SPONGE DIVING - PROFESSIONAL BUT NOT FOR PROFIT

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Sponges and diving are connected by an old tradition, the quest for bath sponges. However, thousands more sponges without elastic-absorbent skeletons were named by early zoologists who did not have the luxury of live observation and provided inadequate descriptions based on dried or pickled specimens. I started to dive in the Mediterranean during the early 1950s because I enjoyed the sport and the technological challenge. Soon I got interested in submarine caves and their colorful occupants, mainly sponges. Studying the animals alive and reading their poor descriptions in the literature convinced me that good spongiology had to start with observation and experimentation under water, and I joined a handful of European scientists with similar interests. Today, thanks to many advances in diving technology, sponge workers are studying many aspects of sponge biology in situ, including systematics, morphology, reproduction, ecology, and physiology. My initial interest in underwater science and sponge biology has proliferated into a multi-disciplinary, long-term research program on Caribbean coral-reef ecosystems (CCRE), based at a field station on the barrier reef of Belize.

INTRODUCTION

People have searched for ways to explore the depths of oceans and lakes at least since antiquity. Bath sponges were among the many treasures divers sought for at least 22 centuries but not more than ten species worldwide qualify for this purpose. This is a small number if one considers that the phylum Porifera is estimated to contain near 10,000 species. About half of these species are fairly well known to science because they are preserved in museum collections. However, the principal problem in spongiology is that most early workers were museum researchers who described perhaps 90% of the known species but had not collected the specimens themselves and may not even have seen a sponge alive, certainly not in its habitat. Instead, they relied on material from dredge hauls and other samples brought back preserved from the classical expeditions that went to far and exotic places but were unable to obtain detailed information on most marine organisms in their natural habitats. Everyone who has seen sponges alive and tried to keep them dried or preserved in alcohol knows about the substantial changes that occur by shrinkage, fragmentation, and loss of surface structure and color.

The use of bath sponges is documented as early as the Minoan, the bronze-age civilization of the Mediterranean island of Crete almost 4,000 years ago. Diving as a method for gathering these firmly attached organisms is probably just as old because the coasts around the Greek islands are steep, and sponges are rarely found within the range of hand-held rakes or hooks. Poems from the days of Greek antiquity describe the dangerous and unprofitable occupation of the sponge diver, mention special diets, prayers, and breathing exercises, weights and tethers for faster sinking and returning, sickles for cutting sponges, dangers from sharks and octopuses, even the use of oil carried in the mouth to smooth waves for better visibility (Arndt, 1937). A well-preserved bath sponge was recently discovered in a burial chamber (Macedonia, Greece, 4th Century B.C.) and was most probably occupied by King Philip II, father of Alexander the Great (M. Mertzani, pers. comm.). Scanning electron micrographs of the sponge fibers by Ms. Mertzani revealed blood platelets, most likely from the deadly wound of the King who was stabbed by one of his body guards during the wedding ceremony of his daughter Cleopatra.

Despite this promising history, serious scientific aspects of sponges ("zoophytes") were not pursued until Linné's monographic series, starting in 1735 (it took another century to establish the animal nature of sponges); and sponge diving as a research technique is less than 50 years old.

NATURE AND USAGE OF SPONGES

The familiar "bath" or "commercial" sponges mentioned above belong to about 15 taxa (species and ecological forms), but fewer than ten are valid species. In contrast, 5,000-6,000 species of sponges are known and another 4,000-5,000 species are estimated to exist worldwide but are not yet discovered or described.

Sponges (phylum Porifera) are defined as aquatic, filter-feeding metazoans with characteristic flagellated collar cells (choanocytes) lining chambers (choanocyte chambers) that propel water through incurrent and excurrent aquiferous systems (Rützler, 1978). Water enters the body through numerous small pores (ostia) and exits through one or a few larger openings (oscula). Food (mainly bacteria), oxygen, and other life-supporting supplies are taken up by choanocytes and other specialized cells from the mesohyle (ground substance; there are no true tissues), waste products are secreted and expelled in a similar fashion. For details of anatomy and terminology consult DeVos *et al.* (1990) and Boury-Esnault and Rützler (in press). Sponges are encrusting or massive, mostly colorful and of a variety of shapes (*e.g.*, cushion, fan, tree, cup, or tube). The body is usually supported by a skeleton of spongin (a collagen-like protein) with or without the addition of mineral components (calcium carbonate, silicic acid). A pure spongin network occurs in the familiar bath sponges (order Dictyoceratida) and is known for its remarkable elasticity and water-holding capacity. Mineral skeletons can be solid (*e.g.*, the limestone base of sclerosponges) but are more commonly secreted as spicules of fanciful shapes that have great importance in the classification of most taxa.

Sponges are sessile except for sexually produced, free-swimming larvae and drifting fragments or asexually generated, reproduction bodies (gemmules). Representatives of the phylum are widely distributed, including freshwater and all ocean depths, but are particularly diverse and abundant in shallow-water ecosystems with solid substrates, such as rocky littoral, coral reefs, and some mangroves.

