Saturation Diving and Underwater Laboratories: How Underwater Technology Has Aided Research on Coral Biology and Reef Ecology

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ABSTRACT. Despite more than a century of coral reef research, the basic biology of reef corals remained poorly understood until the advent of scuba diving and the associated underwater technology that followed. Basic information such as the nature of the coral–algal symbiosis, the importance of coral heterotrophy, specialized structures for space competition, the role of mutualistic crustacean symbionts, the behavior and dispersal ability of coral larvae, the nature of coral protection from ultraviolet radiation and heat stress, and the effects of ocean currents and internal waves on reefs all benefited from the ability of scientists to spend time under water observing, making measurements, and carrying out experiments. In addition to enhancing our understanding of corals themselves, the ability to spend time under water has also provided a huge amount of information about coral reef ecosystems and their component species. These benefits were further enhanced by new opportunities for saturation diving, and technology such as heated suits and underwater habitats or laboratories. One unique example of diving scientists working in concert with underwater technology is the *Aquarius* underwater laboratory (and its predecessors). This asset has allowed hundreds of researchers to spend weeks at a time investigating corals and coral reefs. The availability of underwater habitats/laboratories also fostered the development of other new technology for use on coral reefs and in other subtidal environments, and this technology is now providing the means to examine how changing ocean conditions are likely to impact corals and reefs.

UNDERWATER RESEARCH ON CORAL REEFS AND SUBTIDAL HABITATS

In the early 1800s, naturalists investigating corals reefs had to rely on crude tools such as weighted collecting devices lowered from the decks of vessels to explore the reefs around coral islands. One example was a hollow, bell-shaped weight filled with wax, which brought back impressions of the bottom, such as coral surface topographies, and even fragments of live coral and algae. Charles Darwin used such methods from the HMS *Beagle*, and his findings were sufficient to produce an elegant theory of reef growth and zonation (Darwin, 1842). These naturalists also had a chance to examine corals in the shallows and even at low tide when some reefs were exposed for hours. Commercial diving and submarines became available later in the nineteenth century, and had some utility

for reef studies and specimen collecting, although there does not seem to have been a large number of studies using these methods. Despite more than a century of coral reef research using those techniques, the basic biology of reef corals remained a mystery until the advent of scuba diving and the associated underwater technology it made possible. Such fundamental information as the nature of the coral–algal symbiosis, the importance of coral heterotrophy, specialized structures for space competition, the role of mutualistic crustacean symbionts, the behavior and dispersal ability of coral and fish larvae, the nature of coral protection from ultraviolet radiation and heat stress, and the effects of ocean currents and internal waves on reefs have all benefited from the ability of scientists to spend time under water observing, collecting specimens, making measurements, and carrying out experiments.

Scuba diving has some serious limitations as a research tool for diving scientists. At moderate depths, the amount of time one can spend on the bottom, or in the water column, is limited, from less than an hour to a few hours in a given day. Compare this to the situation for terrestrial ecologists, or even intertidal researchers who can often spend several hours on each low tide, sometimes twice a day, in the relative comfort of the aerial environment. Everything is more difficult under water and often takes more time than on land or in the intertidal zone, so anything that gives a researcher more time at depth is a huge benefit. One option that suffices for some researchers is to work very shallow and thus get more hours without a need for decompression, but that only works when their research subjects are available at those shallow depths. Another option is extended decompression diving, which is generally not supported by university research programs, but has been carried out in some cases by working with agencies that have this capability (Schmitt, 1987). The same is true for mixed-gas diving, which has also had limited availability until the advent of nitrox diving within the scientific (then sport) diving community in the 1980s. Use of nitrox can extend time working at depths significantly, especially in the range of 20–40 m depth where bottom time (i.e., time available to work at depth) can double (Lang, 2001). However, researchers using nitrox are still likely to be limited to less than two hours per day of actual working time at such depths.

