CHAPTER FOUR

ECOLOGICAL INTERACTIONS AND THE DISTRIBUTION, ABUNDANCE, AND DIVERSITY OF SPONGES

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Contents

Abstract

Although abiotic factors may be important first-order filters dictating which sponge species can thrive at a particular site, ecological interactions can play substantial roles influencing distribution and abundance, and thus diversity. Ecological interactions can modify the influences of abiotic factors both by further constraining distribution and abundance due to competitive or predatory interactions and by expanding habitat distribution or abundance due to beneficial interactions that ameliorate otherwise limiting circumstances. It is likely that the importance of ecological interactions has been greatly

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underestimated because they tend to only be revealed by experiments and time-series observations in the field.

Experiments have revealed opportunistic predation to be a primary enforcer of sponge distribution boundaries that coincide with habitat boundaries in several systems. Within habitats, by contrast, dramatic effects of predators on sponge populations seem to occur primarily in cases of unusually high recruitment rates or unusually low mortality rates for the predators, which are often specialists on the sponge species affected. Competitive interactions have been demonstrated to diminish populations or exclude sponge species from a habitat in only a few cases. Cases in which competitive interactions have appeared obvious have often turned out to be neutral or even beneficial interactions when observed over time. Especially striking in this regard are sponge–sponge interactions in dense sponge-dominated communities, which may promote the continued coexistence of all participating species. Mutualistic symbioses of sponges with other animals, plants, or macroalgae have been demonstrated to increase abundance, habitat distribution, and diversity of all participants. Symbiotic microbes can enhance sponge distribution and abundance but also render their hosts more vulnerable to environmental changes. And while photosynthetic symbionts can boost growth and excavation rates for some sponge hosts, in other cases sponge growth proceeds as well or even better in diminished light.

Metrics chosen for evaluating sponge abundance make a substantial difference in interpretation of data comparing between different sites, or over time at the same site. In most cases, evaluating abundance by volume or biomass allows more ecologically meaningful interpretation of influences on distribution and abundance than does evaluating abundance by numbers of individuals or area covered. Accurate identification of species, and understanding how they are related within higher taxa, is essential. Studies in every habitat have illustrated the great power of experimental manipulations, and of time-series observations of sponge individuals, for understanding the processes underlying observed patterns; in many cases, these processes have been revealed to be ecological interactions.

Key Words: sponges; abiotic factors; ecology; interactions; predation; spongivory; competition; mutualism; abundance; diversity

1. INTRODUCTION

A surge of studies on the interactions of sponges with other organisms and with their abiotic environments has bolstered confidence in our general understanding of how sponges fit into their ecosystems. They consume the smaller sizes of particulate organic material and, in collaboration with symbiotic microbes, dissolved organics. Some sponges receive significant nutrition via photosynthetic symbionts. Sponges are in turn fed upon by a small number of charismatic animals such as angelfishes, nudibranchs, sea stars, and hawksbill turtles. Sponges are relatively successful in competition for space against non-sponge taxa, and they are masters of asexual propagation and regeneration after partial mortality. Many of their interactions are moderated by chemistry, produced either by the sponges or by their symbionts. Sponges can have profound effects, both positive and negative, on substratum stability and suitability for other organisms. Sponges are especially adept at striking up collaborative associations with organisms of all types, including other sponge species.

Rapidly changing conditions in coastal marine ecosystems are, however, generating questions that reveal uncertainties in our ability to predict what will happen to particular sponges under particular circumstances, and what the consequences will be for the ecosystems in which they live. Concerns have been expressed about both decreases and increases in sponges. For example, if plankton production rates increase due to increased water column nutrients, will sponges be clogged or grow faster? Conversely, if sponge abundance diminished dramatically, would the water column become murky, and sewage and mariculture effluents become embarrassingly even more evident? If marine protected areas inspire an upwards swing in populations of angelfishes and hawksbill turtles, will sponges be consumed to the point that coral reefs crumble and recovery of damaged reefs is stymied, or will corals flourish? If macroalgae suffer losses to disease, will sponges vanish also or increase? Will sponge pathogens flourish and photosynthetic symbionts flee in response to rapid warming of seawater? If sponge abundance increases, will it be at the expense of other sessile organisms or will it improve water quality and substratum stability? Can sponges perform homeostatic miracles, or will they finally be defeated by deteriorating conditions and vanish, taking with them the enormous number of species with which they have established symbiotic associations? Lurking within each of these questions are the challenging additional questions: Is sponge diversity as important as overall sponge abundance? Does it matter exactly which sponge species are involved, or can all of the sponges be lumped together in prognostications about the trajectories of coastal marine ecosystems?

Although abiotic factors are important first-order filters dictating which sponge species can thrive at a particular site, ecological interactions can play substantial roles in influencing distribution and abundance. Interactions with other organisms modify the influences of abiotic factors on distribution, abundance, and diversity in two main ways: by further constraining habitat distribution or abundance due to competitive or predatory interactions and by expanding habitat distribution or abundance due to beneficial interactions that ameliorate otherwise limiting circumstances. Because of the possibility of reciprocal evolutionary adjustments for ecological interactions, but not for abiotic factors, distinguishing the relative importance of abiotic and biotic influences on sponges is necessary for understanding the adaptive significance of sponge traits. On an ecological timescale as well, predictions cannot be made accurately unless distinctions are made between influences of abiotic and biotic factors. As abiotic factors change, sponge distributions change accordingly, but changes resulting from losses or gains of species with which sponges engage in significant ecological interactions can be much more rapid. Predators can be quickly eliminated by unsustainable fishing, competitors can be lost to disease in just a few months, and symbionts can be sufficiently perturbed to flee in a flash. In this review, I aim to gather current evidence on how ecological interactions with food, competitors, predators, pathogens and parasites, and mutualistic associates are intertwined with abiotic factors to influence distribution, abundance, and diversity of marine demosponges. Space considerations have forced me to defer consideration of many important aspects of sponge ecology (e.g. sponges as biomonitors, population biology and life history strategies, community dynamics, and ecosystem functional roles) in order to focus specifically on how both abiotic factors and ecological interactions have been demonstrated to influence distribution and abundance. Unequal allocation of space for coverage of the habitats considered reflects differences in the degree to which research has been focused on revealing processes.

Underrepresentation of the influence of ecological interactions on distribution, abundance, and diversity of sponges is likely in the literature, in large part because time-series observations and experimental manipulations tend to be required to demonstrate how interactions constrain or enhance distribution and abundance. Some habitats are not amenable to manipulative experiments, and shipboard-based studies are often constrained to a single short visit to each site. In a biogeograpic comparison of sponge distribution patterns on cobbles across oceans, Bell and Carballo (2008) suggest that an apparent pattern of influence by biotic interactions in the Caribbean relative to the Indo-Pacific may simply reflect the greater degree to which sponges have been studied with experimental manipulations in the Caribbean.

Different types of ecological interactions are not equally easy to demonstrate, and this influences how frequently interactions are reported in the literature (e.g., Bergquist, 1978, 1999; Becerro, 2008). Predation can be observed straight away, if experimental design takes into account natural ability of predators to detect and react to prey. Habitat transplants that result in clear bite marks outside cages, but none inside, can give unambiguous answers; but comparisons of size changes inside and outside of cages can be difficult to interpret, as cages may alter sponge feeding. Competition takes longer to demonstrate, as it requires time-series observations of individuals of one species actually overgrowing and killing, or otherwise inhibiting, individuals of another species. Sometimes competition can be inferred if it can be seen that an apparently overgrown species is recently dead under another, although overgrowth could have occurred after death. Clear zones of inhibition can be seen in some cases (e.g. Turon *et al*., 1996). Simple scores of apparent overgrowths are not necessarily evidence of competition for sponges, which are known for their uncanny abilities to tolerate or even thrive under epizoism. Overgrowth by sponges benefits many other species (review in Wulff, 2006d). Sponges growing right up to the edge of living tissue of corals can be either engaging in competition or increasing coral survival, and these possibilities cannot be distinguished without time-series observations (Goreau and Hartman, 1966; Wulff and Buss, 1979). Mutualism is most difficult to demonstrate, as it adds another layer of complexity. A problem must be identified that is only solved in the presence of the mutualistic partner, and thus competition, predation, or inhibition by some abiotic factor has to be demonstrated to differ with and without the mutualistic partner. Benefit must be measured in terms of increased growth, reproduction, or survival, and this requires following the same individuals over time. Sponges are known for their wide intraspecific variation in growth rates and in some cases defensive chemistry, imposing a requirement for control of genotype in experiments. Added to all this is the need to study potential mutualisms for long time periods because long-lived organisms, such as many sponges, may benefit from collaboration only during events that occur at time intervals that are long by human perception.

1.1. Evaluating distribution, abundance, and diversity of sponges

Distribution, abundance, and diversity are not simple, straightforward entities, especially for sponges. Abundance can be measured by numbers of individuals, area, or volume, and each of these can be measured or estimated in a variety of ways. The degree to which species are lumped together in estimating abundance varies from "sponges" (i.e. all sponges lumped together), to groups of sponges defined by growth form or other observable attribute, to painstakingly sorted and named species and subspecies. Likewise, influences on abundance are variously reported as applying to all sponges or only to particular species. Distribution boundaries can be considered at various scales, including microhabitat, habitat, and geographic; and for any particular species, different factors may constrain or extend distribution at each of these scales. Diversity measurement can be simply number of species or can involve an index that combines number of species with relative abundance, compounding interpretation struggles due to inappropriate choice of an abundance metric. Before discussing how ecological interactions influence distribution, abundance, and diversity of sponges, I briefly consider how these variables are evaluated.

1.1.1. Distribution and abundance

Sponges can dominate the biomass and species representation in benthic marine communities to the point that referring to "sponge communities" is apt. On coral reefs, mangrove prop roots, rocky intertidal shores, caves and crevices, subtidal hard bottoms in Antarctica and western Canadian fjords, and even some subtidal soft bottoms, sponge accumulations can be so dense that the underlying substratum appears irrelevant; but in other habitats sponges are minor members. Relative merits of evaluating sponge abundance by numbers of individuals, percentage cover, or volume, and the appropriate situations, for each metric, have been discussed at length and illustrated with examples by Rützler (1978, 2004) and Wulff (2001, 2009).

Conclusions from abundance studies are highly dependent on metrics chosen, as illustrated by the few studies that have provided more than one metric for explicit comparisons. Wilkinson's (1987) summary table of sponge abundance in terms of both number of individuals and biomass at various Caribbean and Great Barrier Reefs (GBRs) highlights how divergent conclusions about sponge biogeography and the environmental parameters influencing abundance can be, depending on the abundance metric used. A figure summarizing distribution patterns of the most prominent 27 sponge species on fore-reef slopes of the GBR illustrates the lack of coincidence of relative abundance in terms of numbers of individuals versus biomass (Wilkinson and Cheshire, 1989). For most of the 27 species they evaluated on 6 reefs, numbers of individuals and biomass do not vary together. On rocky substrata from 0 to 20 m, Preciado and Maldonado (2005) evaluated sponge abundance by both frequency in sampling quadrats and dry weight. Although the five species with the highest frequency of occurrence were all in the top 15 species (out of 85 species total) with respect to dry weight, the authors drew attention to three species with substantial biomass (ranked 11, 14, and 22 by dry weight) that were each found in only 1–3 of the 257 sampling quadrats that included sponges. Description of community composition by growth form in a shallow reef Caribbean community in Panama resulted in massive, encrusting, thick encrusting, and erect-branching sponges equally represented with respect to area. A very different picture of the community is conjured up by volume comparisons, as total volume of erect-branching sponges is 30 times that of encrusting sponges, and volume of massive sponges is 10 times that of encrusting sponges (Wulff, 2001).

Comparisons of community composition between sites also depend heavily on the metric used for abundance. For example, species composition at three mangrove sites in Belize and Panama appears very different when evaluated by numbers of individuals, but very similar by volume, with a single species, *Tedania ignis* Duchassaing and Michelotti, 1864, constituting 49–57% of the total, and the nine species found at all three sites constituting 73–89% of the total volume (Wulff, 2009). *T. ignis*, the "fire sponge", is the icon species for Caribbean mangrove prop roots, consistently standing out as present and dominant in the fauna. But the degree to which it appears to be dominant varies with the metric chosen. *T. ignis* in the above study constituted 8.4–20.4% of the individual sponges, it was recorded on 11–34% of individual roots at nearby sites (Diaz *et al.*, 2004), by photographs of root segments in the Florida Keys it covered 16.7% of the root area (Bingham and Young, 1995), and by line transects along the lengths of prop roots it covered 5–12% of area in Venezuela (Sutherland, 1980). By comparison with these abundance measures, 49–57% of total volume seems to inflate the relative abundance of *T. ignis*; yet this species contributes to the mangrove ecosystem by pumping and filtering water in proportion to its volume and provides shelter and food for inquilines and predators in proportion to volume as well.

Interpretations of community dynamics can vary from "highly stable" to "wildly fluctuating", for the same community, depending on metrics used for abundance. Censuses over 11 years on a shallow coral reef in San Blas, Panama, showed decrease by 53% by number of individuals but only 10.6% by volume (Wulff, 2001). Likewise, data from four complete censuses, at yearly intervals, of mangrove roots at a site in Belize, support a conclusion of enormous change by number of individuals, which varied by 50%. The opposite conclusion of great stability would be warranted based on volume data, which varied by only 12% (Wulff, 2009). In the Florida Keys, over a 4-year period, the opposite pattern emerged from data collected along randomly placed transects: density of sponge individuals increased, while area covered decreased (Chiappone and Sullivan, 1994).

The same site, evaluated by different researchers using different techniques, may appear to have changed quite dramatically in species composition solely due to employment of different evaluation metrics. One of the several illustrative examples gathered by Diaz *et al.* (2004) is Twin Cayes in Belize, which in three different studies was reported to host 20, 54, and 35 mangrove sponge species. Biogeographic comparisons may be misinterpreted if techniques applied differ. Apparently contrasting community dynamics on mangrove root censused in Venezuela (Sutherland, 1980) and the Florida Keys (Bingham and Young, 1995) led Bingham and Young to suggest that tropical systems are more stable than subtropical; but Sutherland included entire roots while Bingham and Young followed particular root segments the size of a camera framer. Because sponges "move" up and down the roots as they grow, it is possible for them to slip out of the spot monitored while still remaining present in the community. Sará (1970) illustrated the degree to which sponge individuals can shift the particular space they occupy while remaining in the community with time-series drawings of encrusting sponges in a Mediterranean cave that show the same individuals participating in the community, but in continuously shifting spots. Hughes (1996) followed sponges and corals in 12 1 m^2

quadrats by taking yearly photographs for 16 years. Sponges were remarkably constant in overall community structure, as measured by numbers of individuals and taxonomic distinction to genus. Because individual sponges could be followed in the time-series photos, he was able to document that apparent stasis was actually the result of very high rates of flux, with high rates of mortality, partial mortality, fragmentation, fusion, and recruitment. On a shallow Caribbean reef in Panama, disturbing losses of 20 of the original 39 species have been revealed by 5 full censuses of 16 m^2 (Wulff, 2006a). Declines in the same set of species on nearby reefs indicated that the problem was not confined to the study reef, but this is the only coral reef site in which individual sponges of all species have been followed over time, so there is no way to know if similar losses have been occurring elsewhere. By contrast, relying on random transects can leave result in unanswerable questions such as whether or not a shift to more but smaller individuals indicates (1) mortality of all residents, followed by recruitment, or (2) fragmentation resulting from partial mortality, or (3) merely chance placement of transects in subsequent monitoring periods. An advantage of censusing the same plots in time sequence is that it eliminates the lurking concern that apparent changes are merely artefacts of the combination of high species diversity and spatial heterogeneity.

Ultimately, the questions at hand must determine which abundance metric is employed. Trophic interactions, such as how much a sponge can filter from the water and how many bites can be taken from it by predators, scale with volume (e.g. Reiswig, 1974; Wulff, 1994), while area covered may be key for mutualisms involving sponges protecting their hosts from borers or consumers (review in Wulff, 2006d). Percentage of the substratum covered by sponges may indicate what space is unavailable to other sessile taxa, if the surface is homogeneous. Percentage cover has been frequently used in coral reef studies because of its appropriateness for corals, of which the live tissue is a consistently thin layer, regardless of overall growth form. But for sponges, ecological interpretation of percentage cover depends on the growth forms represented. Sponge volume can differ orders of magnitude for the same percentage cover, reflecting a range in thickness from 1 mm to over 1 m. Number of individuals can be used appropriately for evaluation of sponge species that do not fragment, and to compare disease prevalence or recruitment rates. More than one metric can be useful. For example, using solely numbers to evaluate the effects of disease may cause interpretation meltdown if fragmentation at lesions increases the number of individuals. However, numbers of individuals can be used in conjunction with volume to understand effects of fragmenting agents such as disease and storms (Wulff, 1995a for a hurricane example). Studies in which both numbers and biomass have been reported are particularly helpful for biogeographic comparisons (e.g. Wilkinson, 1987; Wilkinson and Cheshire, 1989).

1.1.2. Diversity

Taxonomic challenges, combined with high species diversity, prompt the question: Is it really important to accurately identify sponge species in ecological studies? The answer is unambiguously: Yes. Similar, closely related species are likely to share many important traits, but to differ in at least one ecologically important trait. Lumping species, even by genus, can lead to mistakes in estimation of population sizes, habitat distributions, and predicting responses to changes. For example, the common Caribbean mangrove fire sponge, *T. ignis*, was considered to be a habitat generalist that was unusual in inhabiting both mangrove roots and seagrass meadows (Diaz *et al*., 2004). Reciprocal transplant and feeding choice experiments, followed by morphological and molecular study, revealed two species, *T. ignis* and *Tedania klausi* Wulff, 2006, that are distinguished ecologically by differences in palatability to sea stars (and therefore ability to inhabit seagrass meadows), susceptibility to disease, and ability to tolerate wide swings in temperature and salinity (Wulff, 2006c). Likewise, very similar sympatric Mediterranean *Scopalina* species were considered to be a single more variable species until molecular markers were used to distinguish them (Blanquer and Uriz, 2007). Once determined to be two species, life history differences between them could be distinguished that are sufficient to facilitate coexistence: *Scopalina blanensis* Blanquer and Uriz, 2008 responds opportunistically to seasonal environmental changes in temperature and food availability, while *Scopalina lophyropoda* Schmidt, 1862 responds in a more conservative manner, with similar behaviour and relatively low mortality throughout the year (Blanquer *et al*., 2008). These are only two examples among many. Phenomenal sponge species diversity in many habitats motivates attempts to discern categories of sponges that are based on functional roles, intimate associations, suites of morphological characters, and differential vulnerability to hazards. Some divisions into categories can be made by inspection, as whether or not a sponge excavates solid carbonate or has an encrusting, massive, or tubular morphology. Categorization by other attributes, such as relative resistance to smothering by sediments, palatability to a particular predator, or possible benefits from microbial symbionts requires experiments. Grouping sponges as ecological or morphological units for data collection (i.e. not identifying to species) does not provide the same quality of information as grouping taxonomically identified sponges for subsequent analysis.

