

Ecological interactions of marine sponges¹

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Abstract: Sponges interact with most other organisms in marine systems as competitors, symbionts, hosts of symbionts, consumers, and prey. Considerable creative energy has been required to study and describe the amazing variety of sponge interactions, as sponges can hide symbionts deep inside, rapidly regenerate wounds from grazers, carry on important associations with unculturable microscopic organisms, and otherwise foil attempts to determine how they are interacting with other organisms. This review of sponge interactions covers (i) competition among sponge species, and between sponges and other sessile organisms; (ii) predation on sponges by sponge specialists and by opportunistic sponge feeders, and aspects of predation such as the importance of nutritional quality, trade-offs between growth and defense against predators, biogeographic patterns in predation, and the advantages of various techniques for studying predation; and (iii) symbiotic associations of sponges with a variety of organisms representing all types of life, and with results ranging from parasitism and disease to mutual benefit. A hint that some generalizations about ecological interactions of sponges may be possible is just becoming evident, as accumulating data appear to show taxonomic and geographic patterns; however, it is also clear that surprises will continue to emerge from every probing new study.

Résumé : Les éponges réagissent à la plupart des autres organismes des systèmes marins, en tant que compétiteurs, symbiotes, hôtes de symbiotes, consommateurs et proies. L'étude et la description de la remarquable variété d'interactions chez les éponges a nécessité beaucoup d'énergie créative, car les éponges peuvent cacher leurs symbiotes profondément en elles-mêmes, régénérer rapidement les blessures faites par les brouteurs, établir des associations importantes avec des organismes microscopiques impossibles à cultiver et, de diverses manières, contrecarrer les tentatives pour déterminer comment elles interagissent avec les autres organismes. La présente rétrospective des interactions des éponges inclut (i) la compétition entre les espèces d'éponges et entre les éponges et les autres organismes sessiles, (ii) la prédation sur les éponges par les prédateurs spécialisés et par les espèces opportunistes qui les consomment, de même que divers aspects de la prédation, tels que l'importance de la qualité de la nourriture, les compromis entre la croissance et la défense contre les prédateurs, les patrons biogéographiques de la prédation et les avantages des diverses techniques utilisées pour étudier la prédation et finalement (iii) les associations symbiotiques entre les éponges et une variété d'organismes représentant tous les types de vie qui mènent à une gamme de relations allant du parasitisme et de la maladie au bénéfice mutuel. Il commence à y avoir des indications qu'il sera possible de faire des généralisations sur les interactions écologiques des éponges, puisque les données accumulées semblent montrer des patrons taxonomiques et géographiques; cependant, il est aussi évident qu'il y aura des surprises qui émaneront de toute nouvelle étude inquisitrice.

[Traduit par la Rédaction]

Introduction

Sponges are challenging subjects for ecological interaction sleuths. A sponge individual, defined as all sponge material within a continuous pinacoderm (Hartman and Reiswig 1973), is in many ways an aggregation of imperma-

nently specialized, and somewhat independent, cells that are all of the same genotype and capable of coordinated action. These cells, able to change form and function as needed, are also adept at reaggregation following dissociation of the sponge (e.g., Wilson 1907), and sponges "endure mutilation better than any known animal" (de Laubenfels 1949, p. 221). Thus regeneration and remodeling after partial mortality, or to accommodate symbionts, plays a more extreme role in ecology of sponges than it does for any other organisms. Interpretation of one-time observations is hampered by this ability of sponges to quickly heal partial mortality caused by predators, disease, competitors, or abiotic hazards; and to mold their shape to their circumstances, even to the point of receding under unfavorable conditions. Once sponge cells die, most sponges quickly disintegrate and vanish; leaving no telltale skeletons, bones, or shells, like those left behind when animals of most other taxa die. Leaps forward in our

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understanding of interactions of sponges with other organisms, and among sponges of different species, have therefore depended on time-series observations of individuals and communities, controlled experimental manipulations in the field, and combinations of field and laboratory work that elucidate cellular- and molecular-level mechanisms.

That sponges are not only particularly difficult subjects for all aspects of biology, including ecology, but are also particularly intriguing for many of the same reasons, was pointed out by Bergquist (1978) in her book *Sponges*, and also in her keynote address to the sponge scientists of the world in Amsterdam, the Netherlands (Bergquist 1994): “The apparent plasticity and simplicity of sponge organization led to Porifera being ‘sidelined’ for a long time as a group worthy of serious study. They were viewed as odd, difficult, etc. However, these very features have necessitated that students of sponge biology take an integrative view and draw on techniques from many disciplines in order to make progress. This has positioned sponge workers well to make discoveries with impact far beyond sponge systems.” In a keynote address to the same group, in Rapallo, Italy, Rützler (2004) pointed out further that “Conservationists and resource managers throughout the world continue to overlook the important role of sponges in reef ecology. This neglect persists for three primary reasons: sponges remain an enigmatic group, because they are difficult to identify and to maintain under laboratory conditions; the few scientists working with the group are highly specialized and have not yet produced authoritative, well-illustrated field manuals for large geographic areas; even studies at particular sites have yet to reach comprehensive levels.” The many key functional roles played by sponges in marine ecosystems provide great impetus for ecologists to overcome the difficulties presented by sponges: “Owing to their high diversity, large biomass, complex physiology and chemistry, and long evolutionary history, sponges (and their endo-symbionts) play a key role in a host of ecological processes: space competition, habitat provision, predation, chemical defense, primary production, nutrient cycling, nitrification, food chains, bioerosion, mineralization, and cementation” (Rützler 2004).

Undeterred by the sponges, a stalwart company of sponge ecologists scattered all over the world have learned an enormous amount; far too much for justice to be done by a short review. Consequently, this contribution is focused only on ecological interactions of sponges. Other aspects of ecology of marine sponges (i.e., ecological aspects of growth and regeneration, factors influencing distribution and abundance, population structure and dynamics, community structure and dynamics, and functional roles of sponges in marine ecosystems) are sidelined for the moment. Also outcompeted for space in these pages is an important class of ecological interactions — sponges and their food — which are well considered in papers by Reiswig (1973, 1974), Pile (1997, 1999), and Vacelet and Boury-Esnault (1995). All aspects of the ecology of coral reef sponges are covered in a detailed recent review by Rützler (2004); and reviews by Hartman (1977), Rützler (1978), Wilkinson (1983a), Diaz and Rützler (2001), and Wulff (2001) focus on the functional roles of sponges in coral reefs and the importance of choice of study technique in sponge ecology.

Interactions of sponges with organisms of other taxa, and

with sponges of other species, are organized for the following review into 3 sections: (1) competition, (2) predation, and (3) symbiotic associations. Symbiotic associations, in which individuals of two or more species are intimately associated by being adherent to each other or by a host-guest relationship, can range from mutually beneficial, to commensal, to parasitic or pathogenic. These are considered together because often it is not known exactly how an association affects the participating species.

Competition

Competition among sponge species

Elimination by competition has only rarely been demonstrated among sponge species. The few examples involve either great disproportion in size or growth rate of neighboring individuals, very specific chemical mediation, or limited suitable substratum (e.g., mangrove root-dwelling sponges, carbonate-excavating sponges). Hartman (1957) suggested that specificity of substrate shown by nine sympatric species of Adriatic boring sponges reflected competition. Reiswig (1973) observed adult reef sponges overgrowing recent recruits, and Sutherland (1980) reported the common mangrove sponge *Tedania ignis* (Duchassaing and Michelotti, 1864) overgrowing other species on recruitment panels suspended among mangroves. Reef sponges transplanted to mangrove roots were eliminated by overgrowth, most frequently by the three most rapidly growing mangrove species (Figs. 1a, 1b), including *T. ignis* (Wulff 2005). Lack of evidence of chemical warfare and a positive correlation between growth and survival of six of the most common species typical of Caribbean mangrove roots suggest that competitive ranking among sponges of the same growth form in this system is determined by growth rate. Relative growth rates may also play a role in community structure in the Antarctic, where the very rapidly growing *Mycale (Oxymycale) acerata* Kirkpatrick, 1907 might overwhelm sponges of other species if it were not consumed preferentially by a spongivorous starfish (Dayton 1979). Pulling apart partially overgrown sponges revealed that in some cases the basal portions appeared to have been absorbed by the dominant *M. (O.) acerata*.

Chemistry, rather than relative growth rate, has been demonstrated to mediate a specific pairwise interaction on coral reefs in Guam, allowing *Dysidea* Johnston, 1842 to overgrow *Cacospongia* Schmidt, 1862 (Thacker et al. 1998). Likewise, a pattern of negative association with other sponges in the few centimetres adjacent to the borders of *Crambe crambe* (Schmidt, 1862) individuals implicate allelochemicals in allowing this encrusting Mediterranean species to inhibit growth of neighboring sponges (Turon et al. 1996). The great importance of the specific techniques chosen for studying sponge interactions is well illustrated by this study, as the authors point out that simply recording neighbors that were touching would have missed the ability of *C. crambe* to influence neighbors at a distance (Turon et al. 1996).