Saturation diving offers the advantage of unlimited bottom time at saturation depths and greatly extended bottom time at depths much below the saturation depth. Time limits become more a matter of physical stamina of the divers and their support team, and logistical challenges of air delivery and other support. Saturation diving for days to weeks also requires the presence of an underwater structure, such as a habitat or laboratory, to provide comfortable living, sleeping, and eating areas, as well as places for research gear and computers. Once such a system is in place, divers are able to work for many hours each day, often in rotating teams such that even 24-hour studies can be carried out over many days. Such continuous day and night research is very difficult to do from the surface, but becomes relatively routine and comfortable using an underwater laboratory. The ability to work around the clock has been important for studies of zooplankton behavior and distribution, coral physiology, fish behavior, and many others. The purpose of this paper is to review the science that has become possible primarily because of the new capabilities offered by saturation diving, underwater laboratories, and the associated new technologies that have been developed and incorporated by the research teams that have used them.

UNDERWATER HABITATS AND LABORATORIES

The history of saturation diving and underwater habitats has been covered elsewhere and will not be part of this review. However, a bit of this history is necessary to set the stage. There have been a good number and variety of underwater habitats designed and put into regular operation for commercial purposes such as oil exploration, but relatively few that have been constructed and used primarily as scientific research facilities. Saturation diving is being used at great depths in industry (to over 500 m), but has been limited to very shallow depths for research (under 30 m), mostly to increase safety, but also for ease of operation and supply.

An early effort was the Conshelf I (Mediterranean) and Conshelf II (Red Sea) habitats built for Jacques Cousteau's explorations and filming during 1962–1965 (Cousteau, 1965). These habitats, while shallow (10 m), allowed first two and later six aquanauts to stay underwater for seven and thirty days, respectively. In 1965, Conshelf III took six Aquanauts to 100 m for three weeks. The path to successful saturation diving was paved. During 1965–1969, the U.S. Navy used the Sealab I–III habitats for research on diving physiology.

While more than twenty underwater habitats have been constructed and used for science, four facilities have had the largest scientific research and publication impact: the *Tektite I* and *Tektite II* habitats in the United States Virgin Islands (USVI; 1969–1970; Clifton et al., 1970); the Helgoland habitat in the cold Baltic Sea (1969–1979); the *Hydrolab* habitat in the Bahamas (1970–1976) and St. Croix, USVI (1977–1985; Nyden, 1985; Williams, 1985); and the *Aquarius* underwater laboratory, first in St. Croix, USVI (1987–1989), then on Conch Reef, off Key Largo, Florida (1992–present; Shepard et al., 1996). *Aquarius* has had the longest tenure of these facilities and is still in active use at the Florida site as of 2011. Much of the research covered in this review was accomplished using the *Hydrolab* and *Aquarius* laboratories (Figures 1–3).

