ASSESSING AND MONITORING CORAL REEF SPONGES: WHY AND HOW?

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ABSTRACT

Functional roles of sponges in coral reef ecosystems include: increasing coral survival by binding live corals to the reef frame and preventing access to their skeletons by excavating organisms; mediating regeneration of physically damaged reefs by temporary stabilization of carbonate rubble; reworking of solid carbonate through bioerosion; recycling nutrients and adding to primary production through microbial symbionts with special biochemical capabilities; clearing the water column of procaryotic plankton; serving as food for a variety of megafauna; and attracting support for responsible human stewardship of coral reefs with aesthetically appealing colors and morphologies. Nevertheless, sponges tend to be avoided in assessment and monitoring of coral reefs because they are not easy to quantify or identify, and because we have only recently begun to understand the importance of their many functional roles. As we gain more understanding of these roles of sponges in coral reefs, the need to carefully assess and monitor changes in sponges is becoming more clear. Focus on functional roles dictates choice of methods for assessing and monitoring sponges, as follows: (1) volume will generally be the most useful way to quantify sponge populations; (2) accurate identification to genus, family, or even order, combined with a brief description and reference to voucher specimens, is preferable to guesses on species names, in cases for which identification can't be verified by specialists; (3) permanently marked sites must be monitored over time in order to be able to detect community changes and to distinguish beneficial from detrimental effects of sponges on corals.

Sponges play many important roles on coral reefs, but they are often excluded or treated in cursory fashion in coral reef monitoring programs because of the multitude of challenges they present. Sponge biomass can be greater than coral biomass, and sponge species diversity may exceed that of corals. For example, over 640 sponge species have been recorded from the Caribbean, 420 species from Indonesia, and 683 from the W Indian Ocean (van Soest, 1994). The NE Australia sponge fauna has been estimated to include over 1500 species (Hooper, et al., 1999). Not only are these a lot of species to handle gracefully, but many species are difficult to identify in the field, a significant number have not been described, and sponge systematics is in flux on all taxonomic levels. Complex 3-dimensional growth forms that are sometimes tucked under and between corals, and that are alive throughout instead of only on the surface (as in corals), further discourage adequate measurement of sponges. Even more discouraging is the propensity of many sponges to fragment asexually, die partially, and leave no trace after death because dead portions quickly fall apart and disappear.

These difficulties can be compelling reasons to be leery of including sponges in monitoring schemes! However, a very different perspective is gained by focusing on the functional roles that sponges play on coral reefs. Knowing the ways in which sponges are important to coral reefs provides motivation for monitoring sponges, and clarifies how to do so meaningfully. The conclusions presented here on how to quantify sponges on coral reefs do not differ greatly from those published two decades ago by Rützler (1978). What has changed in the intervening years is that motivation for quantifying sponges adequately

has increased, as we have learned more of the sometimes surprising functional roles of sponges on reefs, and as reefs have become more obviously threatened. In this paper, I compare different ways of assessing and monitoring sponges, in order to demonstrate how conclusions about population and community characterization and dynamics can depend on the technique used. To answer the question Why monitor sponges?, a brief summary of what has been learned of how sponges influence coral reef health follows.

CORAL SURVIVAL AND REEF GROWTH: SPONGES AS BINDERS, STABILIZERS AND DISMANTLERS.— Excavating sponges can weaken coral skeletons, making them more susceptible to becoming disengaged from the reef frame. This reworking of solid carbonate into smaller fragments and fine sediment has been long recognized to be a key role of sponges on coral reefs (Rützler, 1975; Hartman, 1977; Wilkinson, 1983a). Patterns of increased excavation rates and abundance of excavating sponges in areas of increased nutrient input have been documented (Rose and Risk, 1985; Holmes, 1997). Three sponge species have been observed to overgrow large areas of reef that were previously inhabited by live coral and other organisms (Vicente 1978, 1990; Rützler and Muzik, 1993). In each of these cases, local effects were dramatic, but only a few of the several hundreds of coral reef sponges in each of the regional faunas appear able to overwhelm corals. Rützler and Muzik (1993) and Vicente (1990) pointed out the intriguing pattern that these few aggressive spatial competitors are all encrusting species with photosynthetic symbionts. Although a few reports have designated sponges in general to be rampant competitors against corals, these reports are based on one-time evaluations from which competition has only been inferred (Suchanek et al., 1983; Aerts and van Soest, 1997). Actual dynamics can only be learned from observations in time series. On casual observation, close contact between sponges and corals can appear to be sponge aggression because coral tissue is a relatively thin layer, partially sunken into the skeleton, whereas sponges grow on top of the solid carbonate provided by dead portions of the coral, inevitably appearing to be in an aggressive stance even when they generally are not.