2. INFLUENCES OF ABIOTIC FACTORS AND ECOLOGICAL INTERACTIONS ON SPONGES IN VARIOUS HABITATS

Substratum type, stability, continuity, and depth; and environmental factors related to water quality, movement, and food availability; as well as ecological interactions have all been implicated as influencing distribution and abundance of sponge species. Factors do not vary alone, and so although abiotic factors often correlate well with the habitat distribution of particular sponge species, the underlying processes that actually curtail or enhance distribution and abundance are often not revealed without experiments and time-series observations. I have attempted to impose some linear organization on what is really a multidimensional interconnected network of causal factors, by focusing in turn on a series of habitat types, in each case seeking to illuminate what has been learned of how interactions with other organisms add to abiotic factors to influence distribution, abundance, and diversity of sponge species.

2.1. Subtidal rocky substrata—walls, plateaus, canyons

2.1.1. Abiotic factors

On subtidal rocky substrata, distribution and abundance of sponge species have been demonstrated to be influenced by water movement, depth, light, inclination, and other aspects of bottom topography, as well as the stability and continuity of the substratum.

Vigour of water movement has presented itself as a consistently important abiotic factor, decreasing overall abundance and constraining growth forms of sponges, and allowing only a stalwart few species to live at very exposed sites. For example, at Lough Hyne, Ireland, sponge faunas on cliffs differed between high- and low-energy environments, indicating the primary influence of wave energy; of the 96 species, only 25 were shared between cliffs and cobbles, indicating additional distinction by substratum stability (Bell and Barnes, 2003). Likewise, a diverse sponge fauna of 82 species on temperate rocky reefs in New South Wales, Australia, was revealed by ordination to consistently divide into distinct sets of species at exposed versus sheltered locations (Roberts *et al.*, 2006). Even at this depth of 18–20 m sponge cover reflected differences, with at least 40% cover of sponges at the four sheltered locations but only 25% cover at four exposed locations. Sponge morphologies reflected hydrodynamic differences, with a preponderance of encrusting forms at exposed sites and erect forms at sheltered sites. The authors pointed out the impossibility of comparing solely exposure, as sheltered sites were also more influenced by pulses of freshwater runoff, as well as human activities.

In addition to directly disturbing organisms, water motion can wreak havoc by setting sediment in motion. An extremely high level of species turnover on shallow subtidal rocky shores at Mazatlán, Mexican Pacific, was caused by physical disturbance involving a combination of wind-motivated water movement and sediment movement and deposition (Carballo *et al.*, 2008). Sand-sized sediment (coarse sand in summer months), which is only suspended by rough water, underscored the importance of the combination of factors. By frequently monitoring permanent quadrats over

6 years, Carballo *et al.* (2008) could follow fates of individual sponges, allowing them to definitively conclude that the influence of physical factors was sufficient to prevent competitive interactions from structuring the community.

A recurrent pattern in studies focused on subtidal hard-bottom sponges is inability to predict species composition of the assemblages at a particular site based on environmental attributes of that site and geographic distance from known sites. Exploration of canyons off of Victoria, SE Australia, yielded 165 sponge species, 79% of which were collected in only one of the five canyons (Schlacher *et al.*, 2007). Species turnover was high between sites within a canyon, as well as between canyons, and geographic distance between sites was a poor predictor of community similarity. The authors pointed out that distribution of rare species can be underestimated, especially by sled sampling, inflating the percentage of species that appear to inhabit only one site. Nevertheless, these data indicate large differences in sponge assemblages among sites. The generally high abundance of sponges in these hydrodynamically and topographically complex canyons was attributed to the great abundance of food for filter feeders. Species diversity decreased with depth in the 114–612 m range collected and increased with heterogeneity of substratum.

On subtidal rocky surfaces representing nine habitat types between 0 and 20 m on the northern Atlantic coast of Spain, Preciado and Maldonado (2005) found that substratum inclination best explained variation in sponge cover and diversity among sites. Sponge diversity (a total of 85 species in the 18 habitat-zones sampled) and biomass per quadrat were significantly greater on vertical than on horizontal substrata. They pointed out that, while the frequent dominance of horizontal surfaces by macroalgae may fuel the assumption that a disjunct distribution of sponges and macroalgae indicates that algae outcompete sponges, algal abundance is not the sole factor that varies with inclination. Sediment on horizontal surfaces may also impede sponges. As well, sponge abundance was higher on vertical substrata even at depths below the range of macroalgae. Lack of influence of competition with algae was also suggested by a pattern of sponges that were distributed independently of the presence or absence of algae, a pattern also found in the Cabrera Archipelago, in the Mediterranean off Majorca by Uriz *et al.* (1992). In the Gulf of Maine, Witman and Sebens (1990) also suggested that decrease in sponge cover by 2/3 between 45 m (i.e. below the lower limit of kelp depth distribution) and 60 m was due to increased sediment cover observed on horizontal surfaces.

The primary constraint on habitat distribution may not reveal itself without experimental manipulation. Focusing on individual species and explicit comparisons between species can help to clarify which processes influence sponge distribution and abundance. In Mazatlan Bay, Mexico, the most abundant organisms between 2 and 4 m, the sponge *Haliclona caerulea*

Hechtel, 1965 and its symbiotic associate, the branching calcareous red alga *Jania adhaerens*, were experimentally demonstrated to be constrained from living more shallowly by high mortality due to wave action (Carballo and Ávila, 2004). In conjunction with water movement, topography can influence the impact of sediment on sponges. Sediment can smother sponges by clogging their aquiferous systems. When growth of an undescribed Western Australia *Haliclona* sp. was compared at high and low levels of light, sediment, and water flow, in order to determine what factors confine it to the undersides of limestone ledges, only the low sediment treatment reduced weight loss of explants (Abdo *et al.*, 2006).

2.1.2. Ecological interactions

Distribution boundaries that coincide with abiotic factors are often caused by interactions with competitors, predators, and symbiotic associates. Macroalgae on continental shelf temperate zone hard bottoms can add their influence to topographical variations. Barthel (1986) described how *Halichondria panicea* Pallas, 1766 improved its ability to cope with medium to strong currents at the entrance of Kiel Fjord, Baltic Sea, by growing on red macroalgae that swayed with the current. Sponges and macroalgae have the opposite interaction in the central Gulf of Maine, where Witman and Sebens (1990) demonstrated clear zonation of sponges on subtidal hard substrata, with differences in sponge species composition with depth and also on vertical versus horizontal surfaces. Where kelps were abundant on horizontal–sloping surfaces above 40 m (the extinction depth of laminarian algae) sponge cover was low. Percentage cover increased with depth to a maximum of 20.8% at 45 m. High incidence of predation by a nudibranch and sea star was deemed to influence small-scale sponge distributions (Shield and Witman, 1993), but not large-scale zonation patterns, which were most influenced by negative interactions with the kelps.

On rocky reefs of the Investigator Group of islands, South Australia, a dense fucoid canopy with green algal understory dominated exposed surfaces, and although sponges were growing beneath the algae at low percentage cover, an especially rich and abundant sponge fauna was found in caves and under overhangs (Sorokin *et al.*, 2008). Likewise, greater sponge cover under rocks at Lough Hyne, Ireland, was attributed to macroalgae growing on the upper surfaces (Bell and Barnes, 2003), and Sará (1970) remarked on decreased persistence of individual sponges nearest the mouths of Ligurian caves, where they shared the substratum with macroalgae instead of other sponges.

Adding additional interactions can reverse sponge distribution patterns relative to macroalgae. At sites near Wollongong, New South Wales, Australia, sponge cover was six times higher among the kelps relative to the adjacent urchin barrens, in spite of physical disturbance by moving kelp fronds and lack of light. The lack of overlap in sponge species in the two habitats (no difference in diversity, with 10 species in each habitat) hinted at an additional factor, which was revealed to be sea urchin grazing on the barrens (Fig. 4.1). Only sponges that are chemically defended from urchins are able to live outside the kelp forests (Wright *et al.*, 1997). In the Mediterranean of NE Spain, experiments revealed that a similar set of taxa (i.e. urchins, macroalgae, and sponges) interacts very differently (Fig. 4.1). Urchin grazing facilitated growth of the sponge *Cliona viridis* Schmidt, 1862 by diminishing the fleshy seaward canopy that otherwise blocks access to sunlight for the zooxanthella symbionts of the sponge (Cebrian and Uriz, 2006; Rosell and Uriz, 1992). A second excavating sponge species that lacks photosynthetic symbionts may be favoured in competition between sponges in the darker environment that results from the absence of urchins. The next trophic level up must therefore be considered, because whether or not fishes that prey on the urchins are over-fished can determine which set of interactions prevails, by influencing urchin abundance (Cebrian and Uriz, 2006).

Aggressively invasive macroalgae have unfortunately offered opportunities to learn more about particular characteristics of algae that can affect sponges more dramatically. In Australia, Davis *et al.* (1997) documented decreased cover of sessile invertebrates, including sponges, from 48% to 23% in the 12 months following the arrival of *Caulerpa scalpelliformis* at Botany Bay, New South Wales. There was no change at reference sites during the same time period. Although sponges can be highly tolerant of epizoism, this tolerance was overwhelmed by the interwoven stolons and dense upright fronds of the *Caulerpa*, combined with the sediment they accumulated. In the Ionean Sea, Italy, Baldacconi and Corrierro (2009) also recorded substantially decreased sponge cover, but relatively little loss of species, in the 2 years during which *Caulerpa racemosa* var. *cylindracea* cover increased from scattered small bits confined to horizontal surfaces to a dense, continuous, sediment-trapping mat on all exposed surfaces. Cavity-dwelling sponges were unaffected, but on horizontal substrata, species diversity dropped from 18 to 11 and cover from 30.6% to 12.2%, and on vertical substrata species dropped from 36 to 26 and cover from 29.4% to 17.6%. The *Caulerpa* could actually anchor its stolons in the surfaces of the sponges, with the sole exception of the encrusting species *Crambe crambe* Schmidt, 1862 which was able to fend the alga off.

Macroalgae constitute a distinct set of spatial competitors against sponges because they are constrained to exposed surfaces, especially horizontal surfaces, by their requirement for sunlight, offering the possibility of refuges in the shade for sponges. Other potential competitors for space on subtidal rocky substrata include bryozoans, ascidians, and other sponges. The importance of spatial competition for sponges of the NW Mediterranean rocky sublittoral is well demonstrated by patterns in toxicity of *C. crambe* specimens, which were more toxic at sites dominated by other sessile animals relative to well-lit algal-dominated sites (Becerro *et al.*, 1997). *C. crambe*

Figure 4.1 Diversity of outcomes of interactions between sponges and mollusc and echinoderm spongivores. In Antarctica, sponge-feeding sea stars may prevent *Mycale acerata*, which grows exceptionally rapidly, from overwhelming other sponges (Dayton, 1979). Photo A. Bill Baker: *Odontaster validus* eating *M. acerata*. Photo B. Bill Baker: *Perknaster fuscus* eating *Mycale acerata*. Photo C. Bill Baker: *Mycale acerata* (lower left of photo) and *Dendrilla membranosa*. In *Alaska*, an unusually dense recruitment of the dorid nudibranch *Archidoris montereyensis* eliminated *Halichondria panicea* from a large area of the intertidal where it had dominated the space for the previous 10 years (Knowlton and Highsmith, 2000). Photo D. Jason Hall: *Archidoris montereyensis* consuming *Halichondria* cf. *panicea* in Olympic National Park, WA. In the *Mediterranean*, NW coast of Spain, herbivorous sea urchins facilitate growth of the zooxanthellate boring sponge *Cliona viridis* by diminishing fleshy algae that otherwise block sunlight (Cebrian and Uriz, 2006). Photo E. Enric Ballesteros *Paracentrotus lividus*. Photo F. Enric Ballesteros: The boring sponge *Cliona viridis*. In *New Zealand*, a nudibranch was two orders of magnitude more

chemistry discouraged not only regeneration of a key spatial competitor, the sponge *S. lophyropoda* Schmidt, 1862, but also the settlement of larvae of the bryozoan *Bugula neritina*. The authors point out that these results do not indicate unimportance of competition for space with seaweeds for sponge habitat distribution, but rather demonstrate the adaptive deployment of toxicity, as chemistry of an encrusting sponge is less likely to be effective against quickly growing single-holdfast seaweeds such as kelps and fucoids.

Topography can be related to sponge distribution constraints by interactions even in the absence of macroalgae. Off the coast of Georgia, USA, Ruzicka and Gleason (2009) related distinct sponge assemblages on vertical scarps versus plateaus to a combination of abiotic factors and predation. Of 32 species, 16 were found in only one of the habitats, and another 14 were significantly more common in one habitat. Species diversity did not differ between habitats, but density of individuals was higher on the scarps. Sponges on vertical scarps were more likely to have to withstand physical disturbance and tended to be encrusting and amorphous forms, while the sedimented surface of the plateau was handled better by erect-branching or pedunculate forms. Spongivorous fishes were more common on vertical scarps, adding a biotic component to distinguishing the sponge faunas. Nine days after four plateau species were transplanted to the scarp, signs of predation were clear, and three of the four species had lost significantly more tissue outside cages than when enclosed. In Ireland, Bell and Barnes (2003) documented another influence of topography on biotic interactions,

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abundant on *Mycale hentscheli* grown on lines for pharmaceutical production, relative to in its natural community (Page *et al.*, 2011). Photo G. Mike Page: Severe grazing damage by *Haplodoris nodulosa* on *Mycale hentscheli*. H Mike Page: Juvenile *H. nodulosa* feeding on *Mycale hentscheli*. In *SE Australia*, a large barnacle increases recruitment success of sponges by providing a refuge from urchin grazing; different sets of sponge species live among kelps versus on urchin barrens, with only sponge species that resist sea urchin grazing in the barrens. Photo I. Andy Davis: The large barnacle *Austrobalanus imperator* and the large common urchin *Centrostephanus rodgersii* with *Tedania anhelans* (orange) and *Chondrilla australiensis* (brown). Photo M. Andy Davis: The physically defended sponge, *T. anhelans*, on vertical surfaces with *C. rodgersii*. In Belize, *Caribbean*, the massive reef sponge *Lissodendoryx colombiensis* is readily consumed by a large seagrass-dwelling sea star but is able to inhabit a seagrass meadow when sponge species that are unpalatable to the sea star overgrow it (Wulff, 2008a). Photo J. Janie Wulff: *Lissodendoyx colombiensis* overgrown by *Chondrilla caribensis* (brown), *Clathria schoenus* (yellow, branching), and *Tedania klausi* (orange-red, in bottom of photo). Photo K. Janie Wulff: The large sea star *Oreaster reticulatis* departing from where it has just consumed a portion of a large *L. colombiensis* that was not overgrown by unpalatable sponge species. Photo L. Janie Wulff: The sea star *O. reticulatis* consuming a reef species, *Mycale laevis*, that was transplanted into a cage in the seagrass, and thrived until the cage was removed, 2 h before the photo was taken.

showing increased risk of sponges being broken off of vertical rock walls due to activities of fishes.

The possibility that predation can have substantial effects on the amorphously massive species *Mycale hentscheli* Bergquist and Fromont, 1988 in New Zealand, if normal inhibitions on the predators are absent, was discovered in the course of monitoring individuals grown on lines in aquaculture for drug production (Page *et al.*, 2011). The nudibranch *Haplodoris nodulosa* was two orders of magnitude more common on farmed sponges, causing severe depletion (Fig. 4.1). The authors suggested that the predator population explosion may have resulted from the continuous monoculture of their food supply, and possibly also the distance of the lines serving as substrata from the habitat of the natural predators of the nudibranch.

Protection of clonal invertebrates from sea urchin grazing by structure provided by large barnacles (Fig. 4.1) was suggested by a positive correlation of cover by sponges and colonial ascidians with barnacle density (Davis and Ward, 1999). The sponge *Clathria pyramida* Lendenfeld, 1888, which was known to discourage urchin grazing, stood out with a contrasting distribution negatively correlated with barnacle density, appearing to confirm the requirement of the other sponges for protection by barnacles. Unsatisfied by interpretations based solely on correlations, the authors designed experiments to test the possibility that other processes were at work. On scrubbed vertical rock faces, 4–14 m deep, they glued plaster filled barnacle tests in natural configurations and at densities spanning the natural range (Davis and Ward, 2009). As they had suspected, the barnacles influenced recruitment, and after 8 months, invertebrate cover and diversity were greater with higher barnacle density. After 56 months, clonal recruits had grown so that cover no longer increased with barnacle density, but the species diversity difference persisted. The complementary experiment of removing barnacles from the midst of established communities revealed that they were not involved in the maintenance of the sponge community, as after 22 months there were no differences between the unmanipulated and barnacles-removed sponge communities. Microhabitat protection of sponge recruits from grazers was also demonstrated to be key for the common Mediterranean sponges *C. crambe* and *S. lophyropoda*. On submerged outcrops near Blanes, sponges that settled in grooves and crevices enjoyed a reduction in mortality due to bulldozing by the sea urchin *Paracentrotus lividus* (Maldonado and Uriz, 1998).