In contrast to this handful of specific examples of one sponge species outcompeting another, many examples of individuals of one sponge species growing over, or adhering to, another have been suggested or demonstrated to be beneficial to both species (e.g., Rützler 1970; Sarà 1970; Sim

Fig. 1. Caribbean examples of ecological interactions of sponges (photographs by J.L. Wulff, except *j*, which is by T.D. Swain and is reproduced with permission). The sole manipulations of the images (all originals are 35 mm slides, scanned, and manipulated in Adobe Photoshop® CS version 8) were cropping from the edges so that only the relevant portions are included, and removal of suspended particles in some of the backgrounds. (a) A small piece of a branch of the typical coral reef sponge *Amphimedon compressa* attached to a mangrove root with a cable tie and (b) the same piece of *A. compressa* 7 months later as it is overgrown by the faster growing typical mangrove root species *Tedania ignis*. (c) Neighboring individuals of *Iotrochota birotulata* and *A. compressa* grow faster and survive better when they adhere to each other. (d) Mangrove roots covered by typical mangrove sponge species such as *Tedania ignis* and *Haliclona (Reniera) implexiformis* grow more rapidly than bare roots, and *H. (R.) implexiformis* grows more rapidly on mangrove roots than it does on a PVC pipe at the same site (Ellison et al. 1996). (e) The starfish *Oreaster reticulatus* consuming the sponge *Lissodendoryx colombiensis* Zea and van Soest, 1986 by everting its stomach on the sponge and digesting the living cells, leaving behind the skeleton of silica and spongin. (f) *Aplysina cauliformis* (transplanted from a coral reef to a mangrove root) beginning to heal wounds left by feeding of the spotted trunkfish, *Lactophrys bicaudalis* (L., 1758). Mangrove sponges of many species, as well as an individual of the reef sponge *Callyspongia vaginalis* that was transplanted from the reef to the mangrove, were growing within 20 cm of this sponge, but were not eaten by the trunkfish. (g) Camouflage among blades of *Thalassia testudinum* does not appear to have inspired this decorator crab's choice of the seagrass meadow dwelling sponge *Clathria* sp. for covering its carapace. (h) The last living portion of a large *A. compressa* individual that had lost most of its live tissue to disease, apparently caused by pathogens. (i) The margins of the scleractinian coral *Montastraea annularis* have grown around the large osculum of *Mycale laevis* living on its undersurface. (j) The colonial zoanthid *Parazoanthus parasiticus* (which hosts zooxanthellae) embedded in the surface of the sponge *Niphates erecta* Duchassaing and Michelotti, 1864. (k) The branching red alga *Jania adherens* appears to serve as the skeleton of the sponge *Dysidea jania*. (l) The excavating sponge *Cliona varians*, which hosts zooxanthellae.

1997; Wulff 1997a; Wilcox et al. 2002; Fig. 1c). In some cases, sponges of many species are mutually adherent (e.g., Sarà 1970; Rützler 1970; Wulff 1997a), and species that tend to be overgrown are morphologically suited to thrive while serving as substratum (e.g., Rützler 1970). These associations, in which competition is not the primary interaction, are described in a subsequent section on symbioses among sponges.

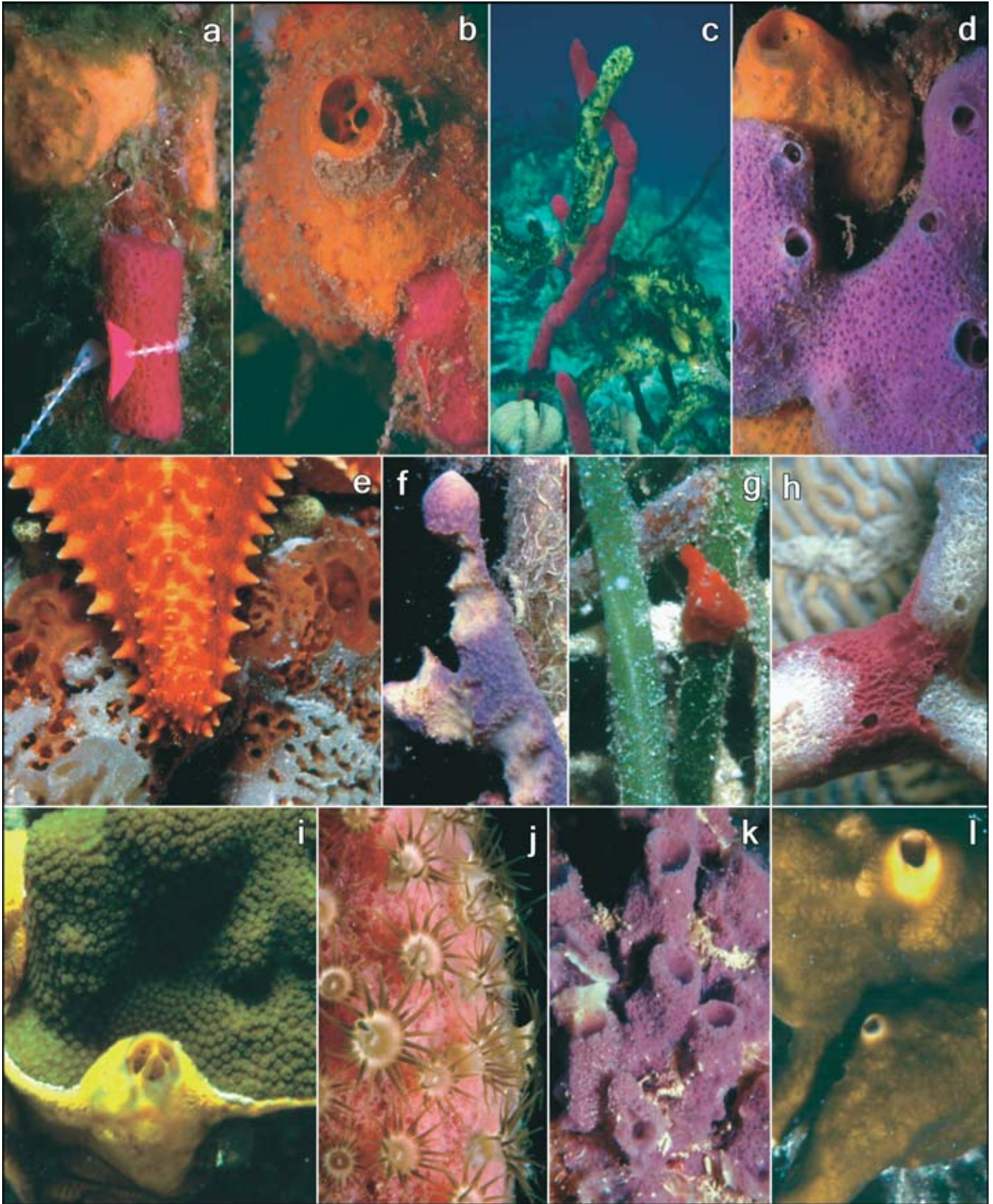
The possibility that sponges might compete with other sponges for food was addressed by Reiswig's (1971) measurements of particles in incurrent vs. excurrent flows for three vase-shaped species in different orders: *Tethya crypta* de Laubenfels, 1949 (= *Tectitethya crypta* (de Laubenfels, 1949)), *Mycale* sp. (= *Mycale (Arenochalina) laxissima* Duchassaing and Michelotti, 1864), and *Verongia gigantea* Hyatt, 1875 (= *Verongula reiswigi* Alcolado, 1984). He related differences among the species in internal morphology and in specific habitat (within the broad habitat of Caribbean coral reefs) to differences in retention of particles of some sizes. In general, food captured was similar among the species, and yet they coexisted, along with dozens of other sponge species using common food resources. Pile (1999) built on these data by adding flow cytometry to the analysis techniques, and compared diets among three species with different growth forms, a tall tube (*Callyspongia vaginalis* (Lamarck, 1814)), a low mound (*Spongia (Spongia) officinalis* L., 1759), and a small-bodied species (*Aplysina fistularis* (Pallas, 1766)) on a reef in the Bahamas. She concluded that competition for food among sponges was unlikely, at least on Caribbean coral reefs, and concurred with Reiswig (1971) that one important reason underlying the great success of sponges is their ability to efficiently consume food resources which other taxa cannot.

Reiswig (1973) pointed out that mechanisms of niche partitioning among sponge species appear to be different from those demonstrated in other phyla, as neither food nor space appear to be resources over which sponges do battle with each other, even though these resources may appear to be limiting. In the more than 30 years since Reiswig published

this insight, no data have been reported to counter the provocative thought that, in this sense, sponges are different from all the other organisms for which the conceptual framework of ecology has been developed.

Competition between sponges and other organisms

Competition between sponges and organisms representing other sessile taxa can be influenced by chemistry and by growth rates and forms. Jackson and Buss (1975) suggested that competitive interactions within a diverse group of encrusting coral reef bryozoans and sponges were mediated at least in part by allelochemicals, on the basis of bryozoan mortality caused by sponge extracts. Buss (1976) pointed out the advantage of allelochemicals that allow a sponge to specifically overgrow an otherwise competitively dominant bryozoan species in a space-limited system. Porter and Targett (1988) specifically tested for the possibility that allelochemicals produced by the Caribbean sponge *Plakortis halichondroides* (Wilson, 1902) could exert influence at a distance from a live sponge, and determined that metabolism of corals of 14 species was inhibited, and their survival chances ultimately decreased, by touching or even being near this species. Greater specificity of allelochemically mediated interactions was demonstrated for four species of Indonesian sponges that scored positive on bioactivity assays (de Voogd et al. 2004). Necrosis for the coral was reported for 85% of sponge interactions with scleractinian neighbors, but less than 25% of overgrown sponges were necrotic. Interestingly, the same sponge individual could cause necrosis in one neighbor, while a neighbor of a different species was unaffected. An intriguing pattern of disproportionately frequent association of a sponge (*Haliclona* sp. 628, which bears nematocysts and zooxanthellae) with dead patches of the coral *Acropora nobilis* (Dana, 1846) appears to be best explained by the sponge larvae settling on and then killing coral tissue, as necrosis of live coral has been observed within a 1 cm radius of this sponge (Garson et al. 1999; Russell et al. 2003).



Overgrowth of other sessile taxa by sponges is not always mediated by chemistry. For example, overgrowth of other fouling community members by an estuarine species of *Halichondria* Fleming, 1828 on eelgrass blades appears to be solely due to the relatively rapid growth of the sponge, perhaps in conjunction with its malleable growth form (Fell and Lewandrowski 1981); and *Haliclona* (*Reniera*) *tubifera* (George and Wilson, 1919) was observed to simply smother neighboring barnacles and tube-dwelling annelids (McDougall 1943). Boring sponges can also cause substantial damage to oysters by weakening the shells with their burrows (see discussion in de Laubenfels 1947).