Many sponge species have a beneficial, rather than destructive, relationship with corals and reef building, at least in the Caribbean. Branching, massive, and cryptic sponges in particular can help corals compensate for their loss of grip on the reef due to erosion by excavators by serving as globs of living glue, binding corals to the reef even when their own carbonate bases are eroded. On fore-reef patch reefs in Panama, 40% of the live coral colonies fell off of reefs within 6 mo of experimental removal of the sponges; whereas only 4% of the coral colonies fell off of unmanipulated reefs (Wulff and Buss, 1979). Even if sponge tissue grows over some coral tissue, this is a small price for corals to pay to enhance coral colony survival by an order of magnitude. In biogeographic provinces in which many sponges rely on photosynthetic symbionts, as on the Great Barrier Reef (Wilkinson, 1987), this role might be less important because sponges requiring sunlight may be less inserted between coral colonies and the reef frame, but this has not been specifically investigated on the GBR. Sponges also help prevent loss of corals due to excavators by covering carbonate surfaces from which live coral tissue has been lost, thereby preventing access to the carbonate by excavating organisms (Goreau and Hartman, 1966).

An additional role sponges play in reef health and carbonate accretion is to facilitate regeneration of physically damaged reefs. The first step in regeneration is stabilization of loose chunks of carbonate. Without stabilization, waves and vigorously foraging fish continuously disrupt rubble, causing crustose coralline algae to grow around individual pieces

of rubble (Glynn, 1974), and preventing binding of pieces of rubble to each other to provide a stable substratum onto which corals can recruit. Corals that settle on stabilized rubble survive substantially better than those on unstable substrata (e.g., 13% vs 1% after 4 yr; Wulff, 1984). Sponges facilitate regeneration because they are able to bind adjacent pieces of rubble together within a few days, stabilizing them until carbonate secreting binders can permanently bind them together. When experimental rubble piles were seeded with sponges, they became tightly bound together with crustose corallines and encrusting bryozoans within 7 mo, and scleractinian corals had recruited to them within 10 mo; whereas initially identical rubble piles that were not seeded with sponges became scattered, were never consolidated and had no coral recruits (Wulff, 1984). Similar experiments were not performed on eastern Pacific reefs, but a positive correlation between rubble consolidation and presence of cryptic sponges in the reef frame was found, matching the pattern on Caribbean reefs.

TROPHIC INTERACTIONS: UNIQUE ROLES OF SPONGES IN CORAL REEF FOOD WEBS.—Sponges play unique roles in coral reef food webs, both as consumers and consumed. They are highly efficient filter feeders, clearing water of organic particle sizes not readily collected by other organisms (Reiswig, 1971; Pile, 1997), and thereby providing trophic links among reef organisms and recycling services that would otherwise be absent. Sponges may serve a unique role as water column cleaners because of their ability to quickly and effectively clear water of procaryotes and other small plankton (Reiswig, 1971; Pile, 1997), with a water turnover rate estimated to be 6–20 ml water ml⁻¹ sponge min⁻¹ (Reiswig, 1971). Directly after Hurricane Allen damaged north coast reefs in Jamaica in 1980 (Woodley et al., 1981), the water column was a cloudy soup of pulverized reef organisms, which soon developed a distinctly rotten smell. Initially, many sponges appeared to have stopped pumping, but as they began to pump again (pers. oberv., confirmed by fluorescein dye), the water column cleared rapidly. No data were collected to demonstrate that harmful material was in that cloudy soup, but it can be imagined that the bacteria colonizing the suspended scraps of necrotic organic material might not have been healthy for other reef organisms, many of which had substantial tissue damage open to the water column. More recently, massive loss of sponges due to unknown causes in Florida Bay has been suggested to have altered water column chemistry and biology (Butler et al., 1995).

Sponges may also contribute substantially to primary production and nutrient regeneration, because of the photosynthetic and non-photosynthetic microbial symbionts harbored by many species. Recent work indicates surprising and important roles of these associations, including nitrification and net primary production (e.g., Wilkinson and Fay, 1979; Wilkinson, 1983b; Rützler, 1990; Wilkinson, 1992; Diaz, 1997; Diaz and Ward, 1997). Internal populations of microbial symbionts can be extremely high, inspiring invention of the term "bacteriosponge" by Reiswig (1981) and also "cyanobacteriosponge" (Rützler and Musik, 1993). Differences in nutrient availability among reefs in the Caribbean, and near shore vs. oceanic reefs in the tropical Pacific have been suggested as a key basis for differences among regions in the degree to which sponges depend on photosynthetic symbionts (Wilkinson, 1987; Wilkinson and Cheshire, 1990).