Symbiotic associations can both enhance and constrain habitat distributions because they combine not only the abilities but also the habitat requirements of both participating species. For example, macroalgal partners in mutually beneficial associations with sponges may limit the depth distribution by their requirement for light. Restriction to depths above 4 m of the association of the coralline red alga *J. adhaerens* and the sponge

Ha. caerulea depends on the alga, which also determines the overall form of the association by growth patterns that reduce self-shading in lower-light environments (Enriquez *et al.*, 2009). Many more associations may significantly influence distribution and abundance of participating species, but establishing both the patterns and their possible adaptive significance can be challenging. For example, the brittle star *Ophiothrix fragilis* settles preferentially on sponges, especially *C. crambe*, and the very small juveniles migrate laterally to recolonize sponges if they are cleared from the sponge surfaces (Turon *et al.*, 2000). The pattern of association is extremely striking and demonstrated to be constituted purposefully, but exactly how these species influence each other is not yet determined.

Associations with microbial symbionts can also mediate the affect of abiotic variables on host sponges, and changes in abiotic variables can diminish the ability of sponges to effectively battle microbial interlopers, such as pathogens. Abundance of Mediterranean species of bath sponges, in the genera *Spongia* and *Hippospongia*, has been dramatically diminished by disease, to the point of near local extinction at some sites (e.g. Pronzato, 1999 and a recent review in Pronzato and Manconi, 2008). Sea water temperatures that were 2–4 °C above normal may have favoured enormous losses that occurred at the end of summer 1999 (e.g. Cerrano *et al.*, 2000b). Exposure time to elevated temperatures was also positively correlated with death in two mass mortality events (summers of 2008 and 2009) of *Ircinia fasciculata* Esper, 1794 in the western Mediterranean Sea (Cebrian *et al.*, 2011). Several lines of evidence implicated symbiotically associated cyanobacteria in the increased vulnerability of *I. fasciculata*: normal cyanobacteria were lost from injured individuals, photosynthetic efficiency was diminished at experimentally elevated temperatures, and the related sponge *Sarcotragus spinosulum* Schmidt, 1862, which hosts only heterotrophic bacteria, did not suffer mortality at the same times and places (Cebrian *et al.*, 2011). Precise documentation of how disease diminished population size was facilitated by conspicuous bare patches that remained on rock for several months after *I. fasciculata* individuals died of disease (Cebrian *et al.*, 2011).

Wilkinson and Vacelet (1979) made explicit comparisons of growth of several Mediterranean species in different flow and light environments by transplanting individual sponges into experimentally altered circumstances. Cyanobacteria-harbouring *Aplysina aerophoba* Nardo, 1833 grew four times as fast under a clear shield as under a black shield, a result that was not unexpected given prior examples of benefits of single-celled algae to animal hosts. Also as expected, if the algae are nutritionally helpful, growth of this species was not diminished as much by low flow conditions. Before the experiments it was less certain if cave-dwelling sponge species prefer low light, or merely accept it because caves are more suitable for some other reason; but *Aplysina cavernicola* Vacelet, 1959 and *Chondrosia reniformis* Nardo, 1847 grew better shaded from light, allowing Wilkinson and

Vacelet to designate these species as truly sciaphilous. Two individuals of the *Chondrosia* even migrated to the underside of the experimental substrata during the experiment. The experiments simultaneously demonstrated the degree to which sediment can inhibit sponges, as *A. aerophoba* control individuals grew half as much as those under clear shields. Depending on water column conditions and flow rates, sponges that gain nutritional boosts from photosynthetic symbionts may constitute a substantial portion of the fauna on subtidal rocky habitats. For example, many of the 61 demosponge species found on rocky reefs in the Investigator Group islands, South Australia, harbour cyanobacterial symbionts, reflecting the extremely clear water (Sorokin *et al.*, 2008).

Photosynthetic symbionts have also been shown to influence trophic interactions of their hosts in an unexpected way. The opisthobranch *Tylodina perversa* was inspired to feed on tissue of sponge species with cyanobacterial symbionts (preferring *A. aerophoba* over *A. cavernicola*) as well as individuals with higher densities of cyanobacteria (i.e. shallow *A. aerophoba* over deep), and even asymbiotic sponges to which cyanobacteria were added (Becerro *et al.*, 2003). In a similar example, the gastropterid opisthobranch *Sagaminopteron nigropunctatum* selects the ectosome over the choanosome of the sponge *Dysidea granulosa* (Becerro *et al.*, 2006). This feeding choice results in *S. nigropunctatum* ingesting high concentrations of cyanobacteria because *D. granulosa* has high concentrations of cyanobacteria restricted to its ectosome (Becerro and Paul, 2004; Becerro *et al.*, 2006).

2.2. Subtidal rocky substrata—cobbles and caves

Caves and cobbles are special cases of rocky substrata, with substratum discontinuity and instability added as complicating factors. Influences of disturbance regime, resource availability, colonization, and competition are so intertwined for these hard-bottom habitats that I here consider abiotic factors and ecological interactions together. Differences among individual substrata can be extreme in the case of cobbles, as substratum size can influence stability, which in turn affects disturbance rate and therefore availability of primary substratum space. An additional aspect of heterogeneity of the habitat experienced by sponges on different parts of a boulder was recently demonstrated in a study in northern France focused on *H. panicea* Pallas, 1766 and *Hymeniacidon sanguinea* Grant, 1826 (=*H. perlevis* Montagu, 1818) living on tops and bottoms of boulders (Schaal *et al.*, 2011). Stable isotope comparisons indicated that a significantly greater proportion of the food consumed by sponges living on the undersurfaces of boulders was based in decomposition of organic matter.

Substratum stability can influence species diversity through its influence on the balance between provision of new space by disturbance and overtaking of space by competitive dominants. Underlying this balance is a trade-off between competitive prowess and recruitment efficiency that directly relates provision of space to recruitment by relatively poor competitors. Rützler's (1965) demonstration that diversity of sponge communities on cobbles in the Adriatic decreased with increasing rock size, from 3 to 30 kg, was the first explicit demonstration of the influence of substratum stability (i.e. levels of disturbance) on diversity of sessile inhabitants. Subsequent studies of algae on intertidal cobbles and of corals on shallow reefs resulted in the designation of this causal relationship between intermediate levels of disturbance and peak levels of species diversity as the intermediate disturbance hypothesis (e.g. Connell, 1978).

Competitive interactions become important only on cobbles or boulders that are stable for long enough that growth of colonizers causes space to become limited. Comparing sponge faunas on boulders at a sheltered and exposed site in each of Ireland, the eastern Pacific at Mazatlan, Mexico, and Palmyra Atoll in the tropical central Pacific led Bell and Carballo (2008) to conclude that an increase in number of sponge species with cobble size in their study was due primarily to the greater area of a larger cobble receiving more larval recruits. The shapes of the curves relating species diversity to surface area varied, but all were monotonic, with no sign of a diversity decrease on larger rocks. In this case, all cobbles had surface areas of less than 3000 cm^2, and the lack of competitive exclusion as a process influencing diversity in this system was confirmed by the authors' report of bare space (30–80%) on even their largest cobbles.

The ability of sponges to profoundly influence the stability of their substrata can disconnect the relationship between cobble size and stability. Cobbles of all sizes in the shallow subtidal and lowest intertidal of the Bay of Panama, in the tropical eastern Pacific, are equally immobilized by being embedded in a colourful matrix of at least seven species of sponges, which can only be seen peeking through from spaces between cobbles. Barnacles, bryozoans, oysters, vermetids, and serpulids crowd into each other on the exposed upper surfaces, regardless of cobble size, while the sponges grip the cobbles from beneath, where they are confined by how quickly they are consumed by one of the most common fish in this habitat, the smooth puffer *Arothron hispidus* (Wulff, 1997c).

Caves are similar to cobbles in the isolation of individual substratum patches and steep gradients in availability of food and light over very small distances. Some studies of distribution and diversity patterns of sponges in caves in the Mediterranean and Ireland (e.g. Corriero *et al*., 2000; Bell, 2002) have focused on influences of water flow and loss of sunlight-requiring potential spatial competitors. Unusual trophic interactions, as well as beneficial associations, that were first studied in Mediterranean caves have stretched our imaginations of what is possible for sponges. One striking discovery that paved the way for similar discoveries at other sites was that sponges could acquire food in such an un-sponge-like way as engaging in carnivory on small crustaceans (Vacelet and Boury-Esnault, 1995).

Indications that sponges may not necessarily abide by the same rules of ecological interaction that elegant experiments have identified for other taxa were first offered by examples of cooperation among sponge species in dense, sponge-dominated cave communities (Rützler, 1970; Sará, 1970). In shallow water caves on the Ligurian Italian coast, Sará (1970) reported more than 60 species in an area of 50 m^2 and 25 species in an area of only 2 m^2. In these particularly dense communities, with continuous sponge cover, number of species increased with increasing density. Near the mouths of the caves, an increase in diversity with decreasing density was attributed by Sarà to the relative precariousness of life as a sponge in circumstances in which space must be shared with algae. He pointed out the similarity to life on small cobbles, on which space is also continuously reopening for recruitment (Rützler, 1965). But deeper in the caves, where sponges reliably abut other sponges, these communities are quite stable. By tracing outlines of encrusting sponges at monthly intervals, Sará (1970) determined that the actual location occupied by a particular sponge at a given moment was quite fluid, but that the same individuals remained in the community over the entire year. Sarà presented his data relating sponge species diversity positively to density in the context of positive interactions among neighbouring sponges of different species and assembled other examples of epibiosis in situations of sponge-dominated communities. He pointed out the lack of the evidence for competitive elimination but at the same time the unavailability of bare space for recruitment of additional individuals into the community as larvae. Rützler (1970) was also attracted to dense and diverse sponge communities, and focused on a community of 34 species thriving in cavities eroded in the base of large boulders in the Adriatic. By field observations, in combination with histological sections, he revealed morphological specializations for supporting epizoic sponges, or for living as epizoic sponges, among the species inhabiting these dense communities. As creatively illustrated by these two papers published in 1970, sponges may be unique in the degree to which they engage in solving space limitation by benign or beneficial overgrowth, thereby maintaining high species diversity in extraordinarily crowded systems.

2.3. Coral reefs

2.3.1. Abiotic factors

On coral reefs, as on subtidal rocky substrata, the clearest direct abiotic influences on sponge distribution and abundance are exposure, depth, available substratum space, and details of topography, such as inclination, as well as water column productivity. Also, as on subtidal rocky substrata, the influence of light is exerted via ecological interactions, but on coral reefs, single-celled photosynthetic symbionts are more likely to be the mediators than macroalgal competitors.

Exposure to overly vigorous water movement in shallow water is the most likely cause of a consistent pattern within the wider Caribbean region and across the GBR of very low densities, biomass, and species diversity in shallow water (e.g. Wilkinson and Cheshire, 1989; Alcolado, 1990; Alvarez *et al*., 1990; Schmahl, 1990). Reiswig (1973) attributed the increase that he documented in total sponge volume between 20 and 50 m on the fore reef at Discovery Bay, Jamaica, to limits imposed by wave action and sedimentation in more shallow water. A critical depth, below which wave energy influence on sponge distribution and abundance drops, was suggested by Alcolado (1994) to occur between 5 and 10 m in Cuba, where diversity increases to 20 m, with a subsequent decrease between 20 and 35 m. On the Australian Barrier Reef, density, biomass, and diversity were also consistently low above 10 m and then increased to a maximum at about 20 m, reflecting a combination of light and physical disturbance (Wilkinson and Evans, 1988; Wilkinson and Cheshire, 1989). Exceptions to this pattern, where dense coral reef sponge communities are found in shallow protected areas such as leeward reefs behind algal ridges (e.g. Wulff, 2001), or at latitudes where hurricanes are rare (e.g. Wulff, 1995a), patch reefs in lagoonal systems (e.g. Schmahl, 1990), and mangrove roots (e.g. Rützler *et al*., 2000) lend credence to the notion that physical disturbance restricts sponges in shallow water at exposed sites.

Comprehensive regional surveys of sponge faunas have provided understanding of abiotic requirements of hundreds of individual species as well as differences among higher taxa in relationships to their environment. Every study has raised intriguing biogeography questions relating especially to faunal heterogeneity among sites. Combining data from nine expeditions allowed Reed and Pomponi (1997) to make a comprehensive analysis of distributions of nearly 300 sponge species at 417 collection sites from 0 m (but especially below 30 m) to 922 m throughout the Bahamas. Diversity was highest (206 species) in the 60–150 m zone, and although they did not quantify abundance it was clear that it peaked in this zone as well, results that concurred with other studies of deep coral reefs. Structure and diversity of sponge assemblages in the second most diverse zone, 30–60 m, strongly reflected the geomorphology, in particular, the variety of subhabitats. Many species were found only in particular depth ranges, and no species was found in all zones. Of the 3059 specimens collected, 429 were unique, a pattern found in other studies. Analysis at higher taxonomic levels revealed a striking shift in relative representation of different orders with depth, although the seven genera found in all depth zones each represented a different order. Similarly, while a geographic signature could be discerned in the species assemblages, 47 species were found in all subregions.

The importance of subhabitats defined by geomorphology was underscored by Lehnert and Fischer (1999), who applied ordination analysis to their collections, combining multiple aspects of the environment into a single analysis of distribution and abundance patterns. They collected at 102 sites at Discovery Bay, Jamaica using SCUBA, and found very clear distinctions between sponges that inhabit exposed reef surfaces versus undersurfaces of plate-shaped corals versus lagoon habitats. They pointed out the degree to which data analysis style can influence conclusions, especially the difficulty of discovering depth-related distribution patterns by using predetermined depth zones. Their collections brought the Jamaican faunal list to 157 species, of which 85% were restricted to shallow water. Of the 60 species found on the deep fore reef (using Trimix diving), only 40% were also found on the shallow reef. Statistically significant environmental variables related to substratum type included substratum inclination, back-reef, fore-reef, deep fore-reef, pinnacle, undersides of platy corals, and coral rubble. On the Bahamian slope between 91 and 531 m, substratum inclination was also a key distinguishing abiotic factor (Maldonado and Young, 1996), in this case confounded with depth because of uneven distribution of horizontal versus vertical substrata over the depth range they traversed with their submersible.

Ordination techniques were also applied to sponges of the Spermonde Archipelago of Indonesia, but on a different scale, with focus on comparing among sites spanning a large geographic area rather than microhabitat details within a set of nearby sites. Cleary and de Voogd (2007) measured a number of environmental variables for 1 day at each of 37 sites and related these to the sponge species at each site. For a total sponge fauna of 150 species, a combination of depth, exposure, and an onshore–offshore spatial component explained 56.9% of the variation in similarity among the sponge species at the sites. de Voogd and Cleary (2008) continued their Indonesian surveys with 30 patch reefs in the Thousand Islands, north of Jakarta, an area profoundly influenced by human inhabitants. Of 148 species, 43 were unique to a single site. As in other studies, the most striking distinction among faunas was related to inner versus outer sites. Faunal differences were evident at the family as well as the species level, as in the Bahamas study by Reed and Pomponi (1997).

Coral reefs and subtidal limestone rocks of the Dampier Archipelago, NW Australia, yielded 150 sponge species from 43 stations that Fromont *et al.* (2006) sorted by non-hierarchical classification. The resulting 11 groups were defined on the basis of depth, exposure, and substratum type and structure. Plotting these groups on a map illustrated a significant geographic component, but 92 of the 150 species (i.e. 61%) were found at only 1 or 2 of the 43 stations with sponges. Strikingly similar are results of Hooper and Kennedy (2002) from 22 sites on the Sunshine Coast of Southeast Queensland. Although a distinction could be made between the faunas of inner (around 2 km from shore) versus outer (around 15 km from shore) reefs, the sponge assortments on adjacent reefs were highly heterogeneous, and about 60% of the 226 species were rare or unique.

On three remote atolls of the southwestern Caribbean, Zea (2001) evaluated sponge assemblages by recording all individuals within 30 m^2 and all species within 400 m^2 at 42 stations between 2.5 and 20 m depth. Comparison with continental shelf reefs shows relatively low densities overall, likely reflecting the low concentration of suspended organic matter. Of the 96 species, 21 were found in a variety of circumstances, and the remainder were associated with circumstances described primarily by depth and exposure. As in other studies, being able to predict environmental circumstances at a site from knowing that a particular species lives there does not mean that the reverse is true. Knowing the environmental conditions at a site does not generally allow prediction of the species present. Distributions were patchy and heterogeneous on scales from tens of metres to hundreds of kilometres.

The almost unanimous finding of highly heterogeneous sponge assortments at sites that are characterized by similar abiotic factors underscores limitations on determining how abiotic factors influence distribution and abundance of individual sponge species by correlating sponge abundance with various parameters. This strong stochastic component to species present at a particular site has been an important theme for discussions of sponge distribution and abundance. History, in the forms of local species loss to disturbance, very low probability of any particular larval dispersal being successful, and enhancement of patchy distributions for some species by asexual propagation after initial recruitment by a larva (detailed discussions in, e.g. Zea, 2001; Hooper and Kennedy, 2002; Hooper *et al.*, 1999, 2002) may play an unusually important role in determining which sponge species inhabit a particular spot.

By focusing solely on species in the order Dictyoceratida, Duckworth *et al.* (2008) were able to eliminate some of the variations that might result in such heterogeneous distributions and to address some of these complications. Dictyoceratids are relatively homogeneous in having larvae that are not likely to disperse far, preference for solid substrata and relatively clear water, and tough skeletons that resist fragmenting agents. Distribution and abundance patterns were strikingly like those found when sponges from all orders are included: 12 of the 23 dictyoceratid species of the Torres Straights, Australia, were only found at 1 location (4 locations, with 5–7 sites at each), and assemblages were often similar on distant reefs but very different at adjacent sites. As predicted if fragmentation is a cause of dense but widely separated patches, the one ramose species that is more likely to asexually propagate did have an especially patchy distribution.

An exception to this pattern of heterogeneous assortments of sponge species at sites characterized by similar abiotic factors may be sites that are quite extreme in at least one abiotic factor. Many species are capable of living at amenable sites, and accidents of history due to the vagaries of larval dispersal and survival of larvae after settlement cause exceptionally large differences in species composition at sites that appear to be very similar by human evaluations. But when conditions are really very poor, only a few species in a regional fauna are capable of surviving. Alcolado (1994, 2007) has pointed out this pattern in the context of sites influenced by anthropogenic pollution, and he has documented which species in the Caribbean fauna are the last to drop out in highly unfavourable sites with comprehensive time-series surveys of the Cuban sponge fauna. *Clathria venosa* Alcolado, 1984 is the species that most reliably serves as an indicator of sites affected by urban pollution in Cuba. Similarly, another thinly encrusting species in the demosponge Order Poecilosclerida, *Mycale microsigmatosa* Arndt, 1927, was the only species able to cope with all sites at Arrail do Cabo, Brazil, including sites that were affected by urban and energy-generation pollution (Muricy, 1989; Vilanova *et al*., 2004).

