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SPONGES ON CORAL REEFS: A COMMUNITY SHAPED BY COMPETITIVE COOPERATION

KLAUS RÜTZLER

Department of Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0163, USA
E-mail: ruetzler.klaus@nmnh.si.edu

ABSTRACT

Conservationists and resource managers throughout the world continue to overlook the important role of sponges in reef ecology. This neglect persists for three primary reasons: sponges remain an enigmatic group, because they are difficult to identify and to maintain under laboratory conditions; the few scientists working with the group are highly specialized and have not yet produced authoritative, well-illustrated field manuals for large geographic areas; even studies at particular sites have yet to reach comprehensive levels. Sponges are complex benthic sessile invertebrates that are intimately associated with other animals and numerous plants and microbes. They are specialized filter feeders, require solid substrate to flourish, and have varying growth forms (encrusting to branching erect), which allow single specimens to make multiple contacts with their substrate. Coral reefs and associated communities offer an abundance of suitable substrates, ranging from coral rock to mangrove stilt roots. Owing to their high diversity, large biomass, complex physiology and chemistry, and long evolutionary history, sponges (and their endo-symbionts) play a key role in a host of ecological processes: space competition, habitat provision, predation, chemical defense, primary production, nutrient cycling, nitrification, food chains, bioerosion, mineralization, and cementation. Although certain sponges appear to benefit from the rapid deterioration of coral reefs currently under way in numerous locations as a result of habitat destruction, pollution, water warming, and overexploitation, sponge communities too will die off as soon as their substrates disappear under the forces of bioerosion and water dynamics. If there is any hope of stopping and possibly reversing this well-documented negative trend in reefs, it lies in concerted efforts arising from forums such as this one.

KEY WORDS

Sponge ecology, biodiversity, productivity, bioerosion, conservation, coral reef, mangrove, Atlantic, Indo-Pacific.

INTRODUCTION

Genova is an ideal location for the Sixth International Sponge Conference: it is not only the center of the Italian sponge universe, but its nearby waters are the birthplace of scientific diving. In the late 1700s and early 1800s, primarily in the Gulf of Naples, early marine scientists from Europe −such as Cavolini, Milne-Edwards, and Delle-Chiaje− were the first to attempt underwater investigations (RIEDL, 1967), which subsequently flourished with the development of scuba and the direct observation and sampling that it allowed (Fig. 1).

Knowledge of coral reefs dates back to when the earliest seafarers and coastal peoples first became aware of reef organisms. However, misconceptions abounded until the middle of the eighteenth century, when DE PEYSSONEL (1752) established the animal nature of corals, and well into the nineteenth century, when scientists began to assess the diversity and geological importance of reefs (DARWIN, 1837, 1842; DANA, 1872).

Coral reefs occur in three of the planet's largest bodies of water: the Indian, Pacific, and Atlantic Oceans (Fig. 2). They are restricted to a latitudinal belt of ca. 30° N and S, in areas of suitable coastal morphology and mean water temperatures of not less than 20°C. Though definitions may vary among sailors, ecologists, and geologists (WOOD, 1999; KLEYPAS *et al.,* 2001), in essence a coral reef is a tropical shallow-water community formed by photosynthetic scleractinian corals, other invertebrates that secrete calcium carbonate, and cementing algae. This massive framework is colonized and strongly affected by macrobenthic algae, sponges, and octocorals, and owing to its spatial complexity it is home to a highly diverse assemblage of associated organisms. The entire system operates through complex animal-plant symbioses, particularly between coral and dinoflagellate algae, and between sponges and cyanobacteria, and functions best in nutrient-poor offshore environments. The principal condition for a healthy reef community is that construction, the buildup of limestone through secretion and cementation, must outweigh erosion, the breakdown by carbonate-excavating organisms and physical forces. Sponges participate in all aspects of these processes.

In certain respects, reefs are not unlike mangrove islands, which, because of their near-tropical temperature requirement, have a similar geographic distribution and often cooccur with hermatypic corals. Saltwater-tolerant pioneering species of the genus *Rhizophora* occupy the low wave-energy niches of the reef, and where the tidal range is small, as in the Caribbean, their elaborate stilt-root system provides ample and protected substrate for sponges and other reef organisms. Mangroves, like corals, stabilize and build geological formations but are also susceptible to environmental stress, which may eliminate them along with the entire community. Unlike reefs, mangroves depend on detritus derived from plant materials for their principal source of energy.

Although sponges have a close association with reefs, numerous species are not restricted to coral environments. Furthermore, despite offering ample substrate and complex habitats of pure calcium carbonate, reefs present many competitive challenges because most of the outer veneer of the coral framework is alive and the cryptic areas are occupied by diverse and evolutionarily successful fauna.

Because of their physical complexity, reefs remained virtually unexplored until the second half of the twentieth century, when World War II's technical inventions and refinements allowed underwater pioneers, particularly in the Mediterranean area, to develop gear suitable for scientific diving and underwater documentation. Along with several others, I applied the new technology to the study of reef sponges in its earliest stages (RÜTZLER, 1996, 2001). That research has spanned almost five decades now and took place at many field locations. Since it would be impossible to cover all work in this brief review, I will touch on only the highlights. I should also warn that my account is biased toward the regions and disciplines of my own interest and expertise.

CORALLINE SPONGES: LIVING FOSSILS

As the fossil record shows, the history of biologically created reefs goes far back in geological time. As early as the Precambrian period, sponges with fused siliceous spicules or solid calcareous skeletons were important contributors to these structures (WOOD, 1999). The first Recent sponge with a solid calcareous base skeleton (*Astrosclera willeyana* Lister), described in 1900, was discovered by dredging, but it was not until scuba and research submersibles appeared that more details about coralline sponges emerged. Their habitat, for example, was found to occur primarily on shallow (25 - 60 m) shaded reefs in the Caribbean and the Indo-Pacific (for instance, HARTMAN, 1969; HARTMAN & GOREAU, 1970; VACELET, 1977, 1981a) or on deep fore reefs (60 - 200 m), where they may still be major contributors to framework construction (LANG *et al.,* 1975; WILLENZ & POMPONI, 1996) (Fig. 3). Coralline sponges are relicts of many diverse Paleozoic and Mesozoic groups (including stromatoporoids, chaetetids, and sphinctozoans) now linked to modern Calcarea and Demospongiae (VACELET, 1985). The discovery of these “living fossils” has made it possible to undertake phylogenetic revisions, conduct histological and finestructure studies, and carry out *in situ* observations and experiments on ecological requirements, calcification rates, and reaction to symbionts, as well as to monitor environmental quality and change over long periods of time (HARTMAN & WILLENZ, 1990; WILLENZ & HARTMAN, 1994, 1999; REITNER *et al.,* 1997; WÖRHEIDE, 1998; LAZARETH *et al.,* 2000).

DIVERSITY AND DISTRIBUTIONAL ECOLOGY

The major provinces supporting coral reefs are the large and extremely rich Indo-West Pacific, the less diverse but large Pacific island region, and the medium-rich and fairly small tropical West Atlantic, including the Caribbean, the Atlantic coast of northern South America, the Gulf of Mexico, Bahamas, Florida, and Bermuda. The sponge fauna of these regions was poorly known until the 1960s (SARÀ & VACELET, 1973), when scientific diving was perfected as a study tool, and since then more than 70 % of the new species described have been collected by divers in coral reef habitats (Fig. 4).

Indo-West Pacific

Among the pioneers in this province was a group of young scientists from the Station Marine d’Endoume, Marseilles, working on the open reef and in caves near Tuléar, southwest Madagascar, during the late 1950s and early 1960s. Using the new technology, they were able to examine the entire fauna alive and *in situ* and discovered many new species (VACELET & VASSEUR, 1965, 1971). One of their particularly interesting finds was the presence of lithistid and coralline sponges in reef caves and other shaded areas, as recorded in similar habitats in the Mediterranean (VASSEUR, 1964). I myself was part of a small expedition to Nosy Bé in northwest Madagascar at that time (1959/1960), but most of my collection of sponges was lost in transit to Vienna, and I was left with only a few specimens of common species, some pictures, and field notes from which I reconstructed reef-sponge distribution patterns (RÜTZLER, 1972). The Marseilles group resumed their work in Madagascar in 1963, under the sponsorship of the International Indian

Ocean Expedition (IIOE) and the International Biological Program, and this research continued until the early 1970s (described in VACELET *et al.,* 1976). Under a U.S. program affiliated with IIOE, participants built a substantial collection of sponges, particularly from the Seychelles in the west (R/V *Anton Bruun*) and from Thailand and Indonesia in the east (R/V *Te Vega* of Stanford University, U.S.A.; RÜTZLER, 1964). Owing to the chronic shortage of specialists, however, most of this material is still awaiting analysis and description. Nevertheless, important descriptions of the sponge fauna and its distribution emerged from studies in the Indo-West Pacific, most notably from Madagascar and the Seychelles (LÉVI, 1961; THOMAS, 1973; HOOPER & KRASOCHIN, 1989; HOOPER, 1996a), Zanzibar (HOOPER *et al.,* 2000), the Red Sea (R/V *Calypso* expeditions directed by J. Y. Cousteau, LÉVI, 1958; MERGNER, 1979; SARÀ *et al.,* 1979), Maldive Islands (SARÀ *et al.,* 1993), India (THOMAS, 1972), Indonesia (VAN SOEST, 1990; DE VOOGD *et al.,* 1999), Western Australia (FROMONT, 1999), and Papua New Guinea (KELLY-BORGES & BERGQUIST, 1988; BERGQUIST & KELLY-BORGES, 1995; PULITZER-FINALI, 1996; PULITZER-FINALI & PRONZATO, 1999), Hong Kong (PULITZER-FINALI, 1982a) and the Philippines (CABEROY, 1979; BAKUS & NISHIYAMA, 1999, 2000).

Many substantial fringing reefs and atolls occur throughout the Indian Ocean, but the most prominent reef feature in the Indo-West Pacific region is without doubt the Great Barrier Reef of Australia and other coral formations along the continent. The first important work in this region took place at a modest field station on Low Isles near Cairns, off northern Queensland (BURTON, 1934). Much of the collecting was done by wading and dredging or snagging from small boats. As subsequent studies have shown, however, the systematic treatment of the collections at the time of their description was of poor quality, unfortunately not an uncommon occurrence in the assessment of sponge diversity. A follow-up study reexamining specimens deposited in the Natural History Museum, London, showed that 42 % of the species were misidentified, and hence that conclusions about their zoogeographic affinities were highly erroneous (HOOPER *et al.,* 1999b). For the next half century, there was little sponge research in Australia until Patricia Bergquist from New Zealand spearheaded new initiatives and Australian systematist John Hooper, first at Darwin, now at Brisbane, entered the field; both inspired numerous colleagues and students (for instance, BERGQUIST & TIZARD, 1967; BERGQUIST, 1969; BERGQUIST *et al.,* 1988, 1999; HOOPER, 1988, 1991; FROMONT, 1991, 1993; HOOPER & BERGQUIST, 1992; HOOPER & WIEDENMAYER, 1994; HOOPER, 1996b; HOOPER *et al.,* 1999a; WÖRHEIDE & HOOPER, 1999; KENNEDY, 2000). At least two studies were conducted off Queensland independently from this group, one on shallow-water sponges of the Heron Island Research Station (PULITZER-FINALI, 1982b) and the other, still ongoing, based in Townsville and dealing with the much neglected systematics of clionaid sponges, a diverse and ecologically important group excavating reef substrates (SCHÖNBERG, 2000).

Pacific Island Region

The peoples of this region have had close ties to the sea and its reefs for millennia, relying on it for both food and items of cultural significance such as shells used for ceremonial purposes or decoration. Their sea skills proved very helpful to the early explorers of reef sponges, who otherwise could only sample by hand during low spring tides (DE LAUBENFELS, 1954; BERGQUIST, 1965). Again, it was a French group that initiated the first large-scale and long-term reef exploration in the West Pacific, at New Caledonia in 1976. Its principal objective was to prospect for novel metabolites among marine organisms. The systematic sponge research was conducted by an international team under the leadership of Claude Lévi, of the Muséum National d'Histoire Naturelle, Paris (LÉVI, 1979), and it culminated in an exemplary illustrated synthetic volume (LÉVI, 1998) and a biogeographic analysis clarifying faunal relationships (HOOPER & LÉVI, 1994). Up to that point, contributed monographs on reef and lagoon sponges had dealt with corallines (VACELET, 1981a), Poecilosclerida (HOOPER & LÉVI, 1993a), Halichondrida (HOOPER & LÉVI, 1993b), Haplosclerida (DESQUEYROUX-FAUNDEZ, 1984, 1987; FROMONT, 1995), and "Keratosa" (BERGQUIST, 1995). These results demonstrate that individual studies are not as effective as comprehensive programs in generating a large body of knowledge, particularly in remote areas. Still, one cannot overlook a number of landmark isolated projects, such as those that dealt with the impact of a new encrusting bacteriosponge deadly to corals in the Ryukyu Archipelago (Japan; RÜTZLER & MUZIK, 1993) (Fig. 5), a small collection from an R/V *Te Vega* cruise to the Fiji Islands (TENDAL, 1969), and samples from numerous locations in Hawaii (DE LAUBENFELS, 1950a; BERGQUIST, 1967). Particularly noteworthy are projects initiated at the University of Guam, including extensive research on secondary metabolites, and collections made by members of the Coral Reef Research Foundation (Koror, Belau) during their biodiversity surveys throughout the Commonwealth of the Northern Mariana Islands (KELLY *et al.,* 2003).

West Atlantic

Systematic evaluation of sponges on western Atlantic coral reefs goes back to DE LAUBENFELS' (1936) monograph on the Dry Tortugas (Florida), which has been the principal reference to genera until the recent publication of the multiauthored Systema Porifera (HOOPER & VAN SOEST, 2002). Although not a diver, de Laubenfels was not shy about getting his feet wet and on occasion was adventurous enough to try out William Beebe's recently developed diving helmet (BEEBE, 1926). He also employed local commercial sponge divers. He expanded his work to elsewhere in Florida, the Bahamas, and Bermuda (DE LAUBENFELS, 1949, 1950b, 1950c, 1953), but no students were available to carry this work further. The only serious young sponge researcher in the United States whose career overlapped de Laubenfels' was Willard Hartman at Yale University. Hartman was not a diver either and at first was primarily interested in the New England fauna, although he provided taxonomic information to a few reef ecologists (for instance, LEWIS, 1965). When I arrived in Washington in 1965, still in an orientation mode and trying to complete projects started in Europe, there was only one other sponge worker with reef interests: George Hechtel, one of Hartman's students, who conducted his thesis research in Jamaica and subsequently worked in Barbados (HECHTEL, 1965, 1969). Hartman then teamed up with famed reef explorer and ecologist Tom Goreau, founder and director of the Discovery Bay Marine Station, Jamaica. Goreau and his students turned their sponge collections over to Hartman and collaborated with him on a number of projects, including one that led to the discovery of coralline sponges in reef caves and crevices, occurring in association with other "living fossils" such as brachiopods (HARTMAN & GOREAU, 1970; JACKSON *et al.,* 1971). About that time, I began my own surveys and collections of coral reef sponges in the Caribbean, which included trips to Bermuda, Puerto Rico, the Virgin Islands, Jamaica, and Bimini, Bahamas, where I first recognized that reef-associated mangrove islands were part of the reef ecosystem and had a similar, albeit specialized, sponge fauna covering mangrove stilt roots and peat banks (RÜTZLER, 1969). Unlike Indo-Pacific mangroves, their Caribbean counterparts have a small tidal range that leaves most available hard substrates under water during its daily cycle. I collected many sponges for later study and returned to my passion at the time, limestone-excavating sponges (RÜTZLER, 1971, 1974).