Sponges of all kinds have been put to good use in many cultures through time. Besides the obvious application of bath sponges for cleaning, blotting, and soaking, they served as stuffing for cushions, as artist's tool for producing patterns on walls and pottery, for polishing, as breast implant and prophylactic for women, as fertilizing aid in cattle breeding, and, their ash dissolved in wine as cure for goiter. Various marine sponges served as agricultural fertilizer, some species were used by fishermen as food or food additive, as scouring pads for their boats and to keep glass face plates of dive helmets from fogging (*Axinella polycapella*, de Laubenfels, 1953), and as tooth brushes. Siliceous sponges were often used as cement, nicely shaped hexactinellids ("glass"sponges) or fossils as jewelry in some cultures. Many more examples were compiled by Arndt (1937). Despite this popularity, most research of the past did not deal much with practical applications or learning about the biology of the group except for chemical analysis of the raw material and experiments with bath-sponge culturing. Part of the difficulty was that most sponges were not accessible for direct observation and only a few survived in aquaria for extended periods of time. The great diversity of marine sponges was not really known until the time of the world-wide oceanographic expeditions and the founding of the great marine stations in the second half of the 19th Century.

Today, bath sponges are gaining renewed popularity in hardware and fashionable bath stores but there are few other direct uses. On the other hand, recent research on natural-product chemistry has shown hundreds of sponge species to be a precious natural resource for they contain substances useful in pharmacology (*e.g.*, Garson, 1994).

HISTORY OF SPONGE DIVING

The first diving for sponges was certainly done by commercial collectors. It is understandable that skin diving for this purpose started in the eastern Mediterranean (Fig. 1) because the rugged rock bottoms of the Greek islands did not allow fishing sponges by harpoon or "gangava" (a heavy drag net), as it was, and in part still is, practiced on the flat, shallow sediment bottoms off Tunisia, Libya, and in the Gulf of Mexico. Travelers from northern Europe report already around 1860 that wealthy citizens of Ikaría (Sporades islands, Aegean Sea) held sponge-diving competitions to pick the best eligible men as husbands for their daughters (Arndt, 1937). Depths of 10-40 m (75 m maximum) were routinely reached by breath-hold diving and dive times of up to 5 min are on record. "Scaphanders" (Fig. 2), dive suits with heavy metal helmets, lead boots, and hose connected to a ship-board air pump, were imported from India by a Greek sponge diver in 1860 and made their way to the West Indies in 1905. Sponge diving in the West Indies and the Gulf of Mexico was mainly conducted by Greek immigrants. These "machines" allowed work times of 2 h at 20 m, 1 h at 40 m, but caisson disease (the bends) were common among sponge divers who often died or ended up crippled, particularly during the first decades of using the new tool. In the early 1920s, many Mediterranean sponge fishermen replaced the scaphanders with a lighter and cheaper type, the Fernez apparatus (Arndt, 1937), comparable to our familiar hookah. This gear consisted of a rubber bag worn on the back attached with a belt and connected to a pressurized air supply in the boat (Fig. 3). Flexible tubing and a mouth piece allowed breathing from the bag that maintained air at ambient pressure. A mask with lenses replaced the heavy helmet.

Figure 1. Skin divers with sickle, collecting net, weight, and tether line (from Arndt, 1937).

Figure 2. Scaphander or hard-hat diver, Tarpon Springs, Florida (J. Vacelet).

In Florida and the Caribbean, the scaphander remained in use and even today is still displayed as a tourist attraction. Its actual use in these days of scuba is no longer practical and by Florida statute all "deep-sea apparatus" is banned to prevent damage to young sponges by heavily weighted divers stepping on them. In fact, commercial sponge fishery all but disappeared in Florida and the Caribbean during the late 1930s because a disease related to a series of red tides (dinoflagellate blooms) killed most suitable species. Interestingly, at just about this time one of the first modern sponge studies took place in Florida employing at least once a "diving apparatus" for walking the bottom to 10 m (de Laubenfels, 1936). Because the author described sponges of the Dry Tortugas, site of a laboratory run by the Carnegie Institution of Washington, one must assume that this apparatus was the same or a similar diving helmet first employed by A.G. Mayor, Director of the Department of Marine Biology at the Carnegie (Yonge, 1930) and made popular through several writings by Beebe (1926, 1932; Fig. 4). De Laubenfels concluded the brief description of his experience with "comparisons to a 'fairyland' are appropriate." In a subsequent paper, the same author described sponges from Bimini, Bahamas, some of which were collected "by using the diving helmet" (de Laubenfels, 1949).

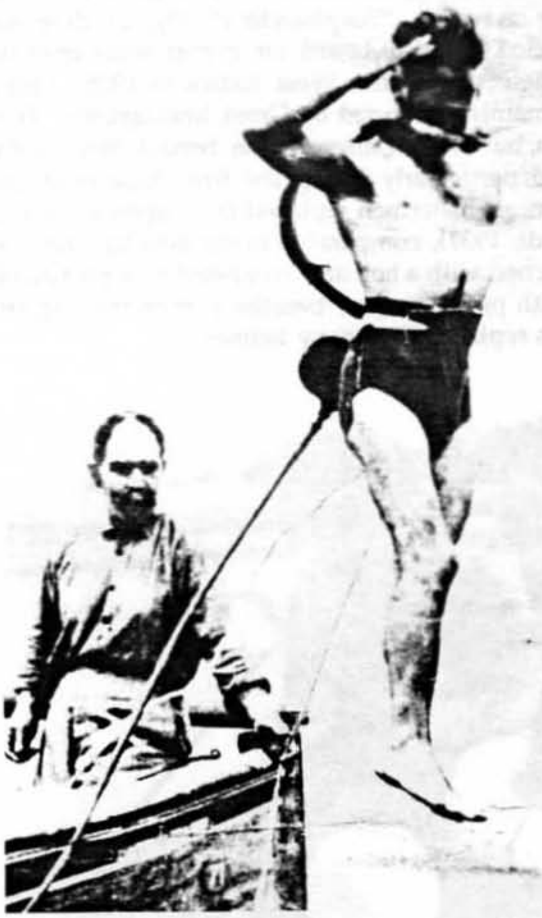

Figure 3. Fernez apparatus (courtesy M. Pansini and R. Pronzato).