A complementary approach to faunal surveys for identifying specific causes of distribution and abundance patterns is to focus on particular sponge species. Results of studies focused on single or groups of species have consistently highlighted how different the ecology of sponge species that look similar can be. Reiswig's (1973) study of factors influencing distribution and abundance of three species of large vase-shaped sponges on the north coast of Jamaica at Discovery Bay has still not been equalled for comprehensive consideration of all factors. *Verongula gigantea* Hyatt, 1875 was confined to the open, exposed habitat of the fore-reef slope platform, clearly unable to tolerate the particle-laden waters within Discovery Bay. Once established on exposed fore-reef substrata, however, *V. gigantea* individuals were undaunted by abiotic factors. Substratum collapse, caused by a combination of storm waves and bio-erosion, was the cause of the few losses from this population. On deep walls, where bases of the platy corals are readily eroded, cascading losses can constitute dispersal downslope, or if the landing spot is sediment, death by smothering. *Mycale laxissima* Duchassaing and Michelotti, 1864 was confined to reef–sand channel interfaces, a distribution coincident with flexible substrata such as gorgonians, that decreased the rate at which this narrow-stalked species was torn off by vigorous water movement. Winter storms were nevertheless the most important mortality source, and 27% of the population was lost to burial, scour, substratum collapse, and tearing loose from the substratum associated with storms in the course of a year. *Tectitethya crypta* de Laubenfels, 1949 was only found on shallow limestone ledges with relatively little sediment deposition, and the sole losses from the population, of very small individuals, were due to burial during storms.

Following in the tradition established by Henry Reiswig of studying trios of species with a common growth form, but in different orders, the erect-branching species *Iotrochota birotulata* Higgin, 1877; *Amphimedon compressa* Duchassaing and Michelotti, 1864; and *Aplysina fulva* Pallas, 1766 were scrutinized with respect to ability to cope with a variety of factors (Wulff, 1997a). They were experimentally determined to differ significantly in susceptibility to smothering by sediment, disease, and predators, as well as breakage, toppling, and pulverization by storms. Loose fragments of these species, that were generated by these factors, also differed in how well they survived, reflecting differences in reattachment success (Wulff, 1997a). In Puerto Rico, focus on *A. compressa* at sites differing in abiotic factors demonstrated increased size with depth, attributed to decreases in both growth rate and survival with increased water movement (Mercado-Molino and Yoshioka, 2009). Larger individuals were more susceptible to getting torn off by rough water, but best survival was in intermediate size classes because small individuals were eliminated by burial in sediments. After a hurricane in San Blas, Panama, this same species exhibited intermediate survival in comparison with two other erect-branching species, with relative rates of survival reflecting a balance of resistance to fragmentation and fragment survival (Wulff, 1995a). Skeletal composition strongly influences resistance to fragmentation. Among the six species with small basal attachments for which sufficient data could be collected to make statistical comparisons, the two species with skeletons solely of spongin were toppled at less than half the rate (22–24% vs. 48–60%) of the species with silica spicules as well as spongin.

In just a few hours, hurricanes can influence sponge distribution and abundance for decades afterwards. Specific effects are not readily observed, however, because they quickly become invisible as damaged sponges heal quickly or deteriorate and vanish entirely. Quantification of hurricane effects requires prior knowledge of sponges at a site and evaluation of storm damage immediately after the waves have calmed. After a major hurricane in Jamaica wrought havoc on the north coast fore reef, 5 weeks of monitoring 576 individual sponges in 67 species revealed a possible mechanism for the maintenance of a full range of growth forms among the sponges in this habitat. The immediate effect of the hurricane was serious damage to 43% of the erect-branching sponges, and less for sponges in four other growth form categories (e.g. 32% for the tough-skeletoned massive species and the least, 20%, for the encrusting species). Recovery was inversely proportional to susceptibility to damage, however, resulting in almost the same proportion of individuals lost from each of the five growth form categories after 5 weeks of either regeneration or continued deterioration (Wulff, 2006b). Curiously, the net result of damage and recovery, in terms of the proportion of the pre-hurricane populations lost, was worst for the tough massive species that were least damaged. Five years after Hurricane Allen, Wilkinson and Cheshire (1988) evaluated recolonization of a portion of the reef that had been devoid of survivors. The five species most abundant among colonists were all in the tough massive category, suggesting that, in addition to the two strategies for coping with hurricanes that were identified in the weeks following the storm (i.e. resistance to damage and recovery from damage on an individual level), a third strategy may be recovery on a population level by efficient recruitment.

Temperature can be an important constraint on latitudinal distribution of coral reef sponges, as illustrated by a geographic gradient in sponge species distributions along the Gulf Coast of Florida (Storr, 1976). Over a 230-km north–south coastline, average temperatures differed by 4 °C and mean low temperatures by 8 °C; only 10 of the 30 sponge species were distributed along the entire coastline. Along the eastern coast of Australia, an abrupt change from tropical to temperate sponge faunas in only 110 km was documented by a comprehensive geographic analysis of a total of 2324 species (Hooper *et al.*, 2002). At the geographic edges of coral reef distribution, temperature fluctuations can veer into the unacceptably low. A January cold snap that persisted for several days in the Florida Keys resulted in sponge mortality, but death was not evenly visited upon all species. Individuals of some species suffered complete mortality, but for other species, only particular portions of each individual died, and some species appeared to be unaffected (B. Biggs *et al.*, Florida State University, in preparation). Lower temperatures at depth were suggested to constrain reproduction and recruitment for two species of coral reef sponges, as adult sponges appeared unimpeded after they were transplanted to depths below where they were found naturally (Maldonado and Young, 1998).

Abnormally warm temperatures that motivate bleaching (i.e. loss of photosynthetic symbionts) in scleractinian corals do not necessarily cause bleaching in zooxanthellate sponges (e.g. Vicente, 1990). On Orpheus Reef, GBR, 84–87% of the corals bleached in March 1998, but all *Cliona orientalis* Thiele, 1900 survived (Schönberg and Wilkinson, 2001). Resistance to bleaching in clionaid boring sponges may be conferred by the ability, demonstrated in *C. orientalis*, to move their intracellular zooxanthellae symbionts deeper into the sponge tissue, in response to stresses (Schönberg and Suwa, 2007). Focusing on symbiotic non-photosynthetic bacteria in the Australian species *Rhopaloeides odorabile* Thompson, Murphy, Bergquist, and Evans, 1987, Webster *et al.* (2008) demonstrated loss of normal symbionts and colonization by alien microbes, including potential pathogens, when temperatures were experimentally increased to 33 °C.

Light, diminishing with depth and in cryptic spaces, plays a direct role in the lives of sponges through reactions of sponge larvae (e.g. see Maldonado, 2006 for a review). This role of light is not restricted to coral reefs, but clear water typical of healthy reefs may allow light to play a role over a much greater depth range in this habitat. Physiological sensitivity of sponges to UV light varied widely among Hawaiian sponge species (Jokiel, 1980), with the encrusting species *Mycale cecilia* de Laubenfels, 1936 succumbing quickly to full exposure, while *Callyspongia diffusa* Ridley, 1884 remained unhampered by UV light. A possible cost of elaborating protective pigments was suggested by the competitive exclusion of *C. diffusa* from water deeper than 3 m by the UV-sensitive *Mycale* (*Zygomycale*) *parishi* (Jokiel, 1980). Many sponges live on tropical reef flats or very shallow seagrass meadows and on intertidal shores in which no refuge from direct sunlight is available. Colour may in some cases protect sponges, and possibly pigments of photosynthetic symbionts also aid in this (discussion in Harrison and Cowden, 1976). Although habitat distribution of the common Australian reef species *R. odorabile* was positively related to light, photosynthesis could not be detected, suggesting that the apparent requirement for light reflects instead correlation of food with light or larval behaviour (Bannister *et al.*, 2011). Light may exert its greatest effects on distribution and abundance of coral reef sponges through its effects on photosynthetic symbionts, a focus of the following section.

2.3.2. Inextricable combination of abiotic factors and ecological interactions: Food for sponges

Factors that exert influence on sponge distribution and abundance through feeding by sponges cannot be readily divided into abiotic and biotic. Water column nutrients can quickly be transformed into pico plankton useful to sponges (e.g. Reiswig, 1971, 1974), and some sponges are capable of directly removing dissolved organics, in collaboration with prokaryote symbionts (e.g. Reiswig, 1981; de Goeij *et al.*, 2008; Weisz *et al.*, 2008). Light is directly transformed into ecological interactions by photosynthetic symbionts that may also feed their sponge hosts. These intertwined influences of abiotic and biotic factors involved in feeding of sponges are not confined to coral reefs, but the relative ease of *in situ* experiments has particularly promoted their study using controlled manipulations on reefs.

Nutrient enrichment of water has often been correlated with increased sponge abundance (table comparing studies in Holmes, 1997), as long as it is not combined with additional pollutants, such as inorganic particles or industrial wastes. Substantial differences in overall biomass of sponges, between the coastal and seaward portions of the GBR, and between tropical Australia and the Caribbean, have been attributed to the greater availability of nutrients near coasts. Wilkinson (1987) reported strikingly higher biomass (measured as weight) on 11 Caribbean reefs (367.5 g/m^2 at Barbados East to 2458.2 g/m^2 at Barbados West, leaving out the Jamaican site at which sponges had been recently eliminated by a major hurricane) relative to 17 reefs on the GBR, Australia (7.9 g/m^2 at Astrolabe Great to 569.9 g/m^2 at Pandora). Confining comparisons between oceans to "oceanic reefs" still yielded eight times the biomass on the Caribbean reefs. An additional related difference was the greater proportion of sponges that rely significantly on phototrophic symbionts in nutrient deficient waters of the outer GBR (Wilkinson, 1987; Wilkinson and Cheshire, 1990).

By comparison with continental shelf reefs, the sponges of three remote atolls in the southwestern Caribbean, showed relatively low densities overall, likely reflecting the meagre concentration of suspended organic matter (Zea, 2001). Zea (1994) also related sponge distribution, abundance, and diversity to a gradient in nutrients along the continental coast of Colombia that may have been natural but has been exacerbated by development of a city near the bay site. He stressed the difficulty of disentangling influences of nutrients from other things that wash off the land, such as sediment. In a survey of sponge distribution and abundance across the 230 km north-south Gulf of Mexico coastline of Florida, Storr (1976) noted that nutrient availability likely influenced the substantially greater sponge abundance and diversity near river mouths. He specifically contrasted the many enormous *Spheciospongia vesparium* Lamarck, 1815 individuals along the Gulf Coast, where nutrients from the Everglades pour into the eastern Gulf of Mexico, with the lower density and smaller individuals of this species in the relatively nutrient-poor Bahamas.

Larger sizes at increasing depth of three common Caribbean tube-shaped sponges, *Callyspongia vaginalis* Lamarck, 1814, *Agelas conifera* Schmidt, 1870, and *Aplysina fistularis* Pallas, 1766, were attributed to superior food availability by Lesser (2006). Energy budgets for *C. vaginalis* revealed a greater rate of food intake at 25 m than at 12 m at a site in the Florida Keys, reflecting significantly higher concentrations of food, especially of heterotrophic bacteria and prochlorophytes, at the deeper site (Trussell *et al.*, 2006). Respiratory costs were also higher at the shallow site, with a clear net result of significantly greater growth rates at the deeper site. Transplants between sites allowed dismissal of the possibility that genetic differences between deep and shallow sponges influenced the growth rate difference. Similarly, three of four species of typical reef sponges transplanted to mangrove roots grew significantly faster among mangroves than on the reef, suggesting response to increased levels of plankton-fuelling nutrients (Wulff, 2005). The one species that did not grow faster in the mangroves, *Desmapsamma anchorata* Carter, 1882, grows unusually rapidly on the reef (Wulff, 2008b).

Excavating sponges, of particular concern for carbonate balance on coral reefs, may be especially spurred on by water column nutrients. Infestation rates of rubble from branching corals by eroding sponge species increased with levels of coastal eutrophication in Barbados (Holmes, 1997). The particularly destructive excavating species *Cliona delitrix* Pang, 1973 was found at especially high abundances in areas influenced by sewage (e.g. Rose and Risk, 1985) and increased abundance over time was related to sewage influence (Ward-Paige *et al.*, 2005). Focusing on patterns of abundance of this voraciously excavating species with respect to a sewage outfall at seven sites in San Andrés Island (Colombia), Chaves-Fonnegra *et al.* (2007) noted that the excavator increased as they moved towards the main outfall, but when they got very close to the outfall it decreased. While increased *Escherichia coli* (the indicator of relative influence of sewage for these authors) may inspire the sponges with more food, the concomitant increase in sediment very near the source may overwhelm the benefit. Because they recorded not only the number of corals infested by *C. delitrix* but also the percentage cover of sponge and dead and live coral, they were also able to determine how the pattern with bacteria abundance was confounded by a positive correlation of sponge cover with coral (live plus dead) cover. The requirement of this species for large, recently dead corals has been identified as a confounding variable in other studies. A comparison by Chiappone *et al.* (2007) of *C. delitrix* at 181 sites in the Florida Keys revealed a distribution pattern of higher density at deeper fore-reef sites, but larger individuals on patch reefs nearer shore, possibly reflecting the need for large recently dead corals; this same requirement was manifested as greater abundance of *C. delitrix* between 12 and 20 m in Los Roques, Venezuela (Alvarez *et al.*, 1990). Deviation from the pattern of increasing boring sponges with increasing water column food at sites within the bay at Discovery Bay, Jamaica, might be due to coincident increase in sedimentation that inhibits efficient pumping of the sponges, resulting in a shift in dominant bio-eroders from sponges to worms and especially bivalves (e.g. Macdonald and Perry, 2003).

Sunlight exerts indirect influence on sponge distribution, abundance, and diversity through ecological interactions, especially by fuelling photosynthetic symbionts such as cyanobacteria, zooxanthellae, and macroalgae and by spurring the growth of photosynthetic competitors.

Photosynthetic symbionts are not just a feature of coral reefs, although clear water may allow a greater depth distribution, and the relative ease of *in situ* experiments on reefs has spurred research in this habitat. Shading sponges that harbour photosynthetic symbionts has demonstrated the potential importance of exposure, but the importance of this type of heterotroph–autotroph association is not uniform across all sponge–alga species pairs. Shading the tropical Pacific species *Lamellodysidea chlorea* de Laubenfels, 1954 for 2 weeks resulted in loss of mass, but symbiont density did not decrease, whereas shaded *Xestospongia exigua* (= *Neopetrosia exigua* Kirkpatrick, 1900) lost symbionts but not mass (Thacker, 2005). Differing reactions of these species were attributed to differences in host specificity of symbiotic cyanobacteria, with the specific association of *Oscillatoria* with *L. chlorea* being mutually beneficial, but the generalist cyanobacterium *Synechococcus spongiarum* hosted by *X. exigua* merely commensal. A pair of Caribbean species also differed in responses to shading, with *A. fulva* growing significantly less in 6 weeks under opaque canopies but *Neopetrosia subtriangularis* Duchassaing, 1850 unaffected with respect to growth, although symbiont density decreased under canopies in both sponge species (Erwin and Thacker, 2008). Significantly greater growth of symbiontbearing *A. fulva* in lower-light mangroves than on reefs (Wulff, 2005) suggests that additional aspects of switching between feeding modes (i.e. heterotrophy vs. reliance on photosynthetic symbionts) remain to be discovered. Variation among species in response to shading may be related to how flexible they can be with respect to modes of feeding, as well as to differences among symbiont clades.

A pattern of constrained depth distribution for photosymbiont-bearing keratose sponges in the Caribbean was experimentally addressed by Maldonado and Young (1998) by transplanting individuals of the common shallow reef species *A. fistularis* Pallas, 1766 and *Ircinia felix* Duchassaing and Michelotti, 1864 from a shallow (4 m) reef to 100, 200, and 300 m. Death within 2 months of all individuals that were transplanted to 300 m was attributed to temperatures (18–9 °C) that were much lower than those of the home environment at 4 m of 26–32 °C; but transplants to 100 and 200 m did surprisingly well. Histological preparations and *in situ* photos of the sponges made before and after transplantation allowed them to conclude that symbiotic cyanobacteria remained in the same concentrations in *A. fistularis*, but the sponges lost their fistules; although cyanobacteria were lost from *I. felix* and the transplants grew unusually tall, narrow chimneys, sponges of both species grew more (although not significantly so) at depth than did controls at 4 m. The authors concluded that the absence of keratose sponges from greater depths may reflect lack of recruitment at depth, due to loss of larval viability or inability to disperse through the pycnocline. This experimental study of a distribution pattern overturned what seemed like obvious explanations of a bathymetric zonation pattern: the need of adult cyanobacterial-hosting sponges for adequate light for autotrophic symbionts, combined with an increasingly oligotrophic water column at depth.

One set of sponges that are confined to illuminated substrata are the photosymbiont-bearing clionaid boring species (e.g. López-Victoria and Zea, 2005). Distributions of three species of zooxanthellate Caribbean excavating sponge species, *Cliona aprica* Pang, 1973, *C. caribbaea* Carter, 1882, and *C. tenuis* Zea and Weil, 2003, were clearly associated with well-illuminated substrata, as well as with recently dead corals. Lack of a positive association with influence from untreated sewage, which has been demonstrated for other clionaids, suggests that zooxanthellae reliably supply their hosts in these species (López-Victoria and Zea, 2005).

The Caribbean excavating species *Cliona varians* Duchassaing and Michelotti, 1864 grows thickly over the substratum as well as excavating burrows, and zooxanthellae near the surface impart a rich golden brown colour. By manipulating light levels and pre-weighing blocks of solid carbonate substrate, Hill (1996) was able to correlate both growth rate and excavation rate with density of zooxanthellae, confirming that the sponge benefits nutritionally from the symbionts. Sunlight-fuelled symbionts also give some encrusting sponge species a significant enough boost in growth rate that they can overwhelm corals, as discussed in Section 2.3.3.2.