Soon after my visit to Bimini, the Swiss paleontologist Felix Wiedenmayer collected sponges during a collaborative project with geologists from the universities of Illinois and Miami who were interested in learning more about the skeletal components of carbonate sediments. Recognizing the inadequacy of the existing sponge literature for the West Indian region, Wiedenmayer embarked on a thorough revision of Bahamian sponges based on his own collections and on exhaustive surveys of the literature and museum material and complemented by a distributional analysis in reef and lagoon habitats (WIEDENMAYER, 1977). About the same time, the young Cuban biologist Pedro Alcolado became interested in sponge communities on reefs and in mangroves of his island nation and despite his academic isolation produced a remarkable series of papers on biodiversity and distributional ecology (ALCOLADO, 1976, 1979, 1990, 1994). By then, similar interests were being pursued on the opposite side of the Atlantic, at the Zoological Museum of Amsterdam, where Rob van Soest had begun a comprehensive study of the sponges of Curaçao "and other Caribbean localities", which was based partly on older collections from the reefs and mangroves of the Netherland Antilles and elsewhere in the region, but also on many from recent surveys (VAN SOEST, 1978, 1980, 1981,1984). As this work continued, he collaborated with a number of students and associates, among them Belinda Alvarez, Cristina Diaz, Eduardo Hajdu, and Shirley Pomponi (*e.g.* DIAZ *et al.,* 1991, 1993; other work discussed below), and most recently Helmut Lehnert. Both Pomponi and Lehnert were among the first to sample the deeper parts of reefs that are not accessible by conventional skin and scuba diving (Fig. 6). Pomponi worked on material obtained by the Harbor Branch Johnson-Sea-Link research submersible for research on secondary metabolites (*e.g.*, POMPONI *et al.,* 1991; REED & POMPONI, 1997), while Lehnert used mixed-gas (trimix) scuba to collect and determine the distribution of sponges to a depth of over 100 m (LEHNERT & VAN SOEST, 1996, 1999; LEHNERT & FISCHER, 1999).

I myself and a handful of colleagues at the Smithsonian Institution spent most of the 1970s developing a long-term, interdisciplinary coral-reef research program. Although many in the group wanted to work on Pacific atolls, for logistical and financial reasons we decided to focus on the Caribbean. After thorough evaluation of many locations, we settled on the barrier reef of Belize (then British Honduras) and founded a field station on Carrie Bow Cay (Fig. 7). The program is now known as Caribbean Coral Reef Ecosystems (CCRE), and its primary purpose is to investigate the systematics, developmental biology, ecology, and paleobiology of reef and mangrove organisms. I dedicated the initial years mainly to methodology, mapping, habitats, and communities (RÜTZLER, 1978; RÜTZLER & MACINTYRE, 1982), but eventually several colleagues and I turned to the rich sponge diversity in the area (*e.g.*, RÜTZLER, 1981; WILKINSON, 1987b; DE WEERDT *et al.,* 1991; RÜTZLER & SMITH, 1993; ALVAREZ *et al.,* 1998; HAJDU & RÜTZLER, 1998; MURICY & MINERVINO, 2000; RÜTZLER *et al.,* 2000; DE WEERDT, 2000) (Fig. 8).

Sponge research on Caribbean reefs took several strides forward during the 1980s when three young South American workers entered the field. Sven Zea started out with research on the systematics and distributional ecology of sponges of the Colombian Caribbean, including the remote oceanic reefs in the southwestern Caribbean, an ongoing program already involving several of his students (ZEA, 1987, 1998, 2001; VALDERRAMA, 2001). Belinda Alvarez and Cristina Diaz did similar thesis work in the Los Roques Islands off Venezuela (ALVAREZ *et al.,* 1990; DIAZ *et al.,* 1990). All three have since expanded their interests to other regions and disciplines of sponge research (see below). An Italian worker, Gustavo Pulitzer-Finali, with credits from many other locations around the world, contributed a systematic study of Caribbean sponges, mostly from reefs (PULITZER-FINALI, 1986).

The same time period saw a renaissance in sponge research in Brazil. Its reefs are much less abundant and less developed than in the Caribbean but belong to the same geographical region, except for some endemism south of the Amazon's freshwater barrier (LABOREL, 1969; WELLS, 1988; VERON, 1995). HECHTEL (1976) found that the coastal sponge fauna too showed strong affinities with the West Indies, but since he was working from older records in both regions, he also postulated that in Brazil endemism was high and many species were cosmotropical. Unlike hermatypic corals, whose zooxanthellae require light, sponges can avoid exposure to freshwater and sediment input by spreading into deeper water, where nutrients from river inputs are ample for these filter feeders (COLLETTE & RÜTZLER, 1977). Coral worker Jacques Laborel and malacologist Richard Foster made substantial collections between 1961 and 1964 (deposited at Yale university and studied by HECHTEL (1976, 1983) and subsequently more samples were taken during a large survey by the R/V *Calypso* (BOURY-ESNAULT, 1973). Several groups of Brazilian researchers, most of them divers, are currently conducting long-term studies in the area (*e.g.*, MOTHES & BASTIAN, 1993; HAJDU & DESQUEYROUX-FAÚNDEZ, 1994; MURICY & MORAES, 1998; MURICY & MINERVINO, 2000; MURICY *et al.,* 2001; MORAES *et al.,* 2003; MURICY *et al.,* 2002).

Another significant zoogeographic barrier long misunderstood because of unreliable taxonomy is the Isthmus of Panama, separating the Caribbean from the Eastern Pacific. Recent research has clarified earlier misconceptions but confirms the long-standing supposition that sponge faunas on either side are quite similar. When traditional taxonomic and ecological characteristics are compared, sibling species can barely be differentiated (WULFF, 1996; BOURY-ESNAULT *et al.,* 1999).

METHODS OF QUANTITATIVE ECOLOGY

Various methods have been used to measure the diversity and quantitative importance of reef sponges. Today, scuba diving is essential for selective sampling, direct observation, and application of a variety of counting and measuring methods, including photogrammetry and videographic documentation (RÜTZLER, 1996). Early studies employing this technique were laborious but provided excellent assessments of sponge habitat quality and the influence of environmental variables (such as depth, substrate, water movement, temperature, and sedimentation) on the number of species and density of individuals (STORR, 1976a; WIEDENMAYER, 1977). Although these surveys relied a good deal on intuitive interpretation, they helped improve our understanding of sponge-dominated environments.

As in all ecological assessments in the field, numerous constraints force the researcher to juggle between the desire for accuracy and the need for expediency. Measures of the sponge population, for instance of a patch reef, to species, number of individuals, and milligram weight are of little value if there is no time to collect information on their context −namely, the extended reef area− or if the measurements can be altered by a single visit from a pair of angle fish. Several colleagues and I who have discussed this problem are the first to admit that for a variety of reasons (such as other priorities or the lack of funds, time, or skilled manpower), we failed to prepare an all-taxa systematic inventory and a quantitative balance sheet for a given reef tract or transect. Instead, many of us apply the same chain-link-count, point-intercept, or frame-counting methods coral workers use (discussed for instance by WEINBERG, 1981; ARONSON *et al.,* 1994) because, despite their shortcomings, they are relatively fast and provide reasonably objective data within the limited time frame of scuba dives and fieldwork (Fig. 9). The resulting data, on species and specimen numbers and area cover, can be used to calculate diversity indices, density, evenness, live cover, zonation, and to perform other statistical exercises. By way of example, these methods have been used in quantitative reef-sponge surveys in the Atlantic in Florida (SCHMAHL, 1990), Cuba (ALCOLADO, 1979, 1990), Jamaica (SCHUBAUER *et al.,* 1990), Belize (RÜTZLER & MACINTYRE, 1982), Venezuela (ALVAREZ *et al.,* 1990; DIAZ *et al.,* 1990), Caribbean Colombia (ZEA, 1993a, 2001; VALDERRAMA, 2001), and Brazil (MURICY, 1989; MORAES *et al.,* 2003); and in the Red Sea in Northern Eritrea (PRONZATO *et al.,* 1994).

Unlike corals, however, most open-reef sponges are massive, rod-shaped branching, or tubular colonies that form only a thin veneer of tissue over the skeleton they secrete. Therefore, their biomass cannot be readily compared if only surface-cover values are obtained. To address this problem, it has been suggested that biomass analyses include three-dimensional measurements of idealized shapes, displacement volume, or wetweight, or extrapolation from wetweight, dryweight, ashless dryweight, and caloric content based on sacrificed subsamples (RÜTZLER, 1969, 1978; DIAZ & RÜTZLER, 2001; WULFF, 2001). So far, disregarding ecophysiological, laboratory, and nonreef research (*e.g.*, DAYTON *et al.,* 1974; BAVESTRELLO *et al.,* 1986), only a few specialized field surveys have taken weight or volume of reef sponges into consideration (WILKINSON & TROTT, 1985; WILKINSON, 1987a; WILKINSON & EVANS, 1989; DIAZ *et al.,* 1990; WULFF, 1990, 1999).

Another approach to estimating sponge diversity, abundance, dominance, and sociability is one used by plant sociologists. It has been adopted in the Mediterranean and in a survey of sponge distribution on the reefs of Tuléar, Madagascar (VACELET & VASSEUR, 1977), but is not suited for statistical treatment. Nevertheless, this and the previously mentioned survey of North Madagascar reefs (RÜTZLER, 1972) further documented the uniqueness of the sponge fauna in reef caves discovered earlier in Mediterranean rock caves.

ENVIRONMENTAL PARAMETERS AND IMPACT ON SPONGE COMMUNITIES

Depth

Water depth is always recorded for surveys or collected specimens. Although this information helps in finding the species again, it is of little ecological import, except in the intertidal. It merely reflects the general conditions of light, temperature, or water movement, conditions that vary greatly with habitat where benthic organisms are concerned. In the intertidal, however, exposure to air and solar radiation at ebb tide may determine distributional limits. Reef corals seem able to cope with frequent exposure in areas such as the Indo-Pacific, where tides measure 3 m or more, but little is known about the effect on sponges. They may survive in pockets of water or by being partly buried in sediment (VACELET & VASSEUR, 1977). Most of the Atlantic reefs occur in areas with a tidal range of less than 50 cm, so corals and sponges are rarely exposed at low tide. At the same time, near-reef mangrove stilt roots support a rich sponge fauna having a distinctive zonation that reflects tidal regime and physiological resistance to desiccation (RÜTZLER, 1996).

Light Exposure

Sponges prevalent in fully illuminated shallow reef environments are subject to competition from photosynthetic benthos, such as algae and symbiotic (hermatypic) corals and octocorals, or to pressure from predators. They meet these challenges with the aid of photosynthetic endosymbionts or protective secondary metabolites, or both. Most photosynthetic sponge symbionts are unicellular cyanobacteria, but they also include filamentous cyanobacteria, dinoflagellates (zooxanthellae), and higher algae (Fig. 10).

The majority of unicellular cyanobacteria are small (<3 µm) and belong to the *Aphanocapsa feldmanni* complex. A much larger prokaryote (>5 µm), superficially resembling zooxanthellae, is described as *A. raspaigellae* and *Synechocystis trididemnum.* Filamentous forms have been assigned to the *Oscillatoria spongeliae* type, also classified as *Phormidium,* depending on the absence or presence of a sheath. All contain chlorophyll *a* and phycobiliprotein pigments, a combination also found in red algae and thought to allow more efficient photosynthesis under low light (COX *et al.,* 1985; LARKUM *et al.,* 1987). But the phycobilin structure and distribution among species are complex, and the genetic expression of extra light-harvesting subunits such as phycourobilin does not necessarily correlate with light intensity (LARKUM *et al.,* 1988).

Dinoflagellate symbionts (zooxanthellae) are primarily known from excavating sponges in the hadromerid family Clionaidae, where they may exhibit different strains and species than the ones in corals and other invertebrates but serve the same nutritional function (VACELET, 1981b; RÜTZLER, 1990; WILKINSON, 1992; HILL & WILCOX, 1998). Curiously, clionaids with zooxanthellae not only grow faster than many others without symbionts but are more destructive; by contrast, the dinoflagellate associates of hermatypic corals aid in the deposition of calcium carbonate (HILL, 1996). At least one non-clionaid sponge from reefs harbors unicellular dinophyceans, an undescribed chalinid, *Haliclona* sp. (Haplosclerida), from the Great Barrier Reef. In this case, the symbionts may have been obtained from live substrate corals (along with nematocysts) after cytotoxic alcaloid metabolites generated by the sponge caused necrosis in the coral tissue (GARSON *et al.,* 1999). Such competitive advantage is common to many symbiotic encrusting sponges and may have a considerable impact on corals, particularly those that are environmentally stressed, but it is still not clear to what degree the symbionts emit toxic substances (BRYAN, 1973; CORTÉS & MURILLO, 1984; PLUCER-ROSARIO, 1987; VICENTE, 1990a; RÜTZLER & MUZIK, 1993; RÜTZLER, 2002).

Multicellular algae can also be counted among the photosynthetic symbionts or, possibly in some cases, parasites. In the Caribbean, species of the rhodophyte (red) alga *Jania* serve as skeletal support for sponges such as *Dysidea janiae,* and the synchronized mode of growth of the two points toward coordinating factors (RÜTZLER, 1990). Another well-studied association occurs in the Indo-Pacific, between the chalinid sponge *Haliclona cymiformis* (also reported as *Gellius* and *Sigmadocia*) and the red alga *Ceratodictyon spongiosum* (PRICE *et al.,* 1984). Rapid growth rates may account in part for this sponge's excellent survival rate in high-energy reef habitats (TRAUTMAN *et al.,* 2000); it also appears to benefit from self-generated nitrogen compounds and algal photosynthate (GRANT & HINDE, 1999; DAVY & HINDE, 1999). Boring green and red algae (genera *Ostreobium* and *Acrochaetium*) penetrate the spongin fibers of *Mycale laxissima* and several other species, including stony corals (RÜTZLER, 1990). Their ability to photosynthesize despite the dark pigmentation of the surrounding host tissue of a sponge such as *M. laxissima* (Poecilosclerida) can be explained by the shallow distribution and thin body wall of the tubular sponge but also by the thick bundles of large monactine siliceous spicules at the core of spongin fibers that work like glass-fiber light guides, as in the hadromerid *Tethya seychellensis* from the Maldive Islands (GAINO & SARÀ, 1994).