Figure 4. Diving helmet (from Beebe, 1926).

DIVING, FROM SPORT TO RESEARCH DISCIPLINE

Like many post-World War II generation marine biologists, I was first attracted by technological challenges of exploring the ocean and only later by the mysteries of the organisms. In 1952, I was 16 years old and growing up in Austria, a tiny central European, land-locked nation. At the time, skiing and swimming were my primary sport interests and my professional ambition after high school was inspired by the Austrian animal behaviorist Konrad Lorenz. But then I acquired books by my fellow countryman H. Hass and by the French L. Boutan, J. Cousteau, and D. Rébikoff, on diving technique, underwater exploration and photography, and I knew my final professional destination. Absolutely no diving equipment was commercially available in Austria at the time and even goggles and fins had to be custom made by one's own design in basement rubber presses. Snorkels had not yet been invented. My first underwater camera housing was an aluminum pressure cooker that sealed well but was quite buoyant. It contained the excellent, now extinct, Robot 24x24 mm survey camera which could advance one entire roll of film with spring-wound motor drive. In these days before o-ring fittings, stuffing boxes were used for more or less leak-proof sealing of turning or sliding controls, such as f-stop, distance, and trigger. Single-shot flash bulbs in ever-corroding sockets were the source of artificial light. A sling shot-like spear gun for hunting food completed the equipment. I also became a (primarily corresponding) member of the First Carinthian Underwater Sports Club in Klagenfurt (capital of Carinthia, a southern province of Austria). This group of enthusiastic and fearless physicians certified me during a weekend dive trip to northern Yugoslavia (the closest sea from Klagenfurt). These people also taught me to build oxygen rebreathers by gluing a rubber bag around a cylindrical, enamel-coated luncheon stew pot (with holes drilled through the bottom) that had a rubber-sealed lid and contained the scrubbing chemicals and filters. Appropriate hoses connected a small oxygen tank (preferably via a pressure-reduction valve) to the rubber bag, and led to the diver's mouth piece and through the scrubber pot back into the bag. Luckily they warned us not to use the contraption below 10 m although experienced divers, they claimed, survived below 20 m.

The first underwater "expeditions" were launched by hitch hiking to Umag, Slovenia, and Trieste, Italy (1952) and to the northwest Italian coast catching ferries to the islands of Elba (1953) and Corsica (1954). Just before entering the University of Vienna, I visited the Zoological Institute there to show off my first underwater pictures and asked what curriculum to take in order to become a marine biologist. I was fortunate to encounter three assistant professors who had recently returned from a pioneering expedition to the Gulf of Naples, the "Austrian Tyrrhenia Expedition," where they used the new skin-diving method in a study of systematics and ecology of littoral organisms. Since I inquired about the many colorful cave sponges shown in my pictures and the Expedition's assigned sponge worker had quit to take a job in applied entomology, I was offered a place on the team after finishing my undergraduate work. My youthful ambitions had found a serious academic framework.

My teacher R. Riedl, University of Vienna, J. Vacelet, University of Marseille, and M. Sarà (then), University of Naples, were the first to recognize the ecological significance of sponges in previously unaccessible Mediterranean submarine cave habitats and, hence, the vital importance of scientific diving in sponge research (Riedl, 1956, 1966, 1967; Vacelet and Lévi, 1958; Laborel & Vacelet, 1959; Vacelet, 1959; Sarà, 1958, 1961). I collaborated by evaluating the data taken by Russ during the Tyrrhenia Expedition (unfortunately without use of the lost sponge collection) and writing the sponge part of the expedition reports (Russ and Rützler, 1959). I continued with my own studies of caves in the Adriatic (Rützler, 1965a,b, 1970) and Tyrrhenian seas (Rützler, 1966).

SCIENTIFIC DIVING AND SPONGE RESEARCH

The now classical early attempts using diving in sponge studies have given rise to a great variety of serious and immensely successful applications to Porifera research, from collecting to long-term *in situ* experimentation. A good indicator for the new trend is the percentage of papers based in some way on the dive technique and presented during past international sponge conferences: London (1968: Fry, 1970), 17 %; Paris (1978: Lévi and Boury-Esnault, 1979), 40 %; Washington/Woods Hole (1985: Rützler, 1990), 51 %; and Amsterdam (1993: van Soest *et al.*, 1994), 71 %. At least 92 % of the papers given during a special sponge symposium of the 8th International Coral Reef Symposium in Panama (1996: J. Wulff, in prep.) used the dive technique, but one should add that the topic of this meeting favored presentations on underwater research. These developments are of course not unique to sponge research but the results of general advances in underwater technology and marine biology. Even the most hardy pioneers will agree that gear development over the past 40 years has made diving much more comfortable and safer and research more efficient and precise. Even the awkward old acronym S.C.U.B.A. has evolved into a familiar noun, scuba. Highlights, for me at least, were inventions such as the snorkel, masks with ground-in correction lenses, easy breathing regulators, buoyancy compensators, precise depth gauges, good quality knives, and advanced, sleek cameras with electronic be custom made by one's own design in basement rubber presses. Snorkels had not yet been invented. My first underwater camera housing was an aluminum pressure cooker that sealed well but was quite buoyant. It contained the excellent, now extinct, Robot 24x24 mm survey camera which could advance one entire roll of film with spring-wound motor drive. In these days before o-ring fittings, stuffing boxes were used for more or less leak-proof sealing of turning or sliding controls, such as f-stop, distance, and trigger. Single-shot flash bulbs in ever-corroding sockets were the source of artificial light. A sling shot-like spear gun for hunting food completed the equipment. I also became a (primarily corresponding) member of the First Carinthian Underwater Sports Club in Klagenfurt (capital of Carinthia, a southern province of Austria). This group of enthusiastic and fearless physicians certified me during a weekend dive trip to northern Yugoslavia (the closest sea from Klagenfurt). These people also taught me to build oxygen rebreathers by gluing a rubber bag around a cylindrical, enamel-coated luncheon stew pot (with holes drilled through the bottom) that had a rubber-sealed lid and contained the scrubbing chemicals and filters. Appropriate hoses connected a small oxygen tank (preferably via a pressure-reduction valve) to the rubber bag, and led to the diver's mouth piece and through the scrubber pot back into the bag. Luckily they warned us not to use the contraption below 10 m although experienced divers, they claimed, survived below 20 m.