Curiously, while harbouring photosynthetic symbionts gives many sponges a significant boost in growth rate and appears to allow a few of them to overwhelm corals, dependence may not be as strong as for corals, and primary habitat constraints may be factors other than sunlight. In addition to the lack of sponge growth enhancement by some of these associations, harbouring photosynthetic symbionts may not be entirely beneficial even in cases of advantage. Wilkinson and Cheshire (1989) suggested that the expense of symbiont upkeep results in decreased representation of symbiont-harbouring species in coastal waters relative to oligotrophic outer reefs on the GBR. Further research into relative importance of differing flexibility in feeding mode among sponge species versus differing contributions among clades of symbionts will contribute to understanding of evolution of mutualism as well as sponge biology.

2.3.3. Ecological interactions

2.3.3.1. Symbiotic associations with macroscopic organisms

Sponges distinguish themselves by their astonishing number and variety of symbiotic associations with macroscopic organisms of all kinds. On coral reefs, many of these associations have been demonstrated to influence distribution and abundance and, in some cases, are the actual causes of distribution patterns that are correlated with abiotic factors. Alvarez *et al.* (1990) pointed out the possibility that apparent abiotic restrictions on depth for a sponge species can actually reflect the depth distribution of favoured microhabitat distributions, such as the association of *Mycale laevis* Carter, 1882 with the massive coral *Montastraea annularis* (Goreau and Hartman, 1966; Fig. 4.2). *M. laxissima*, a vase-shaped sponge with a relatively narrow basal attachment, may survive better on flexible substrata, such as gorgonians, that move with water motion, preventing the sponge from being ripped off (Reiswig, 1973).

In a very different context, overgrowth by *D. anchorata* may be facilitating the invasion of the tropical Pacific by the octocoral *Carijoa riisei*, as nudibranchs, observed on the unfouled octocoral, were absent when it was covered by the sponge (Calcinai *et al.*, 2004). In Hawaii experimental comparisons of feeding by the nudibranch, *Pyllodesmium poindemieri*, on *C. riisei* that was bare versus covered by four species of sponges, confirmed the protection afforded the octocoral by the sponges (Wagner *et al.*, 2009). How growing on *Carijoa* may benefit sponges has not been studied, but sponge associations with other colonial cnidarians on coral reefs can be mutually beneficial. Bright yellow zoanthids, *Parazoanthus swiftii*, conspicuous when embedded in dark forest green *I. birotulata*, discourage the angelfish *Holocanthus tricolor* from consuming the sponge in the Caribbean (West, 1976). Providing another caution on generalization, similar

Figure 4.2 Sponge–coral interactions, positive and negative. In the *Caribbean*, corals associated with non-excavating sponges survived an order of magnitude better than corals from which sponges had been removed because sponges adhere corals securely to the reef frame even if their bases are eroded (Wulff and Buss, 1979). Photo A. Janie Wulff: *Amphimedon compressa* helping to bind *M. annularis* to the reef. Photo G. Janie Wulff: *Niphates erecta* helping to prevent multiple portions of a *M. annularis* colony from becoming disengaged and falling into the surrounding sediment. Photo B. Janie Wulff. The encrusting sponge, likely *Acarnus nicoleae*, covering bare *M. annularis* skeleton, rendering it off limits for recruitment of boring organisms. In the *tropical western Pacific*, the cyanobacteria-bearing encrusting sponge, *Terpios hoshinota*, can rapidly overgrow living corals. Photo C. Keryea Soong: *Terpios hoshinota* overgrowing living coral in Taiwan, where up to 30% of the corals were infested on some reefs only a few years after *T. hoshinota* was first sighted there (Soong *et al*., 2009). In the *Caribbean*, *Mycale laevis* is closely associated with massive corals, which grow to

appearing associations between the zooxanthellae-hosting zoanthid, *Parazoanthus parasiticus*, in grey-blue *Niphates digitalis* Lamarck, 1814 interfered with pumping and in grey-purple *C. vaginalis* it failed to protect from angelfishes (Lewis, 1982) or sea stars (Wulff, 1995b).

Sponges associated with corals on Caribbean reefs can increase coral survival by an order of magnitude as they counter the effects of excavating organisms by gluing corals with eroded bases to the reef frame and protecting exposed skeleton from being colonized by excavating organisms. By measuring and mapping all corals on several fore-reef patch reefs, and then removing sponges from half of them, Wulff and Buss (1979) were able to confirm this benefit of sponges to corals that had been suggested by Goreau and Hartman (1966). Six months after the start of the experiment, 4% of the corals had fallen off of control reefs, but 40% had fallen off reefs from which sponges were removed. Even in cases in which some coral polyps were killed in order to allow a sponge to grip the solid carbonate skeleton, this is a small price for a coral to pay for an order of magnitude boost in colony survival.

The relationship of sponges to substratum stability on coral reefs is unusual in the degree to which the sponges themselves influence substratum

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accommodate its large oscules, as the sponge increases survival of the coral colonies (Goreau and Hartman, 1966; Wulff and Buss, 1979). Photo D. Janie Wulff: *Mycale laevis* adhering a *Porites astreoides* colony, for which the base had been entirely eroded by boring sponges, to the reef frame. Note that the sponge does not overgrow the living coral tissue. Photo H. Janie Wulff: *M. laevis* growing to close a gap in the coverage of exposed *Montastraea annularis* skeleton. In the *Caribbean*, sponges stabilize dead coral skeletons until crustose coralline algae can cement them permanently into a stable structure, suitable for coral recruitment (Wulff, 1984). Photo E. Janie Wulff: *Aplysina cauliformis* fragments, torn from their bases in a hurricane in Jamaica, stabilizing pieces of rubble from branching corals that were also generated by the storm. On coral reefs, boring sponges that harbour zooxanthellae are major agents of destruction of solid carbonate. Photo F. Christine Schönberg: *Cliona orientalis* (lower left) and *Aka mucosa* in the same coral slab in the pavement zone in <1 m of water, in Little Pioneer Bay, Orpheus Island, GBR, Australia. Photo L. Christine Schönberg: The boring sponge *Cliona orientalis* infesting *Platygyra daedalea* in Fig Tree Bay, Orpheus Island, Australia. Although a handful of encrusting sponges that harbour cyanobacteria are capable of rampant and rapid overgrowth of living coral, interpretations of apparent overgrowth must be based on time-series observations. Photo J. Klaus Rützler: *Chondrilla caribea* overgrowing skeletons of the corals *Acropoa cervicornis* and *Agaricia tenuifolia*, Cat Cay, Pelican Cays, Belize; note that the corals had died before the sponge covered them, and that Cat Cay hosts a particularly dense assortment of spongivorous fishes. Photo K. Klaus Rützler: *Cliona caribea* infesting *Diploria strigosa*, at the rate of 0.11–0.25 mm linear growth/day so that the distance from the tip of the knife to the leading edge of the *C. caribea* patch was covered in only 2 years.

stability (reviews in Wulff, 2001; Bell, 2008). On one hand, as discussed in the previous section, a handful of excavating sponge species are responsible for causing disengagement from reefs of chunks of solid carbonate (e.g. Hartman, 1977, Wilkinson, 1983). Non-excavating sponges (i.e. the vast majority of species) can influence solid substrata in the opposite way, by stabilizing coral rubble, significantly improving survival of coral recruits and thereby facilitating recovery of damaged reefs (Wulff, 1984). Among the non-excavating sponges that help corals maintain their grip on the reef frame, one Caribbean species in particular, *M. laevis*, is often found in close association with large massive corals, especially in the genera *Montastraea* and *Porites* (Fig. 4.2). The sponge grows in crevices under and between colony lobes that are covered with living coral tissue, protecting the otherwise exposed coral skeletons from action of excavating organisms, and also serving to glue pieces of coral with eroded bases to the reef frame. As the corals grow, the colony shape continues to accommodate the large oscules of the sponges (Goreau and Hartman, 1966). Consumption of this species by parrotfishes, especially *Sparisoma aurofrenatum* and *Sparisoma viride*, occurred only when the surface was sliced off, and never when it was intact (Wulff, 1997b); thus in return for increasing survival of their host coral, the sponges gain both an expanding substratum and a safe place to tuck vulnerable tissue.

Some coral reef sponges augment their skeletons with macroalgae, perhaps gaining an energetic advantage by not having to expend energy on skeleton formation (examples compiled by Rützler, 1990a). On tropical eastern Pacific reefs in Panama, *Ha. caerulea* perfused with articulated coralline red algae was protected from being consumed by fishes, but when sponge pieces without algae were exposed they were quickly consumed, especially by the angelfish *Holocanthus passer*, which normally engages in planktivory on these reefs that are nearly devoid of exposed sponges (Wulff, 1997c). The Australian sponge–macroalga combination of *Haliclona cymaeformis* Esper, 1794 and *Ceratodictyon spongiosum* Zanardini may fragment more readily than most branching sponges with significant spongin content in their skeletons, because the alga serves as support; but in this case, nutritional advantages allow this symbiotic association to grow rapidly and to recover quickly after fragmenting events (Trautman *et al.*, 2000).

Playing host to photosynthetic microbes not only restricts sponge species to lighted habitats but may influence the evolution of additional associations. Symbiotic associations of sponges with zoanthid species that are obligate sponge symbionts illustrate the complex layers of interdependence resulting from symbionts that require light. Analysis of specificity of associations among 92 Caribbean sponge species and 6 zoanthid species revealed that zoanthid species that host zooxanthellae exhibit a pattern of disproportionate association with host sponges that also host photosynthetic symbionts (Swain and Wulff, 2007). An evolutionary perspective, gained by matching phylogenies, demonstrated that a host switch of a zoanthid to a sponge species without photosynthetic symbionts was accompanied by evolutionary loss of zooxanthellae from this zoanthid species, maintaining the match in requirement for sunlight between the sponge and zoanthid species (Swain, 2009).

Beneficial sponge–sponge associations, first described in temperate North American, Adriatic, and Mediterranean waters (Rützler, 1970; Sará, 1970), are also featured on coral reefs. Mutually beneficial associations among three species of erect-branching sponges, for which growth, and especially survival, is increased by adhering to a sponge of another species, are based on variation among species in susceptibility to a variety of hazards, including breakage by water movement, smothering by sediment, infection by pathogens, and consumption by a variety of predators (Wulff, 1997a). Time-series observations and a variety of experimental manipulations, comparing growth alone versus in combination with other species, confirmed that apparent overgrowths were actually mutually beneficial to participating individuals. Sponge individuals that suffer partial mortality are saved from additional mortality, that can result from being disengaged from the substratum, by firmly adhering to heterospecific sponges that are susceptible to different partial mortality sources. As in dense and diverse sponge-dominated communities in caves in the Mediterranean and Adriatic, mutually beneficial interactions between sponge species may serve to autocatalytically increase diversity by keeping all species in the community.

2.3.3.2. Competition

Competition with algae to the point that sponges are eliminated has not been reported on coral reefs. Zea (1994) was able to clarify a sequence of changes at sites on the Colombian coast near Santa Marta by repeating surveys of number of individuals and percentage cover of corals and sponges after a 2-year interval. At a site that had recently suffered considerable coral mortality due to stress by nutrients and sediment in coastal runoff, sponges had significantly increased and corals had decreased. The actual sequence was that increases in sponges followed on the heels of increases in algae, which had come at the expense of corals. Zea (1994) pointed out that some thin encrusting sponges may have been missed during the first survey when fleshy algal turfs were especially dense, but that even taking that into account, the sponge increase was significant. A recent unusual bloom of a crustose coralline alga in a small semi-enclosed bay in Bonaire has resulted in overgrowth of corals and also sponges, but whether or not sponges will be lost or be able to tolerate the overgrowth is not yet known (Eckrich *et al.*, 2011).

Most sessile animals also appear unable to outcompete adult sponges on coral reefs, although newly recruited sponges are vulnerable. One of the rare examples is overgrowth of thinly encrusting *Chondrilla caribensis* forma *hermatypica* (Rützler *et al.*, 2007) by the corallimorpharian *Ricordea florida* and the gorgonian *Erythropodium caribaeorum* that was documented on the fore reef in Puerto Rico (Vicente, 1990). One coral reef sponge, *Dysidea* sp., has been demonstrated to overgrow another, *Cacospongia,* in Guam. The resulting necrosis can lead to deterioration of the basal attachments of *Cacospongia* such that they lose their grip on the reef (Thacker *et al.*, 1998). Mutually beneficial associations among three branching species (Wulff, 1997a), described in the previous section, were parasitized by a fourth species that behaved conspicuously differently, overgrowing heterospecific sponges to the point of smothering them. *D. anchorata*, with a ridiculously flimsy skeleton, survived significantly better (64.3% vs. 0% after 6 months) when it grew on other erect-branching sponges than on solid carbonate substrata (Wulff, 2008b). Its role as a parasite on the sponge–sponge mutualism did not become evident until after about 12 months, when it began to get large enough to smother its hosts.

2.3.3.3. Special cases of competition: Sponges and corals

Much has been, and continues to be, made in the coral reef literature of how sponges, in general, appear to be increasing on coral reefs at the expense of corals. On the other hand, substantial losses of sponges have been reported, raising concern about loss of their important roles as water filterers, substratum stabilizers, and hosts of diverse symbionts representing every group of organisms. Variation among sponge species in their interactions with corals, ranging from rampant overgrowth of living corals to increasing coral survival by an order of magnitude, mandates that reports of sponge–coral interactions include the names of the species observed and time-series observations. Interactions that appear on initial observation to be competitive overgrowth may either fail to progress over time or actually be beneficial. Results of interactions are not merely species dependent but are also context dependent. Even the outcomes of interactions of excavating sponge species with corals, unambiguously negative for the corals, and obligate for the sponges, depend on details such as angle of encounter, temperature, and water column nutrient levels (e.g. Rützler, 2002; Schönberg, 2002, 2003; López-Victoria *et al.*, 2006). Because of these complexities, and the great importance of sponges to the existence of this threatened ecosystem, I go into much greater detail in this section.

A few sponge species have been demonstrated to be aggressively invasive and capable of overwhelming living coral, when enabled to colonize a community in which they did not evolve. In Kaneohe Bay, Hawaii, *Mycale grandis* Gray, 1867, which is native to Indonesia and Australia, has been wreaking havoc with the corals *Porites compressa* and *Montipora capitata* by smothering their living tissue since 1996. In 10 permanent photo quadrats, cover of this sponge increased 13%, while coral cover decreased 16.3% (Coles and Bolick, 2007). On the Pacific coast of Mexico, an Indo-Pacific sponge, *Chalinula nematifera* de Laubenfels, 1954 is disproportionately associated with branching corals in the genus *Pocillopora*, which it overgrows, adhering tightly to the bared skeleton. This association may be facilitating the invasion of Mexican Pacific coral reefs by *C. nematifera*, because of the relatively low light levels within the coral colonies, or perhaps the protection against predators provided by spikey *Pocillopora* branches (Ávila and Carballo, 2008). Fortunately, it had not increased its representation at the sites monitored during the study, and although the authors searched for it at 150 sites, they only found it at Isla Isabel and Cabo Pulmo.

A small handful of sponge species have been demonstrated to kill corals by chemical means. Experiments and observations of the Caribbean species *Plakortis halichondroides* Wilson, 1902 indicated that corals of 14 species were killed by contact and at distances up to 5 cm (Porter and Target, 1988); and an Australian *Haliclona* species that bears zooxanthellae and also nematocysts appears to be able to settle on and kill living *Acropora nobilis*, as necrosis has been observed within 1 cm of the sponge (Garson *et al.*, 1999; Russell *et al.*, 2003). de Voogd *et al.* (2004) recorded all neighbour interactions of four Indonesian sponge species that had been determined to be bioactive, showing that these species caused necrosis 85% of the time when they overgrew corals. The excavating species *Aka coralliphaga* Rützler, 1971 is also capable of penetrating coral covered by living tissue (Rützler, 2004).

Although only a very small number of species have been observed to consistently overwhelm corals, their effects can be significant when and where they are abundant. An example from Yemen differs from other reports of sponge–coral interactions in that the sponge, a very thinly encrusting *Clathria* species, specifically attacks the massive coral *Porites lutea* as a narrow band along the edge of the living tissue, and as it kills the coral it leaves behind bared skeleton rather than continuing to cover the substratum (Benzoni *et al.*, 2008). Although apparently a local phenomenon, at least for now, it is of concern because *P. lutea* is the primary reef building coral, constituting up to 47% of the benthic cover at the Gulf of Aden site; and *Clathria* sp. was observed in half of the coral colonies. At another Gulf of Aden site, *Clathria* sp. was noted to infest large corals that were transplanted in order to save them from destruction due to construction of a liquefied natural gas plant. Once the corals had a chance to recover from the stress of transplantation, this threat seems to have receded, as survival after over a year was 91% (Seguin *et al.*, 2008).

A small number of encrusting or excavating species, most of which harbour photosynthetic symbionts, have been demonstrated to overgrow living corals (e.g. Vicente, 1978, 1990; Rützler and Muzik, 1993). On Puerto Rican reefs, *C. caribensis* was shown to be an important aggressor against nine species of scleractinian corals (Vicente, 1990); and on coral reefs of the central and western Pacific, another encrusting sponge species that harbours cyanobacteria, *Terpios hoshinota* Rützler and Muzik, 1993, has been demonstrated to overwhelm corals. Because generalizations have frequently been made about "sponges" overwhelming corals, based on reports of these two highly unusual species; and because even these species appear to be greatly restricted in the circumstances under which they overwhelm corals, I go into considerable detail about both in the paragraphs that follow.

