether sponges of species that are consistently rejected by *O. reticulatus* could inhibit starfish from feeding on *L. colombiensis*, the smorgasbord prey-offering technique was modified for 20 trials. Pieces of *L. colombiensis* were attached alone in cage corners diagonal from each other, and in the other two cage corners, pieces of *L. colombiensis* were surrounded by four pieces of other species (*Clathria* sp., *A. erina*, *T. klausii*, and *C. schoenus*) that are commonly found growing over or around the edges of *L. colombiensis* in the seagrass meadow. This row of typical seagrass meadow sponge species was between 0.8 and 1.3 cm high, a trivial physical barrier for large starfish (arm lengths 9–15 cm) capable of moving rapidly in this topographically complex (on a vertical scale up to 25 cm) habitat. A starfish was placed in each cage for 24 h.

Results

Lissodendoryx colombiensis population dynamics, growth, recruitment, mortality

The population of *L. colombiensis* was very similar in the first two censuses, nearly 2 years apart. Size ranges of individuals in June 2005 and March 2007 were respectively 72–6919 cm³ and 4–5861 cm³; total numbers of individuals were 31 and 24; and total volume was 23 834 and 24 694 cm³. Size frequencies of the individuals

differed somewhat (Fig. 2A and B), but are not statistically distinguishable (G-test, $P > 0.1$, with size categories of 0–500, 500–1000, >1000). In both years, the smallest size class (0–500 cm³) has the most representatives. Only two sponges under 100 cm³ were found per census, but this may be an underestimate as they were difficult to see without overturning every piece of coral rubble.

The results of the June 2007 census, only 3 months after the second census (Fig. 2C), reveal this population to be more dynamic than the similarity of the above numbers suggests, although again the size frequency distributions were not statistically distinguishable from those in March 2007 (G-test, $P > 0.1$). Total volume had dropped to 20 645 cm³. The number of individuals was the same (24), but two of the individuals present 3 months earlier were missing entirely, and one large

sponge had been split into three separate individuals. Only one-third of the individuals present in March 2007 gained in size during the 3 months. Size changes of individuals ranged from losses of 90.6% to gains of 116%, and one-third of the individuals either gained or lost more than 80% of their volume (Fig. 3). Extra careful searching at all locations where sponges had been recorded in March 2007 revealed three cryptic individuals under 100 cm³ that were greatly diminished (by 42%, 91%, and 67%) relative to their sizes 3 months earlier.

Overgrowth of the surface or perimeter by other sponges was observed on 70% (28/40) of *L. colombiensis* individuals within and near the censused area. Also overgrowing portions of, or embedded within, *L. colombiensis* were small *Porites furcata* coral colonies, and dense clumps of the green algae *Halimeda opuntia* (Linnaeus) Lamouroux, 1812 and *Dictyosphaeria cavernosa* (Forsskal) Boergesen, 1932. The degree to which the perimeters or surfaces were covered ranged from 5–90%, and the covering sponge species (in decreasing order of cover) were *Chondrilla caribensis* forma *caribensis*, *Clathria schoenus*, *Tedania klausii*, *Clathria* sp., *Amphimedon erina*, *Hyrtios proteus*, *Dysidea etheria* de Laubenfels, 1936, and *Cliona varians* (Duchassaing & Michelotti 1864).

All 12 caged *L. colombiensis* individuals survived, but only two of the 17 exposed individuals survived until 6 months later (significantly different survival by the G-test, $P < 0.001$; Fig. 4). The two survivors had decreased in size to only 2.6 and 6.6 cm³, and were entirely hidden under the rubble on which they were growing, with only small 'snorkels' sticking up around the edges. Neither of these individuals survived to the end of the year. Some of the uncaged individuals were consumed by *Oreaster* within a few days. Specific growth rates of the caged individuals varied from 1.1 to 6.8 in 6 months, with a mean of 3.8 (SE = 1.11); and a mean