Although well known for chemical defenses that cause them to be treated as part of the habitat by most mobile organisms, sponges tend to be specifically defended only against potential predators with which they coexist. Thus, cryptic reef sponges are normally unavailable to generalist herbivores, but are devoured by parrotfishes if exposed to them in both the Caribbean and tropical Pacific (Bakus, 1964; Wulff, 1988, 1997b,c). Likewise,

exposed reef sponges, normally inaccessible to starfish living in adjacent seagrass meadows, are readily consumed by the starfish when they wash off of the reef into the seagrass (Wulff, 1995b). Opportunistic sponge feeding may not tie sponges to these predators in terms of a vast and continuous flow of energy, but episodic addition of sponges to herbivore diets, as more favorable nitrogen sources, may be important (Wulff, 1995b, 1997b). In addition to these facultative sponge-feeders, which only eat sponges when edible species are made available by a disturbance, are sponge specialists, which depend on many sponge species being available at all times. Sponge specialists include hawksbill turtles, which focus their attention on a variety of species within particular orders of sponges (Meylan, 1990; van Dam and Diez, 1997) and angelfishes, which may require even broader taxonomic representation of sponges (Randall and Hartman, 1968; Wulff, 1994). Although angelfishes may prefer to eat some mangrove sponges when these are made available experimentally (Dunlap and Pawlik, 1996), mangrove sponges are normally inaccessible, and so angelfishes appear to cope with chemical defenses and other nutritional challenges of reef sponges by consuming a wide variety of species on a daily basis (e.g., 87% of the 45 sponge species in a 30 × 40 m area on a Panama reef, Wulff, 1994).

EVALUATING FUNCTIONAL ROLES OF SPONGES ON CORAL REEFS.—There may be other important functional roles of sponges that we don't yet imagine. The carbonate skeletons of corals provide such a good record of their history that an expectation of being able to reconstruct important processes from observation of the reef frame or coral skeletons has developed in reef science. The only role of sponges that can be readily detected by simply looking at a live or dead reef is excavation, which leaves a record in the coral skeleton. We have been relatively slow to understand other functional roles of sponges on coral reefs, because sponges are not good about leaving clues: (1) damage from partial mortality or predation is healed quickly, leaving no sign that it occurred; (2) edible sponges are consumed rapidly when available, leaving no clues that they briefly coexisted with their predators; (3) sponges feed on materials that are essentially invisible, and (4) dead sponges disappear, because sponge skeletons quickly become disarticulated once tissue dies, and sponges are not therefore present in fossil scleractinian reefs to indicate roles they may have played in reef regeneration and carbonate binding.

Intimate associations and interactions of sponges on coral reefs are not confined to those with corals or with sponge predators, though these may have the most immediately obvious effects on reef health. Many sponges harbor highly diverse communities of symbiotic animals, including annelids, arthropods, fishes, and molluscs (e.g., Beebe, 1928). Experiments in which recruitment of a variety of organisms was greater onto ceramic tiles with sponges than onto tiles without sponges suggest the intriguing possibility that sponges may enhance reef regeneration in ways beyond rubble stabilization (Bingham and Young, 1991). Investigations of cleaning and predation protection symbiosis between sponges and brittlestars (Hendler, 1984), living space and predation protection symbiosis between sponges and zoanthids (West, 1976; demonstrated to be a parasitic interaction in one sponge-zoanthid species pair by Lewis, 1982), structural support and protection symbioses between sponges and various macroalgae (Rützler, 1990), and support mutualisms among sponge species (Wulff, 1997a) suggest many possibilities of mutually beneficial associations of sponges with other organisms.

Beneficial effects of sponges on coral reef health and growth have already been demonstrated to include increased coral survival, reef regeneration, water column clearing, nutrient recycling, primary productivity, and food for sponge-feeding fishes, starfish, and

turtles. Sponges are highly decorative, as well as functional, and add aesthetic appeal, with their variety of shapes and colors. In times of desperate need for public support for reef conservation, visual appeal is not a trivial aspect of a coral reef. Detrimental effects of the few species of aggressive and excavating sponge species can also be dramatic, and may increase in response to human-caused stresses such as excess nutrients. The need to include sponges in coral reef monitoring programs is therefore clear, and techniques used must allow us to keep track of how sponges are performing these roles. This contribution compares methods of monitoring and assessing coral reef sponges in the context of which methods will provide the most understanding of functional roles and dynamics of sponges on coral reefs.