Terpios hoshinota (Fig. 4.2) was first reported as overrunning corals in Guam in 1973 (Bryan, 1973), and distribution and abundance studies in Okinawa 10 years later revealed a pattern of this thinly encrusting species running rampant over live corals at sites where development had increased turbidity of coastal waters (Rützler and Muzik, 1993). The possibility that *T. hoshinota* was able to gain nutritionally from the living coral tissue as it overgrew was suggested by growth rates on live coral (a mean of 6.5 mm/8 days!) that exceeded those on dead coral (Bryan, 1973). A test of this intriguing suggestion, by comparing growth on live corals versus freshly cleaned coral skeletons, revealed growth on freshly cleaned skeletons to be even faster (Plucer-Rosario, 1987), suggesting inhibition of sponge growth by the fouling community on substrata that have been exposed. The ability of *T. hoshinota* to rapidly infest large areas may be fuelled by symbiotic cyanobacteria that are so dense that the sponge can appear almost black; coupled with an unusual growth form that combines thin encrustations that quickly cover everything with narrow processes by which new substrata can be colonized asexually. On a reef in Taiwan, where an outbreak resulted in 30% of the corals being infested, Soong *et al.* (2009) positioned dark sheets over infested corals to block sunlight from fuelling the cyanobacteria hosted by *Terpios*. Blockage of sunlight caused bleaching in the coral hosts, and the sponges ceased spreading in their usual continuously encrusting growth form. But the sponges advanced thread-like processes across the shaded spaces and resumed their usual expansion once they regained lighted substrata. In spite of an unusual combination of attributes that allow *T. hoshinota* to quickly obliterate large areas of living coral, it also appears to be relatively ephemeral, vanishing at sites where it was abundant, and appearing elsewhere. Fourteen years after *T. hoshinota* had killed 87.9% of the corals at a site in Okinawa, it could not be found among the dense live corals, but it covered 50% of the substratum at a new site on a different island (Reimer *et al.*, 2010), and has now been discovered overgrowing live corals at Lizard Island, Australia (Fugii *et al.*, 2011).

Chondrilla caribensis (Fig. 4.2) also stands out as a species that is capable of overgrowing living coral under some circumstances (Vicente, 1990). When *Chondrilla* was caged with corals in the Florida Keys, it extended laterally over the corals significantly more than when it was not caged, suggesting that spongivores kept the sponge in check (Hill, 1998). Like *T. hoshinota*, *Chondrilla* has unusual abilities for spreading itself and is consequently a difficult organism to manipulate. It tends to break into pieces and migrate (e.g. Zilberberg *et al.*, 2006), entering uncertainty into interpretations of experimental results (e.g. Wilkinson and Vacelet, 1979). Experiments on growth of the closely related species, *C. nucula* Schmidt, 1862, in the Mediterranean required that the specimens be placed in small cups, and still they were able to climb out (at a rate of 2.5 cm/month) and populate the outsides of the cups (Pronzato, 2004). In the Pelican Cays, Belize, one of the sites where *C. caribensis* looks as if it has overgrown corals (Fig. 4.2), the corals had actually died as a result of bleaching before *Chondrilla* overgrew them (Macintyre, 2000), which it did in the presence of a conspicuously dense population of large spongivores, including grey angelfishes, trunkfishes, filefishes, and spadefishes (Wulff, 2000, 2005). Consumption by fish was recorded by video when *Chondrilla* was placed on racks on sand (Dunlap and Pawlik, 1996), and Hill (1998) observed *Chondrilla* with bite marks, indicating that it was consumed, but not entirely. In Panama, it was included as one of 64 species that were consumed by naturally feeding angelfishes a few bites at a time, alternating with bites of other sponge species (i.e. smorgasbord feeding, as described by Randall and Hartman, 1968 and Wulff, 1994). *Chondrilla* ranked 28th in total volume, out of 39 sponge species in a fully censused plot, but 39th in terms of number of bites taken by angelfishes in the genus *Pomacanthus* (Wulff, 1994). It and it is consistently rejected by the large Caribbean sea star, *Oreaster reticulatis* (Wulff, 1995b). A suggestion that variation among individuals and populations may account for at least some of the variation in conclusions about palatability of this species (Swearingen and Pawlik, 1998) is bolstered by the recent distinction of subspecies, one inhabiting mangrove roots, *C. caribensis* forma *caribensis*, and the other inhabiting reefs, *C. caribensis* forma *hermatypica* (Duran and Rützler, 2006; Rützler *et al.*, 2007). Thus interpretation of consumption of *Chondrilla* must take into account the source habitat. Based on literature reports of *Chondrilla* overgrowing corals in the Florida Keys and Puerto Rico (Vicente, 1990; Hill, 1998), and high frequency in hawksbill turtle gut contents, León and Bjorndal (2002) concluded that historically much larger populations of hawksbills prevented this species from overgrowing corals, but it seems that something else must be keeping this sponge uncommon on many reefs that are not currently well populated by hawksbill turtles. For example, in Los Roques, Venezuela, *Chondrilla* was not among the 60 species in 1290 m^2 spanning a depth range from 1 to 35 m (Alvarez *et al.*, 1990); and in San Blas, Panama, it constituted only 0.085% of the total sponge volume of 33,721 cm^3 in completely censused quadrats (Wulff, 2006a). *Chondrilla* was not among the 24 most common species between 10 and 30 m depth at sites in Cuba (Alcolado, 1990); and only 5 of the 3554 (=0.14%) sponge individuals identified at shallow, medium, and deep zones in the upper Florida Keys were *Chondrilla* (Schmahl, 1990). Something besides hawksbill turtles or spongivorous fishes appears to have primary responsibility for restraining *Chondrilla*, at least on most Caribbean coral reefs, while on some reefs it appears to grow unrestrained. It is intriguing that a sponge species that can be extremely common locally, and is capable of overgrowing corals under some circumstances, has been so resistant to our developing a comprehensive understanding of what controls its distribution and abundance.

Aiming to test the hypothesis that sponges are more likely to overgrow corals on reefs that are stressed, Aerts and van Soest (1997) categorized interactions between corals and sponges at three depths at each of five sites near Santa Marta, Colombia, that varied in sedimentation rate and water column visibility. Underscoring the great importance of careful identification of sponges to species, their data analysis revealed that not only was sponge overgrowth of coral not more likely on stressed than on healthier reefs, but the chief determinant of coral overgrowth was not abiotic factors, but the presence of a particular handful of sponge species. Only 16 of the 95 sponge species at these sites engaged in overgrowth of corals at all, and of those, only *D. anchorata*, *Aplysina cauliformis* Carter, 1882, and *Callyspongia armigera* Duchassaing and Michelotti, 1864 overgrew coral in more than 10% of their contacts. Follow-up study of interactions over time revealed that apparent overgrowths often turned out to be standoffs, and that the thinly encrusting species *C. venosa* Alcolado, 1984 overgrew living coral tissue only when the coral colony had been stressed by experimental damage (Aerts, 2000).

D. anchorata, the species that cheats on mutualism among other branching sponge species by overgrowing them to the point of smothering, also bolsters its flimsy skeleton by growing over gorgonians (McLean and Yoshioka, 2008). Although it has been observed to overgrow corals, it does not survive well on rigid substrata (as detailed above). Its ability to grow at rates much faster than other Caribbean coral reef sponges is balanced by a rate of mortality that is also much higher (Wulff, 2008b). Specific growth rates after 3 months were four times those of three co-occurring branching species. The suggestion that fast growth is possible because it invests so little in its own skeleton is bolstered by biomechanical data showing that the extensibility of three other branching Caribbean reef sponges was 5–15 times as great. This flimsiness was reflected in *Desmapsamma* mortality that, after 9 months, was more than eight times that of the other species. These traits allow rapid, but relatively ephemeral, occupation of any particular site. This species that can appear at a particular moment to be overwhelming a reef can also be diminished to small scraps in an afternoon squall.

Effects of one type of ecological interaction are often moderated by another, and so segregating the effects of competition from the effects of predation is a rather futile exercise in rendering something multidimensional into the linear pattern decreed by paragraph structure. Thus many of the examples in the next section "Predation" have been, or could have been, introduced as illustrative of how competition influences sponge distribution and abundance.

2.3.3.4. Predation

Large spongivores on coral reefs include hawksbill turtles, angelfishes, and to lesser extents some trunkfishes, file fishes, puffer fishes, and rabbit fishes. Less is known of the smaller predators, such as nudibranchs and small echinoderms, and even less about inquilines that may munch on their host.

Hawksbill turtles consume a very small subset of coral reef sponge species, most of them in the orders Astrophorida, Chondrosida, and Hadromerida. Many of the species chosen are conspicuously full of silica spicules (e.g. Meylan, 1988, 1990). The large sturdy beaks of hawksbills are capable of reducing large, well-armoured sponges to nothing or to remnants, which are able to regenerate (e.g. Dam and van Diez, 1997). Data on hawksbill feeding, gained by lavage of stomach contents, provide a clear record of what has been eaten, and the relative amount of each species. Every study has confirmed the small number of species, all in a constrained representation of higher taxa, that are ingested. In the Dominican Republic, percentage cover was measured in the field for sponge and corallimorpharian species found in lavage samples in order to calculate selectivity indices. These indicated that a combination of relative abundance and preference influences turtle feeding decisions and indicated positive selection for *Spirastrella coccinea* Duchassaing and Michelotti, 1864 and *Chondrilla nucula* (=*C. caribensis*) at one site and *Myriastra kallitetilla* (=*Stelletta kallitetilla* de Laubenfels, 1936) and *C. nucula* at another site (León and Bjorndal, 2002). Unfortunately, sponge species not found in lavage samples were not included in the field survey, and so these data cannot address the question of persistent choice of these species, and a handful of others, from among the hundreds of sponge species inhabiting Caribbean coral reefs. Additional clues about hawksbill feeding choices came from Mona Island, Puerto Rico, where Dam and van Diez (1997) combined lavage sampling with observations of feeding turtles and noted that the turtles often searched under ledges and in crevices for their prey. At both cliff and reef sites, the species *Geodia neptuni* (=*Sidonops neptuni* Sollas, 1886) and *Polymastia tenax* Pulitzer-Finali, 1986 were most commonly ingested, with differences in relative rates of ingestion of these and other species reflecting differences in the sponge faunas at their sites. Strong hints that *G. neptuni* is nutritionally more valuable to the turtles were provided by reduced foraging time on the cliffs (where *Geodia* was very common), reduced variety of sponge species ingested on the cliffs, and greater growth rates of immature hawksbills living along the cliffs (Dam and van Diez, 1997). The effect on *Geodia* populations included complete consumption of some individuals, but also many individuals showed the typical healing and regeneration patterns after hawksbill bites (photo in Dam and van Diez, 1997); *Geodia* remained abundant at these sites.

Angelfishes are the other large dedicated spongivores on coral reefs. When Randall and Hartman (1968) analysed gut contents of multiple representatives of 212 species of Caribbean reef fishes, they discovered that only 11 of the species consumed sponges, and also that spongivorous fish species tended to distribute their feeding over many sponge species. Based on these data, Randall and Hartman pointed out that coral reef sponges that live on exposed surfaces were not likely to be controlled by predators. Their conclusion, inferred primarily from angelfish gut contents that in the aggregate included 46 sponge species, as well as gut contents of individual fish that had consumed as many as nine species just before the moment they were speared, has been well corroborated by extensive field observations of feeding angelfishes. Hourigan *et al.* (1989) observed feeding on over 22 sponge species in a field study of unimpeded angelfishes, and Wulff, (1994) observed two species of *Pomacanthus* consuming 64 sponge species in the course of 2285 bites. Wulff's data revealed that angelfishes fed on rarer species significantly more than predicted by their relative abundance, both by comparisons of number of bites with sponge volume and by comparisons of number of visits with number of individual sponges. Feeding sequences unambiguously confirmed that individual angelfishes took only a few (mean of 2.8) bites from each sponge, and in 92% of the cases in which they continued feeding they moved on to a sponge of another species. A different interpretation of angelfish preferences among Caribbean reef sponges was made by Pawlik *et al.* (1995) who presented pelletized sponge extracts mixed with powdered squid to wrasses in tanks and scored sponge species as deterrent if the wrasses rejected 4 or more out of 10 pellets. Because some of the species that produced extracts acceptable to wrasses also appeared frequently in Randall and Hartman's (1968) gut content data, these species were deemed preferred. It should be noted that, while gut content data can provide incontrovertible evidence that a particular species was ingested, they cannot distinguish if a prey species was consumed because it was preferred or merely because it was abundant, unless data on relative abundance of sponge species were collected at the sites where fish were collected. Thus gut content data alone cannot validate pellet assays. Some sponge species that appeared especially frequently in the gut contents analysed by Hartman, such as *C. vaginalis*, are among the most common on Caribbean reefs, suggesting that their frequency in gut contents was at least in part due to availability. This species ranked 22nd by number of bites consumed at a site where it ranked 15th by total volume (Wulff, 1994). However enticing its extracts are to wrasses, when mixed with squid powder, this species remains among the most abundant. Bite marks can sometimes be observed on the rims of *C. vaginalis* tubes, indicating the presence of spongivores capable of consuming it, but not inclined to consume very much of it at one go. In a study focused on feeding and growth rate of *C. vaginalis* at different depths, no signs of predation were ever observed, leading the authors to suggest that bottom-up control was more likely than top-down (Trussell *et al.*, 2006). For sponge species that normally live on exposed surfaces on coral reefs in the Caribbean, where most of the spongivore work has been done, predation does not appear to be a primary influence on distribution and abundance patterns.

For sponges that do not live on exposed reef surfaces, predators can play a much greater role in distribution and abundance. Some species are confined to cryptic spaces in the reef frame by spongivorous fishes that eagerly consume them if they are exposed by breaking open their cryptic habitats (e.g. Wulff, 1988, 1997b,c; Dunlap and Pawlik, 1996).

Defences against reef-dwelling spongivores that serve reef-dwelling sponge species well in their normal habitat (i.e. reefs) are not necessarily effective in other habitats. Strict boundaries of habitat distribution where reefs abut seagrass meadows may appear to be caused by inability of reef sponge species to cope with diminished solid substratum or shifting sediments. But in the Caribbean at least, the seagrass-dwelling large sea star *O. reticulatis* efficiently guarantees this habitat restriction by quickly consuming most typical coral reef sponge species if they are washed into the seagrass by a storm or moved there by underwater farmers (Wulff, 1995b). Sponge species typical of other habitats, such as mangroves, are likewise prevented from successfully colonizing coral reefs by reef-dwelling spongivorous fishes (Dunlap and Pawlik, 1996; Wulff, 2005).

Consumption of coral reef sponges by small animals, including some nudibranchs, and endosymbionts, such as shrimps and polychaetes, has also been reported, but challenges in experimental manipulation of inquilines and other small predators have made it difficult to know the extent to which these predators influence distribution and abundance of reef sponge species. Most studies have focused on preferences of the predators. Spread in geographic extent and increase in abundance of the soft coral invader *C. riisei* may be facilitated by its protection from a specialized nudibranch by association with four species of sponges in Hawaii (Wagner *et al.*, 2009). Clear consumption of sponges is demonstrated by photographs of polychaetes inhabiting *A. cauliformis* with their jaws deeply embedded in their host tissue (Tsuriumi and Reiswig, 1997), and syllid polychaetes on the surface of some sponges have been demonstrated to consume their host (e.g. Pawlik, 1983). Shrimps inhabiting canals of *Hymeniacidon caerulea* Pulitzer-Finali, 1986 clearly gain shelter, but bits of this deep royal blue sponge in their guts indicate that they are also ingesting their host (e.g. Rios and Duffy, 1999).

2.4. Coral reefs—cryptic spaces

2.4.1. Abiotic factors

Cryptic habitats, such as caves and cavities in coral reef frameworks, are inhabited by a rich diversity of sponges. Of the 92 species identified by Kobluk and van Soest (1989) in cavities in the Bonaire reef frame, only a small proportion (14%) of the species were found over the entire 12–43 m depth range sampled, but it is unknown what might restrict depth distributions in these species. Many of the species they found in cryptic spaces also inhabit exposed surfaces, raising questions about the relative quality of life for them in these very different circumstances. Do the hidden individuals subsidize the exposed populations? Or are they merely at the fringe, barely eking out a living in cryptic spaces that may constrain size, decrease growth rates, and certainly preclude dependence on photosynthetic symbionts? Distinction must be made between cavity-filling cryptic species that entirely fill gaps between pieces of hard substrata and those, mostly thinly encrusting, species that coat the linings of cavities and crevices and undersurfaces of plate-shaped corals. These are not only morphologically, but also taxonomically distinct, and so while Kobluk and van Soest found that many cavity-inhabiting species also live on exposed surfaces, Lehnert and Fischer (1999) found that sponges inhabiting undersurfaces of platy corals constituted a highly distinct set of species.

Species typical of cryptic habitats were relatively well protected from the ravages of a major hurricane on Jamaican coral reefs; but when they were infrequently exposed by the reef frame being ripped apart, they exhibited unusually poor capacity for recovery, given the usual high regeneration capacity of sponges (Wulff, 2006b). If it is legitimate to interpret their inability to recover when exposed by reef destruction as a hint that this type of insult has not dominated their selective regime, then physical disturbance is an aspect of the abiotic environment that may be evaded in cryptic spaces on coral reefs. Sediment is the other abiotic factor from which sponges in cryptic spaces are protected. Coralline sponges, major framework builders in the Paleozoic, may now be restricted to the undersurfaces of ledges or ceilings of cavities and caves, or to the most vertical of reef walls, by their intolerance of sediment or poor ability to compete for space due to slow growth (Hartman and Goreau, 1970; Jackson *et al*., 1971; Willenz and Hartman, 1999). Their dense aragonite skeletons produced by slow growth are important reef framework reinforcers on deep reefs and in caves (Lang *et al*., 1975; Hartman, 1977).

2.4.2. Ecological interactions

As remarked in the previous section on coral reefs, at least some species have been demonstrated to be restricted to inhabiting crevices in shallow reef frames by eagerness of fishes, including some parrotfishes, to feed on them in the Caribbean (Wulff, 1988, 1997b; Dunlap and Pawlik, 1996), tropical eastern Pacific (Wulff, 1997c), and central Pacific (Backus, 1964). Two species of semi-cryptic sponges, that live with surfaces exposed, but the bulk of their tissue tucked into crevices in corals, were also consumed by parrotfishes when their surfaces were sliced off (Wulff, 1997b). However, not all species that are confined to cryptic spaces are consumed when exposed, suggesting that they fail to thrive due to surface fouling by diatoms, or abiotic factors such as sunlight or wave action (Wulff, 1997a,b).