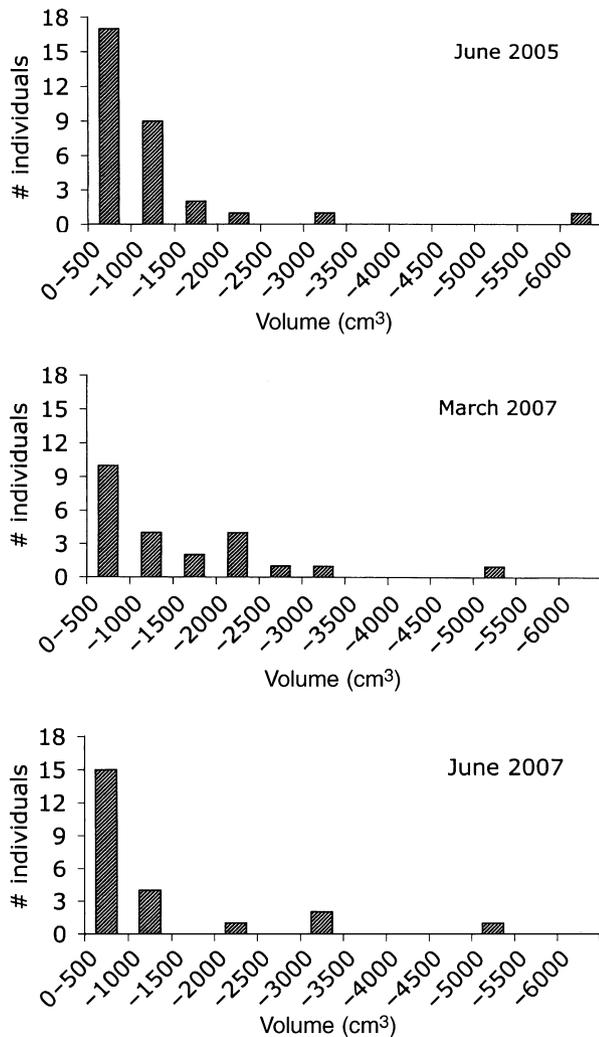


Fig. 2. Size frequency distributions of individuals of *Lissodendoryx colombiensis* in a 10 × 10 m area in a seagrass meadow at Twin Cays, Belize, for three census dates.

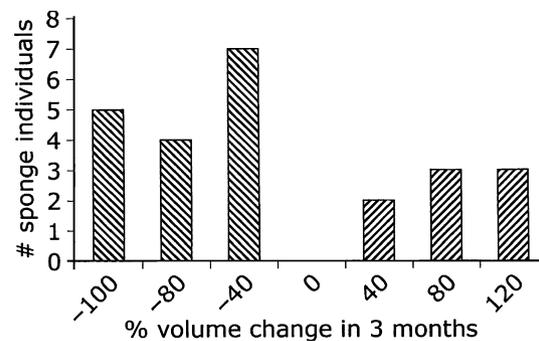


Fig. 3. Number of individuals of *Lissodendoryx colombiensis*, in a 100-m² censused area, that increased or decreased in volume by percentages ranging from –100% to +120% during the 3-month period March 2007–June 2007.

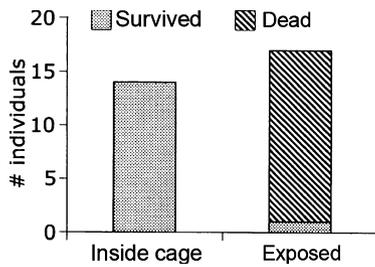


Fig. 4. Survival over 6 months of small *Lissodendoryx colombiensis* individuals that were attached to stakes and placed inside small cages or adjacent to, but outside, the cages in a seagrass meadow at Twin Cays, Belize.

specific growth of 6.9 (SE = 0.84) in 1 year (Fig. 5). After 6 months, portions of most of the caged individuals had grown close enough to the cage walls for *Oreaster* to feed on them by clambering onto the cages and everting their stomachs through the meshes (Fig. 1G), so subsequent size changes inside the cages reflected partial predation as well as growth.