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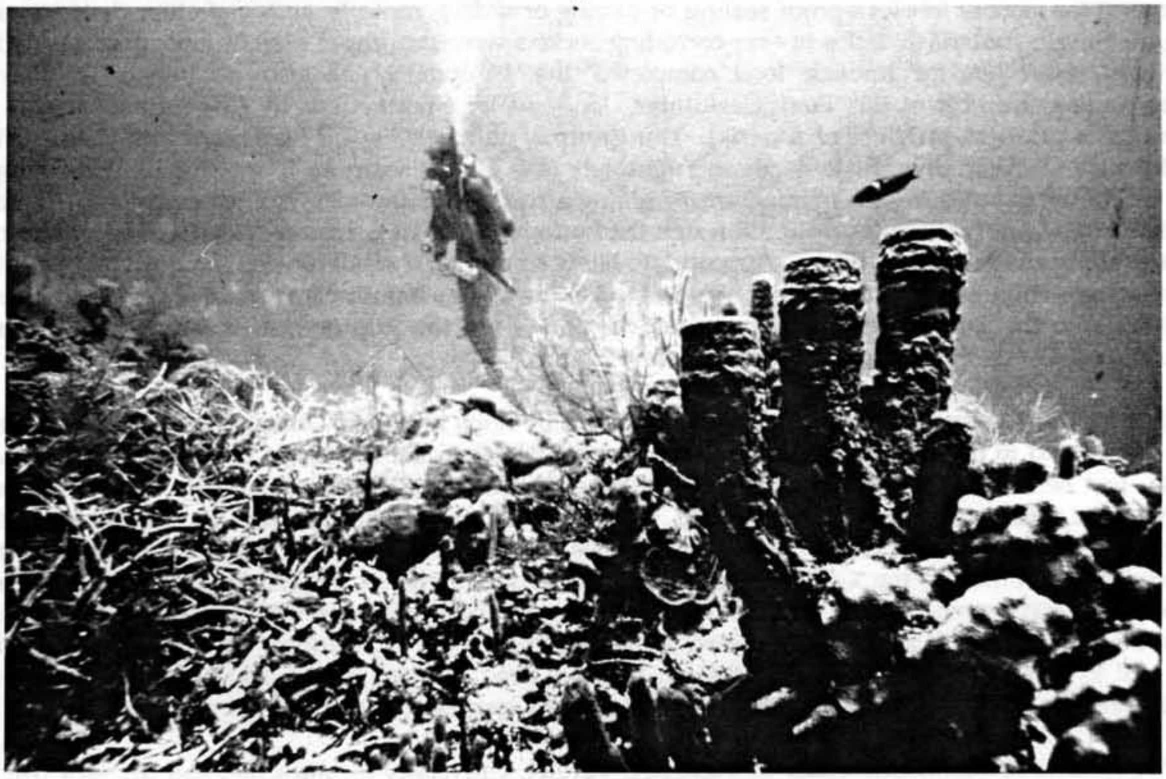

Figure 5. Sponges (*Aplysina fistularis*) and diver, fore-reef, 8 m, Carrie Bow Cay, Belize.

Because hundreds of entries would be eligible, the following summary is in telegraphic style, is selective, and should be considered incomplete. Skin and scuba diving have become so much of a routine tool that many recent authors neglect to mention their use, particularly in observing or collecting, unless the paper is based on a variety of techniques. Representation of diverse topics was given priority.

COLLECTING AND SURVEYING

Mediterranean submarine caves (Fig. 6) were the focus of early research by Vacelet, Sarà, and Rützler, as outlined above. One of the most remarkable discoveries in the darkest tunnels there was a "living fossil" sponge, the calcareous pharetronid (*Petrobiona massiliana*) Vacelet and Lévi (1958); Sarà (1963); Rützler (1966; Fig. 7), soon to be followed by similar discoveries, in tropical reef and Mediterranean caves, of living representatives of groups hitherto thought extinct (sclerosponges); for instance, Hartman and Goreau (1970, Jamaica, West Indies; 1976, Pacific); Hartman (1979, a stromatoporoid, Bahamas); Vacelet (1979, a sphinctozoan from the Indo-Pacific); and, Vacelet and Uriz (1991, a sclerosponge from the Balearic Islands, Spain). More studies in caves and other shaded areas (overhangs, lower surfaces of rock) were done by Vacelet and Vasseur (1965, Madagascar), Macintyre *et al*. (1982, Belize; Fig. 20), Meesters *et al*. (1991, Netherland Antilles), Gischler and Ginsburg (1996, Belize), Pansini and Pronzato (1982, Italy), Biblioni *et al*. (1989, Balearic Islands), and the most recent and exciting one by Vacelet *et al*. (1994, France). The latter study deals with a unique cave near Marseille (Fig. 6) that is sloping down instead of up (as most karst caves in the area) and contains cold water (ca. 14°C) year-round. At least two species of deep-sea sponges (Fig. 8) survive here in only 20 m water depth and allow *in situ* studies of their biology.