RESEARCH AREAS

The ability to spend time under water has facilitated a substantial body of work on coral reefs and other subtidal ecosystems and their component species. The *Hydrolab* and *Aquarius* underwater laboratories have allowed hundreds of researchers
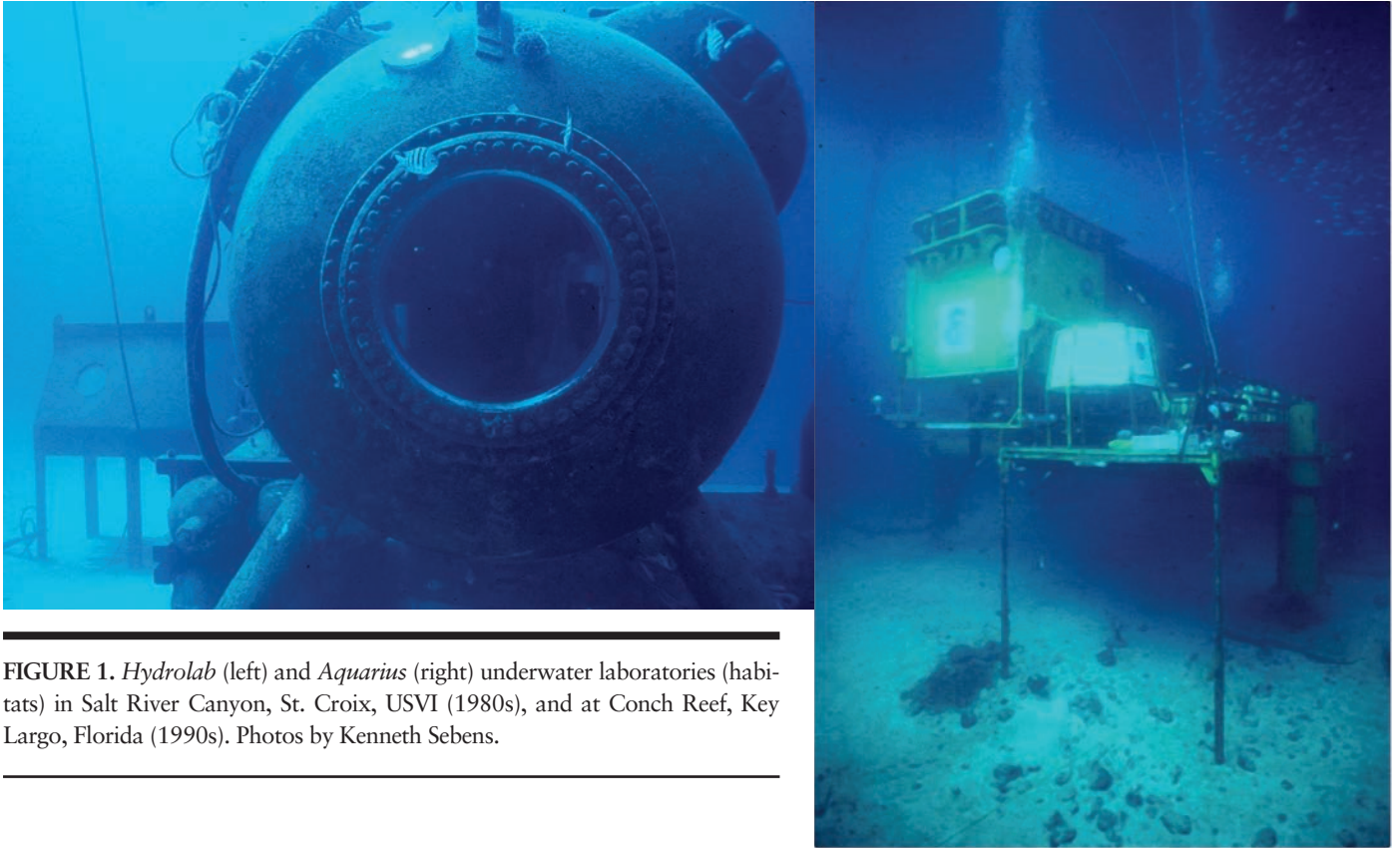
FIGURE 1. *Hydrolab* (left) and *Aquarius* (right) underwater laboratories (habitats) in Salt River Canyon, St. Croix, USVI (1980s), and at Conch Reef, Key Largo, Florida (1990s). Photos by Kenneth Sebens.
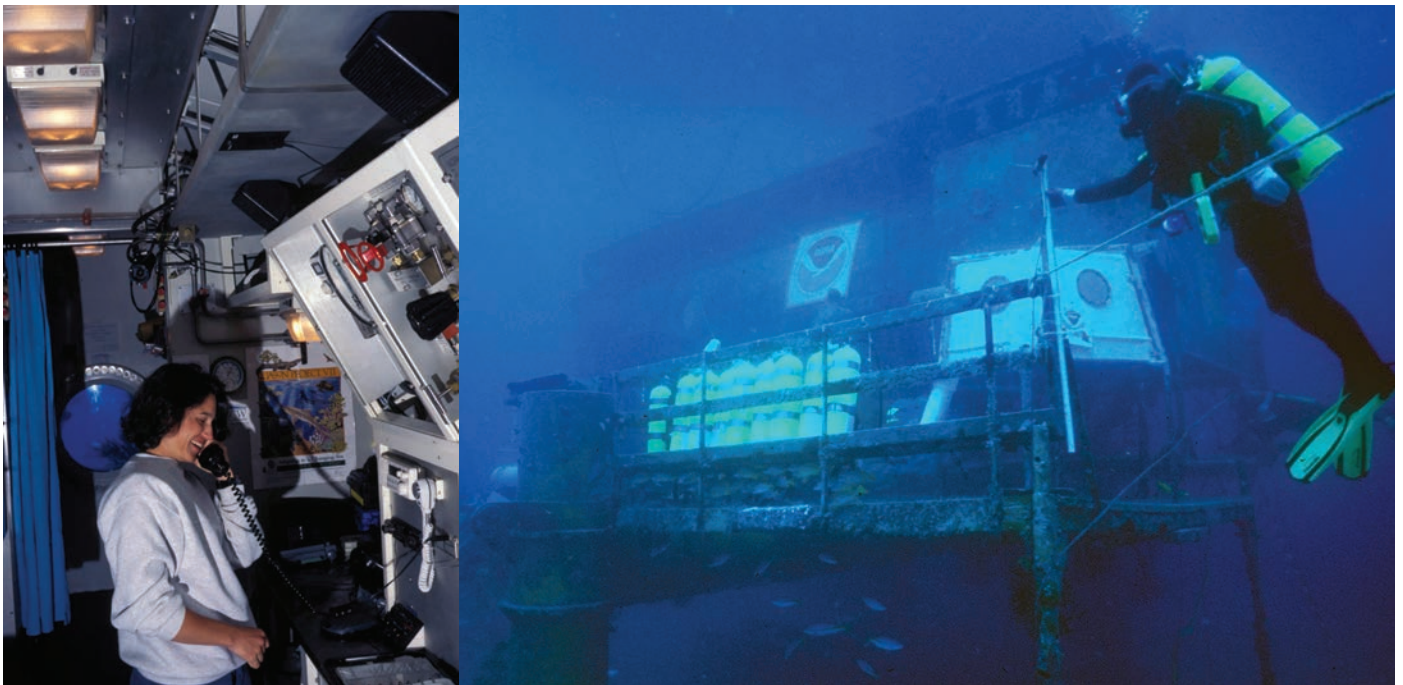