After 1 year, four small *L. colombiensis* individuals (with volumes in cm³ of 0.1, 0.9, 1.1, and 1.3) were found on the five small mounds of sundried rubble. These constituted 27% of the recruits by larvae of the common large-bodied sponge species in this habitat (*i.e.* *L. colombiensis*, *Clathria* sp., *C. schoenus*, *Tedania klausii*) that were found on these recruitment structures. Excluded from this count were one *C. schoenus* recruit that appeared to be by asexual propagation because it was too large (10.9 cm³) to have grown from a larva when first recorded, and all 13 *Chondrilla caribensis* forma *caribensis* because of the propensity of species of this genus for asexual propagation (*e.g.* Milanese *et al.* 2003; Zilberberg *et al.* 2006) and the difficulty of distinguishing recruits that might have been from larvae.

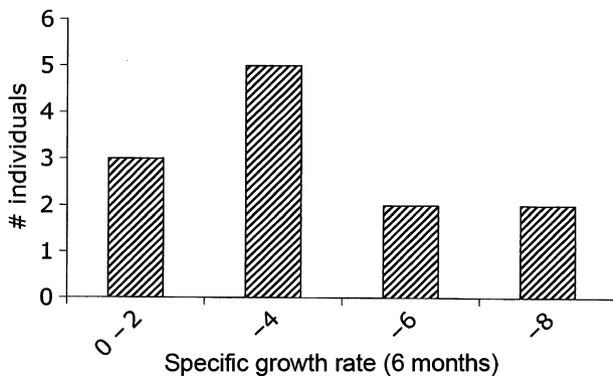


Fig. 5. Frequency distribution of specific growth rates (*i.e.* increase in volume/initial volume) over 6 months for 12 *Lissodendoryx colombiensis* individuals grown inside cages.

Scars from starfish feeding were evident at nearly every starfish census, with a mean of 3.2 scars (SE = 0.4, n = 28 starfish censuses) per census within the 100 m² area. The sponges reconstituted a surface below the portion from which live cells were digested, and the denuded spicule skeleton disintegrated within 4 days after starfish feeding (Fig. 1H and I). Therefore feeding scars on which initial volume of live tissue could be measured indicated feeding within the previous few days. The mean size of these feeding scars (Fig. 6) was 75.2 cm³ (SE = 8.6, n = 28 scars measured). In only six cases (of 90 scars observed) more than one recent feeding scar (*i.e.* the denuded spicule skeleton had not yet disintegrated) was observed on the same sponge individual.

Results of sediment burial experiments were not always consistent among replicates, in part because sediment shifting by mobile organisms buried some sponges deeply and uncovered others. One result was uniform: all eight *Chondrilla* individuals became mushy within the first 24 h, and had completely disintegrated 3 days later. Between 25% and 80% of the tissue was macerated from all replicates of the dense-tissued poecilosclerids in *C. schoenus* and *Clathria* sp., and *Tedania klausii*. How the remaining three species, *L. colombiensis*, *Amphimedon erina*, and *Hyrtios proteus*, fared depended on how deeply they became buried by shifting sediment. Shallow burials resulted in sealing of surface perforations followed by complete recovery; but deep burials caused discoloration followed by death in *A. erina*, and maceration in the other two species.

***Oreaster reticulatus* abundance, unmanipulated feeding, prey choice experiments**

The mean number of starfish in 28 censuses within the 100 m² was 8.9 (SE = 1.83). Starfish ranged in radius from 92 to 150 mm (mean = 121 mm). Combining observations from all censuses, a total of 61% of the starfish were feeding when picked up to be measured, and most of the feeding starfish (80%) were feeding on

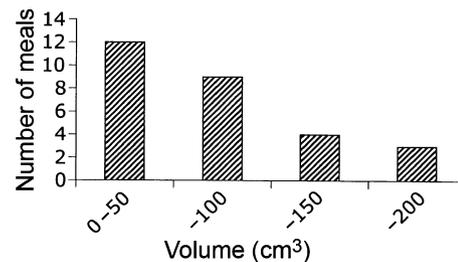


Fig. 6. Frequency distribution of volumes of 28 feeding scars caused by *Oreaster reticulatus* digesting the tissue of *Lissodendoryx colombiensis* from its skeleton.