Observations of sponges apparently overgrowing reef-building corals (e.g., Suchanek et al. 1983; Aerts and van Soest 1997) must be interpreted cautiously unless they have been made in time series, as apparent overgrowths may actually be standoffs (Aerts 2000), or cases in which sponges are increasing survival of corals by adhering to them (e.g., Goreau and Hartman 1966; Wulff and Buss 1979). Sponges have even been demonstrated to increase settlement of larvae of other taxa (Bingham and Young 1991). Most cases of confirmed aggressive overgrowth of corals have involved encrusting or excavating species, most of which harbor zooxanthellae or cyanobacteria (e.g., Vicente 1978, 1990; Suchanek et al. 1983; Rützler and Muzik 1993; Hill 1998; Rützler 2002). Comparisons among reefs where aggressive overgrowth has or has not occurred indicate that corals which are stressed by temperature, sediment, fish bites, or organic pollution may be more vulnerable to overgrowth by these sponges (Rützler and Muzik 1993; Rützler 2002). Likewise, the thinly encrusting *Raphidophlus venosus* (= *Clathria venosa* Alcolado, 1984) was observed to overgrow live coral polyps in 20% of the cases in which the corals had been experimentally damaged, but never to overgrow undamaged living coral (Aerts 2000).

Direct observations of competitive elimination of sponges by other sessile animals have not been reported, but the present habitat distribution of coralline sponges may have resulted from a history of competition for space. Deposition of a dense aragonitic skeleton results in very slow growth of coralline sponges (e.g., Willenz and Hartman 1999), relative to scleractinian corals and other demosponges. Coincidence of very slow growth rates with distribution almost exclusively confined to caves and other cryptic habitats suggests that competition with more rapidly growing sessile animals has placed constraints on coralline sponge distribution (e.g., Hartman and Goreau 1970; Jackson et al. 1971). Confounding factors, such as less sediment in caves and more cavities in scleractinian-built reefs relative to their Paleozoic precursors (Jackson et al. 1971), preclude direct experimental investigation of whether or not this present distribution pattern reflects competition in the past.

Macroalgae, on the other hand, may be successful in spatial competition with sponges. In the rocky intertidal of Alaska, Palumbi (1985) demonstrated that the erect coralline alga, *Corallina vancouveriensis* Yendo, 1901, was able to outcompete *Halichondria panicea* (Pallas, 1766) unless its net growth was decreased by chiton grazing. Consistent negative associations between temperate sponges and macroalgae on subtidal hard substrata have indicated restriction of sponges to sites that are less favorable to algae (e.g., Witman

and Sebens 1990; Bell 2002). Recently, Preciado and Maldonado (2005) have advised caution in interpretation of negative association patterns. By a variety of analyses they demonstrated that, although sponges and macroalgae were sometimes negatively associated, variation in distribution and abundance of sponges among their sites on the north Atlantic coast of Spain was best explained by substratum inclination (i.e., horizontal, vertical, overhangs, or ceilings).

Predation on sponges

Predation on temperate and Antarctic sponges by invertebrates

Invertebrate predators dominate reports of consumption of sponges in temperate waters, where the main sponge-feeding taxa in all oceans include opisthobranch molluscs, asteroid and echinoid echinoderms, and a variety of small crustaceans. Exact color matches between a sea slug species, its prey sponge species, and even its egg masses, are a classic example of apparent camouflage adaptation to evade visual predators (e.g., cover photo of Kozloff 1983), but many of the interactions between invertebrate predators and sponges have required substantial and creative sleuthing.

Typically only portions of adult sponges are consumed, rather than entire individuals, and sponge-predator interactions have not been generally identified as major determinants of community structure in temperate systems. For example, on subtidal hard substrata in New Zealand, two opisthobranch species and a filefish left grazing scars, but did not usually consume entire sponges or remove tissue such that primary substratum was cleared (Battershill and Bergquist 1990). Field and laboratory studies demonstrated that the Mediterranean opisthobranch *Peltodoris atromaculata* feeds only on two sponge species; but even with this degree of specialization, feeding scars are the extent of injury dealt to the prey sponges (Gemballa and Schermutzki 2004). Similarly, predation damage to *Halichondria panicea* in Kiel Bight was minimal (Barthel 1988); and on subtidal walls in the Gulf of Maine, a nudibranch, *Cadlina laevis* (L., 1767), and a seastar, *Henricia sanguinolenta* (O.F. Müller, 1776), consumed sponges but did not appear to exert primary influence on zonation patterns (Witman and Sebens 1990). The boring sponge *Cliona celata* Grant, 1826, inhabiting oyster shells in reefs off the North Carolina coast, was preyed upon by a variety of invertebrates, including two gastropod specialists, and various shrimp, crabs, a limpet, and sea urchin generalists (Guida 1976). Ability of most of these species to consume *C. celata* was a surprise, only learned by feeding experiments and examination of gut contents. Although only the sea urchins were able to break into the excavated galleries to consume sponge tissue, and the other predators were limited to grazing on sponge portions that were peeking out, Guida (1976) suggested that predation might play a role in controlling sponges in the oyster reef. Predation has been demonstrated to have an extreme effect on a temperate sponge in only one case. In south-central Alaska, a particularly successful recruitment of the sponge-feeding nudibranch *Archidoris montereyensis* (Cooper, 1862) entirely eliminated a population of the intertidal sponge *Halichondria panicea* that had previously covered over half of the substratum (Knowlton and Highsmith 2000).

Long-term studies of Antarctic sponges and their predators have left no doubt that these interactions play key roles in structuring the entire benthic system. An assortment of spongivore and omnivore starfish and a nudibranch are the most important sponge predators (Dayton et al. 1974; Dayton 1979; McClintock et al. 2005). The most quickly growing sponge in this system, *Mycale (Oxymycale) acerata*, may be inhibited from taking over all substrata primarily by the preference of the starfish *Perknaster fuscus* for consuming it (Dayton 1979). Further food-web complexity in this system includes an omnivorous filter-feeding starfish that regulates recruitment of spongivorous starfish by consuming their larvae, and thus indirectly influences the sponges (Dayton et al. 1974). As with the intertidal Alaskan example (Knowlton and Highsmith 2000), large swings in community structure and membership may depend on unpredictably heavy or light recruitment of predators and prey (Dayton 1989).

Typically, sponge-feeding temperate and Antarctic invertebrates have preferences among the sponges available. In a particularly detailed study of resource partitioning among six Pacific Northwest nudibranch species, morphological matches of sponge skeletal construction with nudibranch radula structure, and presence or absence of a caecum, played a key role in prey choice (Bloom 1976). Bloom (1981) demonstrated that competitive interactions among the nudibranchs for prey resources were not required to generate the pattern of partitioning observed, as nudibranch growth and reproduction were twice as great on their appropriate sponge species.

An unusual interaction between a sponge, cyanobacteria, and a predator was revealed by observations that the opisthobranch *Tyrodina perversa* (Gmelin, 1790) preferred to feed on the ectosome rather than the endosome of *Aplysina aerophoba* Schmidt, 1862, and preferred to consume specimens from shallow water rather than deep water. Both of these preferences lead the opisthobranch to consume tissue especially rich in the cyanobacteria hosted by the sponge. Confirming that disproportionate ingestion of the symbiont is purposeful, *T. perversa* also preferred *A. aerophoba* over its congener *Aplysina cavernicola* (Vacelet, 1959), which does not host cyanobacteria, and consumed sponge material to which cyanobacteria had been added (Becerro et al. 2003b).

Details of the interaction between the starfish *Henricia sanguinolenta* and finger sponge species of *Isodictya* Bowerbank, 1864 illustrate another type of complexity that can underlie predator-prey interactions involving sponges (Shield and Witman 1993). Size and location of feeding lesions influenced recovery success, and only 16% of the lesions from starfish feeding recovered. Branches weakened by lesions were more likely to break by water movement, resulting in ultimate losses from the sponges far exceeding the amount of tissue actually consumed by the starfish. Similarly, Antarctic sponges on which starfish and nudibranch predation exceeded 20%–30% of their initial volume may have passed a recovery threshold (Dayton 1979).

Sponge feeding by invertebrates and vertebrates in tropical waters

One way in which predator-sponge interactions in the tropics differ from those in temperate waters is that verte-

brates join the ranks of spongivores. Still, only a few fishes and a turtle are able to consume sponges. Randall and Hartman (1968) inferred that “Porifera of the West Indies appear to enjoy relative freedom from predation by fishes” on the basis of the small percentage of 212 reef fish species that had sponge material in their gut contents. Subsequent work has confirmed that sponges are well defended against consumption by most animals with which they coexist. Most of the fishes that inhabit coral reefs, seagrass meadows, and mangroves, including wrasses, surgeonfishes, damselfishes, jacks, snappers, and groupers, are not known to ever consume sponges. Predators that are able to circumvent these effective defenses appear to fall into three categories (each detailed below): (1) smorgasbord feeders that consume small amounts of many species, (2) specialists which concentrate on one or a few sponge species that may be well defended against other spongivores, and (3) opportunistic sponge feeders that are normally herbivores or omnivores, but are able, and even eager, to consume a few poorly defended sponge species that are only available in unusual circumstances (e.g., exposed by storms, or supplied by investigators).

(1) Smorgasbord-feeding sponge specialists

The “smorgasbord-feeding” behavior inferred by Randall and Hartman (1968) when they found remains of 46 sponge species in angelfish gut contents has been well corroborated by field observations of unmanipulated angelfishes consuming 64 sponge species in the course of 1724 bites ingested, including 86% of the 39 species in a completely censused coral reef plot (Wulff 1994). Individual fish typically take only a few bites of each sponge before moving on to a sponge of a different species. Angelfishes have been observed to repeatedly ingest a few undefended sponge species, which have been provided from inaccessible habitats by investigators, until they are completely consumed (e.g., Dunlap and Pawlik 1996; Wulff 2005). Most of the time, however, angelfishes do not have the choice of consuming highly palatable sponge species from mangroves or cryptic reef spaces, and must consume the generally unpalatable exposed reef sponges in a rotating fashion. In an experimental study, angelfish also moved among seven mangrove sponge species, taking only a few bites at a time from all but the two most edible species (Wulff 2005). No sponges appear to be eliminated from the reef community by smorgasbord feeding and some of the most frequently consumed sponge species remain the most abundant (e.g., Wulff 1994).