FIGURE 2. The *Aquarius* underwater laboratory (right) at Conch Reef, Florida, and the communications and data center inside the habitat during the Jason Project (1996, with A. Grottoli). Photos by Kenneth Sebens.

FIGURE 3. Full face mask (K. Sebens, 1999) and helmet (G. Wellington, Jason Project, 1996) systems supplied air from *Aquarius* (left) and from the surface barge above *Aquarius* (right). Photos by Kenneth Sebens (left) and Karla Heidelberg (with permission, right).

to spend weeks at a time gathering information on corals and coral reef ecosystems. Typically, a research mission in *Aquarius* lasts seven to ten days, thus providing longer single observation times (each dive lasts several hours), with a total dive time for a mission corresponding, approximately, to six months of intensive "classical" diving field work. The availability of these laboratories also stimulated the development and adaptation of many technologies for use on coral reefs and in other subtidal environments. These technologies are now providing the means to examine how changing ocean conditions are likely to impact corals and reef ecosystems.

We concentrate on a few research areas that have benefitted greatly from the availability of underwater laboratories: coral biology and physiology, coral reef hydrodynamics and flow effects on benthos, zooplankton ecology and behavior, fish behavior and ecology, and coral reef community and ecosystem ecology. There

are many other areas of research that have also benefited, including everything from human behavior (as a space station analog) and physiology to instrument development and testing (engineering), that will not be covered in this review.

CORAL REEF HYDRODYNAMICS AND THE EFFECTS OF WATER FLOW ON CORALS AND OTHER REEF BENTHOS

Coral reef communities experience a broad range of flow conditions, from crashing waves in the surf zone to strong unidirectional currents along deep reef walls and almost-still water in some lagoonal and backreef habitats (Sebens and Johnson, 1991; Sebens and Done, 1994; Monismith, 2007). Corals and other reef organisms must thus deal with limitations imposed on their physiology and structure by these flow conditions, as well as by the extreme conditions that occur during storm events. Water

FIGURE 4. An InterOcean S4 electromagnetic current meter in place on a shallow reef, and a Sontek ADV flow meter on a stand that allows vertical profiling from just above coral tentacles to 2 m above the bottom. These and several other recently developed instruments have been used to characterize flow on coral reefs. Photos by Kenneth Sebens.

flow also is important for delivery of nutrients and plankton to reefs (Leichter et al., 1998, 2003, 2007), and for transport of larvae from one reef to another. Current meters can be deployed from surface vessels or by divers on no-decompression dives, but such meters generally give only mid-depth flows. More recently though, acoustic doppler current profilers (ADCPs) have been mounted on the bottom to provide comprehensive data on flow at all depths above the bottom, but not within centimeters of substratum.