Competition for space can be extreme in cryptic habitats. Cavity-filling species can bind disjunct pieces of solid carbonate to each other, stabilizing them until crustose coralline algae and other carbonate secreting encrusters can bind them together permanently, rendering them suitable for recruitment of coral larvae (Wulff, 1984). Internal architecture of cavity-filling cryptic sponges tends to be "cavernous", facilitating water flow in enclosed spaces and also encouraging inquilines. At least one cavity-filling species, *Hy. caerulea*, hosts eusocial shrimp (Rios and Duffy, 1999).

Encrusting sponges that line cavities or coat undersurfaces of plate-shaped corals, interact very differently, and competition for primary substratum space may dominate their lives. The ability of encrusting filter-feeding animals to evade elimination in a habitat of discontinuous substrata was explored by Buss (1976) and Buss and Jackson (1979) in a system of at least 300 species that inhabit the undersurfaces of foliaceous corals. Non-transitive competitive relationships were demonstrated by scoring overgrowth in 152 interactions among 20 species of encrusting organisms, including 8 sponge species. Buss and Jackson's resulting notion of competitive networks provides a mechanism for enhancing species diversity in habitats characterized by multiple discrete patches. A combination of position effects with multiple mechanisms of competition can increase diversity by slowing elimination from a particular discrete substratum and also by increasing the probability of different winners in each patch.

2.5. Mangroves

2.5.1. Abiotic factors

Prop roots of mangrove trees, and the associated peat banks, can support extremely dense communities dominated by sponges, at least in areas where tidal amplitude is not great. Root surface area covered by sponges can be 100%, with mean coverage reported as 31.7% in the Florida Keys (Bingham and Young, 1995), and 10–50% cover in Belize (Farnsworth and Ellison, 1996). In a comparison of diversity and abundance of sponges on mangrove roots at scales ranging from within individual roots to between cays on the Belize Barrier Reef, a striking pattern revealed by Farnsworth and Ellison (1996) was the complete lack of sponges on windward sides of cays. Luxurious sponge growth on mangrove roots in less exposed sites (e.g. 15.7 and 20.8 cm^3/cm root length on mangrove prop roots at two sites on offshore cays in Belize; Wulff, 2009) may be facilitated by relatively benign physical disturbance levels and high food availability, although extreme variations in other abiotic factors such as temperature, salinity, and turbidity can be mortal stressors.

Rützler *et al.* (2007) compiled tolerances of sediment and of temperature and salinity extremes, for 25 mangrove-dwelling sponge species, demonstrating the astonishing capacity of these fragile appearing, and uniquely porous animals to cope with environmental challenges, including temperatures of 19–41 °C, salinities of 20–38 ppt, and layers of fine sediment as thick as 5 mm. In a single tidal cycle, temperatures can vary from 18 to 32 °C in winter and from 28 to 41 °C in summer (Rützler *et al*., 2004). Species vary widely in tolerances, and distribution patterns reflect this variation. On an offshore mangrove cay, Twin Cays Belize, differences in sponge faunas between a main channel site and a tidal creek (only 330 m away) that consisted mainly of deletions in the tidal creek (17 vs. 39 species) spurred transplant experiments to see if deletions were best explained by colonization history or by more extreme temperature and salinity fluctuations. Transplants thrived for the first 10 days, but all replicates of five of the six species had vanished 1 year later, implicating episodically unfavourable abiotic factors in constraining distribution for at least these five species (Wulff, 2004). Similarly, transplants of four species between sites in Belize that differed in abiotic factors grew during the first 16 days but then began to decline such that by 6 months later all had died (Farnsworth and Ellison, 1996). More extreme negative conditions delete more species, to the point that only a single species was found on prop roots at one Belize coastal site (Farnsworth and Ellison, 1996). At mangrove sites in the Florida Keys, where temperature and salinity fluctuate dramatically, sponge species typical of coral reefs did not fare well after transplantation, and at one of three sites, the usual mangrove species were killed as well (Pawlik *et al*., 2007). Torrential rains in the Florida Keys entirely eliminated mangrove sponges from sites at Long Key (C. Lewis, personal communication), underscoring the degree to which episodically extreme abiotic conditions can influence sponges at sites that are vulnerable not only due to their proximity to land but also because of their geographic position at the extreme boundaries of faunal distribution.

On Caribbean mangrove roots, where low tidal amplitudes generally allow sponges to live reliably submerged very near the water line, occasional very low tides expose sponges. Even during a period of unusual tides 40 cm below MLW in the middle of sunny days, some sponges survived, providing information on variation among sponge species in ability to cope with air exposure (Rützler, 1990b). Vertical zonation patterns on mangrove roots could then be interpreted as the signature of previous low tides. Just as in rocky subtidal and coral reef habitats, negative effects on sponges of episodically unfavourable abiotic factors can be moderated or worsened through microbial symbionts in mangrove habitats. Rützler (1988) documented disease in a cyanobacteria-bearing species, *Geodia papyracea* Hechtel, 1965, in a Belizean mangrove channel, that was caused by its normal cyanobacterial symbiont multiplying at an overwhelming rate. The sponges appeared unable to control their symbionts, which may have outstripped their hosts in response to conditions, possibly temporarily warmer temperatures, that were more favourable to cyanobacteria than to sponges.

2.5.2. Ecological interactions

Heterogeneity of species distribution at spatial scales ranging from within individual roots to between geographic subregions has been the conclusion of most studies of mangrove sponge species distribution patterns (e.g. Farnsworth and Ellison, 1996). Although much variation in distribution and abundance can be attributed to variation in abiotic factors, high heterogeneity remains a characteristic even in comparisons between sites that are abiotically identical. At least some of the apparent heterogeneity reflects methods of evaluating abundance, as illustrated by three sites in Belize and Panama that appear to differ substantially in composition if evaluated with respect to numbers of individuals, but are very similar when compared in terms of volume (Wulff, 2009). Vagaries of recruitment to small separate substrata contribute to heterogeneity among roots at a particular site (e.g. Sutherland, 1980; Wulff, 2004), and current direction can influence movement of larvae within a site, with the importance of this effect strongly dependent on life histories of individual sponge species (Bingham and Young, 1991, 1995; Bingham, 1992). Understanding differences in life history strategies among sponge species that are typical of mangrove roots allows at least some of the heterogeneity among roots within a site to be interpreted as differences in successional stage (Wulff, 2009), with younger roots covered by quick recruiters and older roots tending to have accumulated poor recruiters that are adept at out-competing early successional species.

As in other communities, substratum continuity can influence the degree to which a competitively superior species can eliminate other species from a community. Rare leaps from one mangrove root to another via long flimsy extensions are possible for a few species, but in general recruitment is by larvae, as in other habitats with discrete small substrata that are separated by uninhabitable matrix. Among the sponge species in a mangrove-root system in Bahia de Buche, Venezuela, Sutherland (1980) documente an inverse relationship between efficiency of recruitment onto experimentally provided substrata and ability to acquire and hold space. This result was corroborated by Wulff (2004) in a Belizean mangrove cay where early recruitment to artificial roots (pvc pipes suspended among the roots) was disproportionately of species that were either uncommon, or not reported at all on roots.

Sutherland (1980) documented community structure and followed dynamics for 18 months on mangrove roots dominated by sponges. By explicitly comparing community development on roots versus large flat recruitment panels that he suspended among the roots, he was able to garner clues about mechanisms by which community assembly results in heterogeneous species composition from root to root. Sutherland interpreted the rapid domination of some of the panels by the single species *T. ignis*, which was not among the top recruiters, as an illustration of the extreme importance of stochastic recruitment events in this system. Because each panel had at least 10 times the surface area of an individual root, they were more likely to sample all of the larvae in the water column and, therefore, to gather species that recruit less efficiently but that may be particularly effective at gaining and maintaining control of space. Competitive elimination in this system was slowed by a disproportionately low probability that a superior competitor species recruited at all to a particular root. Just as for community dynamics on undersurfaces of coral plates, the interplay between size of continuous substrata, provision of bare space, recruitment, and competition on mangrove roots is influenced by addition of new space via growth of individual substrata.

Sutherland's (1980) remark about the Venezuelan mangrove community, "In spite of the taxonomic richness of this community, most species are extremely rare", has turned out to aptly describe other mangrove-root communities in which relative abundance has been measured. For example, nearly 54.9% of the space on Florida Keys mangrove roots was covered by just three species (Engel and Pawlik, 2005), and on mangrove props roots at three sites in Belize and Panama, 73–89% of the volume was concentrated in the nine species that all the sites had in common (Wulff, 2009). Curiously, at many Caribbean sites, the same species, *T. ignis*, dominates by whatever metric is used for abundance, even though it often does not appear on a particular root, and its presence on a root or panel does not guarantee that it will dominate that substratum (e.g. Sutherland, 1980; Wulff, 2009).

Epizoism is common among sponge species that typically inhabit mangroves, and interactions between neighbouring sponges that are overgrowing each other can be beneficial or neutral, as well as negative. An apparent competitive hierarchy of 10 species growing on mangrove prop roots in the Florida Keys was erected by Engel and Pawlik (2005) by recording whether or not sponges appeared to be growing over each other. They pointed out a counter-intuitive pattern that the most abundant species occupied a middle level in the overgrowth hierarchy, and individuals of the most basal species in the hierarchy often grew to be very large. While this pattern appears puzzling in the context of many marine systems in which competition has been demonstrated to be a key structuring process, evidence continues to accumulate that it may be normal for some sponges to not compete with sponge neighbours. Sponge-dominated communities appear to stand out in the degree to which overgrowth can increase the representation of participating species. It is important to note that this does not apply to early successional mangrove sponge species, which do get eliminated, but are also less likely be observed on roots during a one-time survey (e.g. Sutherland, 1980; Wulff, 2009). Overgrowth by non-sponge taxa, such as dense mats of the filamentous cyanobacteria genera *Lyngbia* and *Schizothrix* (Rützler *et al.*, 2004) or compound ascidians and bryozoans (personal observation), can have negative effects on sponges. Mangrove roots that are not in abiotically extreme circumstances fall into Sará's (1970) third category of sponge community types, that of "continuous sponge populations, with practically negligible intervention of other elements of the sessile macrofauna and macroflora", a situation that has consistently provided illustrations of how sponges can benefit by their neighbours also being sponges.

Differences in sponge species diversity at mangrove sites are extreme, ranging from 3 to 147 species on a list of sites compiled by Diaz *et al.* (2004). Very low diversity reflects abiotic variables that are simply unfavourable for most sponges, but diversity differences between sites characterized by abiotic variables that are generally favourable may be strongly influenced by ecological interactions. Mangrove prop roots in the lagoons of three mangrove-covered islands of the Pelican Cays, Belize, were inhabited by 147 sponge species, in contrast to only 57 species on roots at three sites in Twin Cays and 54 at Blue Ground Range (Rützler *et al.*, 2000). All of these islands are far from the coast, but the Pelican Cays mangroves differ from the others in their close association with coral reefs. Spongivorous fishes that normally inhabit coral reefs, but not mangroves, were abundant among the prop roots, and many of the sponge species inhabiting Pelican Cays roots were typical of coral reefs. Reciprocal transplant experiments of sponges between the Pelican Cays (very high sponge diversity, coral reef-associated sponge fauna) and the Twin Cays (lower sponge diversity, mangrove-associated sponge fauna) demonstrated that typical mangrove species that were moved to the Pelican Cays were quickly consumed by spongivorous fishes, unless protected inside cages, and typical reef species that were moved to Twin Cays survived well until the mangrove species resident on the roots began to overgrow and ultimately eliminate them (Wulff, 2000, 2005). Reef species grown on otherwise bare pvc pipes (i.e. without competitors) that were suspended among the roots continued to thrive, and their growth rates were significantly faster than they were on a coral reef for three of four typical reef sponge species. Faster growth of coral reef species among mangrove roots highlights the possibility that ecological interactions can inhibit sponge species from living in a habitat that is otherwise superior to the one where they normally live. As in other habitats, high diversity does not necessarily indicate more favourable conditions but may result from continuous cropping of competitive dominants by consumers. In the Pelican Cays, fast-growing mangrove species that are not defended against spongivores are prevented from overwhelming slower-growing reef species by a dense assortment of angelfishes, trunkfishes, and spadefish.

Predation by fish is not routinely responsible for distribution and abundance of mangrove sponge species in typical mangrove stands that are not embedded in the tops of coral reefs. Sutherland (1980) found no differences attributable to spongivory when he compared caged versus uncaged panels situated among mangrove roots, and Bingham and Young (1995) reported no direct observations or signs of fish predation on mangrove sponges in the Florida Keys in over 270 h of diving. In a prop root community that was censused four times, at yearly intervals, abrupt decreases in relative abundance of sponge species that are known to be favoured by angelfishes were observed to result from brief and unusual residence of juvenile angelfish at one site (Wulff, 2009).

Proximity to coral reefs was the only variable that appeared to explain differences in species composition in comparisons among 8 sites (with a total of 22 sponge species) in Aruba and Curaçao that differed by the addition of typical reef species to the typical mangrove species assemblages. Within sites however, an unexpected positive association between sponge percentage cover and tannin content of mangrove roots hinted at the possibility of influence of tannins on sponge nutrition (Hunting *et al.*, 2008) or larval settlement (Hunting *et al.*, 2010). Mangroves may also influence at least some of the sponges inhabiting their roots by nutrient trading, carbon for nitrogen, via adventitious roots embedded in the sponges (Ellison *et al.*, 1996). One species, *Haliclona implexiformis* Hechtel, 1965, grew significantly faster on roots than on pvc pipes for the 1-month duration of the experiment. In turn, the sponges increase the longevity of the roots on which they live by protecting them from boring isopods (Ellison and Farnsworth, 1990; Ellison *et al.*, 1996).

2.6. Sediment dominated habitats, including seagrass meadows

2.6.1. Abiotic factors

A small number of marine sponge species are capable of inhabiting sediments as their primary habitat, by employing a variety of special tricks. Functional differentiation within sponge individuals is illustrated by some sediment dwellers, such as Caribbean *Oceanapia* spp., which have a basal portion embedded in the sediment, and an upright portion through which water flow is directed downwards through the sponge body (Werding and Sanchez, 1991), and *Cervicornia cuspidifera* Lamark, 1815, which not only takes in water through its upright portion but also harbours zooxanthellae there (Rützler, 1997; Rützler and Hooper, 2000). An excavating species, *Cliona inconstans* Dendy, 1887, also lives buried in lagoon sands in south-eastern Japan; but its tall chimneys, surmounted by oscules protruding above the surface (Ise *et al.*, 2004), indicate that water flow is in the opposite direction from that in fellow clionaid *C. cuspidifera*. *Bubaris ammosclera* Hechtel, 1969 stabilizes carbonate sand as it grows as a mat over the surface (Macintyre *et al.*, 1968). One of the clear differences observed among the extremely diverse sponge species inhabiting the various reef-associated habitats of Tulear, Madagascar, was the incorporation of carbonate particles by the relatively few sediment-dwelling species (Vacelet and Vasseur, 1977).

Details of how this occurs have been studied for the common Caribbean seagrass-dwelling sponge, *T. crypta*, which rolls when small, organizes course sediments near its base to stabilize it when medium-sized, and then lives partially buried and incorporates unsorted coarse sediment when it is large (see Cerrano *et al.*, 2004b, 2007 for a recent review). Its ability to entirely close its osculum and to strongly contract its body may further aid its success in a habitat in which resuspended sediments might clog openings and impede water flow through aquiferous systems of the sponges (Reiswig, 1971).

In sediment-dominated habitats in which there are also scattered pieces of hard substrata, sponges may settle on the hard substrata and then grow to appear as if they are growing on the sediment (e.g. Battershill and Bergquist, 1990). A dense sponge garden on a deep reef flat in northeastern New Zealand is established on sediment-covered base rock, where the asexually generated fragments or buds, by which resident sponges propagate, first attach to other sponges, or rock and shell fragments, and ultimately to the underlying rock. They are then able to survive as they develop especially long oscular tubes (in *Polymastia* spp.) or tolerate being covered by sediment (e.g. *Cinachyra* sp., *Aaptos aaptos* Schmidt, 1864), as described by Battershill and Bergquist (1990). Similarly, a Red Sea sponge, *Biemna ehrenbergi* Keller, 1889, is attached to beach rock underlying the sediments that can bury the sponge bodies to depths of 20 cm. This species may benefit from the organic richness of the sediment as it intakes interstitial water (Ilan and Abelson, 1995). The authors point out a counterbalancing issue, which is the risk of oxygen levels diminishing too much in the interstitial water. Coral reef sponge species transplanted to a seagrass meadow inside cages (for protection from consumption by sea stars), but growing on small pieces of coral rubble, grew faster than sponges of the same genotypes and initial sizes on the reef (Wulff, in preparation), as expected if sediment-dominated habitats are richer in sponge food.

As part of a project focused on habitat for juvenile spiny lobsters, Butler *et al.* (1995) mapped all sponges of several species that are large enough to provide shelter at 27 sites in Florida Bay Unanticipated data included documentation of dramatic sponge mortality coincident with a cyanobacterial bloom. Over 80% of the individuals representing the genera *Ircinia*, *Aplysina*, *Callyspongia*, and *Hippospongia* died, as well as 40% of the *S. vesparium* Lamarck, 1815. During a second bloom in the following year, all the remaining sponges died at some sites. Although the sponges were attached to hard substrata, this habitat is predominantly seagrass meadow, and massive loss of seagrasses also occurred. Consideration of how this ecosystem might ever be fully reconstituted illustrates some of the considerable risks for sponges of living in a particularly food-rich habitat. Water that is murky with phytoplankton impedes passage of adequate sunlight for seagrasses, and loss of seagrasses eliminates binding of sediments, which are readily resuspended from shallow bottoms. Although sponges filter phytoplankton, sediment in the water column can overwhelm their canal systems. The sponge populations that were present before the mortality events have been demonstrated to account for sufficient filtering capability that subsequent blooms could be attributed to the loss of sponges (Peterson *et al*., 2006). It is hard to see how Florida Bay can recover, unless the sponges and the seagrasses are all added back simultaneously at densities that are sufficient to clear the water and bind the sediment. Yet sponge recovery has been progressing at some sites, suggesting that sponges may contribute significant homeostatic mechanisms to this system (Stevely and Sweat 2001), although the particularly large-bodied species that had contributed much of the biomass to the community before the mortality events are taking longer to return.