Details of the feeding behavior of the widely distributed tropical sea urchin *Eucidaris tribuloides* (Lamarck, 1816) are not known, but a study of gut contents revealed a pattern reminiscent of the angelfishes. All 20 individuals that were collected in Todos os Santos Bay, Bahia, Brazil, had only sponge remains in their guts (Santos et al. 2002). Individual urchins had evidence of up to six sponge species in their guts, representing five orders of demosponges, and including material from species not previously known to inhabit Bahian waters. Reiswig (1973) also noted significant predation by the urchins *E. tribuloides*, *Lytechinus variegatus* (Lamarck, 1816), and *Tripneustes ventricosus* (Lamarck, 1816) on the seagrass-inhabiting sponge *Tethya crypta* (= *Tectitethya*

crypta), which may have slowed its net growth rate but did not result in mortality of entire individuals.

(2) *Specialists on particular sponge species*

Hawksbill turtles specialize on sponges as adults, but concentrate their feeding on sponge species in only 3 of the 13 recognized (Hooper and van Soest 2002), extant demosponge orders (Meylan 1990; Anderes and Uchida 1994; van Dam and Diez 1997). Focus on species of Astrophorida, Chondrosida, and Hadromerida is extreme, such that Meylan's (1990) hawksbill gut contents from around the Caribbean showed more than 97% by dry mass from these three orders. Caribbean trunkfish appear to prefer a limited selection of sponges in the order Verongida (Fig. 1f) (in Panama, Wulff 1994; Belize, J. Wulff, personal observation; and Navassa, T. Swain, personal communication), which is mostly avoided by angelfishes (Wulff 1994, 2005).

A very different type of specialist predator is represented by the small crustaceans that inhabit sponges. In most cases the sponges serve only as a dwelling place, but some copepods, amphipods, isopods, and alpheid shrimps consume their host sponges (Rützler 1976; Ríos and Duffy 1999; Mariani and Uriz 2001). The sponge *Hymeniacidon caerulea* Pulitzer-Finali, 1986, which hosts, and is consumed by, the snapping shrimp *Synalpheus williamsi* Ríos and Duffy, 1999, stands out as unpalatable to all other potential predators tested so far (Wulff 1995, 1997b, 1997c). Thus, consumption of *H. caerulea* by this shrimp fits with a pattern of small crustaceans that inhabit generally unpalatable algae being able to consume their chemically defended host plants (e.g., Hay et al. 1988; Duffy and Hay 1994). Other crustacean endobionts are more general in their choice of host for living and feeding. For example, Rützler (1976) found *Synalpheus gambarelloides* (Nardo, 1847) in all six of the Tunisian dictyoceratid sponge species that he studied.

Some sponge-feeding nudibranchs have taken specialized interactions with prey a step further by sequestering secondary metabolites from the sponges (e.g., Thompson et al. 1982; Faulkner and Ghiselin 1983; Pawlik et al. 1988; Proksch 1994). As tempting as it is to generalize about something that makes such a good story, caution is advised by a detailed study of three species of the nudibranch genus *Glossodoris* on species of the dictyoceratid sponge genus *Hyrtios* Duchassaing and Michelotti, 1864 (Rogers and Paul 1991). Nudibranchs did not necessarily simply sequester defensively useful metabolites, but disabled some apparently useful metabolites ingested from their prey, excreted others, and enhanced the concentration of others even though that did not increase the protection of the nudibranchs from their own predators (e.g., Rogers and Paul 1991).

(3) *Opportunistic feeding on sponges that are not usually available*

Opportunistic sponge feeding is well illustrated by the large seagrass-dwelling Caribbean starfish *Oreaster reticulatus* (L., 1758) (Fig. 1e), which only consumes 1 of 14 (7%) sponge species typical of the seagrass meadows/rubble beds it inhabits, but readily consumes 16 of 20 (80%) typical reef species tested (Wulff 1995). When a hurricane swept reef sponge fragments into a seagrass meadow, the starfish consumed them rapidly; and when fragments of four common reef

sponges were scattered in a seagrass meadow, the starfish had already completely consumed 33 of 60 fragments of the palatable species by the 5th day (Wulff 1995). Parrotfishes were observed to opportunistically consume some species of sponges that were revealed by overturning coral slabs at Fanning Island and Eniwetok in the tropical Pacific (Bakus 1964, 1967), and restricted at least two Caribbean species of reef sponges to cryptic spaces within the reef frame by consuming them whenever they were exposed (Wulff 1988, 1997b). Two species of mangrove sponges living under rubble were consumed when the rubble was overturned (Dunlap and Pawlik 1996), and parrotfishes quickly consumed two semi-cryptic species when their surfaces were sliced off (Wulff 1997b). Likewise in the tropical eastern Pacific at Panama, angelfish, parrotfish, trunkfish, and Moorish idols completely consumed four species of cryptic space-inhabiting sponges in 20%–30% of 20 min trials, when they were exposed by breaking into the reef frame (Wulff 1997c). Parrotfishes have also been observed to consume some species of mangrove sponges, preventing them from living on reefs (Dunlap and Pawlik 1996, 1998; Wulff 2005). These examples of opportunistic sponge feeding illustrate another difference between temperate and tropical spongivory: predators have been demonstrated to entirely constrain habitat distribution of some tropical sponges. Because of opportunistically feeding predators, (i) some mangrove species cannot inhabit exposed surfaces on coral reefs, (ii) some cryptic reef species cannot inhabit exposed surfaces, and (iii) many reef species cannot inhabit seagrass meadows.

Studying predation on sponges

Convenient bioassays of palatability for tropical marine sponges have ranked dozens of species according to consumption of pellets (made of sponge extracts, a feeding attractant, and a hardening agent) by generalist predators that do not consume living sponges (e.g., Pawlik et al. 1995). Some species consumed in pellet form by wrasses were also abundant in fish gut contents analyzed by Randall and Hartman (1968), apparently confirming accuracy of this type of assay for judging palatability. However, these same species are also among the most common sponges on shallow Caribbean reefs, so commonness in gut contents may simply reflect availability in the field. To infer preferential consumption or rejection of particular sponge species from gut content analysis requires knowing the relative abundance of sponges in the habitat where predators were captured. Other disadvantages of using gut contents to understand predator-prey relationships include lack of data on feeding behaviour, and the destructive sampling of predators (except in the case of turtles, from which gut contents can be obtained by lavage, e.g., van Dam and Diez 1997). An advantage of gut content data is the unambiguous evidence that particular prey were ingested, without having to spend many hours following fish in the field, hoping to observe feeding. Gut content analysis can also demonstrate presence of rare or hidden species as illustrated by sea urchin gut contents in Brazil that contained species previously unknown from Bahia (Santos et al. 2002).

Pellet consumption can be used to answer specific questions relating to nutritional content or biogeography, as de-

scribed in the following section. However, some aspects of predator deterrence by sponges are not captured by pelletizing procedures, as palatability designations based on wrasses consuming pellets are at odds with field observations of unfettered spongivores consuming living sponges. For example, sponge species that are palatable to angelfishes are rejected by starfish, and starfish readily consume sponges avoided by angelfishes (Wulff 1994, 1995); while trunkfish specialize on sponge species rejected by angelfishes (Wulff 1994; Fig. 1f) and ignore species preferred by parrotfishes (J. Wulff, unpublished data). Parrotfishes and angelfishes differed in how much they consumed four mangrove sponge species (Dunlap and Pawlik 1996). Hawksbill turtles also consume one of the mangrove species preferred by angelfishes (Dunlap and Pawlik 1996), but otherwise concentrate their feeding on yet another set of sponges (Meylan 1990; van Dam and Diez 1997). "Palatable" is clearly a characteristic of the relationship between a sponge species and a particular predator species, rather than the sponge species alone. Consequently, there is no easy substitute for experimental manipulations and field observations of various potential predators feeding on living sponges.

Some sponge species concentrate predator deterrents at their surfaces (Uriz et al. 1996a; Wulff 1997b; Becerro et al. 1998; Schupp et al. 1999; Furrow et al. 2003; McClintock et al. 2005), apparently optimizing deployment of defensive metabolites. Practical aspects with respect to research techniques are that cut surfaces must be allowed to heal before live sponges are used in preference experiments, and palatability tests with either living sponges or extracts must be made with both surface and inner tissue to be certain that deterrence is not missed.

Predator deterrence and nutritional quality

Clear patterns in the relationship of nutritional content to predator preference have been elusive. Randall and Hartman (1968) pointed out that the two sponge species they found most frequently in fish gut contents, *Callyspongia vaginalis* and *Chondrilla nucula* Schmidt, 1862, had low spicule content to organic matter ratios (although much of the organic matter is in the form of spongin), and they suggested that these species may be sought by the fishes. But for the next 20 most abundant sponges in the gut contents, there was no particular pattern relating proportion of organic matter to consumption rates. Likewise, nutritional composition and spicule contents of Antarctic sponges had no consistent relationship to feeding patterns of four species of starfish and one nudibranch (McClintock 1987), and sponges that figure prominently in diets of hawksbill turtles were either especially high in silica (orders Hadromerida and Astrophorida), or especially high in protein content (order Chondrosida) (Meylan 1990). Comparison of sponge nutritional quality with the number of extract pellets consumed by wrasses also revealed no consistent patterns, except a higher lipid content in sponges from which less palatable pellets were made (Chanas and Pawlik 1995). Spicules added to pellets were only a deterrent when the nutrient content of the pellets was lower than that of sponges (Chanas and Pawlik 1996). Tests of the possibility that effectiveness of chemical defenses is enhanced by physical defenses, such as spicules, have

shown a synergistic effect for some sponge species, but not for the majority of species tested (e.g., Hill et al. 2005; Jones et al. 2005).

Explicit consideration of how nutritional content is confounded by chemical defenses may help to reveal some patterns. When Duffy and Paul (1992) provided food pellets varying in nutritional quality and in concentrations of secondary metabolites from two sponge species, *Dysidea* sp. and *Luffariella variabilis* (Poléjaeff, 1884), to reef fishes on Guam, food quality influenced choices significantly, and chemistry was less of a deterrent in higher quality food. In a comparison of the two Mediterranean species *Crambe crambe* and *Dysidea avara* (Schmidt, 1862), chemical defenses were more concentrated in *C. crambe*, which has higher energy content (Uriz et al. 1996b), as predicted if predators respond to a balance between chemical defenses and nutritional quality.