Figure 6. N. Boury-Esnault collecting in cold water cave near Marseille, 16 m (J.G. Harmelin).

Figure 7. *Petrobiona*, first "living fossil" calcified sponge (J. Vacelet).

Figure 8. Carnivorous *Asbestopluma* (J. Vacelet).

Many more environments that are difficult to sample (or types of sponges, such as excavating clionids) have been surveyed by the new technology, primarily by scuba and, below scuba's reach, by research submersibles. The results were valuable collections for systematic study, chemical extractions for biomedical research, and data on the distributional ecology of sponges. Some sponges (sclerosponges, hexactinellids) are particularly difficult to preserve and process for study by electron microscopy and have to be fixed *in situ*. Examples from Mediterranean and Atlantic hard bottoms are Vacelet (1959), Laborel *et al.* (1961, "soucoupe" *Cousteau*, France); Borojevic and Boury-Esnault (1987, submersible *Thalassa*, Bay of Biscay, France); Voultsiadu-Koukoura (1987, Greece); Witman and Sebens (1990, submersibles *Johnson-Sea-Link, Mermaid II*, Gulf of Maine, USA); Messing *et al.* (1990, submersible *Alvin*, Florida); Diaz *et al.* (1991, 1993); Pomponi *et al.* (1991); Reed and Pomponi (1996, submersible *Johnson-Sea-Link*, central-western Atlantic, Bahamas; Figs. 9, 10); Uriz *et al.* (1992); Biblioni *et al.* (1993, Balearic Islands, Spain); Bavastrello *et al.* (1993, Italy); and, Muricy *et al.* (1993, Brazil).

Similar studies on reefs were by Rützler (1964, Indonesia; 1972, Madagascar; 1974, Bermuda); Lang *et al.* (1975, *Nekton* submersible, Belize); Wiedenmayer (1977, Bahamas); Rützler and Macintyre (1982, Belize; Figs. 18-21); Zea (1987, Colombia); Alcolado (1990, Cuba); Alvarez *et al.* (1990, Venezuela); Schmahl (1990, Florida); van Soest (1990, Indonesia); Zea (1996, southwestern Caribbean). Examples for special tissue fixations *in situ* are given by Reiswig (1979, hexactinellid, Long Island, British Colombia); Gallissian and Vacelet (1990, calcified sponge *Petrobiona*, cave near Marseille, France); Boury-Esnault and Vacelet (1994, hexactinellid, cave near Marseille, France); Hartman and Willenz (1990); Willenz and Hartman (1994, sclerosponges, reef tunnel, Jamaica, West Indies).

Figure 9. Hexactinellid *in situ*. (9, 10, Harbor Branch Oceanographic Institution; courtesy S. Pomponi and J. Reed).

Figure 10. Submersible *Johnson-Sea-Link* with lock-out diver.

QUANTITATIVE ECOLOGY AND RESPONSES TO THE ENVIRONMENT

These studies require extended periods under water, counts and measurements using calibrated lines or frames (Fig. 19), standardized photographic documentation, and *in situ* experiments. Observations on effects of pollution and other stresses are included here. Quantitative assessments and analysis of environmental parameters of sponges were made by Sarà (1958, 1961); Russ and Rützler (1959); Rützler (1965a, b); Vacelet (1959); Wilkinson and Vacelet (1979); Pansini and Pronzato (1982); Biblioni *et al.* (1989, Mediterranean caves); Rützler (1972, Madagascar reefs); Dayton (1979, 1989, hard bottoms, Antarctica); Pansini and Pronzato (1985, Mediterranean seagrass meadows); Alvarez *et al.* (1990); Alcolado (1990); Diaz *et al.* (1990); Zea (1993a, Caribbean reefs); and, Battershill and Bergquist (1990, rock bottoms, New Zealand). Modification of growth form of *Halichondria* in response to currents was studied by Barthel (1991, Baltic Sea) and hurricane impact by Wulff (1995a, Panama). Effects of pollution and other stresses were determined by Verdenal *et al.* (1990, Mediterranean); Zea (1994, Colombia); Rützler (1995, Belize), Carballo *et al.* (1996, southern Spain); Holmes (1996, Barbados); and, Steveley and Sweat (1996, Florida).