microalgae, nearly always filamentous epiphytes on the seagrass, *Thalassie testudinum*, the calcium-reinforced green alga *Halimeda*, or other macroalgae among the seagrasses. *Oreaster* were feeding on *L. colombiensis* in 12.5% of the observations, and on seagrass sponges in 4.5%. Except for three cases (two starfish feeding on *Tedania klausii* and one on *Clathria* sp.) the other sponges on which feeding was observed were not the conspicuous seagrass species, but small and/or cryptic, e.g. *Oceanapia peltata* (Schmidt, 1870), which lives partly buried in sediment, or *Mycale (Aegagropila) americana* van Soest, 1984, which in the seagrass lives under rubble or entangled within *Halimeda* clumps. In 3% of the observations, starfish were feeding on sponges from other habitats that had been transplanted into the seagrass meadow inside cages [e.g. the reef sponges *Mycale laevis* (Carter, 1882), *Callyspongia vaginalis* (Lamarck, 1814), *Iotrochota birotulata* (Higgin, 1877), and *Aplysina fulva* (Pallas, 1766)] and subsequently grew too close to, or through, the edges of their cages.

During 24-h trials within cages in the field, starfish consistently rejected two of the seagrass species, *Hyrtios proteus* and *Clathria* sp., and nearly always rejected *Tedania klausii*. By contrast, they always consumed *L. colombiensis*. This pattern of rejection of seagrass species and consumption of *L. colombiensis* was indistinguishable from previous results from San Blas, Panama, in which starfish generally ate reef species but rejected seagrass species, some of which also inhabit this seagrass meadow in Belize (Fig. 7; Wulff 1995).

When *Oreaster* were given an explicit choice of pieces of *L. colombiensis* alone versus surrounded by pieces

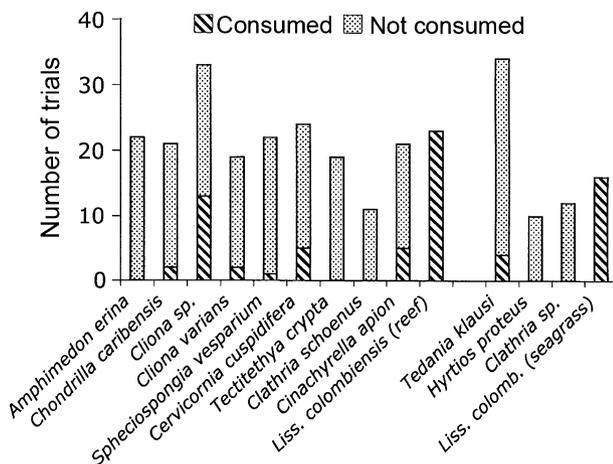


Fig. 7. Number of trials in which a variety of seagrass meadow/rubble flat sponge species and *Lissodendoryx colombiensis* were consumed or rejected by *Oreaster reticulatus* in prey choice trials in the field. Data for the first 10 species along the x-axis, provided for comparison, are from Wulff (1995); and the data for *Tedania klausii* were also presented in Wulff (2006c).

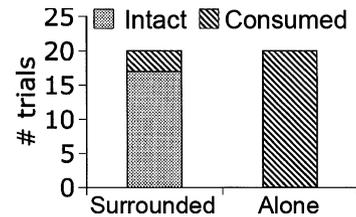


Fig. 8. Number of trials in which *Lissodendoryx colombiensis* was consumed or rejected by *Oreaster reticulatus* when it was offered alone versus surrounded by pieces of the seagrass meadow sponge species *Tedania klausii*, *Clathria schoenus*, *Clathria* sp., and *Amphimedon erina*.

of the typical seagrass sponge species, they consumed *L. colombiensis* when it was presented alone in every trial, but only three times (of 20 trials) crawled over the barrier of other species to consume it (Fig. 8).