Trade-offs between defenses and growth, and variation in deterrence by life-history stage

Sponge growth rates would be predicted to be inversely related to defenses against enemies, if defensive chemistry or structures are expensive, and this has been demonstrated in a few studies. A particularly thorough and compelling study of trade-offs within a single species demonstrated that *C. crambe* individuals with the greatest investment in chemical and physical defenses grew more slowly, and survived better, than conspecifics in a more illuminated, less animal-dominated habitat (Uriz et al. 1995; Turon et al. 1998). In this case, defenses may protect especially against spatial competitors as well as predators. At McMurdo Sound in Antarctica, the starfish *P. fuscus* specializes on *Mycale (Oxymycale) acerata*, which stands out in this sponge-dominated community by its very rapid growth rate (Dayton 1979). On shallow Caribbean coral reefs, growth rates of three common erect branching species (*Iotrochota birotulata* (Higgin, 1877), *Amphimedon compressa* Duchassaing and Michelotti, 1864, *Aplysina fulva* (Pallas, 1766)) are positively related to relative preference (i.e., frequency of consumption in terms of number of bites/relative abundance in terms of volume) by unmanipulated angelfishes (Wulff 1994), and growth rates of an assortment of 12 reef and mangrove sponge species were positively related to predation by unconstrained parrotfishes and angelfishes (Wulff 2005). Rate of regeneration of wounds, made by cutting holes through the walls of vase-shaped sponges, was positively related to palatability by pellet assays (Walters and Pawlik 2005). Substantial (i.e., up to a couple of orders of magnitude) differences between growth and regeneration rates in the same sponge species (e.g., Reisinger 1973; Ayling 1983) raise interesting questions about differences in allocation to each of these processes relative to predator defenses.

Chemical defenses in the large, slow-moving larvae of two Caribbean sponge species decrease their vulnerability to planktivorous fishes, allowing them to be safely released during the day (e.g., Lindquist et al. 1997). As adaptive as this must be, it is not a general rule. Larvae of the Mediterranean species *D. avara* are rejected by fish, but larvae of the sympatric *C. crambe* are consumed, although metamorphosed stages deter predators as early as 2 weeks after settlement

(Uriz et al. 1996b; Becerro et al. 1997). These studies indicate that examination of life stage-dependent predator deterrence in other sponge species may be a particularly interesting aspect of further studies of trade-offs among defenses and growth or reproduction.

Biogeographic patterns in predator–prey relationships

A geographic pattern of more effective chemical defense against predators, demonstrated for many groups in tropical latitudes relative to temperate latitudes, has not been supported as data accumulate for sponges. Predation has been demonstrated to play a key role in population and community dynamics of Antarctic sponges (Dayton 1979), and chemical defenses are clearly involved in mediating those interactions (McClintock 1987; Furrow et al. 2003; Amsler et al. 2001; McClintock et al. 2005). Experimental comparison of feeding by suites of large and small generalist fishes from tropical (Guam) vs. temperate (Mediterranean) sites on sponge pellets incorporating extracts of tropical vs. temperate sponges also revealed no consistent biogeographic differences (Becerro et al. 2003a).

The only biogeographic pattern in sponge–spongivore relationships that seems certain at this point is that invertebrates, especially molluscs and echinoderms, are important spongivores at all latitudes, but significant sponge feeding by vertebrates is a feature of tropical systems only. An apparent biogeographic pattern at this point is that predation may be more generally important in curtailing habitat distribution of particular sponge species and in structuring benthic communities dominated by sponges in the tropics and Antarctica. However, there is yet much to be learned about spongivory, and the many challenges of studying predator–prey relationships in all systems are magnified for sponges by the speed with which partially consumed sponges are able to efface all traces of injury (e.g., Fig. 1f), and skeletons of sponges from which tissue has been consumed disarticulate and disappear. For example, the surprising importance of spongivory in Antarctica is only known because of logistically demanding, long-term studies (e.g., Dayton 1979, 1989; McClintock et al. 2005). Likewise, the sole demonstration that sponge-feeding predators can exert significant control on their prey in temperate waters depended on long-term study of particular sites through years in which predator recruitment varied (Knowlton and Highsmith 2000). Even in the tropics where logistics of directly watching spongivory in action are far easier, it is only by long hours spent hovering over fishes, or setting up and monitoring manipulative experiments, that we have any idea how completely predators are able to constrain sponge habitat distribution (Bakus 1964; Wulff 1988, 1995, 1997b, 1997c, 2005; Dunlap and Pawlik 1996, 1998; Hill 1998; Pawlik 1998) and to influence sponge diversity (Wulff 2005). There was no reason to imagine that the starfish *Oreaster reticulatus* could prevent reef sponges from living in seagrass meadows, but for chance observations of rare natural opportunities for the starfish to consume reef sponges (Fig. 1e), followed up by feeding choice experiments (Scheibling 1979; Wulff 1995), and there may be many other unexpected spongivore–sponge interactions to be discovered. Thus, it is still too early to be certain about general patterns in interactions of sponges with their predators.

Symbiotic associations

Sponge structure, homogeneous, malleable, and simple, but pervaded by canals, may facilitate development of intimate associations with other organisms. This was one of the earliest aspects of sponge ecological interactions to be closely examined and quantified (e.g., Arndt 1933; Arndt and Pax 1936; Pearse 1934, 1950; de Laubenfels 1947). William Beebe illuminated the fascinations of sponges for a public readership in his record of early diving helmet explorations *Beneath Tropic Seas* (1928), which includes an enthusiastic account of the many hundreds of crustacean and piscine inhabitants of a large *Sphaciospongia vesparium* (Lamarck, 1815) individual that he examined in a rustic laboratory on board a four-masted schooner anchored off Haiti (pp. 123–131). Rützler (1976) summarized earlier accounts and reported on finding representatives of 11 animal phyla, and up to 1500 individuals/kg of sponge, in 6 species of Tunisian sponges in the order Dictyoceratida. An interesting pattern emerging from his data was a positive association of sponge canal volume with total mass of endofauna, but negative association of canal volume with numbers of individual endofauna (Rützler 1976). In one recent and well-quantified example of the astounding diversity and abundance of inquilines possible in sponges, Ribeiro et al. (2003) found 2235 individual symbionts of 75 invertebrate species, representing 9 phyla in the encrusting (0.5–4 cm thick) sponge *Mycale (Carmia) microsigmatosa* Arndt, 1927 in southeastern Brazil. Likewise, Villamizar and Laughlin (1991) reported 139 and 53 species inhabiting the two Caribbean vase-shaped species, *Aplysina lacunosa* (Pallas, 1766) and *Aplysina archeri* Higgin, 1875, respectively, in Venezuela. Most commonly represented in these sponge hotels are crustaceans, polychaetes, ophiuroids, cnidarians, molluscs, and fishes.

Sponge species vary widely in the number and types of symbionts they host. And within each of the common symbiont higher taxa are species that represent every type of association with their host, ranging from facultative sponge associates that also live in other sheltered habitats, to obligate sponge associates that occupy a variety of sponge species, to obligate specialists on particular sponge species. Net results of symbioses involving sponges likewise run the gamut from mutualism to commensalism to parasitism. Some associations recur in similar taxa in different oceans, hinting at the possibility of future generalizations. Sponge symbioses appear to be more diverse and ubiquitous in tropical waters, and Cerrano et al. (2006) have pointed out that this may not only reflect higher biodiversity in these systems, but that these associations are also a source of increasing biodiversity. Besides these observations, perhaps the sole reliable generalization about sponge symbioses is that every probing study of a particular symbiosis is sure to reveal intriguing surprises.

Molluscs (Bivalvia and Gastropoda) and sponges

Associations of sponges with dense populations of bivalves have been described in most oceans. Scallops inhabiting an oyster bank on the Atlantic coast of Ireland have been demonstrated to gain protection from starfish predators when their valves are overgrown by *H. panicea*, while the sponges gain a favorable feeding location by the inhalant feeding

currents of their hosts (Forester 1979). In a similar interaction in South Australia, sponges not only deterred an asteroid predator, but also prevented boring sponge damage in scallop shells, resulting in faster growth (Pitcher and Butler 1987). In both Ireland and Australia, sponges seemed to facilitate escape of scallops by interfering with the starfish ability to manipulate the scallops, but in Australia, one sponge species inhibited starfish even when the scallops were immobilized (Pitcher and Butler 1987), implicating tactile or chemical defenses. Sponges appeared to preferentially settle on the scallops. In another association that seems to benefit both partners, sponges of 19 species inhabit shells of the byssate bivalve *Arca noae* L., 1758 in the Mediterranean. The sponges may benefit from water flow generated by the bivalve, and all six species of boring sponges that were present on the rocks were missing from the shells (Corriero et al. 1991), suggesting that non-boring sponges might protect shells from borers. As well, the sponge *C. crambe* encrusting *A. noae* shells inhibited predation on their hosts by a starfish, a non-native invasive snail, and octopus (Marin and Belluga 2005).

Siliquariid molluscs are obligate commensals of sponges. Host-commensal associations are not specific, but only a limited number of sponges appear to have the skeletal architecture desirable to these sessile gastropods (Pansini et al. 1999). Presumed benefits for the molluscs are living space and protection from predation, while the sponge may benefit from the mollusc pumping and the fine particles not retained by the ctenidia.

Polychaetes and sponges

Polychaete worms are common sponge symbionts, sometimes conspicuous, as when large sabellids inhabiting *Mycale (Carmia) microsigmatosa* obscure their host from view with their fans spread in filtering (J. Wulff, personal observation). The large Caribbean sponge *Neofibularia nolitangere* (Duchassaing and Michelotti, 1864) can host a dense population of tiny white polychaetes, genus *Haplosyllis* Langerhans, 1879, embedded in the surface of its atrium (photo in Humann 1992). Non-filter-feeding polychaete species may feed on their hosts. For example, the small errant polychaete *Branchiosyllis oculata* Ehlers, 1887 was found to live and feed on 9 of 16 sponge species surveyed in Bermuda (Pawlik 1983).