COMMUNITY PARAMETERS

This section includes papers on seasonal changes, space competition, recruitment, reproduction, and predation. Changes of individuals or populations are usually monitored by periodic measurements or by photography of marked specimens, particularly if monitored over long periods of time or when presence of a diver might be disturbing: Rützler (1965b, population changes with substrate mobility, Adriatic); Randall and Hartman (1968, predation by fishes, Caribbean); Rützler (1970, space competition, epizoism, Adriatic); Reiswig (1976, timing of gamete release, Caribbean); Dayton (1979, population dynamics, Antarctica); Ayling (1980, 1983, recruitment to settling plates and space competition, New Zealand); Dayton (1989, interdecadal population changes due to anchor ice formation, Antarctica); Pansini and Pronzato (1981, test panel study, Mediterranean); Suchanek *et al.* (1983, space competition on deep open-reef habitats, from *Hydrolab* habitat, U.S. Virgin Islands); Wulff (1985, 1991, asexual reproduction and dispersal through fragments, Panama); Pansini and Pronzato (1990, community dynamics, Mediterranean); Schubauer *et al.* (1990, population changes in 5 species, Jamaica); Vicente (1990, changes in *Chondrilla*, Puerto Rico); Wulff (1990, changes in shape and size of branching sponges, Panama); Gaino *et al.* (1991, changes in calcareous sponge, Italy); Rützler and Muzik (1993, coral-killing *Terpios*, Pacific); Zea (1993b, recruitment to settling plates, Colombia); Fromont (1994, reproductive biology, Australia); Wulff (1994, predation by fishes, Panama); M. Lesser (1995, pers. comm., sponge-growth dependence on habitat depth, by saturation diving from *Aquarius* habitat Florida); Aerts (1996, space competition on stressed reef, Colombia); Leys and Lauzon (1996, growth and seasonal regression of hexactinellid, Vancouver, British Colombia); Rützler and Feller (1996, mangrove environment, Belize; Figs. 22-24); Wilkinson and Thomson (1996, success of asexual reproduction by fragmentation, Australia).

OBSERVATION AND MEASUREMENT OF PROCESSES

This section includes outputs to the environment, such as ecological and ecophysiological studies of filter feeding, production, regeneration, bioerosion, metabolism, and energetics. Reiswig (1971, 1973, 1974, 1990) pioneered studies on *in situ* pumping, particle feeding, growth, and respiration (reef, Jamaica; Figs 13, 16; Senanus Island, British Colombia); Gerrodette and Flechsig (1979), during a *Hydrolab* saturation dive, conducted experiments on the effects of sediments on pumping rates (reef, Bahamas); G. Silver (*fide* Mackie, 1979) monitored pumping by two species of hexactinellids *in situ* (Vancouver Island, British Colombia); Lewis (1982) compared *in situ* pumping rates and predation of sponges with and without epizoic zoanthids *Parazoanthus* (Belize); Rützler (1996) examined pumping and ecological function of sand-buried sponges. The unusual case of feeding in a sponge by carnivory was discovered by the French group of the Endoume Laboratory, who studies deep-sea organisms (including the sponge *Asbestopluma*) in a shallow cave near Marseille (Fig. 8). Dayton (1979) studied growth and dispersal processes of sponges under the annual sea ice (Antarctica). Rützler (1981) monitored growth and pigment formation of a cyanobacteriosponge under different light intensities. Hoppe (1988) studied growth, regeneration of lesions, and predation of three sponges *in situ* (Netherlands Antilles). Storr (1976b) and Jackson and Palumbi (1979) conducted experiments on wound healing *in situ* (Florida, Jamaica). Rützler (1975) measured rates and periodicity of bioerosion on reefs. Rützler and Macintyre (1978) assessed the importance and fate of siliceous sponge spicules in reef sediments, and Tunnicliffe (1979) measured the drag force of water necessary to break coral weakened by clionid borings. Various metabolic studies involving sponges and photosythetic symbionts were conducted *in situ*. For instance, Wilkinson (1981, Great Barrier Reef, Australia); and, Pile and Patterson (1994, Lake Baikal, Siberia). Sponge energetics, including pumping, food retention, and secretion of metabolic products were studied *in situ* by Pile (1995) and Pile *et al.* (1996) using saturation diving (from *Aquarius* habitat; Fig. 14) or scuba and special underwater metabolism chambers (Key Largo, Florida; Gulf of Maine; Fig. 15).

METHODOLOGY

Many devices aiding the study of sponges by scientific diving method have been developed over the past few decades and range from simple photographic gadgets to sampling gear and fairly sophistica-

Figure 13. H. Reiswig sampling exhalant water *in situ*, 29 m, Jamaica (courtesy H. Reiswig).

ted recording instruments; only some can be mentioned here and many are not described in the literature. General techniques of sponge field research on coral reefs are discussed by Rützler (1978). Forstner and Rützler (1970) constructed a thermistor flowmeter to measure oscular currents and discussed other sensors for measuring the microclimate surrounding a sponge. Similar devices were built or used by Reiswig (1971; Figure 16), LaBarbera and Vogel (1976), and M. Patterson (A. Pile, pers. comm., 1996). Respiration and metabolism chambers have been built by modifying plastic bell jars and equipping them with magnetic stirrers and polarographic electrode ports (G. Bretschko and K. Rützler, unpubl.) or constructed from scratch (C. Wilkinson and J. Vacelet; Fig. 17; M. Patterson, pers. comm.). A stationary plankton sampler to capture near-bottom plankton, such as sponge larvae, was built for use on the reefs and in the mangroves of Belize (Rützler *et al.*, 1980; Figs 25, 26). Examples of special photographic techniques for sponge studies are found in Balduzzi *et al.* (1981), Pansini (1983), and Pansini and Pronzato (1990).

Figure 14. Divers getting tanks near air-filled "gazebo," *Aquarius* habitat, Florida (M. Lesser).