More difficult is the characterization of water flow at the microscale, from just above the bottom down into the interstices of reefs and among tentacles of corals (Reidenbach et al., 2006a, 2006b, 2007). Getting this type of data involves delicate positioning of instruments and use of video and other technologies by divers who reposition their instruments (thermistors, ADVs, and electromagnetic flow meters) continuously and move them to various habitats and depths (Figure 4). Such studies are often paired with physical, biological, and/or chemical sampling over the same time period, including temperature, zooplankton, nutrients, coral physiology, and other chemical parameters of the water column (Patterson et al., 1991; Sebens and Done, 1994; Leichter et al., 1996, 2005).

Flow on reefs originates from a number of sources including waves, currents, and internal waves (Monismith, 2007). On reefs with strong longshore currents, the biotic communities can experience strong flow at any depth (Sebens and Done, 1994), but

reefs without such currents often experience the highest flows in wave-dominated forereef environments and have a sharp drop in flow with depth (Sebens and Johnson, 1991; Sebens, 1997; Sebens et al., 2003). Deep reef and shallow lagoonal habitats with very low mean flow conditions are likely to experience reduced delivery of particles for suspension feeders (Sebens, 1997) and reduced uptake of nutrients by corals and algae (Hearn et al., 2001). Low flows also affect biological processes such as bleaching, recovery from bleaching, and development of heat shock or stress responses (Carpenter and Patterson, 2007; Carpenter et al., 2010). As a rough approximation, reef habitats with flow speeds normally under 5 cm s^{-1} present physiological and nutritional challenges for corals, affecting their photosynthesis, respiration, tissue growth, and calcification (Sebens, 1997). Flows in the range of 10–30 cm s^{-1} may be in the optimal range for particle capture and lack of diffusional limitation, whereas flows well above that range present challenges for corals in retaining particles, keeping tentacles extended, and avoiding mechanical damage and dislodgment.

Moderate to deep reefs can experience variable flow regimes when internal waves shoal at those depths, as happens in Florida (Leichter et al., 1996, 1998, 2003, 2005, 2007). Benthic suspension feeders experience pulsed periods of high flow, as well as pulsed delivery of zooplankton and nutrients, during the wave events. This important source of nutrients and particulate material for reefs was first recognized and documented by researchers

using the *Aquarius* laboratory. In addition to flow magnitude, turbulence also affects delivery of dissolved and suspended materials (Monismith, 2007). Davis and Monismith (2011) found that turbulence in the reef boundary layer was highly variable in time and was modified by near-bed flow and shear, as well as stratification concurrent with shoaling internal waves (Davis and Monismith, 2011) at Conch Reef.

CORAL PHYSIOLOGY AND NUTRITION

Ideally, researchers would like to understand the physiology and nutrition of reef corals under natural reef conditions. Recirculating respirometry chambers deployed on the seafloor next to underwater habitats (e.g., *Hydrolab, Aquarius*) have allowed interesting insights into coral ecophysiology that would have not been obtained any other way (Patterson et al., 1991). Because the chambers are exposed to the same ambient conditions of irradiance, temperature, and water chemistry as nearby corals, the perturbation to the test subjects is minimal, a significant advantage when conducting experiments with needed ecological relevance. Chambers developed by Mark Patterson and colleagues were used to manipulate flow over coral colonies in a controlled fashion. The chambers were the first to be completely computer controlled from inside the habitat (*Hydrolab*), and to our knowledge this was the first use of a desktop computer (Apple IIe) in a pressurized underwater environment (Figure 5). A regular CRT screen could not be used under pressure, so Patterson acquired one of the first flat-screens on loan from the manufacturer, before they were available on laptops. Subsequent experiments in *Aquarius* used an early Apple Macintosh Plus to control experiments, including monitoring the data, performing QA/QC, and performing self-diagnostics on the progress of the experiment.

These and later experiments from *Aquarius* (Figure 6) resulted in data on a diversity of coral species and provided strong evidence that flow modulates both respiration and photosynthesis in scleractinians (Patterson et al., 1991; Finelli et al., 2005; Carpenter and Patterson, 2007; Carpenter et al., 2010). *Aquarius* was also used to test gas microelectrodes moved by a micromanipulator under control of a scuba diver to measure diffusive boundary layers over individual coral polyps (Patterson, 1992a). These data were valuable in constructing a theory of metabolic scaling in lower invertebrates and algae that demonstrated the effect of shape and flow on the allometric exponent (Patterson, 1992b) that relates metabolic rate to organism size.