By comparing absorption spectra of acetone extractions of sponges and of gut-free worm tissue, Pawlik (1983) confirmed that the color of *B. oculata* individuals matched colors of two host sponge species (*Tedania ignis*, *Cinachyra alloclada* (= *Cinachyrella alloclada* (Uliczka, 1929))) as the result of the worms ingesting their hosts. Tsuriumi and Reiswig (1997) illustrated this aspect of polychaete-sponge associations with clear photomicrographs of the polychaete *Haplosyllis spongicola* (Grübe, 1855), with its proboscis engulfing the tissue of its host *Aplysina cauliformis* (Carter, 1882) (Fig. 1f). Polychaetes identified as this same syllid species have been reported from 36 sponge host species in a variety of sponge orders and biogeographic regions (Lopez et al. 2001). Consistent differences between temperate examples (a few large worms, not necessarily obligately associated with a particular host sponge) and tropical examples (huge numbers of small worms, which complete their entire life cycle within their sponge host) suggest that what is pres-

ently referred to as *H. spongicola* may actually be a species complex (Lopez et al. 2001).

Crustaceans and sponges

Sponge associations with crustaceans attracted early attention (e.g., Arndt 1933) with their great variety. An association that seems as if it must be mutually beneficial is that of hermit crabs and suberitid sponges. The sponges encrust gastropod shells inhabited by hermit crabs and then continue to grow, apparently relieving the crabs of the necessity of finding new shells as they grow. However, closer investigation of one of these associations in the northern Gulf of Mexico (Sanford 1994) revealed that mutual benefit might be a hasty conclusion in some cases, as hermit crabs left sponge-covered shells in favor of clean shells, if they were of the right size and type. An assumption of mutual benefit also seems obvious in the case of sponge-decorated decorator crabs. But, although many interesting ideas have been advanced and experiments have shown clear choices among sponge species (e.g., Woods and Page 1999), the adaptive significance of crab choices of sponge species for decorating has not been often identified (Fig. 1g). Camouflage seems a likely purpose in one case in which sponge species decorating crabs most frequently were also the most common in the habitat (Schejter and Spivak 2005). By contrast, seasonal preference for decoration with the sponge *Hymeniacidon heliophila* (Parker, 1910) may confer predator protection on decorator crabs in North Carolina in winter and spring when their preferred algal decoration, *Dictyota menstrualis*, is unavailable, as this sponge is unpalatable to local fishes (Stachowicz and Hay 2000). Sponge-dwelling snapping shrimps have attracted attention as the only known example of eusocial marine organisms (Duffy 1996a). Sponge host specificity may have played a key role in the evolution of the particularly high species diversity of snapping shrimps (Duffy 1996b). At least one shrimp both lives in and consumes its host, as evidenced by bits of this deep royal blue sponge visible in shrimp guts (Ríos and Duffy 1999).

Other small crustacean inhabitants of sponges include copepods, isopods, and amphipods, some of which also consume their hosts (e.g., Rützler 1976; Poore, et al. 2000; Thiel 2000; Mariani and Uriz 2001). These associations are common in every biogeographic region, including the Arctic and Antarctic (review by McClintock et al. 2005). Sponge-dwelling barnacles appear to be especially diverse and abundant in coral reef sponges (Ilan et al. 1999; Cerrano et al. 2006). Large sponges can be important shelters for juveniles of the Caribbean spiny lobster, *Panulirus argus* (Latreille, 1804), which feed in food-rich, but shelter-scarce, seagrass meadows before moving onto coral reefs as adults (Butler et al. 1995).

Echinoderms and sponges

Brittle stars are common sponge associates in tropical and Mediterranean waters. By a combination of time-lapse filming, gut content analysis, and predation experiments, Hendler (1984) was able to demonstrate that the association of adult brittle stars, *Ophiothrix lineata* Lyman, 1860, with the tubular Caribbean sponge *Callispongia vaginalis* was mutually beneficial. Brittle stars clean the inhalant surface of sponges as they feed and derive protection from predators on

their inedible perches. In another study of this association, small individuals were found only on the outside of tubes, while large ones were found inside (Henkel and Pawlik 2005). The Mediterranean brittle star, *Ophiothrix fragilis*, settles on, and recently settled individuals also crawl onto, the surfaces of particular sponge species, especially *Crambe crambe*, *Scopalina lophyropoda* Schmidt, 1862, and *Dysidea avara*, reaching densities of over 50 individuals/cm² (Turon et al. 2000). Demonstrating the limits on generalization from one interaction to an apparently similar one, in this Mediterranean example the tiny brittle stars appear to gain a feeding advantage from the inhalant currents, but once they are larger than 1 mm in disk diameter they leave the sponges.

Bryozoan and sponge

About 90% of the colonies of the bryozoan *Smittina cervicornis* (Pallas, 1766), in a variety of habitats in the northwestern Mediterranean, are overgrown by the thinly encrusting sponge *Halisarca* cf. *dujardini* Johnston, 1842. The association elevates the sponge above the substratum, which it could not achieve on its own, as sponges in this genus lack skeletal fibers or spicules, and the feeding currents appear to be strengthened for both partners by their collaboration (Harmelin et al. 1994).

Colonial cnidarians (Anthozoa, Scyphozoa, Hydrozoa) and sponges

Cnidarians, representing Anthozoa, Scyphozoa, and Hydrozoa, are conspicuous sponge associates, with sponge and cnidarian individuals sometimes completely interwoven with each other. A colonial, branched scyphozoan inhabits a variety of dictyoceratid and dendroceratid sponges on subtidal walls in the northwestern Mediterranean, conferring on its hosts a substitute for, or enhancement of, skeletal fibers (Uriz et al. 1992). For the sponges *Dysidea* spp., the scyphozoan partner constitutes the primary support. It is not clear exactly what this widespread association offers the scyphozoan, possibly protection against predators and physical disturbance, but the scyphozoan is not found apart from host sponges (Uriz et al. 1992). Experimental investigation of another scyphozoan inhabitant of sponges showed that it increases survival of its host *Mycale fistulifera* (Row, 1911) in the Red Sea, protecting it from predation by a starfish and one of the echinoids in the system (Meroz and Ilan 1995).

Zoanths are conspicuous sponge associates (Fig. 1j) in all oceans and, in some cases, are colored in striking contrast to their hosts. Zoanths in the genera *Parazoanthus* Haddon and Shackleton, 1891 and *Epizoanthus* Gray, 1867 appear to be obligate symbionts, hypothesized to gain substratum space in space-limited systems, as well as protection from predators, by intimate association with sponges. Net effect of the association has been investigated in three Caribbean examples, with the intriguingly varied set of results that (i) *Parazoanthus swiftii* (Duchassaing de Fonbressin and Michelotti, 1860) hosted by *Iotrochota birotulata* was determined to be mutually beneficial, with the sponge gaining protection from a specialist angelfish predator (West 1976), *Holocanthus tricolor* (Bloch, 1795) (Randall and Hartman 1968; Wulff 1994); but (ii) *Parazoanthus parasiticus* (Duchassaing de Fonbressin and Michelotti, 1860) hosted by

Niphates digitalis (Lamarck, 1814) appeared to interfere with host pumping and did not provide predator protection for *Callyspongia vaginalis* (Lewis 1982); and finally, (iii) a zoanthid epizoic on the coralline sponge *Calcifibrospongia actinostromarioides* Hartman and Willenz, 1990 inspires the sponge to alter its skeletal deposition in a way suggesting reaction to a parasite (Willenz and Hartman 1994).

An unusual association of a sponge with another anthozoan, the octocoral *Carijoa riisei* (Duchassaing and Michelotti, 1860), has been reported from Indonesia (Calcinai et al. 2004). The sponge may receive support and the octocoral some protection against predators, although the octocoral appears to react against the sponge. Curiously, both the octocoral and the sponge *Desmapsamma anchorata* (Carter, 1882) are Caribbean species that may be invading the tropical Pacific as a pair.

Reef-building corals gain survival advantages from intimate association with non-excavating sponges. When the Caribbean sponge *Mycale laevis* (Carter, 1882) is associated with corals, especially species in the genus *Montastraea*, the margins of the corals respond to the oscular flow by creating folds around the large oscula (Fig. 1i). As the corals grow they provide space in which the sponges can expand, and as the sponges grow they cover exposed portions of the coral skeletons, protecting the bases and undersurfaces of corals from invasions by bioeroders (Goreau and Hartman 1966). An experimental investigation of the importance of sponge protective and binding services to coral survival had surprisingly dramatic results. Removal of all non-excavating sponges from fore-reef patch reefs in San Blas, Panama, resulted in 40% loss of coral colonies (46% of surface area of live coral) in only 6 months, whereas only 4% of the corals (3% of living surface area) were lost from control reefs with intact sponges (Wulff and Buss 1979). On these moderate depth fore-reef patch reefs, corals cannot afford to be without their sponges, as this rate of loss is not long sustainable.

Hydroids of many species associate with sponges in every possible configuration from growing over the surface, to being completely intermingled with host tissue, to augmenting the skeletal framework of the host sponge, and even having hydrorhiza enveloped by the spicule tracts of the sponge (Bavestrello et al. 2002; Puce et al. 2005). Very different from the sponge-inhabiting zoanths, which are in just two genera of obligate symbionts, the sponge-inhabiting hydroids are scattered among a number of genera, some of which do not have a particular tendency to be symbiotic (Puce et al. 2005). As details of these hydrozoan associations are worked out, comparisons with scyphozoan and anthozoan sponge symbionts are certain to be informative about the evolutionary and ecological constraints on development of sponge–cnidarian associations.

Sponges associated with other sponges

Especially intriguing among the intimate associations of sponges are those between sponge species. Intimate association among highly efficient filter feeders of multiple species is not what would be predicted by theories of interactions, but many sponges clearly thrive in close association with each other. Very specific two-species associations are one form of symbiosis; North American examples (from de Laubenfels 1950) include *Calyxabra poa* de Laubenfels, 1947

being consistently covered by *Hymeniacidon sanguinea* (Grant, 1826); European examples (from Sarà 1970) include *Haliclona cratera* Schmidt, 1862 growing over *Ircinia oros* Schmidt, 1864, and *Coelectys insinuans* (= *Chaetodoryx insinuans* (Topsent, 1936)) growing over *Oligoceras collectrix* Schulze, 1879; and a Korean example (from Sim 1997) involving an association between species from the genera *Poecillastra* Sollas, 1888 and *Jaspis* Gray, 1867. Although it is not always clear exactly what each species derives from the association, the covered sponge does not appear to be traumatized by the lack of access to water over most of its surface. The inner species of a specific pair (*Haliclona* sp. over a species in the genus *Geodia* Lamarck, 1815) described in the Florida Keys (Wilcox et al. 2002) may derive protection from predators.