A helpful technique for assessing photosynthetic performance is to measure oxygen production rates, as has been done for symbiotic sponges from several depths on the Great Barrier Reef (CHESHIRE & WILKINSON, 1991) (Fig. 11). Another tool, pulse amplitude modulated (PAM) fluorometry, shows great promise for rapid, nonintrusive *in situ* measurement of chlorophyll fluorescence, as has been demonstrated for sponges of the genera *Theonella* and *Cliona* in the Red Sea (BEER & ILAN, 1998; ILAN & BEER, 1999). Although this method does not take into account respiration, it can be used to evaluate photosynthetic performance at different depths as well as the health of organisms.

The distribution of photosynthetic symbionts is closely associated with their impact on reef-sponge biomass. On the Great Barrier Reef, in nearshore habitats shallower than 10 m, suspended sediments scatter and filter available light, so sponge biomass is low; in the clear waters of outer reefs above 40 m (with 5 % or more of surface irradiance), biomass is considerably higher, despite much lower levels of nutrients (WILKINSON & TROTT, 1985). At the same time, certain species that do not harbor symbionts may have light-exposure preferences or tolerances that reflect competitive resistance to fish and invertebrate grazing and sediment exposure (RANDALL, 1967; BAKUS, 1964; 1968; RÜTZLER, 1972). The effect of ultraviolet radiation (UV) on sponges is still poorly understood but detrimental effects have been demonstrated in very shallow (<10 m) reef environments penetrated by UV light. Pigment filters demonstrated for some species appear to protect those growing fully exposed in clear shallow water (JOKIEL, 1980). Species restricted to shaded habitats and artificially exposed die quickly, but factors such as sedimentation and fish grazing also play a role (BAKUS, 1964; RÜTZLER, 1972; WILKINSON & VACELET, 1979).

Temperature and Salinity

For the most part, coral reefs exist in areas that are not exposed to large fluctuations in temperature. Because long-term elevations and extremes can have adverse effects on reef distribution, the increases in mean highs recently experienced in some areas are particularly worrying. Stress of this nature may lead zooxanthellae to leave coral tissue and thereby cause coral bleaching, which may be followed by the death of the host cnidarian; over the past two decades, cases of such bleaching have been reported worldwide (GATES, 1990; JOKIEL & COLES, 1990; MACINTYRE *et al.,* 2000). From our observations in Belize, either sponges are less affected by adverse temperatures or symbionts are not as readily expelled. Where bleaching has occurred among reef sponges, those with both cyanobacterial and dinoflagellate symbionts have been affected (VICENTE, 1990b; HILL & WILLCOX, 1998; FROMONT & GARSON, 1999). Whereas temperature and salinity are not environmental determinants in the case of coral reefs, because hermatypic corals can only tolerate small deviations from oceanic conditions, they are selective factors for sponge distribution in reef-related lagoons and mangroves (RÜTZLER & FELLER, 1996; RÜTZLER *et al.,* 2000). Temperatures ranges of 16 - 39° C and salinity of 28 - 41 ‰ were recorded in tidal ponds and creeks that provide habitat for a few species of the demosponge genera *Suberites, Terpios,* and *Halisarca* (RÜTZLER, 1995).

Shaded and Dark Habitats

Many reef sponges do not flourish in illuminated habitats but are important community components on the deep fore reef and below, and in caves, crevices, and under overhangs. Most cavity-dwelling reef sponges, known as coelobites, are small or encrusting forms and do not require much space (Fig. 12). Even pieces of coral rubble, particularly platy shapes, are suitable cryptic habitats as long as they are not directly exposed to sediments and allow regular flushing to bring in nutrients and remove waste products. Their diversity, ecological impact, geological and paleoecological importance, and contribution to the trophic balance of reef ecosystems have been well documented (VACELET & VASSEUR, 1965; JACKSON *et al.,* 1971; JACKSON & WINSTON, 1982; MACINTYRE *et al.,* 1982; LOGAN *et al.,* 1984; KOBLUK, 1988; KOBLUK & VAN SOEST, 1989; MEESTERS *et al.,* 1991; GISCHLER & GINSBURG, 1996; RICHTER & WUNSCH, 1999; RICHTER *et al.,* 2001). Reef cavities off Bonaire, Netherlands Antilles, revealed more than 90 species of sponges (KOBLUK & VAN SOEST, 1989), probably nearly one-quarter of the entire population, though only a small part of the biomass. Because of their thinly encrusting morphology, such sponges tend to expand rapidly in these limited spaces and form competitive hierarchies (JACKSON & WINSTON, 1982), particularly under the more stable conditions in deeper water, below the reach of storm surges that may periodically disturb the habitat structure.

One problem with cryptic reef habitats is their structural complexity and poor access. Crevices too small for divers to enter or too large to expose without damaging parts of the reef are only now being explored with the development of underwater endoscopic techniques. The CaveCam (WUNSCH & RICHTER, 1998) is a diver-operated video system that is enabling scientists to observe animals, map habitat structure and populations, and study the microclimate in spaces measuring a few cubic centimeters. With the aid of such techniques, it has been found that the rich fauna of cavernicolous sponges on reefs in the Red Sea far outweigh sponges of the open reef.

Occupants of reef crevices in ancient reefs, such as brachiopods and coralline sponges, were clearly able to survive competition from the fast-growing hermatypic corals that appeared in the Middle Jurassic (JACKSON *et al.,* 1971). However, the importance of those sponges has been greatly underestimated because many assemblages have been misinterpreted or were not preserved in the fossil record (KOBLUK & VAN SOEST, 1989).

Sediments and Impact from Storms

Reefs sediments consist largely of biogenic limestone in grain sizes from gravel to silt derived from protozoan and invertebrate skeletons, calcareous red and green algae (genera *Amphiroa, Neogoniolithum, Jania, Halimeda, Penicillus,* and many more), foraminiferids (*Homotrema*), cnidarians (milleporids, gorgonaceans, scleractinians), and assorted crustaceans, molluscs, bryozoans, and echinoderms. Calcareous sponges exist but do not attain large biomass. Reef sediments are the product of various forces: storms that pound shallow corals and intertidal coralline algal formations; mechanical abrasion through the movement of sand, gravel, and rock; grinding by grazers such as parrotfish, chitons and other molluscs, sea urchins, and starfish; and bioerosion by limestone-penetrating bacteria, fungi, filamentous algae, sponges (see below), worms, crustaceans, molluscs, echinoids, and others (CARRIKER *et al.,* 1969; SCHWARZ, 1982) (Fig. 13). Noncalcareous fragments may derive from terrestrial sources (quartz particles washed in by rivers), but on reefs distant from land, they are made up of siliceous skeletons or spicule fragments produced by resident organisms such as diatoms and sponges. Sponge spicules are composed of hydrated silicon dioxide and are not very stable in the Si-undersaturated, high-pH environments of reef sediments. Hence they are rapidly dissolved and recycled by consumers such as sponges (RÜTZLER & MACINTYRE, 1978).

Sediments have a marked effect on the distribution, ecological importance, and developmental biology of most sponges. Some sponges are themselves sediment producers. For instance, Clionaids and some haplosclerids participate in the breakdown process and produce extremely fine or microgranular (silt-size) particles by using archaeocyte filopodial cell processes for chemical coring (RÜTZLER, 1971, 1975; RÜTZLER & RIEGER, 1973; POMPONI, 1979a, b, 1980; ACKER & RISK, 1985). Other sponges are adapted to live in sediment as part of the endopsammon or incorporate sands in their skeleton and tissue for reinforcement. Some species of the genera *Oceanapia* (Haploclerida), *Biemna* (Poecilosclerida), and *Cervicornia* and *Tectitethya* (= *Cryptotethya*) (Hadromerida) have adapted to life in sandy substrata. Several mechanisms help support this unusual way of life for such filter feeders:

Oceanapia and *Cervicornia*, both from the Caribbean, have large incurrent fistules protruding from the sediment surface, the choanosome is buried and sealed from the surrounding loose particles, and exhalant ducts allow water to exit into the porous sand (WERDING & SANCHEZ, 1991; RÜTZLER, 1997). A Red Sea species of *Biemna* lives in shallow lagoons with soft bottoms rich in organic content and takes in water through buried ostia, while the oscula are located on top of siphons above the substratum surface. In addition, ostia may avoid clogging by cellular displacement, and oscula are closed by contraction to avoid penetration by sediments (ILAN & ABELSON, 1995). Similar mechanisms may be adopted by sponges surviving in soft sediments for extended periods of time after having been dislocated from solid substrates such as mangrove roots or rock (RÜTZLER, 1995; unpubl. data from Bermuda). One report on sediment-covered *Spheciospongia vesparium* (Hadromerida) from the Gulf of Mexico suggests periodic backwashing as a mechanism to clear the incurrent canal system (STORR, 1976b). The Caribbean *Tectitethya crypta* is usually buried in coarse sand; its top portion, including porus sieves and oscula, protrudes but is thickly covered by fine sediment. This species produces a strong ventilation current alternating with shutdown periods that may aid in the flushing or cellular elimination of unwanted particles (REISWIG, 1971a). Psammobiontic sponges may ensure habitat stability by settling in low-energy lagoons or attaching to buried pieces of rock. In Belize, sponges such as *Tectitethya* appear to incorporate sand to help stabilize small specimens or asexually produced fragments on soft bottoms until they become buried in the substrate where they are adapted to survive (CERRANO *et al.,* 2002).

Many keratose sponges (Dictyoceratida, Dendroceratida) incorporate sediment particles in their skeleton fibers or in ectosomal spongin and may distinguish between sand particles and fragments of foreign (siliceous) sponge spicules, which may be considered a taxonomic character in species lacking the ability to form proper spicules (DE LAUBENFELS, 1950b; SARÀ & VACELET, 1973). In experiments with reef species such as *Dysidea etheria,* explants deprived of sediment (a situation not likely to occur in nature) were found to change the shape and slow the growth of new skeletal fibers (TERAGAWA, 1986). Sediment may also be incorporated throughout the body, as is the case in the order Hadromerida and the artificial (heterogenous) “Psammascidae” (see the relevant chapters in HOOPER & VAN SOEST (2002).

Aside from the aforementioned specializations, the distribution of reef sponges may be affected by the interaction of sediment and water flow. In their extremes, fine-grained material in stagnant water is smothering, while coarse sand in strong currents acts as an abrasive (BAKUS, 1968; RÜTZLER, 1972). The West Indian hadromerid *Cliona* (= *Anthosigmella*) *varians* may be encrusting or excavating (forma *incrustans;* WIEDENMAYER, 1977) and has a tough consistency that allows it to prevail in shallow reef habitats with coarse sediment and strong wave action, where it can cover areas up to 46 m^2. The same species attains massive to digitate and ramose shape in turtle grass beds of sediment-rich lagoons (forma *varians*). Distribution and growth form appear to be governed by sediments and wave action, possibly combined with resistance to predatory fish (VICENTE, 1978; HILL, 1999). Strong water movement also plays a role in the zonation of certain reef sponges. In a tidal creek in the Red Sea, current force combined with sediment grain size is considered to be responsible for the structure of four distinctive sponge associations that differ from that in a nearby fringing-reef community (SARÀ *et al.,* 1979). Experiments with Caribbean reef sponges, including the verongid *Aplysina* (= *Verongia*) *lacunosa,* indicate that exposure to high concentrations of very fine suspended sediment slows down pumping rates significantly (GERRODETTE & FLECHSIG, 1979). During extended storms, reduced intake of organic matter and the need to expend energy to clear unusable particles will doubtlessly influence species distribution and cause population loss. Extreme storms such as hurricanes may have various effects depending on local geomorphology, but those effects cannot be fully judged without data on pre-storm populations. When the powerful hurricane Gilbert of 1988 passed directly over Cozumel, Mexico, the sand layers deposited over sponges did not appear to have long-lasting effects, but there are no records of pre-storm sponge diversity or biomass (FENNER, 1991). In the same year, hurricane Joan affected reefs in the San Blas Islands, Panama. Because it struck from the opposite direction of the usual north-east trade winds, the nonadapted benthic community suffered severe damage (WULFF, 1995a). Hardest hit were the large erect and branching sponges, while spongin-dominated skeletons were more resistant than those with a high spicule content. However, many fragments reattached, and there may have been an increase in sexually produced propagules as a result of the storm.

POPULATION DYNAMICS AND ECOPHYSIOLOGICAL PROCESSES

Recruitment, Growth, and Competition for Space

Information is available on several aspects of sexual and asexual reproduction in coral reef sponges (Fig. 14). Spectacular synchronous sperm release by populations of male demosponges ("smokers") and parallel exuding of egg masses in gelatinous encasement have been observed in a number of Caribbean locations. Although not the rule, these occurrences provide a superb tool for research into biological processes. Such a tool may facilitate prediction based on environmental conditions, season, and lunar phase and make it easier to determine sex ratio and reversal, separate populations genetically, and carry out artificial fertilization (REISWIG, 1970, 1976; HOPPE & REICHERT, 1987; FROMONT, 1988). Several studies have detailed the reproductive biology of haplosclerid species (genera *Chalinula, Haliclona, Niphates*) from the Great Barrier Reef and the Red Sea, adding histological and fine-structure data to the ecological observations obtained *in situ* (ILAN & LOYA, 1988, 1990; FROMONT, 1994). Once larvae are developed and released, their ecological preferences and a large degree of luck help determine settlement and survival of the adult. Depending on species, larvae measure from less than 100 m to more than 6 mm, their swimming speed ranges from several mm/sec to mere drifting, and they slow down and settle after periods of hours or a few days (WAPSTRA & VAN SOEST, 1987; WOOLLACOTT, 1993; RÜTZLER *et al.,* 2003). No matter how strong their swimming ability, nearly all of them swim very close to the substratum; to catch them, divers need to pull or push plankton nets or use a stationary net that generates currents (RÜTZLER *et al.,* 1980). The only exception known are the armored propagules of certain excavating sponges (genera *Alectona* and *Thoosa*) that are found among open-water plankton and were previously identified as gemmules but recently shown to be sexually produced larvae (VACELET, 1999). The swimming behavior of larvae is closely associated with environmental parameters such as light and water flow, but not necessarily with the presence or abundance of adults of the same species. Low temperature, however, seems to limit larval swimming speed, the life of tropical species, and dispersal into cold water (MALDONADO & YOUNG, 1996). Temperature, along with season and depth, was found to affect sponge recruitment in an area of periodic coldwater upwelling in the Colombian Caribbean (ZEA, 1992, 1993b). As in other areas, the poor swimming capability of larvae appears to account for the higher settlement rates and success in the vicinity of established populations of adults and for the great heterogeneity among communities subject to very similar environmental regimes (RÜTZLER *et al.,* 2000; ZEA, 2001). Whereas most reef sponges recruit and grow slowly and live for extended periods of time, some opportunistic species grow and mature quickly, produce larvae (parenchymella is the common type) in great quantities throughout the year, and settle and metamorphose rapidly. Among these generalists are species of the poecilosclerid genus *Mycale,* such as *M. laxissima* studied on the reefs of Jamaica. It is relatively short-lived, grows quickly, and maintains populations on a large variety of substrata, which it colonizes rapidly as soon as they become available. These characteristics give the species a clear advantage after a catastrophic event such as a hurricane. Like some of its more specialized competitors, however, it grows larger with increasing depth below 20 m, where it is protected from storm effects and heavy sedimentation (REISWIG, 1973; SCHUBAUER *et al.,* 1990).