CARIBBEAN CORAL REEF ECOSYSTEMS PROGRAM (FIGS. 18-25)

What does sponge research have to do with the development of a major coral-reef research program? When I first arrived at the National Museum of Natural History 30 years ago, I was one of a few specialists on marine sponges worldwide. Because I was a diver I realized the need to study sponge

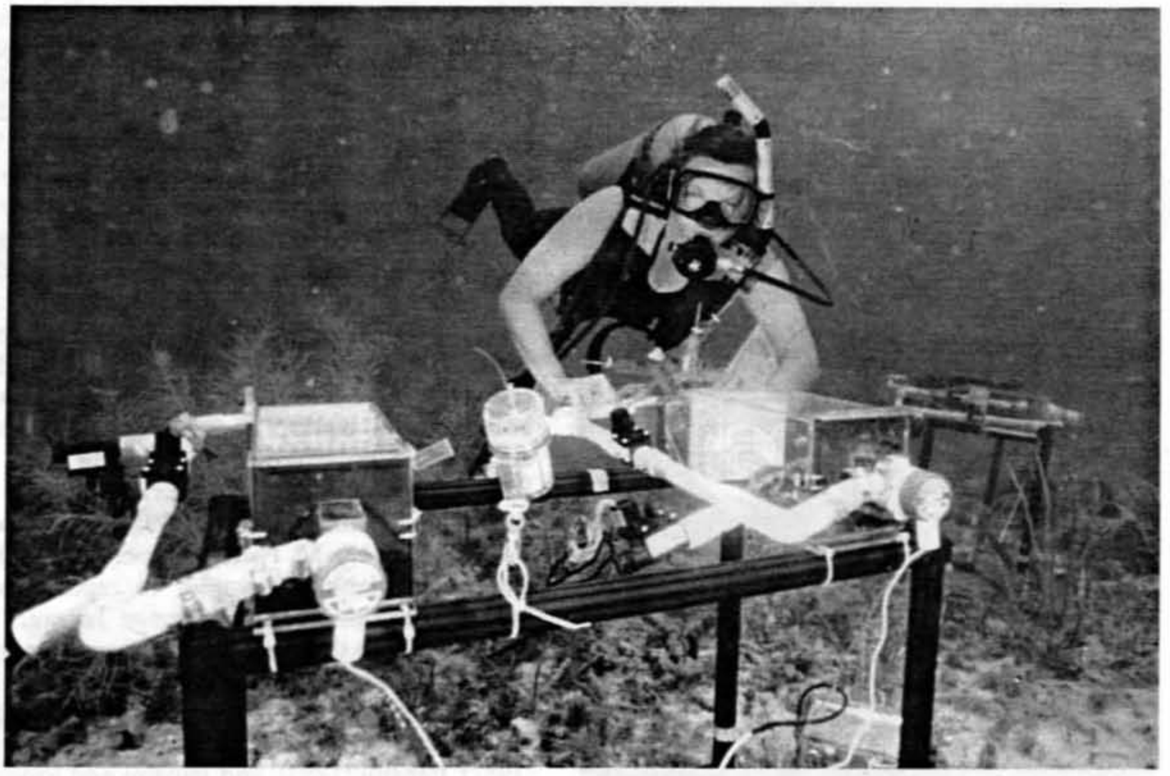

Figure 15. A. Pile with metabolism chambers near *Aquarius* habitat, Conch Reef, Florida (D. Gouge).

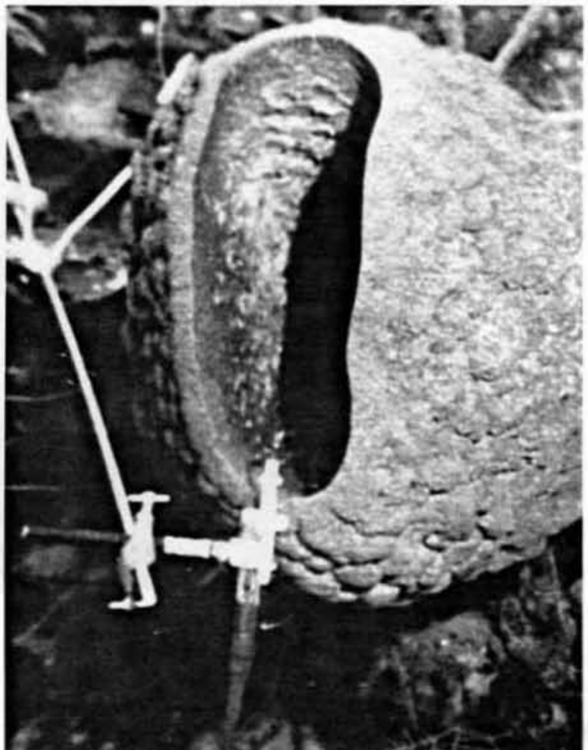

Figure 16. Current meter set up on *Verongula reiswigi*, Jamaica, 40 m (H. Reiswig).

systematics and biology within the context of the entire community and its controlling physical factors. Since this was a big task I hoped to connect with colleagues with similar interests and complementary disciplines. And indeed, in the late 1960s, six of us at the Museum, representing the fields of marine zoology, botany, geology, and paleobiology, decided to collaborate in a comprehensive study of a Caribbean coral reef. Because we planned to expand our studies to other environments, we named the program IMSWE (Investigations of Marine Shallow Water Ecosystems). The switch to CCRE came in 1985 when, during the Caribbean Basin Initiative, Congress approved an increase to the NMNH budget base for the study of Caribbean reefs, mangroves, and seagrass meadows.

Figure 17. C. Wilkinson's metabolism chambers set up on the Great Barrier Reef, Australia (courtesy J. Vacelet).