METHODS

Sponge abundance was studied on a shallow reef in San Blas, Panama. All sponge individuals in 16 m² arrayed within a 8 × 8 m area of depth -2.5 m to -2.8 m were counted, measured, and identified five times between 1984 and 1998. This area is on a shallow reef to the leeward of Guigalatupo, a small island near what was, until June 1998, the San Blas Field Station of the Smithsonian Tropical Research Institute (map in Wulff, 1995b). The substratum is uniformly covered with rubble from ramose corals, and small to medium-sized live corals, with the genera *Diploria*, *Porites*, *Agaricia*, *Siderastrea*, and *Montastrea* (in decreasing order of relative abundance) constituting 90% of the cover of live coral. Sponges are the most abundant sessile organisms on this reef, and the dense and diverse sponge fauna is characteristic of reefs throughout the greater Caribbean region.

Populations of each sponge species were quantified in three ways: (1) by combined volume of all individuals; (2) by combined substratum area covered by all individuals; and (3) by number of individuals. Volume was measured by approximation to conglomerations of various geometric solids, such as hemispheres, cylinders, prisms, wedges, cubes, and cones. These volume estimates are not exactly comparable to biomass estimates because, although all concavities visible from the surface were subtracted from the calculated external volume, internal canal volumes were not subtracted from the external volume occupied and no correction was made for different ratios of skeleton and live tissue. For vase-shaped sponges, atrial cavity volumes were subtracted from outer volumes of each tube to calculate actual volume occupied, with the edge defined as the surface pinacoderm. For branching species, diameters as well as lengths were measured for each branch segment.

Area was measured by approximation to assortments of two-dimensional geometric shapes. For erect sponges, area was measured as the projected image on the substratum rather than just the attachment point, to most closely approximate the viewpoint of increasingly popular census methods which use video or still photos. Area approximations by number of transect line units draped over the organisms were not used because these merely provide estimates of actual surface area. This popular technique may provide fairly accurate estimates of surface area of encrusting organisms or those which, like corals, only maintain live tissue in a thin layer at the surface of three-dimensional structures, but for complexly shaped three-dimensional sponges the results of such estimates are difficult to interpret in an ecologically meaningful way. In addition, for purposes of evaluating volume, area, and numbers as means of quantifying sponge populations, all three measures need to be comparable, requiring that each be made directly on every sponge within the designated area, i.e., all must be census techniques rather than estimation techniques.

For counting numbers of sponges, individuals were defined by physiological independence. Depending on the species of sponges, physiologically-defined individuals may or may not correspond to genetically defined individuals.

RESULTS

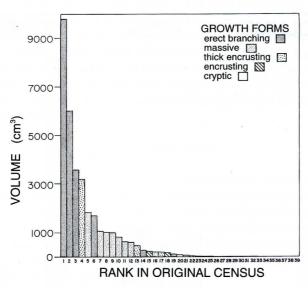
Assessing Sponges: Overview.—Initially this sponge community consisted of 39 species representing 8 orders of Demospongiae. Some changes from the species list published in Wulff (1994) that have resulted from taxonomic revisions and additional identifications can be obtained from the author. Total volume of live sponges was 33,721 cm³ and was distributed, highly unevenly, among 1395 sponge individuals. Individuals were defined by physiological independence, indicated by physical discontinuity. Because of asexual fragmentation, it is not known how many genetically defined individuals there were in this community. Pairwise somatic tissue grafting experiments among the 60 largest individuals of each of the three most common species indicated that as few as 12–24 genotypes were represented among those 60 physiologically defined individuals of these erect branching species (Wulff, 1986). Thus the number of genetically defined individuals is smaller than the number of physiologically defined individuals, especially for erect branching species and thin encrusting species that fragment readily (Wulff, 1986, 1991).