Anoxic mud, the extreme case of sediment-dominated habitat and seemingly anathema to sponge species that normally inhabit hard substrata, was nevertheless tolerated by a set of mangrove-root inhabiting species. Frequent observations of large sponges of 10 species that inhabit mangrove roots partially buried in fine, organic-rich sediment, but apparently perfectly healthy, inspired Rützler *et al.* (2007) to experiment. Their experimental burials with four species confirmed that the sponges could continue to pump, and even to incorporate detritus from the sediment, even while buried for as long as 10 days.

2.6.2. Ecological interactions

Abrupt habitat distribution boundaries that happen to coincide with the edge of sediment may not necessarily indicate that sediment is the primary constraint on sponge distribution. Although reef sponge species may appear constrained by lack of continuous hard substrata where reefs abut sediment-dominated seagrass meadows, it is actually a seagrass-dwelling sea star, *O. reticulatis*, that enforces this habitat distribution boundary in the Caribbean. In feeding trials in the field, *Oreaster* consistently rejected all 6 of 6 typical seagrass meadow sponge species and 7 of 8 typical rubble bed sponge species that were offered in choice experiments in the field; but they consumed 11 of the 14 reef sponge species offered (Wulff, 1995b). While on the reef, the reef sponge species are protected from the sea star because parrotfishes and butterflyfishes bite the sea stars if they move onto the reef; but if a storm washes reef sponges into the seagrass or a poriferologist redistributes them there, the sea stars discover and consume them within days (Wulff, 1995b).

Very different constraints shape the interaction of another seagrass meadow spongivore and its prey. In their report on unambiguous sponge-consuming equipment of the shrimp *Typton cameus* Holthuis, 1951, living in *T. klausi* in Belize, Duris *et al.* (2011) pointed out the need for relatively gentle consumption of ones' home. They suggested that a clever mechanism by which the shrimp can reduce damage to their host is to serve as effective defence against colonization by additional conspecific shrimp.

Growing on eelgrass or large bivalves and even on mobile organisms, including decorator crabs and hermit crabs, is one way in which hard substratum sponges inhabit sediment environments. Although it is a clear advantage for sponges to be on a host that has effective mechanisms for preventing burial, this is still not a simple cost-free strategy. Living substrata tend to not only be discontinuous, and sometimes mobile, but also relatively ephemeral, imposing a requirement for highly effective recruitment on sponges that utilize this option for coping with sediment. Fell and Lewandrowski (1981) demonstrated the extreme degree to which the life history of a *Halichondria* species that lives on eelgrass blades in New England estuaries is opportunistic, with high mortality balanced by very high growth rates and early, and heavy, devotion of resources to reproduction. Some sponge-living substratum associations are quite specific, such as the hermit crab sponge *Pseudospongosorites suberitoides* Diaz, van Soest, and Pomponi, 1993, which lives on shells inhabited by hermit crabs in the genus *Pagurus* on the Gulf coast of Florida (Sandford, 1994). The preference of the hermit crabs for shells of a suitable size, rather than a sponge, even if that sponge appears to confer an advantage due to its ability to grow as the crab grows, adds an additional risk for the sponge. Hermit crabs that find a shell that fits may simply discard their sponges, causing them to languish on the sediment (Sandford, 1994, 1997).

Collaborative interactions between sponges of different species can also allow hard substratum sponges to inhabit sediment-dominated habitats. Multi-species piles of sponges deposited in sand channels of a reef by a hurricane were able to stay alive by a sort of snowshoe effect (Woodley *et al*., 1981; Wulff, personal observation), and Cerrano *et al.* (2004b) observed that sponges of different species that adhered to each other could prevent rolling on the sediment bottoms of the Belize Barrier Reef lagoon. A *Geodia* species in a seagrass meadow in Florida hosts a haplosclerid on its surface that may protect it from predators (Wilcox *et al*., 2002). Similarly, in a seagrass meadow in Belize, a species of extremely cavernous internal architecture, which may render it relatively unaffected by shifting sediments, provides additional substratum for dense-tissued sponge species that are more vulnerable to smothering if buried. The cavernous host species, *Lissodendoryx colombiensis* Zea and van Soest, 1986, is in turn protected from being devoured by the large sea star, *O. reticulatis*, to which it is palatable (Wulff, 2008a), when it is overgrown by the dense-tissued species which are deterrent to the sea star (Fig. 4.1).

2.7. Intertidal shores

2.7.1. Abiotic factors

The extreme porosity of sponges seems as if it would render them exceptionally unsuited for inhabiting intertidal zones, but some species thrive in, and others are able to tolerate, the low intertidal, or occasional exposure by unusual tides. Even in an area of monsoon rains and intense anthropogenic pressures due to industrialization, along the NW coast of India, six sponge species were recorded at each of two sites described as rocky–muddy (Vaghela *et al*., 2010), although the authors expressed concern for diversity loss under increasingly challenging circumstances.

In Mozambique, a diverse assemblage of sponges (33 species) dominated the sessile fauna of a wide intertidal zone in spite of extremes in temperature, salinity, and currents (Barnes, 1999). Analysis of community composition distinguished two clusters, one on exposed rocks and the other in protected caves and on boulders, reflecting the importance of current velocity to sponge distribution.

The importance of water flow for intertidal sponges is reflected in morphological alterations as well as mortality patterns that curtail distribution. McDonald *et al*. (2003) noted that intertidal *Spongia* sp. individuals in Darwin Harbour, in northern Australia, were oriented with their longest axis perpendicular to the water flow. When individuals were experimentally twisted 90°, they reoriented themselves to again have long axes facing the current. Another intertidal species in Darwin Harbour, *Cinachyrella australiensis*, produces thicker oxeas, and a higher proportion of its total mass consists of skeleton, at more disturbed sites where water flow is greater (McDonald *et al*., 2002). Concerned about reduced current flow with the implementation of new storm surge controls at the Oosterschelde estuary in The Netherlands, Hummel *et al*. (1994) experimentally subjected *H. panicea* to different flow rates in tanks. At low flow, the sponges became covered by bacteria and died, and this effect was exacerbated by higher temperatures. Both high and low extremes of flow can make life intolerable for sponges. On the wave-dashed rocky coast of Washington, USA, *H. panicea* grows in low mounds with stiff tissues in surge channels, and thinly encrusting with less stiff tissues where water motion is less extreme. Transplants from less to more wave stress rapidly developed stiffer tissues, but transplants from more to less stress delayed switching to less stiff tissues, an adaptive choice in an unpredictable habitat (Palumbi, 1984).

Water flow in the intertidal, as in other habitats, does not have a monotonic relationship to sponge distribution and abundance, and too much water flow disrupts intertidal organisms and their communities. Sessile invertebrates, including sponges, on rubble at One Tree Island, GBR, were least abundant and less diverse at low shore levels at exposed sites. Wave action overturned rubble, exposing inhabitants to desiccation and abrasion, and significantly decreased cover in spite of the regeneration abilities of the sponges (Walker *et al*., 2008).

2.7.2. Ecological interactions

Even in this habitat in which elegant experiments have demonstrated that upper distribution limits tend to be controlled by abiotic factors (e.g. Connell, 1961), interactions with other species have been demonstrated to either extend or constrain the distribution and abundance of sponge species. Explicit demonstrations have been made of the importance of beneficial interactions in extending the depth zone range for intertidal sponges. On wave-washed shores of the Pacific northwest of the USA, *H. panicea* inhabits the lowest intertidal but is enabled to live higher in the intertidal when associated with an erect coralline alga that protects it from desiccation (Palumbi, 1985). The association is not reliably beneficial for the sponge, as the alga is able to outcompete the sponge unless chiton grazing keeps it trimmed. In a parallel association in the tropical eastern Pacific at Mazatlan, association of *Ha. caerulea* with another erect coralline alga extends the range of the sponge by more than 1 m into the subtidal by improving resistance to waves (Carballo and Ávila, 2004).

Predation has been demonstrated to influence intertidal sponge distribution and abundance, sometimes to a great extent. In a study focused on reproductive timing of the encrusting intertidal species *Haliclona permollis* (=*Haliclona cinerea* Grant, 1826) in Oregon (Elvin, 1976), sunlight, nutrition, and tissue temperature were related to reproduction and growth, but asides about how ephemeral individuals are, due to merging with neighbours or disappearing or being broken or eaten, hint at the possible importance of interactions even in this physically challenging habitat. The intertidal sponge *H. panicea* was eliminated at a site in southcentral Alaska where the nudibranch *Archidoris montereyensis* Cooper, 1862 settled especially strongly (Figure 4.1), although the sponge had previously covered more than 50% of the substratum and had been the dominant space occupier for at least 10 years (Knowlton and Highsmith, 2000). Nudibranch numbers at the 550 m^2 site increased from the 12–42 individuals to 156 by this single recruitment event, and once the sponge was consumed, the nudibranch population plummeted as well. Underscoring the speed at which ecological interactions can alter communities, and the degree to which the alterations can be difficult to undo, the site quickly became colonized by annual macroalgae.

Cover of intertidal sponges (and also mussels and ascidians) increased when a small omnivorous grapsid crab was excluded by caging, demonstrating that preference of the crab for animal food favoured dominance of macroalgae at sites in São Paulo State, in subtropical Brazil (Christofoletti *et al.*, 2010). Restriction of sponges to spaces between and underneath cobbles in the lowest zone of the exceptionally wide intertidal on the Pacific coast of Panama is imposed by the eagerness of the smooth pufferfish *A. hispidus* to consume six species, representing five demosponge orders, if they are removed from the protection of the cobbles (Wulff, 1997c).

2.8. Antarctic hard bottoms

2.8.1. Abiotic factors

Boisterous water flow is not the only physical disturbance influencing sponge depth distribution. In the Antarctic, sponges are restricted by frequent ice scour as deep as 10–25 m (and infrequently to as deep as 600 m) and by anchor ice, which can hoist the entire bottom community to the surface with dire consequences (Dayton *et al.*, 1970; McClintock *et al.*, 2005). Below 33 m, however, sponges can cover at least 55% of the substratum (Dayton *et al.*, 1974). Species diversity increases, and then decreases, with depth. McClintock *et al.* (2005) reported 62 species in 1–100 m depth, 99 from 100 to 500 m, 25 from 500 to 1000 m, and only 16 below 1000 m in Antarctica, a pattern similar to that reported in a recently revised list of deep-sea sponges off Brazil by Hajdu and Lopes (2007), who listed 59 species in 100–200 m depth, 49 between 201 and 500, and only 7 from 1000 to 2000 m.

Temperature may seem an obvious factor influencing sponges in Antarctica, but how this abiotic variable is reflected in the sponges may not be simple. Slow growth is often a result of very low temperatures, and in general, this has been confirmed in Antarctica by time-series size measurements, in particular of common large-bodied hexactinellids. However at least two demosponges, *Homaxinella balfourensis* Ridley and Dendy, 1886 and *Mycale acerata* Kirkpatrick, 1907 can grow extremely rapidly as well as recruiting so efficiently that a *Homaxinella* population that was nearly eliminated by anchor ice quickly rebounded to 80% cover (Dayton, 1989). Thus no automatic restriction to slow growth or meagre reproduction appears to be imposed on sponges by low temperatures. Seasonal variations in available sunlight influence plankton production, and plankton can be seasonally extremely sparse to the point that it is somewhat mysterious how sponges maintain themselves (Barthel and Gutt, 1992). Sponges that are unable to at least temporarily exist under conditions of metabolic semi-quiescence may be excluded from Antarctic waters (e.g. McClintock *et al.*, 2005)

Low temperature may also have profound influences by slowing rates of larval development. Antarctica stands out in the similarity of sponge faunas among distant sites, a pattern that may reflect greater distance travelled by larvae that develop more slowly in the prevailing very low temperatures (McClintock *et al.*, 2005). Highly clumped distributions of some species suggest, however, that their larvae do not travel (Barthel and Gutt, 1992).

2.8.2. Ecological interactions

Diatoms can foul some Antarctic sponges to the point of clogging water intake pores, especially during the early summer bloom (Amsler *et al.*, 2000). Sympatric diatoms were discouraged by extracts of seven of the eight species tested. A lack of correlation of predator deterrence and diatom deterrence suggests that diatom fouling may be a significant enough issue to select for specific deterrents. Even with deterrent chemistry, sponges were thickly fouled, indicating that the diatoms are not repelled, but rather controlled by the sponges. Diatoms may even parasitize the internal tissue of sponges. From SEM analyses, Cerrano *et al.* (2000a,b) determined that diatoms of *Melosira* sp. embedded in the hexactinellid *Scolymastra joubini*

Topsent, 1916 (=*Anoxycalyx joubini* Topsent, 1916) gain nutritionally at the expense of their hosts. By contrast, *M. acerata* appears to be able to use diatoms as food (Cerrano *et al.*, 2004a).

Antarctic sponges are consumed by spongivore and omnivore sea stars and a nudibranch (Dayton *et al.*, 1974). *M. acerata*, which grows exceptionally fast in the context of this habitat (Fig. 4.1), is preferred by the sea star *Perknaster fuscus*, which prevents it from simply taking over all the space (Dayton, 1979). Larval settlement of sponge-feeding sea stars may be moderated in turn by a filter-feeding sea star (Dayton *et al.*, 1974). Chemical defences against predators have been revealed to be at least as prevalent in Antarctic sponges as in tropical sponges (Peters *et al.*, 2009). Far from being a system in which cold temperatures slow everything to a pace at which interactions are irrelevant, Antarctic sponges are engaged in a complex web of ecological interactions strong enough to influence distribution, abundance and diversity (see McClintock *et al.*, 2005 for a comprehensive review).

3. CONCLUSIONS

Influences of abiotic and biotic effects are inextricably intertwined: details of abiotic environmental context can determine the outcomes of ecological interactions, and biotic interactions often moderate the influence of abiotic factors. Determining how these factors interact, and which are the primary influences on the distribution and abundance of particular sponge species in particular situations, is still a worthy endeavour, despite the challenges. Studies in every habitat have illustrated the great power of time-series observations of the same individuals and of experimental manipulation for understanding the processes underlying observed patterns. Influence of ecological interactions on distribution patterns may coincide with abiotic factors to the point that the causative factor is entirely obscured unless experiments are performed.

Experiments have revealed opportunistic predation to be capable of enforcing sponge distribution boundaries that coincide with habitat boundaries (e.g. coral reef–seagrass meadow) or distinct microhabitats (cryptic—exposed, kelp forest—urchin barrens). Within habitats, by contrast, dramatic effects of predators on sponge population sizes seem to occur primarily in cases of unusually high recruitment rates or unusually low mortality rates for the predators, which are often specialists on the sponge species affected (e.g. temperate rocky intertidal and subtidal, Antarctic hardbottoms). Competitive interactions have been demonstrated in a few cases to diminish populations or exclude sponge species from a habitat (e.g. reef species in mangroves, early successional species in mangroves).

Cases in which competitive interactions have appeared obvious have often turned out to be neutral or even beneficial interactions when observed over time (e.g. mangrove roots, coral reefs). Especially striking in this regard are sponge–sponge interactions in dense sponge-dominated communities, which appear to promote the continued presence of all participating species (e.g. temperate caves, coral reefs, seagrass meadows). Mutualistic symbioses with other animals, plants, or macroalgae have been demonstrated to increase abundance and habitat distribution in several habitats (e.g. coral reefs, subtidal hardbottoms, temperate, and tropical rocky intertidal). Symbiotic microbes can enhance distribution and abundance, but also render their hosts more vulnerable to environmental changes (e.g. temperate subtidal, mangroves). And while photosynthetic symbionts can boost growth and excavation rates for their sponge hosts, in other cases sponge growth proceeds as well or even better in diminished light (e.g. temperate subtidal, coral reefs).

Metrics chosen for evaluating sponge abundance make a huge difference in interpretation of data comparing between different sites or over time at the same site. In many circumstances, volume or biomass is likely to allow interpretation of influences on distribution and abundance better than numbers of individuals or area covered. Accurate identification of species and understanding how they are related within higher taxa is essential. Sponge species that look similar because they share growth form and colour can differ in attributes, such as symbionts they harbour or predators they deter, that influence their interactions and the roles they play. Even closely related species tend to differ in at least one key ecological attribute and must be distinguished for any studies relevant to conservation, as two smaller populations are not equivalent to one large one.

Predicting the outcome of ecological interactions for distribution and abundance of sponges depends on substantial understanding of details and dynamics of the ecology of the actual species involved. Apparently similar sets of species have been shown to interact completely differently. Sublittoral rocky substrata provide one good example, from among the many habitats in which sponges play major roles. In order to accurately gauge interactions outcomes in this habitat type, it must be known not only if the sea urchins are herbivores or carnivores, but also what their relative preferences among the available prey are. Whether or not predators of sea urchins control their populations must be known. Seaweed strategies must be well understood, as macroalgae can play roles ranging from outcompeting sponges to providing havens for sponges that are vulnerable to urchin grazing. Sponges may be disturbed by kelp fronds as they are whipped about by waves, and sponges with photosynthetic symbionts may suffer from diminished sunlight within algal stands; but it is the unstoppable stolons of *Caulerpa*, with their ability to spread forever asexually, accumulate sediment, and grip any sort of bottom, including sponges, that makes this green seaweed anathema for sponges. However, a sponge with a particularly effective multipurpose chemical arsenal, like *C. crambe*, can resist the stolons, perhaps paying for devoting energy to keeping its arsenal at the ready by reduced growth rates that make it vulnerable to other competitors. Knowledge of particular attributes of the sponge species in addition to resisting algal stolons is required, for example, resistance to sea urchin herbivory is a pre-requisite to thriving in urchin barrens, and dependence on photosynthetic symbionts can restrict habitat distribution even as it enhances growth rates. Striking site-specific differences in the interactions between seaweeds and sponges were only revealed by experimental manipulations, long-term observations, and application of a variety of approaches to learning about growth rates, recruitment, chemistry, and other sponge attributes, with careful attention to distinguishing individual sponge species. This rocky subtidal example is only one of many, from every type of marine habitat, that illustrate the surprises that sponges hold in store for us. The many instances in which biotic influences have been identified as important determinants of distribution and abundance of sponge species hint that many more ecological interactions of sponges await illumination.

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