Studies of multispecies interactions among sponges in dense and diverse assemblages have consistently suggested or demonstrated mutual benefit (Sarà 1970; Rützler 1970; Wulff 1997a). Sarà (1970) demonstrated a clear positive association of diversity (the diversity index $d = (S - 1)/\ln N$, where S is number of species per group and N is total number of individuals) with density for 5 microhabitats in a cave in the Riviera Ligure di Levante and as many as 25 species in an area of only 2 m². By detailed monitoring of these complex sponge communities, Sarà (1970) was able to demonstrate remarkable stability over time, in spite of variation in abiotic factors. From his own work and a review of previous work, Sarà (1970) concluded that "... the complexity of continuous sponge populations, with the coexistence of a large number of species, examined from the three aspects of species diversity, community structure and stability in time, suggests that some cooperation phenomena may play a very important role". Rützler (1970) recorded 134 incidences, in 54 species combinations, in which individuals of the same or different species were growing upon each other (Fig. 2). By analyzing histological preparations of sponges of different species that were adherent to each other, he demonstrated that species which are typically covered by other sponges are morphologically suited to maintaining access to the water column. Facultative, non-specific associations among three species of erect branching sponges (*Iotrochota birotulata*, *Amphimedon compressa*, and *Aplysina fulva*), which are among the most common on shallow Caribbean coral reefs (Fig. 1c), increase growth and survival of participating sponge individuals (Wulff 1997a). The mechanism for increased growth is still a mystery, but the mechanism for increased survival was experimentally demonstrated to depend on each species being differentially affected by a variety of biotic and abiotic environmental hazards (e.g., fish and starfish predators, infectious pathogens, basal smothering by sediment, breakage by storm waves, etc.). Adherent heterospecific neighbors have synergistic effects on each other's ability to withstand mortality agents (Wulff 1997a). Further complicating these associations, the unusually quickly growing and readily fragmented sponge *Desmapsamma anchorata* can act as a parasite on species that participate in the mutualism, gaining benefits without reciprocating (Wulff 1999).

Sponge associations with macroalgae and flowering plants

Associations with photosynthetic organisms are well de-

veloped for many sponges and in many cases are quite specific. Rützler (1990) identified five types of associations of sponges with non-vascular autotrophs: unicellular cyanobacteria, filamentous cyanobacteria, dinoflagellates, filamentous algae embedded in skeletal fibers, and calcified red algae. Erect calcified red algae are important collaborators of sponges in at least three demosponge orders. A Caribbean reef sponge makes use of the articulated coralline red alga *Jania adherens* Lamouroux, 1812 as its primary skeleton (Fig. 1k) to the point that the association is reflected in the specific name of the sponge *Dysidea jania* (Duchassaing and Michelotti, 1864) (discussion in de Laubenfels 1950). Wulff (1997c) demonstrated a benefit for a sponge species from harboring macroalgae by exposing *Haliclona caerulea* with and without symbiotic articulated coralline reds to predators in the tropical eastern Pacific at Panama. Sponges without algae were readily consumed by the angelfish *Holocentrus passer* Valenciennes, 1846 and even by the Moorish idol, *Zanclus cornutus* (L., 1758). The same association has been studied by Carballo and Ávila (2004) in the Bay of Mazatlán in Mexico, where resistance to physical damage by water movement is an advantage gained by the sponge from the alga, and the alga only lives below 1 m when associated with the sponge. On the wave-washed temperate rocky coast of the Pacific northwest of the USA, Palumbi (1985) demonstrated experimentally that association of *Halichondria panicea* with the erect coralline alga *Corallina vancouveriensis* improved survival of the sponge in higher intertidal zones by providing desiccation protection. Complicating this association is the ability of the coralline algae to outcompete the sponge if herbivorous chitons that feed on the alga are absent (Palumbi 1985).

The possibility of nutritional collaboration between sponges and macroscopic algae has been studied for the apparently obligate association of the tropical Australian *Haliclona cymiformis* (Esper, 1794) with the red alga *Ceratodictyon spongiosum* Zanardini, 1878 (Grant et al. 1999), which is able to propagate efficiently as an association (Trautman et al. 2003). Although some photosynthate transfers from alga to sponge, the sponge still gains most of its nutrition from filter feeding, and the authors conclude that the primary function of the alga is more likely to be structural. However, the alga may benefit in nutrient poor water by the cycling and conservation of nitrogen within this association (Davy et al. 2002).

One alga-sponge association reminds us to keep our minds open while studying sponges, as they have come up with devices that we are unlikely to have even imagined: Gaino and Sarà (1994) discovered that a siphonaceous green alga, *Ostreobium* Bornet and Flahault, 1889, may be enabled to grow along the radially arranged silicious spicules of *Tethya seychellensis* (Wright, 1881) by the spicules working like fiber-optic lights, directing sunlight deep into the body of the sponge.

Different from these algal associations, in which the sponge and alga live interspersed with each other, are sponges that live on vascular plants, such as seagrass blades in estuaries (Fell and Lewandrowski 1981) and water hyacinth roots (Taveres et al. 2005). In these cases, the plants serve primarily as substrata and the plant life cycle can impose a degree of ephemeralness on the life history of the sponges (e.g., Fell and Lewandrowski 1981).

Fig. 2. A cluster of Adriatic sponges growing upon each other “from miniature cave in Polari Bay (drawing after photograph and preserved specimens before dissecting). The main supporter of most of the assemblage is *Fasciospongia cavernosa* (a). Epizoic species which in parts are also supporters are: *Ircinia spinosula* (b), *Crambe crambe* (c), *Ircinia oros* (d), *Clathrina falcata* (e), *Buska* sp. (Bryozoa, f), *Sycon* sp. (g), *Antho involvens* (h), *Leuconia solida* (i), *Cornularia cornucopiae* (Anthozoa, j) (1/2×).” The figure and caption are from Rützler (1970), reproduced with permission of *Oecologia* (Berl.), vol. 5, p. 87, © 1970 Springer Science and Business Media.



Mangrove roots provide stable, long-lived substrata for a diverse and abundant sponge fauna (e.g., Sutherland 1980; Rützler et al. 2000), and the associations between these trees and the sponges living on their prop roots are complex. Sponges living on mangrove roots (Fig. 1d) have been demonstrated to increase root elongation rate (2- to 4-fold) and decrease root infestation by boring isopods (Ellison and Farnsworth 1990; Ellison et al. 1996). Mangrove roots grew adventitious roots into some sponges, and at least one of the most common sponge species, *Haliclona* (*Reniera*) *implexiformis* (Hechtel, 1965), grows significantly faster on roots (Fig. 1d) than on PVC pipes in the same location (Ellison et al. 1996). Stable-isotope analyses suggest transfer of dissolved inorganic nitrogen from sponge to mangrove and transfer of carbon from mangrove to sponge (Ellison et al. 1996).

Sponges as hosts of single-celled autotrophs

Photosynthetic single-celled organisms, from cyanobacteria to dinoflagellates, are common symbionts of sponges and have been demonstrated to be beneficial in a wide variety of taxa (e.g., Wilkinson 1978; Wilkinson and Fay 1979; Wilkinson 1983b; Rützler 1981; Rossell and Uriz 1992; Thacker 2005). A substantial majority (80%) of sponge individuals, and 9 of the 10 most abundant species, inhabiting Great Barrier Reef sites far from shore harbor cyanobacteria; and many sponges exhibit growth forms that appear well designed to expose their guests to sunlight (Wilkinson 1983b). Wilkinson (1987) pointed out substantial differences in the proportion of photosymbiont-harboring

sponge species near shore (0%) vs. middle distances from shore (20%–64%) vs. far from shore (5%–90%) on the Great Barrier Reef, and suggested that these reflect differences in the nutrient content of the ambient water, and therefore the relative ability of sponges to support themselves solely through filter feeding. Taking the comparison a step further, Wilkinson (1983b) suggested that the relative rarity of phototrophic (i.e., relying on their photosynthetic symbionts for at least 50% of their energy requirements) sponges in the Caribbean reflects ocean-scale differences in water column nutrient availability in tropical seas.

The enormous populations of cyanobacteria that can be hosted by a sponge is reflected in the term cyanobacteriosponge (Rützler and Muzik 1993). One indication of the great advantage that might be gained by the hosts is the ability of encrusting host sponge species to grow rampant over live reef corals on stressed reefs (Rützler and Muzik 1993). Although cyanobacteria are found in many sponge species, in a phylogenetic sense the association is not random: all of over 100 sponge species found to host cyanobacteria are in only 26 of the recognized 72 demosponge families (Diaz and Ward 1999). Four genera (*Aplysina*, *Xestospongia* de Laubenfels, 1932, *Dysidea*, *Theonella* Gray, 1868) are particularly rich in these associations, with 5–10 species in each genus hosting cyanobacteria (Diaz and Ward 1999).

Filamentous cyanobacteria have been documented in the dictyoceratid *Oligoceras violacea* (Duchassaing and Michelotti, 1864) in the Caribbean by Rützler (1990), and in another dictyoceratid, *Dysidea herbacea* (Keller, 1889), on the Great Barrier Reef by Hinde et al. (1999). In both cases, the

proportion of cyanobacterial biomass to overall biomass was particularly high, in *O. violacea* as much as half of the total cell volume of the association. Some symbiotic prokaryotes collected in different oceans are indistinguishable by electron microscopy (Rützler and Muzik 1993) or by 16S rRNA (e.g., Usher et al. 2004a, 2004b), suggesting that these are long and well-established associations. Shading of another dictyoceratid – filamentous cyanobacterium association, *Lamellodysidea chlorea* (de Laubenfels, 1954) – *Oscillatoria spongelliae* (Schulze) Hauck, 1879, for 2 weeks resulted in loss of 40% of the area covered by shaded individuals, indicating dependence of the host sponge on these symbionts (Thacker 2005). Coevolution of sponges and cyanobacteria is further indicated by vertical transmission of symbionts in *Chondrilla australiensis* Carter, 1873, via incorporation into eggs (Usher et al. 2001), and in the unusual giant larvae of *Svenzea zeai* (Alvarez, van Soest and Rützler, 1998) (Rützler et al. 2003).