A Caribbean congener, *M. microsigmatosa,* exhibits similarly opportunistic behavior in mangrove lagoons, where it colonizes seagrass blades and stilt roots (HAJDU & RÜTZLER, 1998). An r-selected species, *Mycale fistulifera,* from the Red Sea has a similar life history; it prefers an opportunistic coral species as substrate (MEROZ & ILAN, 1995a). By contrast, K-selected species —for instance, the Caribbean *Tectitethya crypta* (Hadromerida), *Agelas clathrodes* (Agelasida), *Neofibularia nolitangere* (Poecilosclerida), *Ircinia strobilina* (Dictyoceratida), and *Aplysina* (= *Verongia*) *fistularis* and *Verongula reiswigi* (= *Verongia gigantea*) (Verongida)— have relatively stable populations in selected habitats and use their available energy for regeneration and maintenance (REISWIG, 1973; HOPPE, 1988; SCHUBAUER *et al.,* 1990).

Of course, reef sponges may be dispersed by other than larval means. Several species among the genera *Cinachyrella* and *Tethya* (RÜTZLER & SMITH, 1992; SARÀ, 1993) reproduce by gemmules, though the actual mechanism of dispersal and settlement has not been investigated. There is also strong evidence that storm events that break up shallow-water sponges, particularly those having a ropy branching morphology, contribute substantially to dispersal if the fragments come to rest on suitable substrates and attach (WULFF, 1985; BATTERSHILL & BERGQUIST, 1990). At the same time, experiments show that susceptibility to fragmentation and successful reattachment depend to a large degree on anatomical adaptations; species high in spongin are resistant to tearing but do not easily reattach, whereas sponges of more cellular composition (less spongin) tear readily and reattach with a high success rate (WILKINSON & THOMPSON, 1997).

For the most part, the growth rates of species are difficult to establish because measuring techniques vary and specimens for which data are available differ in shape, size, age, environmental conditions, genetic make-up, and health. Reported linear growth rates vary from 0 (indeed, negative values owing to shrinkage, predation, or partial die-off are common) to several cm per year. Encrusting clionaids, such as the zooxanthellae-bearing *Cliona varians* and *C. caribbaea,* may spread as much as 13 cm/year, while excavating their substratum to depths of 10 mm or more (AERTS & KOOISTRA, 1999; RÜTZLER, 2001) (Fig. 15). The linear increase for massive reef species (demosponge genera *Agelas, Neofibularia, Xestospongia, Ircinia*) can reach 4 cm/year (HOPPE, 1988; SCHMAHL, 1999). A particularly aggressive opportunistic Caribbean species, the poecilosclerid *Desmapsamma anchorata,* reportedly overgrows its substratum at a mean rate of 45 cm^2/month, which amounts to about 80 cm linear growth a year (AERTS *et al.,* 1999). Specimens of this species are known to grow faster when attached to other sponge species rather than on carbonate substrata because it saves energy by reducing skeletal reinforcement (WULFF, 1999). On the other hand, loose fragments reattach to rock more rapidly than in any other species, which may be an advantage for sponges torn from their substrate.

Heavily damaged sponges regenerate more slowly than slightly injured specimens (SCHMAHL, 1999). Experimental lesions generally heal quickly: 4 mm diameter holes in thinly encrusting species may take only 3 days to regenerate (JACKSON & PALUMBI, 1979); 10 mm holes (5 mm deep) in the opportunistic *Desmopsamma anchorata* take 12 days; and 30 mm lesions (10 mm deep) in the expansive encrusting *Cliona* (= *Anthosigmella*) *varians* heal in 60 days, faster if less deeply cut (AERTS *et al.,* 1999; AERTS & KOOISTRA, 1999).

As sessile occupiers of substrata, reef sponges must compete for space with other sponges and with many algae, bryozoans, and tunicates, but particularly with corals, the very organisms that provide them a home. The Caribbean sponge *Mycale laevis* is associated with several massive coral species, particularly *Montastraea annularis* (GOREAU & HARTMAN, 1966). The sponge first encrusts the free lower (dead) surface of the coral and grows in step with the cnidarian, which spreads sheet-like because of the low level of light in the typical habitat where the association occurs (10 m and below). Characteristic folds along the coral's edge corresponding to oscular regions of the sponge appear where the current flow is strong and may assist the host in feeding. Since the coral is protected from the clionaid and other borers that tend to penetrate the dead base, the sponge is presumed to benefit from an expanding substratum free of competitors. Sponges that compete best in very shallow water with strong currents and wave action are small forms in cryptic habitats (under platy rubble) or thinly encrusting and excavating species, as already mentioned. A very tough competitor in very shallow (<3 m) open water in the Virgin Islands, West Indies, is one previously identified as the octocoral *Erythropodium caribbaeorum,* with sponges in the genera *Chondrilla, Hemectyon, Ircinia,* and *Aplysina* (= *Verongia*) next in importance (SUCHANEK *et al.,* 1983). Information from other locations indicates that *Chondrilla* cf. *nucula* and several species of *Cliona* (including *"Anthosigmella"*) are just as aggressive and successful, particularly in environments stressful for corals (VICENTE, 1978, 1990a; AERTS & KOOISTRA, 1999; MACINTYRE *et al.,* 2000; RÜTZLER, 2002).

As has been amply demonstrated, secondary metabolites aid in sponge aggression. On the lower surfaces of platy coral and rubble in Jamaica, for example, thinly encrusting sponges, bryozoans, and ascidians fiercely compete for limited space and, in the absence of physical disturbance and predation, the prevailing species are able to succeed through complex allelochemical mechanisms (JACKSON & BUSS, 1975). Similar chemical means were identified in a study of sponge-sponge competition on reefs in Guam (THACKER *et al.,* 1998). The haplosclerid excavating sponge *Aka* (= *Siphonodictyon*), common on and in live coral heads in the Caribbean, maintains and possibly acquires its space through the secretion of a metabolite (SULLIVAN *et al.,* 1983). In the U.S. Virgin Islands, extensive cushions of the homosclerophorid *Plakortis halichondrioides* kill the sheet coral *Agaricia lamarcki,* not only upon direct contact but also through waterborne toxic compounds (PORTER & TARGET, 1988). Similar effects on corals, with or without direct contact, have been shown for several species in different orders of Demospongiae in Caribbean Colombia, the Great Barrier Reef, and the Philippines (AERTS & VAN SOEST, 1999; GARSON *et al.,* 1999; NISHIYAMA & BAKUS, 1999). Surveys of Colombian reefs also confirm observations elsewhere in the Caribbean indicating a hierarchy in the competition for space among sessile reef organisms: algae predominate in very shallow, strongly illuminated, and turbulent water; corals (somewhat limited by seasonal coldwater upwelling) and octocorals on mid-depth reef terraces and slopes; and sponges at the deeper-water reef base. And where specialized, aggressive species are lacking or are not quantitatively important, even stressed corals are not significantly affected by sponge overgrowth unless they are severely damaged (ZEA, 1993b; AERTS & VAN SOEST, 1997; AERTS, 2000). A comparison of reefs off Curaçao with high coral cover and those off Caribbean Colombia with low cover has shown that high cover (and not species composition) is positively correlated with overgrowth by sponges with diverse populations, including aggressive species (AERTS, 1998).

Sponges as Reefs

Despite their abundance, most recent species of reef sponges do not contribute to the reef framework because their spicules are siliceous and hence are rapidly dissolved in undersaturated waters (HARTMAN, 1977; RÜTZLER & MACINTYRE, 1978; MALDONADO *et al.,* 1999). Rare exceptions are the few coralline sponges ("sclerosponges") that secrete an aragonitic base skeleton, but at best they only somewhat strengthen the walls of caves and the framework of the deep fore reef. Nevertheless, sponges perform some functions that put them in the category of reef-builders, which range from generating framework to colonizing surfaces, tissues, and internal cavities. Some examples are the modern sponge bioherms found on the Bahama Bank and elsewhere in shallow tropical carbonate environments, which are not unlike certain paleoecological facies of the Tethyan Mesozoic. The lithification process starts when certain sponges —most notably species among the Hadromerida (for instance, *Spheciospongia vesparium, Tectitethya crypta*)— accrete and incorporate sediment, and it continues with the secretion of calcium carbonate by colonizing organisms such as algae, cnidarians, polychaete worms, and bryozoans, as well as other sponges (WIEDENMAYER, 1978, 1979; CERRANO *et al.,* 2002).

Faced with limited space and resources, reef organisms have developed many mechanisms of coexistence, as a result of which sponges have become probably the most utilized hosts (Fig. 16). Various terms have been used to describe such coexistence —symbiosis, commensalism, mutualism, parasitism— but not enough is known about the biology of the associates to apply the terms correctly (see review in

CASTRO, 1988). The taxonomic spectrum of endosymbionts ranges from microbes to fishes. Photosynthetic (cyano-) bacteria and dinoflagellates are known to provide nutrition to their host and to the rest of the system. The nutritional contributions of blue-pigmented bacteria are not yet understood, but the characteristic symbionts of some species in the genera *Terpios* (Hadromerida) and *Hymeniacidon* (Halichondrida) seem to be sensitive to full solar radiation and to the ultraviolet portion of the spectrum, which restricts the host to semishaded environments (SANTAVY, 1985; RÜTZLER & SMITH, 1993). Heterotrophic bacteria are present in all Porifera and may be highly diverse, as observed in the mesohyle of a coralline sponge, *Ceratoporella nicholsoni* (SANTAVY *et al.,* 1990). However, it is difficult to assess the role and contribution of the different morphological types, particularly the obligate anaerobic forms, because only a small percentage can be isolated and cultured. Heterotrophic bacteria make up nearly 50 % of the total biomass of quite a few reef sponges, hence named bacteriosponges (REISWIG, 1981; RÜTZLER *et al.,* 2003). Unlike non-bacteriosponges, these sponges use dissolved organic matter as their primary energy source (WILKINSON & GARONNE, 1980; REISWIG, 1981).

Whereas many sponges endeavor to keep their outer surface clear of settlers, with the aid of antibiotic or cell-mechanical defense mechanisms, some are specialized for supporting algae and certain encrusting invertebrates without compromising their own water-exchange needs. Such organisms include dictyoceratids with spongin-reinforced ectosome in the genera *Spongia* and *Hyatella* living on crowded stilt roots and peat banks in mangroves, or tetractinellids such as *Geodia* with a cortex of special spicules (RÜTZLER, 1981; RÜTZLER *et al.,* 2000; WILCOX *et al.,* 2002). Field experiments with sponges and other sessile invertebrates in Belize and Florida have demonstrated that allelochemicals are involved in both antifouling and attraction among certain species (BINGHAM & YOUNG, 1991). Some sponges are intimately associated with species of the epizoic zoanthid *Parazoanthus,* for example. In a study on the barrier reef of Belize, the frequency of zoanthid colonization increased with size (age) of members of the host population and the mutualistic arrangement tended to turn into parasitism when epizoan density exceeded a certain threshold, because pumping rates were then depressed (LEWIS, 1982). Such an association is obviously beneficial for many parazoanthids because their host's toxicity protects them from fish grazing; what the host gains in return is less clear. Some algae, hydroids, and gorgonaceans form stolons that use very little attachment space on a sponge's surface and are generally tolerated by many species. As already mentioned, calcified branching red algae often serve as skeletons, and there are other curious associations, such as intertwining with a tubiporan octocoral described from Indonesia (VAN SOEST & VERSEVELDT, 1987). Many sponges even have scyphozoan polyps and barnacles embedded in their outer tissues (MEROZ & ILAN, 1995b; ILAN *et al.,* 1999; VICENTE *et al.,* 1991), and the resulting openings have often been misidentified as systematic features of the host.

It has long been known that reef sponges are rich in endofaua. In his now classic report on loggerheads (*Spheciospongia*) and other large species (genera *Ircinia, Spongia*) from the Dry Tortugas, Florida, PEARSE (1932) extracted thousands of syllid polychaetes, amphipods, ostracods, isopods, alpheids and other decapods, and ophiurid echinoderms and differentiated between mere dwellers and parasites. A more recent account of the organisms living in *Spheciospongia vesparium* from the

Dutch West Indies reported similar diversity and related species richness, and also found (with the aid of biogeographic methods) that sponge inhabitants from hosts larger than 1 l make up a predictable, stable community (WESTINGA & HOETJES, 1981). Another study, comparing the endobionts of tubular and cavernous *Aplysina* species (Verongida) at Los Roques islands, Venezuela, found that diversity depends greatly on interstitial volume and distribution of space (VILLAMIZAR & LAUGHLIN, 1991). Off the Bahamas, the endofaunal diversity of *Niphates* (= *Gelliodes*) *digitalis* has been shown to correlate more with specimen size and volume available for colonization than with sponge age and habitat location (UEBELACKER, 1977). Various taxa such as fishes and thallassinid and alpheid decapods have also been described living cryptically in large Caribbean shallow-water sponges (TYLER & BÖLKE, 1972; SCOTT *et al.,* 1988), and a recent study at Carrie Bow Cay, Belize, revealed a high diversity of snapping shrimp in reef sponges and provided the first marine example of eusociality, the kind of cooperation observed among ants and honeybees, which has a strong reproductive benefit (DUFFY, 1996). A rare contribution from the Indo-Pacific (Papua-New Guinea) describes endobiotic barnacles and syllid polychaetes, and their effect on anatomy and ecology of the verongid host sponge, genus *Anomoianthella* (MAGNINO *et al.,* 1999).