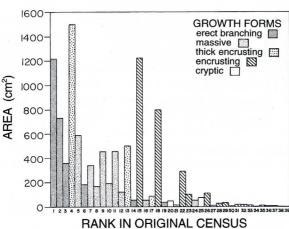
Volume.—Combined volume of all individuals of each of the 39 sponge species (Fig. 1A) shows the enormous disparity between the most common and most rare species: a ratio of 49,000:1. To facilitate direct comparison among representations of this sponge community derived by different methods, abundance is given on a linear instead of a log scale. Contribution to overall community biomass by the least abundant 2/3 of the species (i.e., ranks 14–39) therefore is clearly indicated to be minimal by this graph, as indeed it was (only 8.2% of the combined volume)! Volume was the most time-consuming method of evaluating abundance. Each census took at least 30 h, much of that underwater, and the rest used calculating volumes from the many linear measurements. Evaluating volume non-destructively requires a close, and sometimes rather long, look at each individual as an assortment of geometric solids. Often dozens of linear measurements with a ruler or calipers were required in order to closely approximate the actual volume, especially in branching species, as small differences in branch diameter measurements are magnified when used to calculate volume.

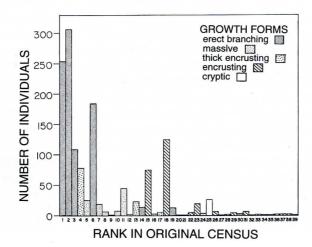
A_{REA}.—Combined area covered by all individuals of each of the 39 sponge species is presented (Fig. 1B) using the ranking derived from volume measurements to facilitate comparison. Relative abundance of sponges of encrusting growth forms was greatly inflated by this measure. The ratio of most to least abundant is decreased to only 1500:1. Area measurements required less than 10 h census⁻¹, again most of that time underwater, and a small amount for calculations.

Number of Individuals.—Number of individuals of each of the 39 species is presented (Fig. 1C), again using the rankings derived from volume measurements. The most and least abundant species are least differentiated from each other by numbers of individuals, with a ratio of only 300:1. This is the easiest method, because it requires no calculations

Figure 1. (opposite page) Top (A). Combined volume of all individuals of each of the 39 species found in 16 m² on a shallow reef in San Blas, Panama. Species are ranked by relative abundance, according to volume. Center (B). Combined area covered by all individuals of each of the 39 species found in 16 m² on a shallow reef in San Blas, Panama. Species are ranked by relative abundance, according to volume (i.e., the same ranking as in a). Bottom (C.) Total number of individuals (defined by physiological independence) of each of the 39 species found in 16 m² on a shallow reef in San Blas, Panama. Species are ranked by relative abundance, according to volume (i.e., the same ranking as in a).







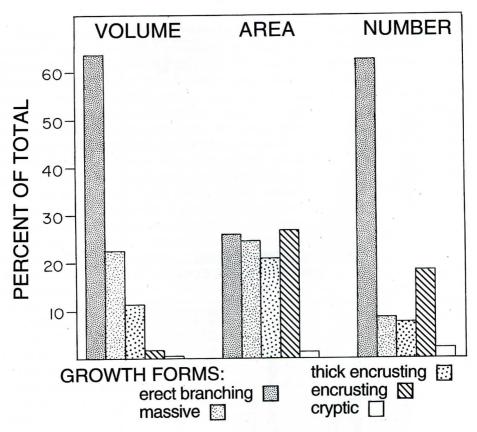


Figure 2. Summary of relative abundance of sponges of different growth forms in 16 m² on a shallow reef in San Blas, Panama, as measured in terms of total volume, area, and number of individuals.

and only one record for each sponge individual, and could be accomplished in less than 5 h underwater.

Characterizing the Sponge Community by Growth Forms.—Characterizations of this sponge community based on growth forms are very different, depending on the method used to evaluate sponge abundance (Fig. 2). When described by either volume or number of individuals, the community is dominated by branching sponges. However, massive sponges constitute the second most abundant growth form by volume, whereas encrusting sponges appear to be second in abundance when evaluated by number of individuals, even though by volume they constitute only 1.8% of this community. Characterization by growth form using area covered is most different, and shows approximately equal representation of erect branching, massive, thick encrusting, and encrusting sponges.

Monitoring Changes.—Some changes in this community over the 14 yr study were dramatic, while others were subtle; and the dynamics are sufficiently complex to require a separate report. For purposes of discussing what sort of monitoring approach would be required to detect important changes, the overall changes during the first 11 yrs of monitoring, will be presented here. These included a net decrease in volume of 10.6%, a net decrease in number of individuals of 53%, and a loss of 41% of the original sponge

species, as well as a gain of three species. The rank numbers (by volume in the initial census) of the species lost during the first 11 yr are: 4, 5, 7, 8, 9, 12, 13, 19, 20, 21, 23, 27, 30, 31, 33, and 34; and the lack of any relationship between loss and initial volume, area, or number of individuals, can be readily seen by referring to Figure 1A,B,C. As one example to underscore the lack of predictive value of any of these descriptors for the others: during the single year June 1994—August 1995, the total sponge volume decreased 8.1%, and the number of species decreased by 21.9%, but the number of individuals increased by 19.6%.