As previously pointed out by Rützler (1990), one curious pattern shared by the Caribbean, Mediterranean, Red Sea, and tropical Pacific is that dinoflagellates (zooxanthellae) in sponges inhabit primarily excavating sponge species in the order Hadromerida. Rich brown colors, ranging from the golden medium brown of *Cliona varians* (Duchassaing and Michelotti, 1864) (Fig. 1l) to an almost black brown in *Cliona caribbaea* Carter, 1882, indicate excavating species that can be packed with zooxanthellae. Clear positive influence of zooxanthellae on growth rate of *Cliona viridis* (Schmidt, 1862) was demonstrated by comparisons of shaded and unshaded individuals (Rosell and Uriz 1992). Another hadromerid, *Cervicornia cuspidifera* (Lamarck, 1815), that lives with its base anchored in sediments and its spire-shaped top exposed, also harbors zooxanthellae in the erect portion (Rützler and Hooper 2000). Dinoflagellates morphologically similar to scleractinian zooxanthellae are also found in *Haliclona* sp. 628 growing in channels at Heron Island, Great Barrier Reef (Garson et al. 1999; Russell et al. 2003). Alkaloids produced by the sponge cause coral tissue necrosis, and the authors suggest that zooxanthellae are co-opted by the sponge (along with nematocysts) as it kills the coral.

Heterotrophic single-celled organisms hosted by sponges

Heterotrophic prokaryotes appear to be ubiquitous symbionts of sponges, even though sponges are efficient consumers of bacteria (Reiswig 1971, 1974; Pile 1997, 1999). The great proportion of a “sponge” that can actually be bacteria is reflected in Reiswig’s (1971) term “bacteriosponge” applied to *Verongia gigantea* (= *Verongula reiswigi*). The difficulty of culturing symbiotic bacteria has stymied identification, but molecular and microscopy techniques have begun to ease this difficulty. For example, fluorescence in situ hybridization has been used to analyze bacterial symbionts of *Aplysina cavernicola* (Friedrich et al. 1999), and this technique was combined with 16S rRNA sequencing to analyze bacterial diversity in *Rhopaloeides odorabile* Thompson, Murphy, Bergquist and Evans, 1987 (Webster et al. 2001). An enormous variety of heterotrophic bacteria, including representatives of seven divisions, have been identified by comprehensive surveys using 16S rDNA sequences (Hentschel et al. 2002).

Intriguing patterns in distribution among taxa and among oceans are being discovered. One indication of the possibility of tight coupling between host sponges and their symbionts is the similarity of symbiotic bacteria over time, even after 11 days of starvation or antibiotic treatment of their sponge hosts (Friedrich et al. 2001). A hypothesis of co-speciation of sponges in the order Halichondrida and their bacterial symbionts has been supported by comparative phylogenetic analysis based on the gene coding for cytochrome oxidase subunit I (*COI*) (Erpenbeck et al. 2002). A group of filamentous Archaea is likewise consistently found embedded in the perispicular collagen of sponges in the genus *Axinella* Schmidt, 1862, but was not found in sponges of 15 non-axinellid species (Margot et al. 2002). Host sponges retained their Archaea while living in aquaria for 3 and 6 months, and each of three sponge species harbored a species-specific single phylotype, suggesting a co-evolved symbiosis (Margot et al. 2002). Maternal transmission of symbionts is not confined to prokaryotes. A yeast hosted by three species of *Chondrilla* Schmidt, 1862 is also transmitted to the next generation via the oocytes (Maldonado et al. 2005). The development of this first reported yeast–sponge symbiosis is likely to date from before or during the diversification of species of *Chondrilla*, as the three species in which the yeast was discovered represent different biogeographic regions: Mediterranean, Caribbean, and Australian Pacific (Maldonado et al. 2005).

The difficulty of culturing heterotrophic prokaryote sponge symbionts renders determination of their function in their host extremely challenging. Nitrifying symbionts add significant amounts of biologically meaningful nitrogen to tropical shallow benthic communities (Wilkinson and Fay 1979; Diaz and Ward 1997), and antifungal properties have been discovered in the prokaryote symbiont of *Theonella swinhoei* Gray, 1868 (Schmidt et al. 2000). Osinga et al. (2001) and Hentschel (2004) list a variety of possible functions of prokaryote symbionts in sponges, but in most cases what the symbiosis provides for the sponges, if anything, is largely mysterious, though these may be ancient associations (Wilkinson 1984; Sarà et al. 1998).

Pathogens in sponges

One type of symbiont differs from all the others in that the net result of the symbiosis is clear, but the identity of the symbiont is rarely known. These are the infectious pathogens. Pathogens can play decisive roles in sponge population and community dynamics. Diseases in sponges have been reported from most habitats, including Caribbean and Pacific coral reefs (e.g., Smith 1941; Reiswig 1973; Goreau et al. 1998; Cervino et al. 2000; Wulff 2006a), Caribbean mangroves (Rützler 1988), and subtidal hard bottoms in temperate North America (Shield and Witman 1993), the Mediterranean (Pansini and Pronzato 1990; Pronzato et al. 1999), and Antarctica (Dayton 1979); and many of these diseases have characteristics suggesting that they are caused by infectious pathogens. Striking in every case is that only some species, often within the same higher taxon, are affected by a particular incident of disease. In at least some cases, this pattern appears to result from species-specific pathogens (Fig. 1h). For example, disease transmission between adherent Caribbean coral reef sponges depended on whether or not they

were conspecific (Wulff 1997a, 2006a). Even adjacent sponges of different species of the same genus may differ in susceptibility, with one species consistently affected while the other remains healthy (e.g., in *Tedania* spp. (Wulff 2006b) and in *Callyspongia* spp. (K. Koltjes and J. Tschirky, personal communication (January 2006))). But in other cases, species representing particular higher taxa of sponges may be more vulnerable. A pattern of disproportionately frequent disease in keratose sponges (e.g., Smith 1941; Pansini and Pronzato 1990; Pronzato et al. 1999; Cervino et al. 2000; Wulff 2006a) was suggested by Vicente (1989) to reflect increased vulnerability owing to temperature stress in these sponges that may have evolved in cooler water. Etiologic agents have rarely been identified in sponges. In the case of disease in the mangrove sponge *Geodia papyracea* Hechtel, 1965, normally beneficial cyanobacterial symbionts appear to have become unbalanced by abiotic stresses to their host and have ended up causing disease by overwhelming their hosts (Rützler 1988). The agent causing sponge disease that decimated commercially valuable species in the Caribbean in the 1930s (Smith 1941) was presumed to be a fungus, as hyphae were observed in diseased tissue; however, the rapid colonization of necrosing sponge tissue by other microorganisms makes it uncertain what agents caused disease and what organisms colonized afterwards.

Sponges and mutualistic symbioses

An astounding array of intimate associations in which sponges participate are mutually beneficial. Although in some cases in which mutual benefit seemed obvious, closer scrutiny, especially with experimental manipulations, has demonstrated that they are not necessarily beneficial; other associations that appeared to be obvious cases of competition (e.g., sponges–corals, sponges–sponges) have been experimentally demonstrated to be mutually beneficial for participants. Summarized from the foregoing discussion of symbiotic associations of sponges (references are supplied throughout the above text) are the following demonstrated benefits.

Benefits that sponges offer intimate associates include (a) protection from boring organisms by coating the host surfaces (e.g., scleractinian corals, mangrove roots, bivalves); (b) protection from predators by coating surfaces (e.g., bivalves, octocorals, other sponges); (c) protection from predators by providing shelter (e.g., juvenile spiny lobsters, small crustaceans, ophiuroids, scyphozoans, zoanthids); and providing (d) food (e.g., polychaetes, snapping shrimps, copepods, isopods, amphipods) and (e) nitrogen (e.g., erect red algae, mangroves).

Benefits gained by sponges from intimate associates include (a) protection from predation (e.g., coralline red algae, scyphozoans, zoanthids); (b) protection from desiccation (e.g., coralline red algae); (c) skeleton reinforcement that might help the sponge both withstand water movement and avoid expenditures on skeletal production (e.g., coralline red algae, scyphozoans, hydroids, other sponges); (d) substratum on which to live (e.g., corals, bryozoans, mangrove roots, seagrass, other sponges); (e) nutrition (e.g., cyanobacteria, heterotrophic prokaryotes, dinoflagellates); and (f) enhanced water currents (e.g., bivalves, bryozoans).

The variety of types of mutual benefit, and the array of organisms that truly collaborate with sponges, suggests that the uniquely homogeneous and readily rearranged structure of sponges preadapts them to development of intimate associations which synergistically improve life for both partners. Clonal organisms in general may be more susceptible to the evolution of mutually beneficial intimate associations, as both host and guest, by increasing the probability that each step in the development of mutualism will progress (Wulff 1985) as follows: (i) clonality may increase the chances of an intimate association developing at all, because of the relatively low dependence of each portion of an organism on the integrity and functioning of the other portions; (ii) once an association has developed, clonality may also increase the chances of an intimate association becoming permanent and being able to spread, as host and guest can grow and propagate as a unit, potentially forever; and (iii) as well, clonality may increase the chances that a permanent association can transform into a mutualism, because the possibility of eternal association increases the value of the host and guest to each other (Wulff 1985). Sponges are clonal to an extent far beyond any other multicellular animals in that they can be dissociated even to the point of individual cells (e.g., Wilson 1907). They can accommodate intimate association with organisms of any shape or habit without mortal disruption of their overall integrity, because they rely so little on that integrity. Likewise, tandem proliferation of an intimate association involving sponges can proceed on any scale. Sarà et al. (1998) have suggested that epigenesis plays a key role in regulating intimate associations with sponges. If this is the case, the perception that these associations verge on behaving as superorganisms is close to the mark. The assertion that sponges are incredibly simple must be modified to acknowledge that they have devised ways of being complex by collaboration with other organisms, while simultaneously retaining the many advantages of informality and simplicity.

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