Filter Feeding and Photosynthesis

Despite all the known complexities of nutrition in sponges, with or without symbionts, the primary feeding mechanism remains water pumping by means of a cleverly designed incurrent and exhalant hydraulic system, with choanocyte chambers in the center (Fig. 17). Although many methods have been devised to measure pumping volume and current flow —from dye injection to thermistor flow meters and tubes with floating spheres (FORSTNER & RÜTZLER, 1969; VOGEL, 1981)— it is still difficult to obtain long-term continuous signals *in situ* and to avoid water leaks into electronic compounds or influences from ambient currents. Even so, these techniques have produced substantial information. For example, a recording current meter with thermistor sensor has demonstrated water-pumping activity in three species of Demospongiae from Jamaican reefs: *Tectitethya crypta* (= *Tethya;* Hadromerida), *Mycale laxissima* (= *Mycale* sp.; Poecilosclerida), and *Verongula reiswigi* (= *Verongia gigantea;* Verongida) (REISWIG, 1971a). *Tectitethya* shows periods of activity followed by inactivity that are synchronized throughout the population on a daily basis but not on a biweekly scale, at least not during the calm season; periodic storms, however, caused synchronization of the contractions that indicate inactivity. By contrast, *Mycale* maintains a constant level of pumping activity. *Verongula* holds the middle ground, ceasing activity about once a day for nearly an hour, nonsynchronized among the population. A seasonal temperature decrease of merely 2° C depresses the activity patterns of these species. The pumping rate for a 0.51 ml specimen of a verongid, *Aplysina* (= *Verongia*) *lacunosa,* in the Bahamas was found to be 1 - 6 l/h, which decreased with the presence of suspended sediments, as mentioned earlier (GERRODETTE & FLECHSIG, 1979). By comparison, a population of the haplosclerid *Xestospongia muta* in a similar reef setting off Jamaica has a mean pumping rate of 2.6 ml/min for a 1 ml sponge (REISWIG *et al.,* 1979). Even though these extrapolations are quite disparate (a maximum of 12 l water/hour/l for *Aplysina* versus a mean of 156 l water/hour/l for *Xestospongia*), the volume of seawater filtered by reef sponges each hour may be more than 6 m^3 per m^2 per day, which demonstrates the strong influence these filter feeders have on the carbon budget. Particles available for filtration by sponges range from colloidal organic material to 1 μm bacteria; larger cells, to 50 μm, are presumed to be captured by amoebocytes and transported into the body for phagocytosis or, as in the case of armored cells, are discarded (REISWIG, 1971b). Some reef sponges, such as the ropy *Aplysina cauliformis,* possess distinctive choanosomal cell strands that facilitate nutrient transport through the body (LEYS & REISWIG, 1998). A study of resource partitioning among ultraplankton (<5 μm) feeders on Bahama and Florida reefs using flow cytometry has revealed that sponge species differ in their retention efficiency with regard to food groups such as bacteria, cyanobacteria, and autotrophic picoeucaryotes, and that food availability increases toward the bottom, putting low-growing forms at an advantage over tall morphologies (PILE, 1997, 1999).

Like reef corals, sponges in nutrient-poor water rely on autotrophic symbionts for dietary enrichment, which in turn promotes growth. Indo-Pacific and Atlantic sponges harbor very similar microbial associates (WILKINSON, 1980; VACELET, 1981b; LARKUM *et al.,* 1988; RÜTZLER, 1990), although Caribbean Porifera appear to be less effective as photosynthesizers and consume considerably more organic matter than their Great Barrier Reef counterparts (WILKINSON, 1987b). In some areas of the Great Barrier Reef, common foliose cyanobacteriosponges have a predominately phototrophic nutrition, with most of their energy derived from symbiont photosynthesis; oxygen production may exceed consumption by a factor of three (WILKINSON, 1981, 1983, 1987a; HINDE *et al.,* 1999). But a large variety of heterotrophic bacteria are also common in reef sponges (WILKINSON, 1978; BURJA *et al.,* 1999; FUERST *et al.,* 1999). These, together with cyanobacteria, may contribute to nutrient production on coral reefs by fixing dissolved inorganic nitrogen (WILKINSON & FAY, 1979; CORREDOR *et al.,* 1988; DIAZ & WARD, 1997; WILKINSON *et al.,* 1999).

Bioerosion versus Stabilization of Reefs

Not surprisingly, a great variety of limestone-excavating sponges have evolved in the rich calcium carbonate environment of coral reefs (Fig. 18). Excavating (or boring, burrowing) sponges belong primarily to the hadromerid family Clionaidae, but they are joined by a number of species in the poecilosclerid *Paracornulum* and *Zyzzya* and the haplosclerid *Aka* (= *Siphonodictyon)*, and possibly others capable of destroying reef coral (RÜTZLER, 1971; PANG, 1973; MACGEACHY, 1977; POMPONI, 1980; ROSE & RISK, 1985; RÜTZLER & STONE, 1986; SCHÖNBERG, 2000). A few species of *Cliona* (for instance, *C. delitrix*) and most *Aka* are especially destructive and commonly seen penetrating the live surface of otherwise healthy coral heads. Species of excavating *Aka* are also known from the Jurassic and considered a good indicator of early carbonate cementation in habitats dominated by siliceous sponges (REITNER & KEUPP, 1991). As far as is known, all excavating sponges apply the same method of chemical coring mentioned earlier. As has been long recognized, the impact of such an invasion is far greater in deeper coral communities than in shallow ones because calcification rates there are slower and wave surge is weak (GOREAU & HARTMAN, 1963). Excavating activity can erode the base of large coral colonies and cause them to break off, and it can produce large quantities of muddy sediments. At the same time, as Goreau noted with his characteristic optimism, dislodged coral that rolls down the fore-reef slope and comes to rest on the soft sediments at the reef base provides substrata for dense new reef populations, Evidently this is what happened with the staghorn coral, *Acropora cervicornis,* that used to be a dominant member of the Jamaican shallow-water community. Clionaids weaken these structures and accelerate breakage, which leads to an increase in asexual reproduction and dispersal (TUNNICLIFFE, 1979). Up to the late 1960s, it was widely believed that clionaids always attack the dead bases of reef coral, never the live surfaces, but this idea has now been refuted with increasing observations of encrusting sponges boring over and under live coral surfaces, at least in the Caribbean, particularly during periods of environmental stress, such as extended periods of high or low temperatures (RÜTZLER, 1975, 2001; VICENTE, 1978; MCKENNA, 1997). Since less is known about such activity in the Indo-Pacific, efforts are under way to clarify neglected clionaid systematics, to determine how sponge erosion spreads and is influenced by environmental factors, and what steps in reef management should be taken to arrest this structural damage (SCHÖNBERG *et al.,* 1997; SCHÖNBERG, 2000, 2001; SCHÖNBERG & WILKINSON, 2001).

Although modern sponges can no longer be included with framework builders, they clearly contribute to stabilization of the reef, as well as its destruction. The aragonitic base of coralline-sponge skeletons helps to strengthen the deep fore-reef framework and the walls of caves and tunnels in shallow water (HARTMAN, 1977). Moreover, coral framework includes many occupied cryptic spaces that will eventually fill with sediments and be reinforced by slow lithification, unless disturbed by wave surge, fish grazing, and other physical forces. Sponges have also been shown to help counteract such disturbances by binding reef components together until the consolidation process is completed and the newly formed stable substratum can be occupied by new framework builders (WULFF & BUSS, 1979; WULFF, 1984; RASSER & RIEGL, 2002).

Disease and Reaction to Pollutants

Actual diseases of reef sponges —that is, conditions clearly caused by a pathogen— are still poorly understood, although, for obvious reasons, much research and speculation has been dedicated to commercial species (see PRONZATO, 1999). In the Caribbean, fungal pathogens, smothering macroalgae associated with red tides, high temperatures, and various other environmental conditions were blamed for the demise of bath sponges during the 1930s and 1940s, from which these once abundant populations never truly recovered (SMITH, 1941; GALTSOFF, 1942; STORR, 1964; STEVELY *et al.,* 1978; VICENTE, 1989; STEVELY & SWEAT, 1994). Today, commercial sponges are no longer restricted to the small spectrum of species with a soft, dense, and absorbent skeleton that used to serve many a household. Another use, sparked by the increasing demand for secondary metabolites, makes it desirable to cultivate sponges in order to produce large quantities of biomass, either *in situ*, as in the traditional bath-sponge cultures, or under more controlled conditions, in closed systems or as cell cultures, in vitro (POMPONI & WILLOUGHBY, 1994; POMPONI *et al.,* 1997; OSINGA *et al.,* 1999). Such efforts remain in the developmental stages, however, owing to poor unerstanding of factors such as proper food supply, diseases that easily develop and spread in confined spaces, and the effects of metabolite concentrates. One study found that a usually well-adjusted symbiosis, exemplified by the cyanobacteria-containing Belize mangrove sponge *Geodia papyracea,* goes awry during periods of stress, which can turn the endobiotic microorganism into a disease agent that causes histolysis of the host (RÜTZLER, 1988). A similar process may be responsible for cases of the partial necrosis or death of large barrel sponges (*Xestospongia muta*) reported from Curaçao (NAGELKERKEN, 2000) and observed by divers on the Belize barrier reef. Some sponges, such as the dictyoceratid *Ircinia felix* common in these waters, may counteract this abnormality by producing furanosesterterpine tetronic acids (FTA's), antimicrobial compounds that may also prevent infection by food bacteria (ZEA *et al.,* 1999).

As already pointed out, certain encrusting and boring sponges may be more robust than reef corals and take advantage of the weak resistance of the stressed cnidarians. Except for extended cold or hot spells, the only factors directly or indirectly implicated in the demise of sponge populations are various land-generated pollutants entering reef water via runoff and currents. Some have suggested that sponges may act as sinks by filtering out toxic substances or pathogenic bacteria, but this is unlikely to occur except in modest amounts. Habitat proximity to land runoffs has been shown to increase sponge biomass, both in the Caribbean and on the Great Barrier Reef, whereas the same conditions (high nutrients and turbidity) are unfavorable to coral growth (WILKINSON, 1987c; ZEA, 1994). With increasing concentrations of organic contaminants, sponge diversity decreases, leaving only few specialists but allowing identification of species usable for pollution monitoring (ALCOLADO & HERRERA, 1987; MURICY, 1989; DIAZ & RÜTZLER, 2001; WULFF, 2001), such as the encrusting poecilosclerid *Clathria venosa* near Havana, Cuba.

Interestingly, bioerosion rates seem to increase on polluted reefs, with clionaid sponges prominent among the participating organisms. In the Cayman Islands, the highly corrosive *Cliona delitrix* may increase fivefold in biomass, in concert with sixfold counts of bacteria in the water column, including coliforms (ROSE & RISK, 1985). Similar observations involving several clionaid species in Barbados and on Indonesian reefs suggest that pollution might be monitored by analyzing branching coral rubble, which is stable and abundant and could be examined without causing damage to live specimens (HOLMES, 2000; HOLMES *et al.,* 2000). Clionaids are also thought to be one of the main causes of increased bioerosion in a case of thermopollution in Guam (SIEGRIST *et al.,* 1992).

Predation and Chemical Defense

Although reef sponges produce a host of toxic metabolites, which of course makes them attractive to the pharmocological industry, they can also be prey to a number of organisms (BAKUS, 1981; FAULKNER, 1984; GARSON, 1994; MUNRO *et al.,* 1994) (Fig. 19). There is a voluminous literature on sponge-generated chemical compounds and their effects on other organisms in laboratory tests, often at very high concentrations, but far less information on the ecological impact *in situ* at "ecologically relevant" concentrations (GARSON *et al.,* 1999). One complication with field studies is that feeding-deterrent chemical compounds, for instance, in the Caribbean haplosclerid *Xestospongia muta* and the hadromerid *Chondrilla* cf. *nucula,* are not present in the same composition and concentration throughout the population of a species (KERR & KELLY-BORGES, 1994; CHANAS & PAWLIK, 1997; SWEARINGEN & PAWLIK, 1998). As mentioned above, many endobionts, such as alpheid shrimps, eat modest quantities of their host, usually not more than can be easily replaced. Apparently, secondary metabolites that are successfully employed in space competition do not fully protect against predation, just as they are not equally effective against all competitors. The common Caribbean fire sponge, the poecilosclerid *Tedania ignis,* is a good example. Though toxic to humans who handle it, causing severe dermatitis in some, it supports a sizable community of endo- and ectobionts (YAFFEE & STARGARDTER, 1963; HALSTEAD, 1965; RÜTZLER, 1968; unpubl. data).

Organisms that can inflict considerable damage on sponges or cause mortality and shifts in population structure include mollusks, echinoderms, fishes, and sea turtles. The large and common Caribbean starfish *Oreaster reticulatus* lives in seagrass meadows and feeds primarily on sponges, which it digests after everting its stomach over them (WULFF, 1995b). This animal prefers sponges knocked loose after heavy storms and thrown into the adjacent lagoon and rubble fields (and during researcher's experiments). It is less fond of native lagoon sponges, which are presumed to have developed defense mechanisms. A stomach content analysis of more than 200 Caribbean reef fishes revealed sponge fragments in about 10 % of specimens, but only 11 species, primarily angel angle- and file-fish, contained large enough quantities to classify them as sponge feeders (RANDALL & HARTMAN, 1968). These specialists eat a large variety of sponges and are not particularly attracted or repelled by color, shape, or spicule content. WULFF (1994; 1997a) added trunkfish to the list, which seem to prefer a diet of the verongid *Aplysina fulva,* and discovered that parrotfish, usually herbivores, are strongly attracted to cryptic sponges when they become exposed. Parrotfish were also implicated in bites taken from the reef sponge *Xestospongia muta,* particularly bleached specimens, and those with distribution in mangroves showed significant quantities of spicules in their gut, primarily from the tetractinellid *Geodia* (DUNLAP, 1999). A comparison of Caribbean and Pacific populations across the isthmus of Panama has shown that, unlike their Caribbean cousins, Pacific sponges are generally species-poor and small, and are confined to cryptic habitats by their predators (WULFF, 1997b). Experiments indicate that Caribbean sponges could be substantially reduced or lost if Pacific fishes were able to cross the isthmus. Spongivory may also be beneficial to the reef community because it keeps in check aggressively spreading coral competitors such as the encrusting hadromerid *Chondrilla* cf. *nucula* and thus helps maintain species diversity (HILL, 1998). The population structure of sponges can also be affected by feeding pressure from fishes, which is responsible for large differences in the species spectrum and relative abundances between reefs and different types of mangroves (WULFF, 2000). The hawksbill turtle, one of the few reptiles on Caribbean reefs, is known to feed almost entirely on sponges (MEYLAN, 1988, 1990; VICENTE & CARBALLEIRA, 1991; VAN DAM & DIEZ, 1997). Direct observation and study of the contents of turtles' intestinal tract and of fecal pellets show that many sponges targeted for food sustained substantial injury or were removed entirely from their substratum. Most of the prey species regularly consumed belong to the spicule-rich Tetractinellida and Hadromerida and have a low energy content per weight, even for ash-free tissue, compared with other animal tissue; the advantage of feeding on them may be a low level of toxic metabolites.