Discussion

Extending habitat distribution into enemy territory

A conservative estimate of the mean amount of sponge tissue consumed by starfish each day in this 100 m² area can be made from the mean feeding scar volume multiplied by the mean number of recent, or in progress, meals at each census, divided by 4 (the number of days over which the spicule skeleton remained visible once the tissue had been digested from it). The result, 59.8 cm³ per day, produces an estimate of 21 820 cm³ per year – very close to the total standing volume of *L. colombiensis* within the censused area. Field trips were not evenly distributed throughout the year (most were in March, June, December), so if there are seasonal differences in sponge-feeding by starfish these might have been missed. But even if this is an overestimate of the amount consumed, *L. colombiensis* and *O. reticulatus* clearly play significant roles for each other in this seagrass meadow. Sizes of *Oreaster* differed among eight seagrass meadows in San Blas, Panama, with larger individuals at sites where episodic access to reef sponges (i.e. when storms washed them off the reef) was more likely (Wulff 1995), possibly reflecting the superior quality of sponges over their usual microalgal diet that was demonstrated experimentally by Scheibling (1979). Sizes of *Oreaster* at this Belize site (mean radius 121 mm) were at the larger end of the ranges reported from Panama (overall mean in San Blas, Panama, was 117.8 mm, and for the three sites with reef sponge access means were 120.7, 122.7, and 123.7 mm), but comparisons with other Belize populations are required to determine whether feeding on *L. colombiensis* influences starfish sizes there. The starfish fed on other sponge species, but most were cryptic, with volumes of

less than 5 cm³ each, making their contribution to starfish diets small in comparison with a 75-cm³ meal on *L. colombiensis*. Reef sponges that were consumed when they grew close to their cage edges were only present as experimental transplants, and could not have persisted in this seagrass meadow outside of cages.

That experimentally demonstrated differences in starfish consumption of reef and seagrass sponges have direct consequences for habitat distribution, was confirmed by observations in San Blas, Panama, of *Oreaster* consuming 33/60 individuals of three common reef sponge species (*Iotrochota birotulata*, *Aplysina fulva*, and *Callyspongia vaginalis*) within 5 days of their experimental placement in the seagrass, and 22/51 individuals of these same species between the 3rd and 4th week after a hurricane washed them into the seagrass (Wulff 1995). Vulnerability of reef-dwelling *L. colombiensis* to *Oreaster* predation was also confirmed by observations in San Blas, where the starfish were inhibited from scaling the reef to consume the reef sponges by parrotfishes biting their spines. When all the parrotfish were abruptly eliminated, the most conspicuous early indication that *Oreaster* were no longer discouraged from being on the reef was that they rapidly consumed two large *L. colombiensis* that had served as underwater landmarks for years.

The very similar total volume of *L. colombiensis* in censuses of June 2005 and March 2007 indicate that this seagrass meadow population is holding its own in spite of losses to predation that appear to equal the total standing volume in the course of a year. High rates of partial mortality due to *Oreaster* suggest that every sponge individual may have gone through several cycles of loss to meals, regeneration, and regrowth during the 21 months between censuses, and this is confirmed by the huge changes in size measured for the majority of individuals in the 3 months between March and June 2007. Starfish meal volumes of 42–84 cm³ indicate that small *L. colombiensis* are at risk of annihilation in a single feeding episode, although cryptic remnants of two of the 17 small individuals placed outside of cages demonstrate that partial survival is possible. More very small remnants from starfish meals might have been found during censusing if all pieces of hard substrata had been overturned, but that was deemed too disruptive of the habitat.

Whether this seagrass meadow *L. colombiensis* population replenishes itself or larvae travel from a coral reef population is unknown. The nearest known reef population is in the Blue Ground Range, 4 km away. Whatever the source of larvae, efficient recruitment is demonstrated by finding four successful *L. colombiensis* recruits, among a total of 15 recruits of large-bodied sponge species, on recruitment assessment structures with a combined total area of only 1/5 m² that had been deployed 1 year earlier.

The recruitment structures had to be picked up, turned over, and examined closely to see and identify the very small sponges on them, so it is likely that similarly small and cryptically located recruits were missed during the censusing of the 10 × 10 m area.