DISCUSSION

Comparison of Techniques for Quantifying Sponges.—Abundance measures can be compared with respect to efficiency, i.e., data acquired per effort unit, and the usefulness of those data. Efficiency and usefulness may not both be maximized by the same technique, and may vary with particular situations. A 5 h technique may seem preferable to a 15 h technique, if rated by efficiency alone; but if the data accumulated fail to inform us of processes we intend to detect or quantify, instead of saving 10 h, this choice wastes 5 h and does not lead to the desired results.

Counting the number of sponge individuals took much less time than measuring area or volume, but it is not clear that important functional roles of sponges are related to numbers of individuals. Volume of individual sponges ranged over three orders of magnitude, from 0.1 cm³ to 770 cm³. Perhaps the only way in which sponges of such disparate sizes are ecologically equivalent to each other is if each represents a successful recruitment event. For sponges shaped like erect tubes and vases (i.e., with distinctive upright morphologies, featuring very high volume to basal attachment ratios), and for sponges with extremely tough (i.e., unfragmentable) skeletons, this may be a reasonable assumption. Population dynamics of three species of vase-shaped sponges have been very effectively described by Reiswig (1973), using a combination of numbers of individuals and volumes of individual sponges. However, for sponge species that are susceptible to fragmentation, especially branching and encrusting species, the number of individuals is highly unstable and does not reflect the number of larval recruitment events. In these sponges, number of individuals can greatly increase in a single short storm, while simultaneously the amount of sponge biomass decreases due to partial mortality associated with fragmentation. Size-dependent mortality can also influence changes in volume and numbers of individuals differently. For example, during a hurricane a shallow reef population of the erect branching species Amphimedon compressa decreased 42.9% by number of individuals, but only 4.9% by volume (Wulff, 1995a). Countering losses by partial mortality, fragmentation may enhance genotype survival and growth rates of branching species (Wulff, 1990, 1991) due to dispersal of fragments and to an inverse relationship between size and specific growth rate, which has also been found in tube-shaped and massive species (Reiswig, 1973; Hoppe, 1988). Thus changes in number of individuals can be an important aspect of population ecology, but must be considered in conjunction with size frequency distributions based on volume.

Area covered by a sponge might be related to competition for space with other sessile organisms; and, for monitoring the few aggressive encrusting sponge species, area covered is an effective and easy abundance measure. Photosynthetic symbionts in these few aggressive encrusting species also ensure that these sponges live on exposed surfaces,

facilitating their evaluation using photographic techniques. Protection of coral skeletons from excavating organisms is another role related to area covered by sponges. Sponges providing this service are disproportionately found on sides and undersurfaces of corals, and are therefore greatly underestimated by photographic surveys.

Sponge volume best addresses trophic relationships, as sponges can roughly be assumed to consume food and to provide food as a function of their biomass. Sponges do vary in percent organic content, nitrogen content, mineral components, etc. (e.g., Reiswig, 1973; Rützler, 1978; Meylan, 1990; Chanas and Pawlik, 1995), and thus going a step beyond volume measurements, by converting volumes to actual biomass, would be ideal in evaluations of sponge communities. However, variation among sponge species in live tissue/volume gives rise to much smaller inaccuracies in estimating sponge biomass from volume than the gross inaccuracies, amounting to differences of as much as several orders of magnitude, caused by evaluating massive or erect species by area or by number of individuals rather than by volume.

Although still or video photography can greatly decrease time spent in the field, data collected in this way are meaningful in only a limited set of circumstances. Photographic records can be used to accurately monitor cover and dynamics of encrusting sponge species or recruitment to flat surfaces of dock pilings or sunken ships. However, many reef sponges are not confined to exposed flat surfaces. In areas stressed by heavy sediment loads, sponges may live disproportionately on vertical and under overhanging surfaces. Many sponges that enhance coral survival by holding corals on the reef and protecting coral skeletons from excavators live tucked under corals where they are invisible to a camera. Even for fully exposed sponges, volume can be difficult to estimate from photos, and may require more than one view of each individual.