CONCLUSIONS

Sponges clearly contribute to many of the processes that enable a coral reef to flourish. Although they are not exclusive to the reef ecosystem, they are a conspicuous and ubiquitous component. Both partners in this association, sponges and reefs, have much to lose if one should succumb to environmental pressures.

Today, sponges play only a minor role in the construction of carbonate reef framework, but they are the organisms that started the process, back in the early Cambrian, more than 500 million years ago. Recent descendants of Paleozoic and Mesozoic stromatoporoids, sphinctozoans, and chaetetids —"living fossils"— still reinforce some cryptic habitats and their characteristics have shed light on the evolution and ecological significance of their ancient relatives.

Modern reef sponges are extremely diverse, mainly because of niche differentiation in their structurally complex habitat, which also encompasses mangrove islands and seagrass meadows. Biomass is equally significant and contributes energy and habitat resources. One of the next steps in research should be to standardize the methods used to assess mass, growth, and regeneration.

Of all the environmental parameters acting on a reef, light, water movement, and sedimentation are the most influential in determining the distribution and health of sponges. Solar radiation is vital for many common species associated with photosynthetic symbionts, from microbes to macroalgae. At the same time, shaded and dark habitats are adequate for species that have no direct investment in photosynthesis. Water movement has an impact on physical stability, food supply, and reproduction and in combination with coarse or fine sediment may have a detrimental effect, in eroding the substrate or smothering sessile organisms. Temperature and salinity are less limiting to sponges than to corals and may create temporary advantages in the battle for space.

The majority of reef sponges grow slowly and live long. Under favorable environmental conditions, they may spread rapidly, reproducing through larvae or asexually by fragmentation. During the reproductive seasons, larval production is high, but the parenchymellae are generally poor swimmers, are active for but a brief period, and stay close to the bottom. Dispersal over large distances is haphazard, and hence population structure is highly heterogeneous. Owing to toxic metabolites, sponges are successful space competitors, but they occupy special niches on the reef and rarely overpower healthy corals.

Despite their toxic tissue and exudate, sponges are occupied within and without by a multitude of specialized symbiotic, commensal, or parasitic associates spanning the phylogenetic spectrum from microbes to fishes. Most large epi- and endofauna use their host for shelter, but microbial symbionts contribute substantially to nutrient cycling, to the benefit of both the host and the entire reef ecosystem. Sponges feed mainly by filtration, targeting mainly ultraplankton.

Sponges having the greatest impact on their substratum are those living on reefs. Limestone-excavating species participate in bioerosion, which destroys framework and releases large quantities of dissolved and finely particulate calcium carbonate.

Encrusting and creeping-branching forms help hold fragmented corals together until calcification processes have restabilized them.

Their competitors and environment may affect the well-being of individual sponges in many ways, including the spread of microbial diseases. The mechanisms of these diseases are still unclear, though it is known that antimicrobial metabolites protect sponges from infection by many microorganisms functioning as food or symbionts. Land runoff and organic pollution in moderate concentration may benefit sponges by providing nutrients for the increased food bacteria, but the associated stress on reef corals can affect a sponge's substratum and shelter.

Predators of the sessile sponges range from microscopic endofauna to giant sea turtles. Except for the adapted specialists, most predators are deterred by the toxic qualities of secondary metabolites. These powerful chemicals have evolved as a defense mechanism over hundreds of million years and are now being investigated for their structure and multiple pharmacological properties, and thus for their antibiotic, anti-inflammatory, antiviral, and antitumor potential.

Research and assessments during the past decade have raised serious concern about the health and future of the world's coral reefs, including those in my own group's scientific field base in Belize (see, for instance, WILKINSON, 1993; LESSIOS & MACINTYRE, 1997; RISK, 1999; MACINTYRE *et al.,* 2000; KLEYPAS *et al.,* 2001; ARONSON *et al.,* 2002; BUDDEMEIER & FAUTIN, 2002). Their message is unmistakable: the reefs in some areas are degrading faster than scientists can monitor, even with rapid, large-scale techniques often criticized for not being rigorous enough. The obvious causes are overpopulation, overfishing, and overdevelopment, all of which can create adverse conditions such as water warming, pollution, and sediment production and can lead to the loss of grazers and predators, bleaching (through the expulsion of zooxanthellae), disease, algal and toxic microalgal blooms, excessive bioerosion, and reduced resistance to natural stressful events such as hurricanes and population shifts.

Coral reefs are unique ecosystems that flourish under low-nutrient conditions. They fortify tropical coasts, build islands, and through their structural complexity maintain the highest biodiversity in the sea, including a plethora of sponges. Reefs are among the richest resources on earth, both in economic and aesthetic terms. As sponge biologists, we should and must participate in their conservation.

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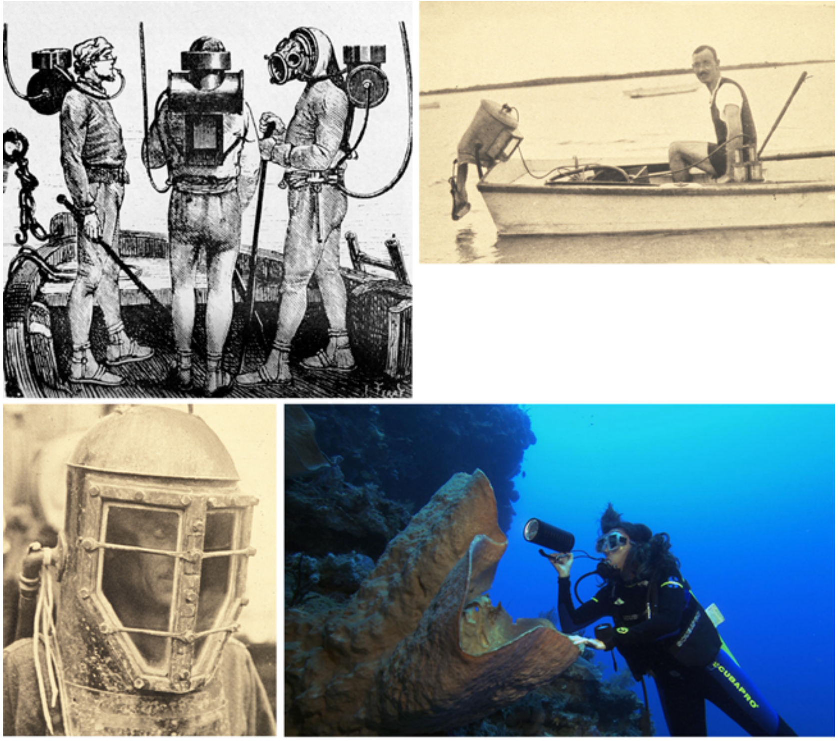

Fig. 1. Scientific diving, an essential tool for reef-sponge research (clockwise from top left): Surface-dependent breathing apparatus introduced during the founding of the first great marine stations (woodcut from Sonrel, 1880); diving helmet, hose, and pump used by members of the Great Barrier Reef Expedition (from Yonge, 1930); today's scientific sponge diver using scuba and wetsuit (photo by Sea Studios); Beebe's dive helmet occasionally employed in the Caribbean by American spongiologist M.W. de Laubenfels in the 1930's (from Beebe, 1926).

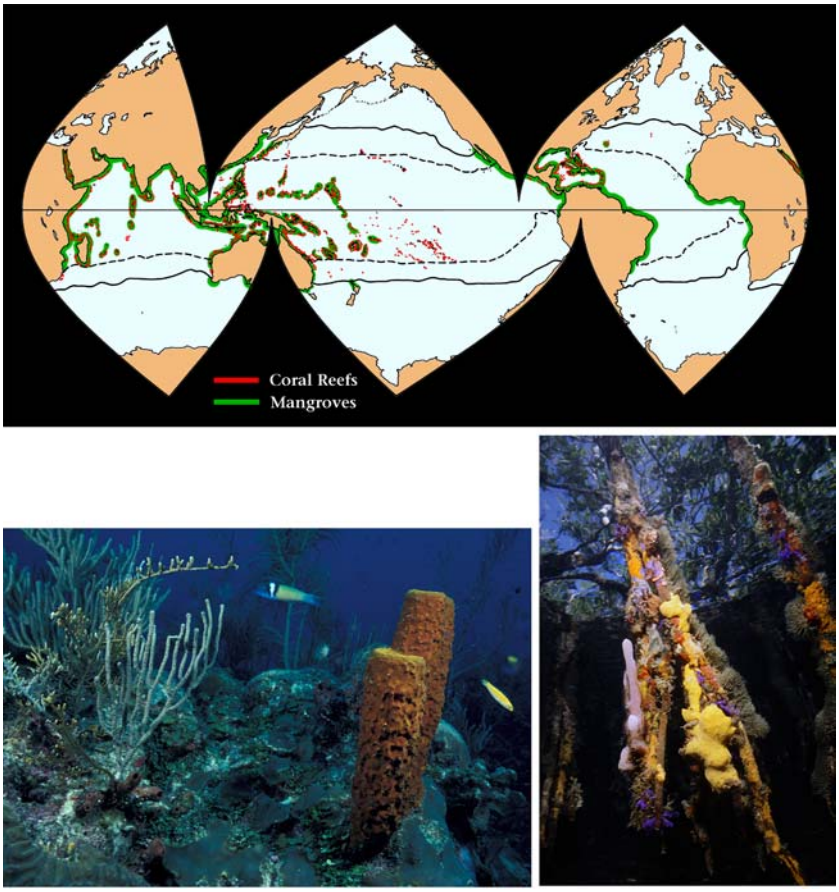

Fig. 2. Distribution of reef and mangrove sponges (top): World map showing distribution of reefs (red) and mangroves (green) in relation to the 23° C isotherm during the warm (solid line) and cool season (dashed line) (based on WELLS 1957); *Aplysina fistularis,* a typical representative of Caribbean reef sponges (bottom left; photo by C. Clark); species of *Biemna* and *Haliclona* are common on stilt roots in Caribbean island mangroves (bottom right; photo by C. Hansen).

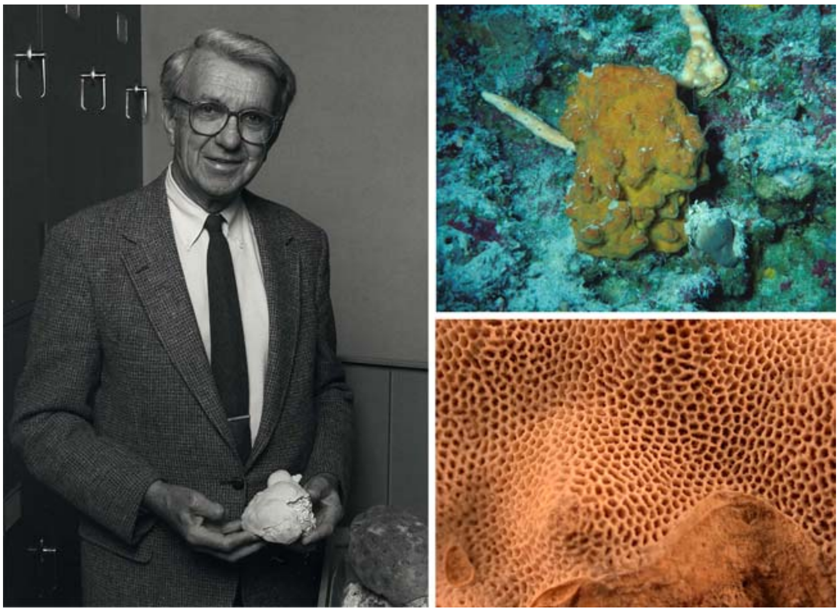

Fig. 3. Several modern sclerosponges, discovered by scuba divers, were recognized as “living fossils” by eminent American spongiologist Willard D. Hartman (left; with specimen of *Ceratoporella* sp.) (photo by B. Sacco, Yale University; 1992); *Willardia caicosensis* Willenz & Pomponi, named after Hartman, was photographed (top right) and sampled by the research submersible Johnson Sea Link (photo by Harbor Branch Oceanographic Institution, Biomedical Marine Research); dried and cleaned specimen of *Acanthochaetetes wellsi* Hartman & Goreau (bottom right), shows the structure of the calcareous skeleton base.

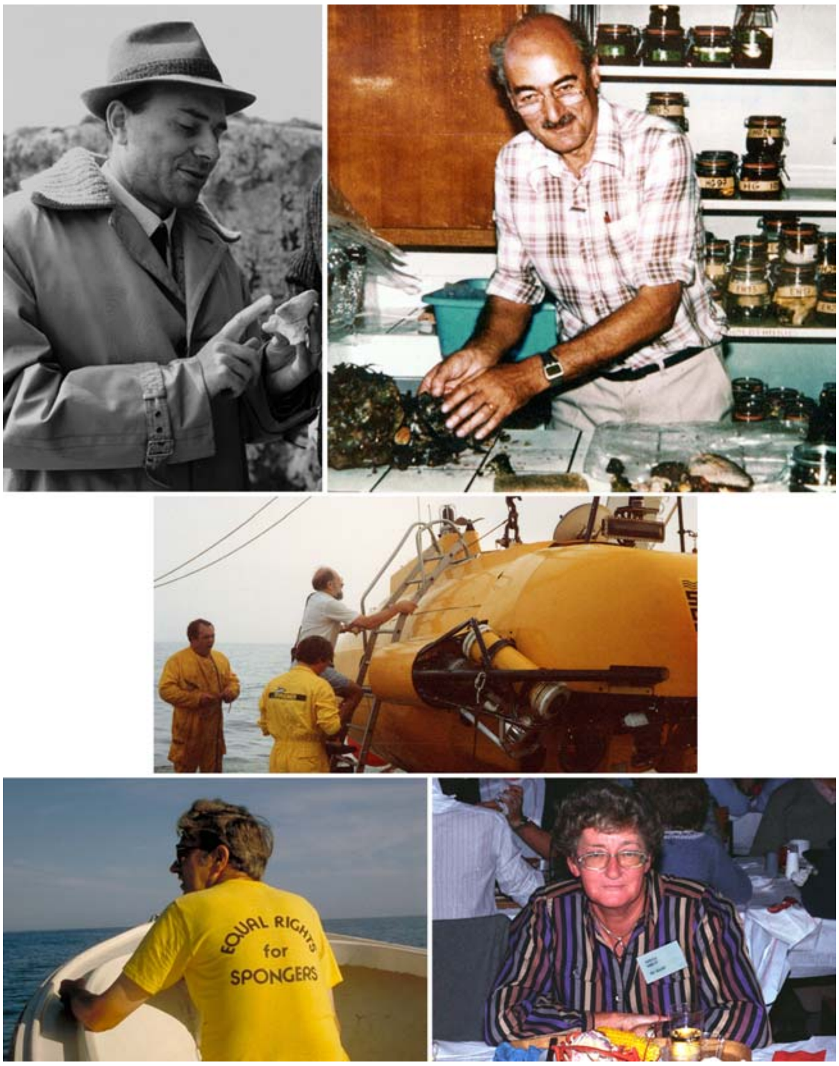

Fig. 4. Pioneers in the study of sponge biodiversiy on coral reefs (top left to bottom right): Michele Sarà, University of Genova, Italy (Capo di Sorrento, 1964); Claude Lévi, National Museum, Paris, France (Nouméa, New Caledonia, ca. 1978; photo by B. Thomassin); Jean Vacelet, University of Marseille, France (climbing on board of research submersible Cyana, 1991); Willard D. Hartman, Yale University, New Haven, Conn., U.S.A. (Jamaica, 1980; photo by P. Willenz); Patricia R. Bergquist, University of Auckland, New Zealand (Woods Hole, 1985).