Rapid growth and efficient recruitment certainly help to prevent this population of *L. colombiensis* from succumbing to *Oreaster* predation, but they are not sufficient to explain how the large sponge individuals avoid being completely consumed. The possibility that large *L. colombiensis* have genotypes conferring lower palatability is not supported. Recent feeding scars, or starfish in the midst of feeding, were observed on most of the large individuals; and eight of the 10 individuals larger than 500 cm³ suffered partial mortality between March and June 2007. The relative rarity of *L. colombiensis* individuals with more than one feeding scar suggests the possibility of inducible defenses in this sponge species. However, this pattern may also reflect *Oreaster* behavior with very large prey, as *Oreaster* individuals were also observed to move away after they had digested a single circular area of tissue, on the rare occasions in which they fed on large massive corals in a seagrass meadow in San Blas (Wulff 1995). If induced defenses are present, they are not quickly effective, or perhaps only some individuals are capable of this response. A few times starfish were observed consuming different portions of a large sponge on successive days; and up to three feeding scars, each at a different stage of recovery, were observed on an individual sponge. Overgrowth of portions of *L. colombiensis* individuals by unpalatable sponges may be the most effective way by which they evade complete elimination by starfish feeding. As in the experiments, starfish avoided portions of *L. colombiensis* individuals that were covered or surrounded by unpalatable sponges. Thus, in this example, associations among sponge species aid the overgrown species in extending its habitat distribution into enemy territory.

Sponge epizootic associations

Overgrowth, and other forms of intimate association among sponges, can be specific interactions between only two species (de Laubenfels 1947; Sim 1997; Thacker *et al.* 1998; Wilcox *et al.* 2002; Cruz-Barraza & Carballo 2006), or a more general community-wide phenomenon (Rützler 1970; Sarà 1970; Wulff 1997a; Schaft & Mebs 2002). Likewise, overgrowing or being overgrown by another sponge appears to be an obligate condition for some species (*e.g.* Sarà 1970; Wilcox *et al.* 2002; Cruz-Barraza & Carballo 2006), whereas other species engage in intimate associations facultatively (*e.g.* Rützler 1970; Sarà 1970; Wulff 1997a). Curiously, although obligate interactions tend also

to be specific, the specificity of an interaction does not predict the net result – *i.e.* if it is beneficial or antagonistic.

One pattern in sponge epizooism is that overgrown species tend to have morphological attributes that are consistent with coping gracefully with being overgrown. Microscopic examination of sections through the interface between adherent sponges revealed gaps between the overgrowing and underlying sponges in studies by Rützler (1970) and Wilcox *et al.* (2002). Sponges in the Order Astrophorida, characterized by a densely spiculed cortex, often serve as overgrown species. It may not be coincidental that members of at least one astrophorid genus (*Geodia*) are also particularly palatable to a variety of vertebrate predators (*e.g.* Meylan 1990; Dunlap & Pawlik 1996, 1998; van Dam & Diez 1997; Wulff 1997b,c; León & Bjørndal 2002; Wilcox *et al.* 2002).

Lissodendoryx colombiensis lacks an armored cortex, but does have other characteristics that may help it thrive when overgrown. It stands out among seagrass meadow and coral reef sponges in being riddled with wide canals. In their original description, Zea & van Soest (1986) remarked that it is 'extremely cavernous' and measured channels from 260 μm to 1 cm in diameter. It is also able to build tubes of a few mm to over 1 cm in diameter, and up to several cm in length, which it uses as 'snorkels' for water circulation when covered by sponges or living within rubble or corals (Fig. 1). The use of oscular tubes to gain access to the water column, although entirely overgrown, was also previously demonstrated by Rützler (1970; illustrated in his Fig. 9) for the Adriatic species *Spongia virgultosa* Schmidt, 1868. On coral reefs *L. colombiensis* is not covered with other organisms, but it often grows tucked into crevices or between branches of corals; and on mangrove roots in the Pelican Cays (Rützler *et al.* 2000) it is often covered by an encrusting sponge species. The cavernous interior and ability to form oscular tubes, or 'snorkels', that help *L. colombiensis* thrive while overgrown may also help it to cope with sediment. The sediment burial experiments indicated that *L. colombiensis* is among the species in this seagrass meadow that are least likely to perish by chance burial, adding to its attractiveness as a stable perch for other sponges in this sediment-dominated habitat.