Sponge Taxonomy.—As tempting as it may be to name all sponges encountered, even if based on a color and morphology key or photo guidebook, many sponges are difficult to distinguish without using more characters. Photos with poor resolution, such as those taken primarily for the purpose of estimating coral cover, may not allow accurate sponge identification, even by experts. Mistakes in identification can result in underestimation of number of species. For example, in the census area in Panama, there were four massive orange sponge species, representing three different orders; and five red encrusting species, representing three different orders. Without careful attention to characteristics that allow distinction among species, these nine species could be recorded as only two common species, one orange and one red. Another red sponge, Cliona delitrix, can appear by casual observation to be an encrusting or massive species, but instead it is actually an excavating species that erodes deep caverns within massive coral skeletons (e.g., Rose and Risk, 1985). This example brings up what is perhaps the most important reason for careful sponge taxonomy, which is that functional roles of sponges vary widely, and previously gathered information on roles of particular sponge taxa cannot be accessed without correct names. For example, hawksbill turtles can consume large amounts of sponges, but confine their attentions to species in only a few orders, especially the Astrophorida and Hadromerida. Some members of the Hadromerida are excavating species, engaged in dismantling the reef rather than holding it together. The genus Ircinia, in the order Dictyoceratida, is characterized by extremely tough skeletons that render its members nearly immune to fish bites (Wulff, 1994) and damage by physical disturbances. These sponges are therefore especially effective at holding the reef together, even in the face of hurricane-force water movement (Woodley et al., 1981; Wulff, 1995a). Many

Dictyoceratida also appear to be particularly susceptible to pathogens, and include the commercial sponges, which have suffered dramatic population decreases apparently due to pathogen epidemics (e.g., Smith, 1941). Keratose sponges (i.e., orders Dictyoceratida, Dendroceratida, and Verongida) tend to be less tolerant of sediment, whereas members of the Poecilosclerida, Haplosclerida, and Halichondrida appear to be characterized by particularly graceful acceptance of turbid conditions (Reiswig, 1971; Alcolado, 1994; Zea, 1994; and Wulff, 1997a). Correct sponge names are the only means by which published insights into the roles the sponges might play can be accessed.

Monitoring Changes in this intensively monitored 16 m² community were dramatic, but the actual data were surprising at every census because the sponge community did not look very different from census to census. Perhaps in part because of the minimal changes in total sponge volume, the loss of nearly half of the original species was not immediately obvious. Loss of half of the species in such a diverse group could be a signal of important changes in environmental context, especially when those lost were not just rare species, but species that previously contributed a significant proportion of the sponge biomass. The species lost during the 11 yr period had initially contributed 25.3% of the total sponge volume in the community and included species ranked as high as 4, 5, 7, 8, and 9 in volume. It is possible that this degree of sponge loss has occurred in other places, but has gone unnoticed due to lack of permanent long-term census sites. Previous reports of dramatic decreases in commercial sponges in the Caribbean (e.g., Smith, 1941) may partly reflect the greater attention paid to farmed sponges. Declines in commercial sponges, and especially their lack of recovery, have been particularly conspicuous (Vicente, 1989), but we have no reports of whether or not commercially unimportant species might have been affected by disease at the same times.

The techniques chosen and the detail with which monitoring is done make an enormous difference in our resulting understanding of community dynamics. For example, if sponges in the community monitored in Panama had been evaluated only by numbers of individuals, they would have appeared to be thriving between the 1994 and 1995 censuses, with an increase of nearly 20% in number of individual sponges. However, the contrasting simultaneous decrease of 8.1% by volume in this single year might cause concern if indicative of a trend. Going beyond quantification of sponges to keeping track of taxonomy of all individuals revealed the loss of 21.9% of the species during this single year, surely indicating serious environmental challenges and unequivocal cause for concern.

High diversity of coral reef sponges causes methodological problems beyond taxonomy. If the actual quadrats or transects censused do not include all the species in an area, a recensus of any points other than the exact original points could spuriously appear to document additions or deletions of species. The $16~\rm m^2$ censused here were representative of the surrounding area in that a 5 h search of the $30 \times 40~\rm m$ relatively homogeneous area of surrounding reef revealed no additional sponge species except for three that are characteristic of seagrass meadows, all found in a small patch of seagrass on the edge of the designated area. However, moving slightly deeper $(1.5~\rm m)$ on the reef, or up on top of the adjacent *Porites* reef $(1~\rm m$ vertically), or farther into the seagrass meadow $(3~\rm m$ horizontally), quickly added an additional 37 species, giving a total of 76 species for this small $(50~\rm m \times 50~\rm m)$ area spanning a depth range of only 3 m. De Voogd et al., (1999) describe a useful method for objectively determining minimum sampling area by counting sponge

species included in one quadrat, and continuing to double the sampling area until a doubling adds fewer than 10% more species.