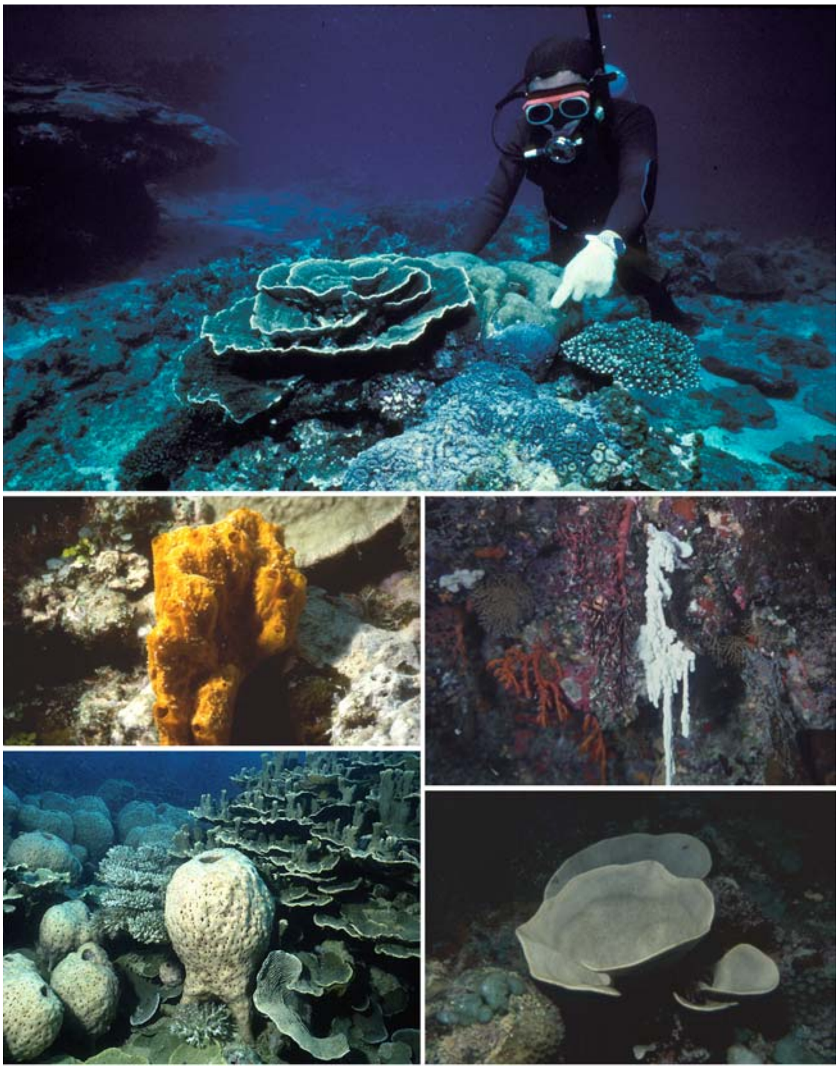

Fig. 5. Sponges on Pacific reefs (clockwise from top): Ryukyu Archipelago, Japan), the diver points to an encrusting, coral-threatening hadromerid, *Terpios hoshintota* (photo by Y. Itagaki); cave habitat on the Great Barrier Reef, with "dripping" calcareous sponge *(Leucetta* sp.) (photo by J. Hooper); lamellate phototropic sponge *(Phyllospongia lamellosa),* Vanuatu (photo by J. Hooper); *Melophlus sarasinorum* on reef off Guam (photo by V. Paul); *Stylissa massa* from Palau which contains palauamide, a potent metabolite with possible anti-cancer properties (photo by G. Paulay).

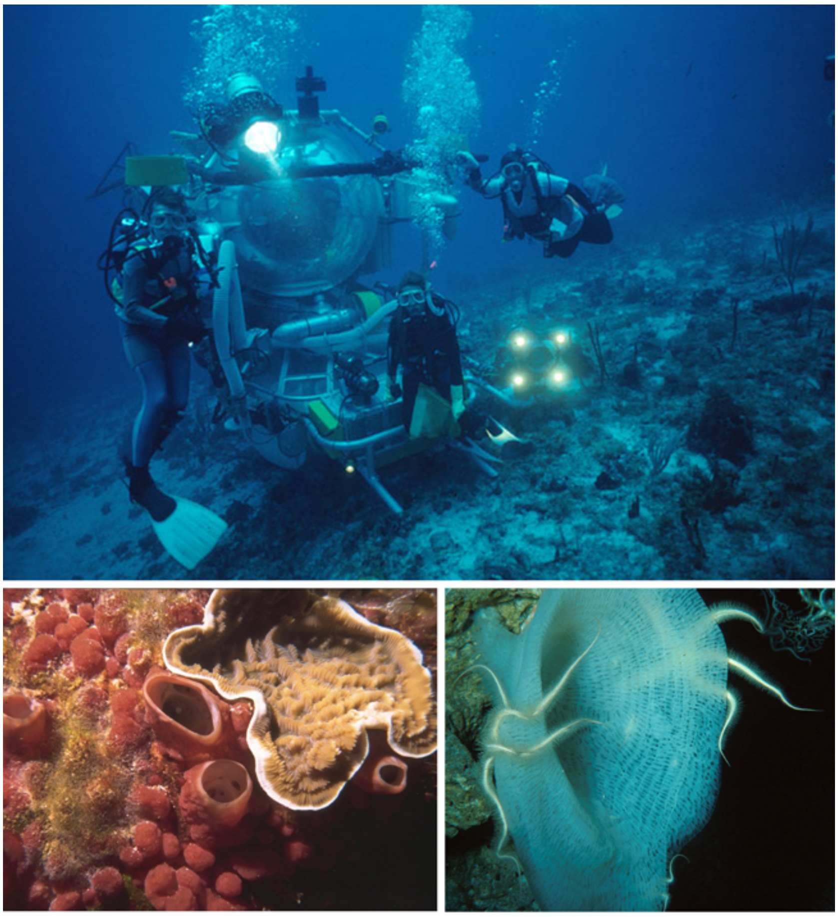

Fig. 6. Exploration of deep fore-reef sponges in the Caribbean (clockwise from top): The research submersible Johnson Sea Link with support divers in 1997 (photo by J. Reed, Harbor Branch Oceanographic Institution); a member of Hexactinellida associated with ophiuroid echinoderms (photo by Harbor Branch Oceanographic Institution, Biomedical Marine Research); a species of *Polymastia* sharing space with an *Agaricia* coral (photo by H. Lehnert).

Fig. 7. Belize barrier reef from the air looking northwest (top): Carrie Bow Cay (foreground), South Water Cay and the continuous barrier reef, and Twin Cays mangrove (background; photo by J. Smith); Carrie Bow Cay Marine Field Station (center; photo by C. Hansen); fore-reef slope community with spiny lobster (bottom; sponges are red branching *Amphimedon compressa* next to purplish chimneys of *Aiolochroia crassa* and yellowish tubes of *Aplysina fistularis*) (photo by C. Clark).

Fig. 8. Biotopes and recent sponge research, Carrie Bow Cay Marine Field Station (clockwise from top left): Shallow patch reef off Carrie Bow Cay dominated by large head corals (genera *Montastraea* and *Diploria)* (photo by C. Clark); a rich red-mangrove community anchored on a thriving coral patch reef (mainly *Agaricia* spp.) in the Pelican Cays (photo by C. Hansen); Renata Manconi and Maurizio Pansini, members of the 2001 sponge–sediment interaction team (University of Genova) (photos by T. Pazella); mangrove-sponge workshop (1997) participants (left to right) Cristina Diaz, Kate Smith, Janie Wulff, Belinda Alvarez, Klaus Rützler, Sven Zea, and Rob van Soest (photo by L. Manes).

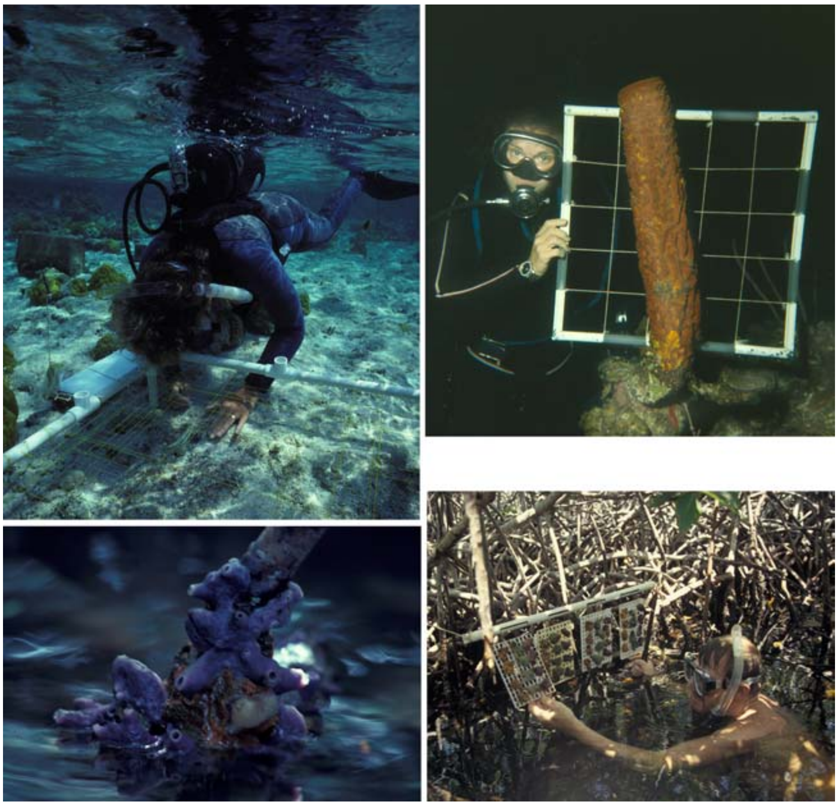

Fig. 9. Assessment of sponge populations and stress of exposure to air (clockwise from top left): The frame-counting method is relatively fast and suitable for encrusting species (photo by C. Clark) but requires added parameters for massive, three-dimensional growth forms such as this tubular *Aplysina fistularis* from the Belize barrier reef; exposed experimental frames with sponge explants attached for determining desiccation resistance of different species (photo by M. Ryan); Caribbean mangrove sponge *(Haliclona tubifera)* on a *Rhizophora mangle* stilt root becomes uncovered at low tide.

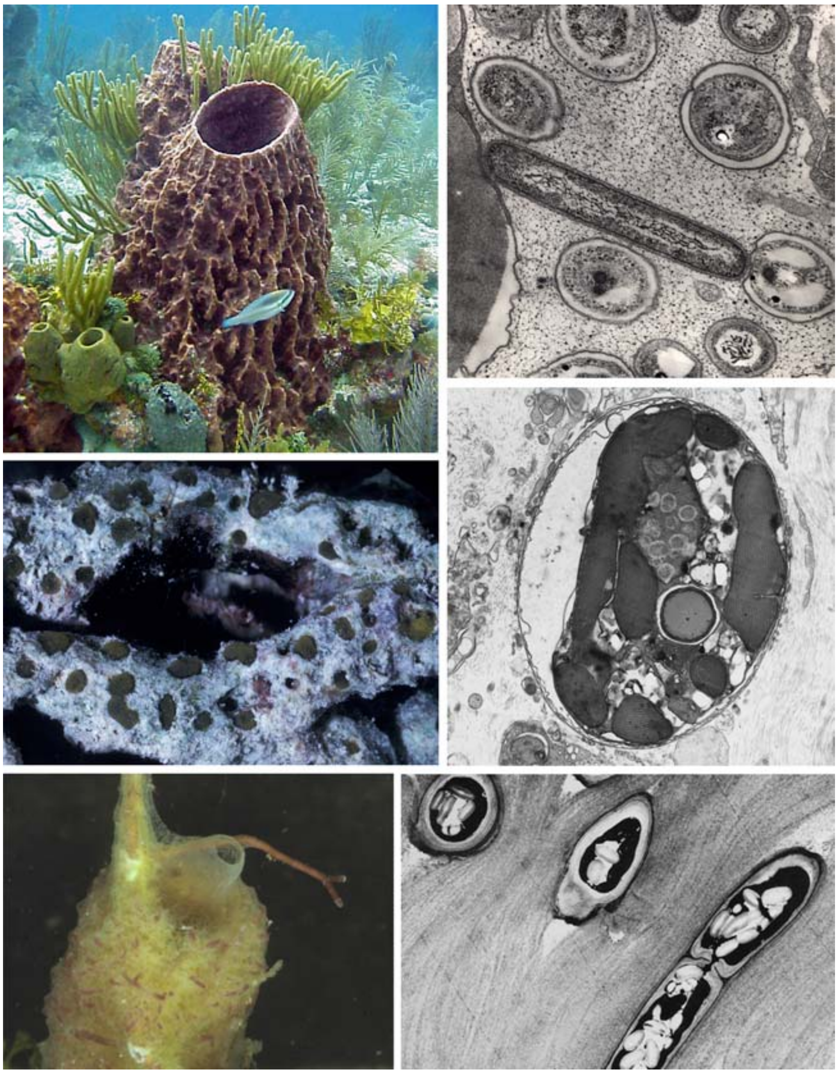

Fig. 10. Symbiosis with unicellular cyanobacteria and dinophyceans (top left to bottom right): Large reef sponge *Xestospongia muta* (photo by J. Sanchez); *Xestospongia* bacterial symbionts (13000x mag.); *Cliona caribbaea* in coral rubble; *Cliona* zooxanthella *(Gymnodinium;* 6200x mag.); *Dysidea janiae* incorporating branches of calcified red algae (genus *Jania);* section of red alga *Acrochaetium* (1500x mag.) embedded in spongin fiber of *Mycale laxissima* (from RÜTZLER, 1990).