Collaboration between sponge species for substratum space and protection from predators has been reported before. In Florida Keys seagrass meadows, Wilcox *et al.* (2002) studied a common (0.075–0.91 individuals per m^2) two-sponge association in which the overgrown species belongs to the particularly palatable genus *Geodia*. Dynamics of growth, recruitment, or mortality were not measured, but at two of their sites, the authors found that 3% and 10% of the internal sponges had been damaged

by predators. In some cases almost all that remained after predation was the outer 'rind' of the overgrowing haplosclerid species (Wilcox *et al.* 2002; Fig. 5). This example differs from *L. colombiensis* in that it is specific, always involving the same pair of species; and it is obligate, with neither of the species found alone in the seagrass meadows. A recent report of another haplosclerid species that has only been found living epizoically on *Geodia media* Bowerbank, 1873 in the Mexican tropical eastern Pacific (Cruz-Barraza & Carballo 2006) underscores the prevalence of epizoic associations among sponges. These are not rare oddities, but can constitute significant proportions of the biomass and species diversity in marine hard bottom habitats. The collaboration-mediated presence of *L. colombiensis* in the Belize seagrass meadow adds 200 cm^3 of sponge volume per m^2 directly; and by increasing attachment space for the other sponge species, it may indirectly increase sponge volume far more.

Sponges and community ecology theory

Competition for substratum space among sessile organisms has played a key role in the development of community ecology theory aiming to explain species diversity patterns. Ideas falling under the heading 'compensatory mortality' focus attention on processes that disproportionately decrease space occupation by competitively dominant species, increasing diversity by making space available for other species (Tansley & Adamson 1925; Paine 1966). The extension of these ideas known as the 'intermediate disturbance hypothesis' points out that diversity is low not only when a competitively dominant species is able to usurp space, but also when disturbance is so intense or frequent that it defeats the ability of most species to hold space (*e.g.* Connell 1978). These ideas have provided insight on diversity patterns in some sponge-dominated systems. For example, very high sponge diversity on mangrove roots in one set of cays in Belize may reflect preferential consumption of rapidly growing species by spongivorous fishes, whereas lower diversity in another mangrove cay reflects the success of superior spatial competitors (Wulff 2005). The first explicit report of highest diversity at intermediate disturbance levels, 13 years before the 'intermediate disturbance hypothesis' was named, featured Adriatic sponges (Rützler 1965). Low diversity on small cobbles reflected high disturbance rates, while low diversity on stable substrata reflected dominance of superior spatial competitors. Moderate rates of disturbance on medium cobbles ensured space for the highest diversity of sponge species (Rützler 1965).

Sponges have also played a prominent role in demonstrating that competition is not necessarily the default

interaction between neighbors that have common requirements for space (reviews in Sarà 1970; Wilcox *et al.* 2002; Rützler 2004; Wulff 2006b). Facultative, non-specific, positive interactions allow more species to co-exist and may also influence community stability, in the sense of resistance to change. Sarà (1970) pointed out the intriguing pattern that diversity of sponges, in a community in which many individuals were growing over each other, increased with density. By following all the sponges within a defined area month by month throughout a year, he documented high stability of the individuals making up this community, although the actual space covered by each individual was somewhat fluid, with individuals increasing and decreasing in size and altering the exact space occupied. Rützler (1970) likewise pointed out the enhanced diversity of communities in which space limitation is solved by epizoisism instead of competitive elimination. The Adriatic cave community he studied was stable in composition over 6 years of observations, with no successional sequence of different sponge species (Rützler 1970). Similarly, in a small area on a coral reef from which 20 of the original 39 sponge species vanished during a 14-year period (Wulff 2006a), the three species that maintained the highest abundance were those for which intimate associations had been demonstrated to be mutually beneficial (Wulff 1997a).

Early in the study of diversity patterns, Hutchinson (1961) included mutually beneficial interactions among his suggestions for explaining paradoxically high phytoplankton diversity in a general guiding statement about processes influencing diversity; but most ecologists chose to focus instead on competition. Collaborative phenomena may result in relationships between diversity and stability that are different from those predicted, and demonstrated, for communities in which competitive relationships dominate assembly. The next important step will be to discover what aspects of a system determine whether competitive or collaborative interactions dominate dynamics. As functionally important, abundant, and diverse inhabitants of marine hard bottom ecosystems, which also have a knack for collaboration, sponges will be ideal subjects with which to pick up this lost thread of community ecology.

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