Difficulty in distinguishing competitive from beneficial interactions between sponges and corals by simple observation is another compelling reason for establishing permanent quadrats for monitoring. This is essential when the outcome of interactions between neighboring coral and sponges can be as different as (1) sponges overgrowing and killing entire corals, vs (2) sponges enhancing coral survival by gluing coral colonies onto the reef and protecting exposed coral skeletons from colonization by excavators. Actual advance of sponges over living coral must be demonstrated before a conclusion of aggression is made, regardless of prior assumptions about how nature works.

REALISTIC SPONGE EVALUATION IN A WORLD OF LIMITED FINANCIAL RESOURCES, BOTTOM TIME, AND SPONGE EXPERTS.—Approaches chosen for sponge assessment can be tailored to the purposes of the study. Where single aggressive species appear to be overgrowing corals, use of photographic techniques may maximize both efficiency and usefulness. However, because most other known roles of sponges are related to sponge volume, estimation of sponge volumes is required for community characterization, assessment, and monitoring. Differences in data resulting from evaluating sponge abundance by area, number of individuals, and volume are so large that approximating volume with less detailed measurements is likely to provide more meaningful results than using area covered or number of individuals. Time in the field can be reduced, for example, by using a single average diameter for large branching individuals, rather than by measuring and recording the actual diameter of every branch segment. Depending on the assortment of sponge shapes represented on a reef, other techniques by which volume measurements can be streamlined without major loss of accuracy can be devised and tested for relative accuracy. For example, Reiswig (1973) constructed a regression curve of sponge volume and linear measurements from which he could accurately determine volume of individual specimens in the field.

Communication among widely dispersed reef scientists and managers, and access to published ecological and distribution information, requires accurate names of sponges. Although the sponges in a local area can be drawn from regional pools of 400-1500 species, typically many fewer species are found on a particular reef (e.g., Hooper, et al., (1999) provide a comparison of regional sponge faunas in northeastern Australia). In Venezuela, Alvarez et al. (1990) found 60 sponge species in transects across a depth gradient; Schmahl (1990) found 84 sponge species on reefs in the Florida Keys, USA; Alcolado (1990) reported 130 species from Cuban reefs; and Hooper et al. (1999) found 176 species at Lizard Island, Australia. These species numbers are less overwhelming once it is known which species they are. Techniques for collecting and preserving sponges are detailed in Rützler (1978) and in Hooper (1998), who also provide methods for gathering additional information on the sponges which can be used for determinations of species and higher taxa. If names are required more quickly than they can be provided by an expert, it is preferable to give a brief description and make voucher specimens avail-

able than to publish an uncertain species name.

If field time or diver experience is limited to the extent that only some sponges can be included in a monitoring scheme, the choice can be based on consideration of the functional roles of greatest interest. For example, large individual sponges each provide vast filtering capacities that are of particular importance in maintaining water column clarity, excavating sponges may be of special interest in nutrient enriched areas, and species favored by hawksbill turtles might be of special interest in other situations.

Using sponges as temporary binders of coral rubble, until carbonate secreting organisms or submarine lithification can bind them permanently, may be a promising aid to reef restoration. Sponges in this role have not been investigated beyond the experiments described in the Introduction (Wulff, 1984), but the potential is great, as sponges would offer aesthetically more appealing and less expensive glue than underwater cement, as well as providing other unique ecosystem services of sponges. Not all sponges are equally able to reattach quickly or even respond gracefully to being cut. For Great Barrier Reef sponges, these differences correspond closely to morphological differences, some of which are related to dependence on photosynthetic symbionts (Wilkinson and Thompson, 1997), but in other faunas they might be related to taxonomic relationships or local habitats.

Motivation for keeping track of coral reef sponges is provided by their functional roles on reefs. Human caused degradation appears to increase the carbonate-dismantling and coral-overgrowing activities of some sponge species. Loss of other sponges from coral reefs can decrease coral survival, reef regeneration, water column clearing, nutrient recycling, primary production, abundance of sponge-feeding fishes and turtles, and aesthetic appeal.

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