The principal objective of CCRE: It is a multi-disciplinary, long-term research program to study diversity, function, origin, development, and environmental predictability of a tropical marine ecosystem, the coral reef. (In the Caribbean at least, mangrove island swamps and seagrass meadows are integral parts of the reef). It was essential to the program from the beginning to have a permanent field station. This was founded in 1972 on Carrie Bow Cay, a small island situated on the barrier reef of Belize (Rützler and Macintyre, 1982; Rützler and Feller, 1996). Belize was chosen for its great diversity of habitats and species; it has the longest barrier reef in the western hemisphere, separated from the mainland by a wide lagoon, and three open-water atolls. Belize also has the least disturbed marine environment in the Caribbean.

Figure 18. Carrie Bow Cay, site of the Smithsonian coral-reef field station.

The main research questions of the CCRE program cover the entire science range and can be summarized as follows:

1. What are the community components of the reef system; diversity of animals, plants, microbes; systematics, morphology, growth, reproductive and developmental biology?
2. Where do organisms live, in what numbers and biomass?

Figure 19. Diver assessing species composition using frame.

Figure 20. Columbus Cay cave.

Figure 21. Sponge study on fore-reef slope.

3. What is the nature of the physical and chemical environment such as habitat topography, structure (substrate), and zonation; solar energy, including temperature, air and water movement, tides and precipitation; water and substrate chemistry; and, how does it impact on species and communities?
4. What was the geological history of reefs and mangroves, the evolution of species and communities; the changes of community structure over time?
5. What are the processes and interactions between organisms and environment, including nutrient cycling, productivity, food chains, bioerosion, symbiosis, parasitism, disease, behavior, algal blooms?
6. How does the reef compare to and interact with adjacent systems, such as deep-sea bottoms, blue-water, and mainland communities?
7. What is the human impact, and which questions of modeling and predictability, habitat conservation, and education can be addressed?

Figure 22. Photographic mapping of fouling community.

Figure 23. Examining settling plates among red mangrove roots.

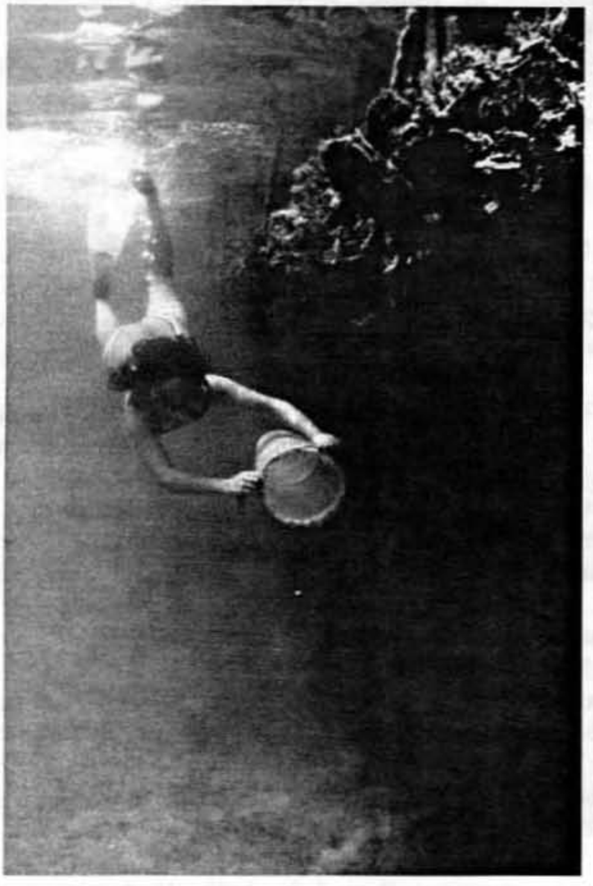

Figure 24. Sampling sponge larvae in front of peat-bank cave.

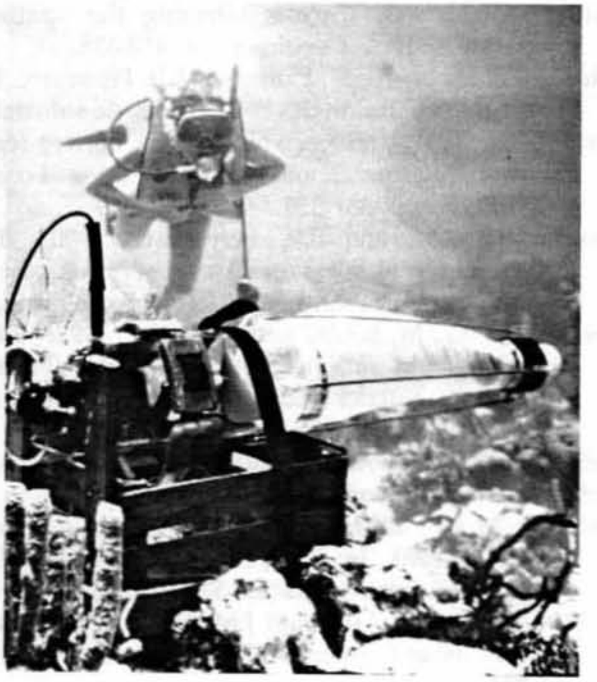

Figure 25. Stationary near-reef plankton sampler (hoplasa) installed on patch reef.

It is obvious that scientific diving will continue to be a powerful tool in answering these questions, and we look forward to further developments and refinements of the technique and hope for expedient access to its advanced technological accomplishments.

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