Fig. 11. Ecophysiological experiments measuring productivity (clockwise from top left): Recording photosynthesis in situ on the Great Barrier Reef (photo by J. Vacelet); incubation of sponge fragments on the Belize reef flat to measure oxygen production at maximum radiation; cyanobacterio-sponge *Ulosa funicularis* on a patch reef; new growth of *Ulosa in situ* after shading by polarizing foil to determine changes in pigment composition.

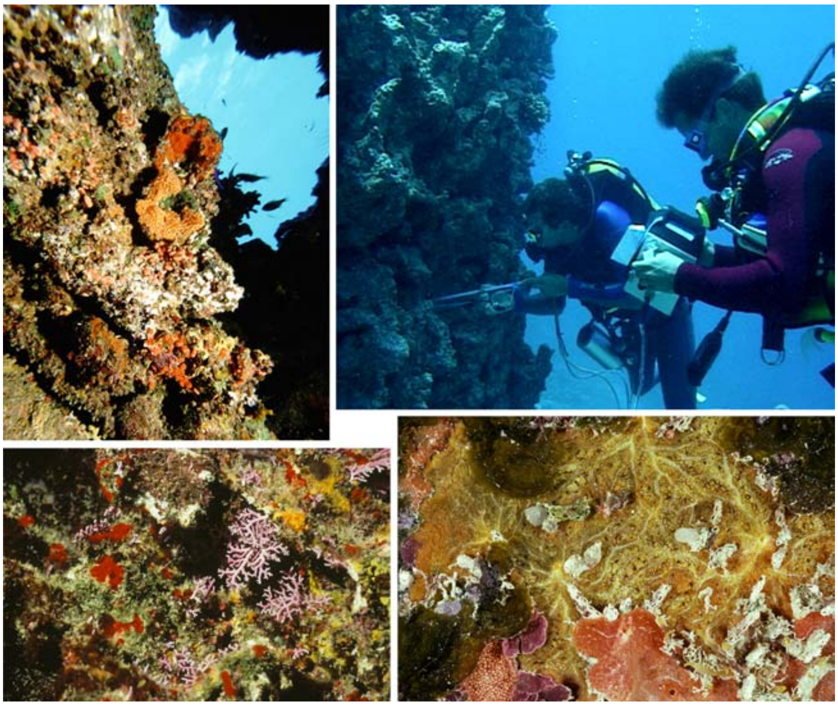

Fig. 12. Cryptic reef habitats dominated by sponges (clockwise from top left): Red Sea cave habitat (Aqaba, 4 m) as seen through the endoscopic CaveCam (photo by M. Wunsch); the CaveCam in use (photo by I. Kötter); lower surface of platy coral rubble covered by competing encrusting sponges (*Clathria*); cave wall community, Belize fore reef (10 m), with diverse organisms including red encrusting sponges *(Monanchora),* crustose corallines, and stylasterid coral.

Fig. 13. Storms and sediments (top; center left to bottom right): Carrie Bow Cay on the Belize barrier reef during hurricane Iris (October 2002) (photo by D. Hurlburt); calcium carbonate chips produced by clionaid bioerosion (120x mag.); etched siliceous sponge spicules from reef sediments (60x mag.) (from RÜTZLER & MACINTYRE, 1978); Spongin fiber (*Dysidea* sp.) cored by calcareous particles (60x mag.); cut through small specimen of *Spheciospongia vesparium* from the Belize lagoon showing incorporated sediments; *Cliona varians* forma *incrustans* from high energy reef.

Fig. 14. Reproductive properties (clockwise from top left): Stationary self-propelled plankton sampler for capturing benthic larvae on a reef (from Rützler et al., 1980); larvae, *Dysidea etheria; Agelas* sp. covered by egg mass (photo by D. Fenner); asexual buds covering specimen of *Cinachyrella apion* (from Rützler & Smith, 1992); rapidly reproducing, opportunistic (r-strategist) *Desmapsamma anchorata* (branching pink) overgrowing tubular *Callyspongia vaginalis* (photo by C. Hansen).

Fig. 15. Competition for space (clockwise from top left): Crustose *Cliona caribbaea* advancing over brain coral *(Diploria)* (nails mark growth edge 4 months earlier) (from RÜTZLER, 2002); *Mycale laevis* covering dead lower surfaces at growth edge of *Montastraea* coral (photo by D. Fenner); competing *Tedania ignis* and *Biemna caribea* on red-mangrove stilt root; *Chondrilla* cf. *nucula* overgrowing coral stressed by hurricane-generated water warming.

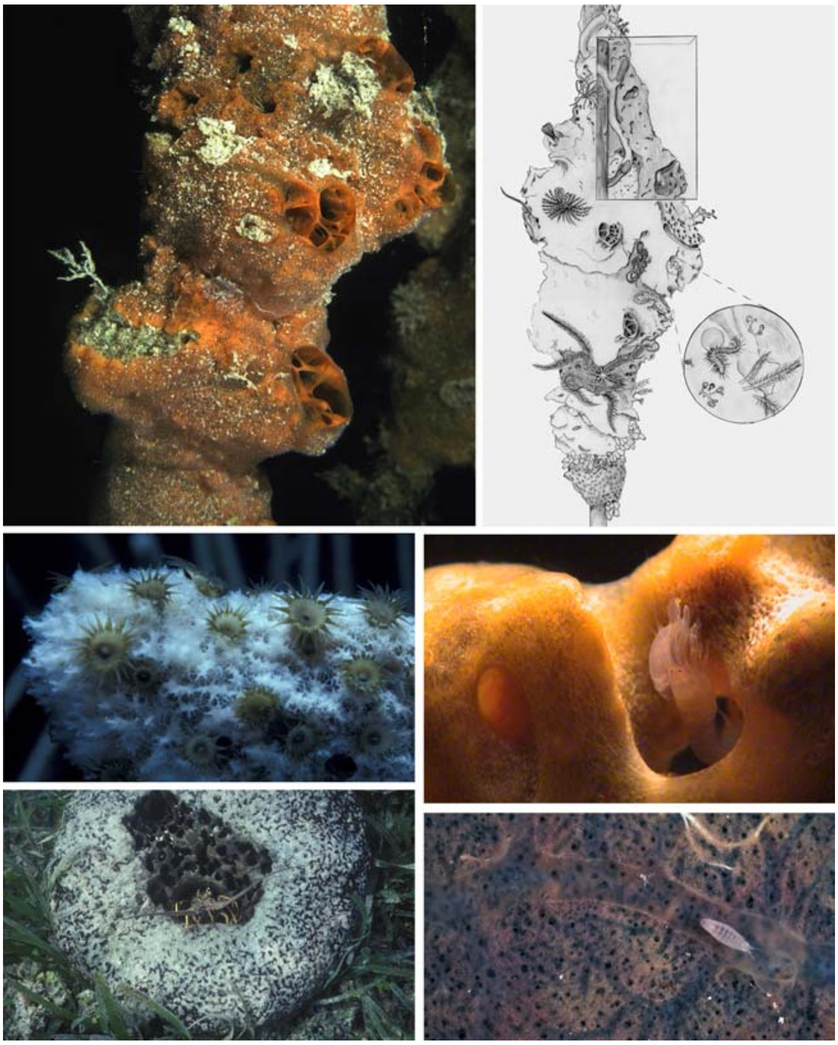

Fig. 16. Sponge associations (clockwise from top left): The toxic (to humans) mangrove sponge *Tedania ignis* harbors a great variety of endobionts; examples of *Tedania* associates (drawing by M. K. Ryan); eusocial *Synalpheus regalis* male guarding one of the oscula of *Lissodendoryx* sp. (photo by J.E. Duffy); amphipod crustacean traveling through an exhalant canal of encrusting *Mycale microsigmatosa* (8x mag.); small spiny lobster inhabiting a loggerhead sponge *(Spheciospongia vesparium),* which has a large interior cavity system and harbors a reef-like diversity of invertebrates and fishes; epizoic *Parazoanthus parasiticus* on *Niphates erecta.*

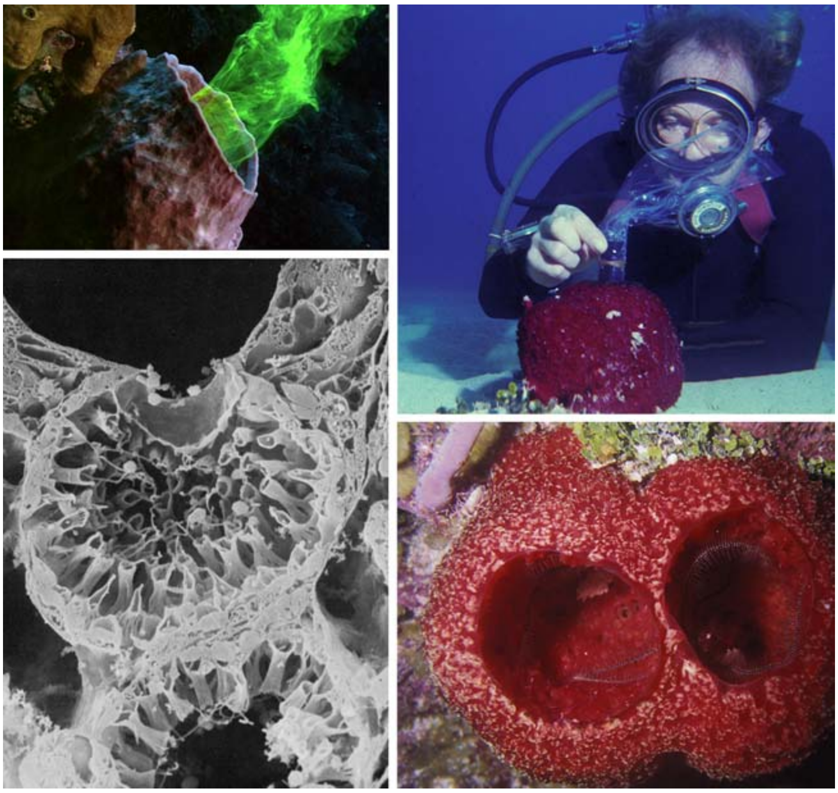

Fig. 17. Sponge nutrition by filter feeding (clockwise from top left): Exhalant water flow in a *Xestospongia* sp. made visible by injecting fluorescein dye into inhalant canals (photo by Sea Studios); Henry M. Reiswig (ca. 1969) sampling exhalant water from *Mycale laxissima* on a Jamaica reef; *M. laxissima,* looking into the double atrium (photo by D. Fenner); typical choanocyte chamber revealed by freeze fracture (1000x mag.) (from DE VOS *et al.,* 1991).

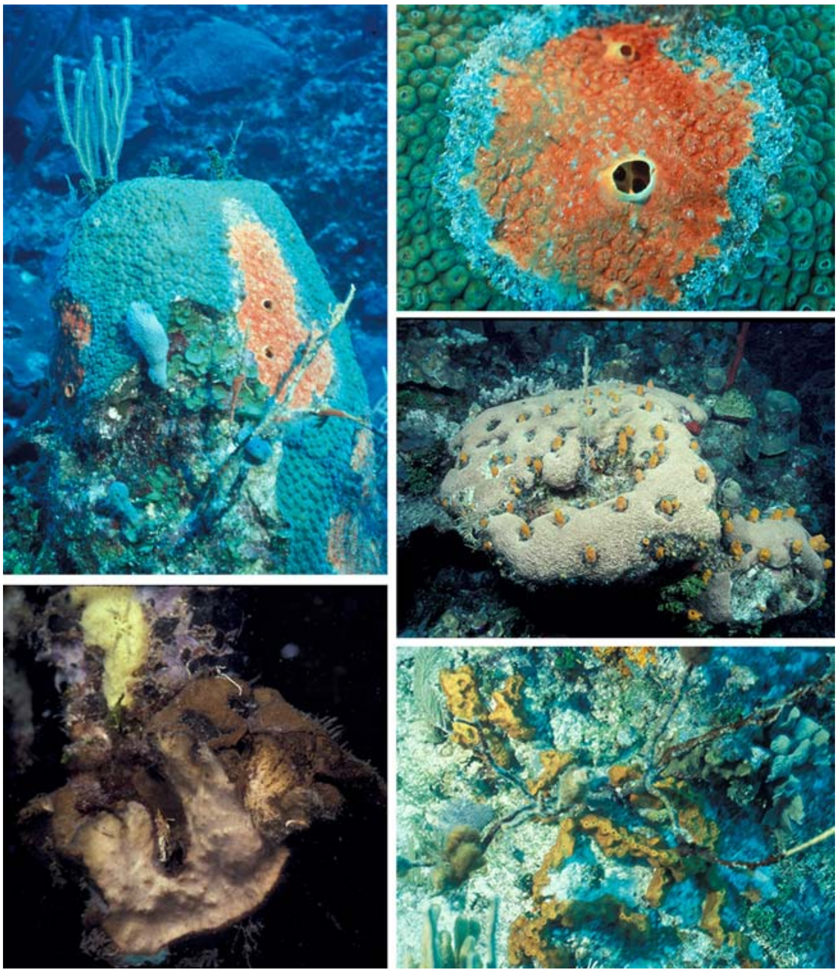

Fig. 18. Bioerosion, cementation, and disease (clockwise from top left): Massive *Montastraea* coral on Belize barrier reef invaded by *Cliona* (photo by C. Hansen); close-up of aggressively bioeroding *C. delitrix* on *Montastraea* coral (photo by L. Penland); head coral, *Siderastrea,* riddled by *Siphonodictyon* (= *Aka*) *coralliphagum* (photo by C. Clark); *Ectyoplasia ferox* cementing hurricane-generated coral rubble (photo by L. Penland); mangrove sponge *Geodia papyracea* succumbing to disease caused by its own symbiotic cyanobacteria (from Rützler, 1988).

Fig. 19. Secondary metabolites and predation (clockwise from top left): In memoriam D. John Faulkner, distinguished biochemist and ever-sarcastic friend teaching us the importance of sponge secondary metabolites (photo by J. Pawlik); sponge-feeding snail *Cyphoma* on deep-reef *Agelas* (photo by H. Lehnert); starfish (*Oreaster*); angel fish (*Holacanthus*) (photo C. Hansen); and hawksbill turtle (*Eretmochelys*), with remoras attached (photo by C. Clark).