As concern grew about the impact of global warming on reefs, experiments were devised to expose corals to elevated water temperature in situ using modifications of the prior technology (Figure 7). Thermofoil avionics heaters were applied inside the metabolism chambers and precise temperature control was achieved from sophisticated industrial controllers inside *Aquarius*. These experiments would not have been possible without the ample power from *Aquarius* available to run the associated heaters and pumps. More recent work has demonstrated that within-colony variation in photosynthetic performance (Carpenter and Patterson, 2007) and heat shock protein expression (Carpenter et al., 2010) is modulated by flow in a non-linear, unimodal fashion. The heated chambers also made possible development of a new minimally invasive method for measuring the production of heat shock proteins in single polyps by carefully excising small bits of tissue in situ using a special tool (Bromage et al., 2009).

Another instrument developed for test and evaluation by saturation diving was a handheld profiler for temperature, dissolved oxygen, and pH (Figure 7). This instrument could be precisely emplaced for quick profiling over the bottom 3 m of the
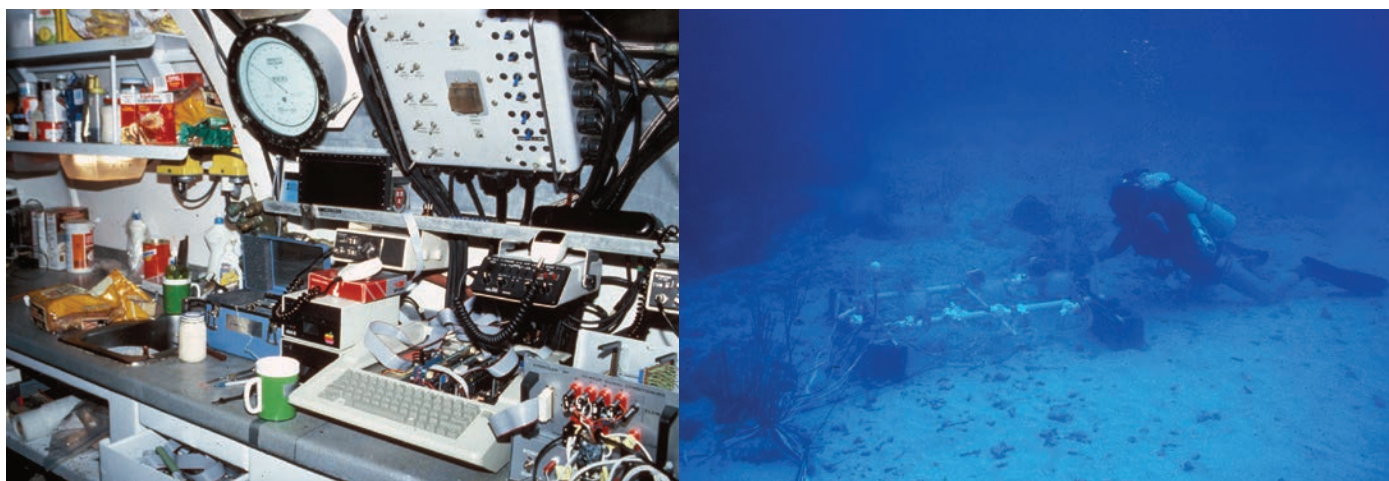

FIGURE 5. The first computer (Apple II) used in *Hydrolab* (by M. Patterson and colleagues), including a prototype flat-screen monitor on loan from the manufacturer (1984) (left). Chambers used for respirometry and flow studies, deployed adjacent to the reef at *Hydrolab* (1984) (right). Photos by Kenneth Sebens.

FIGURE 6. Respirometry chambers used for coral production and respiration measurements at a range of flow speeds being prepared for use in *Hydrolab* by M. Patterson and colleagues (left) (Patterson et al., 1991; photo by Kenneth Sebens), and similar chambers being used for nutrient uptake studies (right) (Leichter et al., 2003; photo by James Leichter).
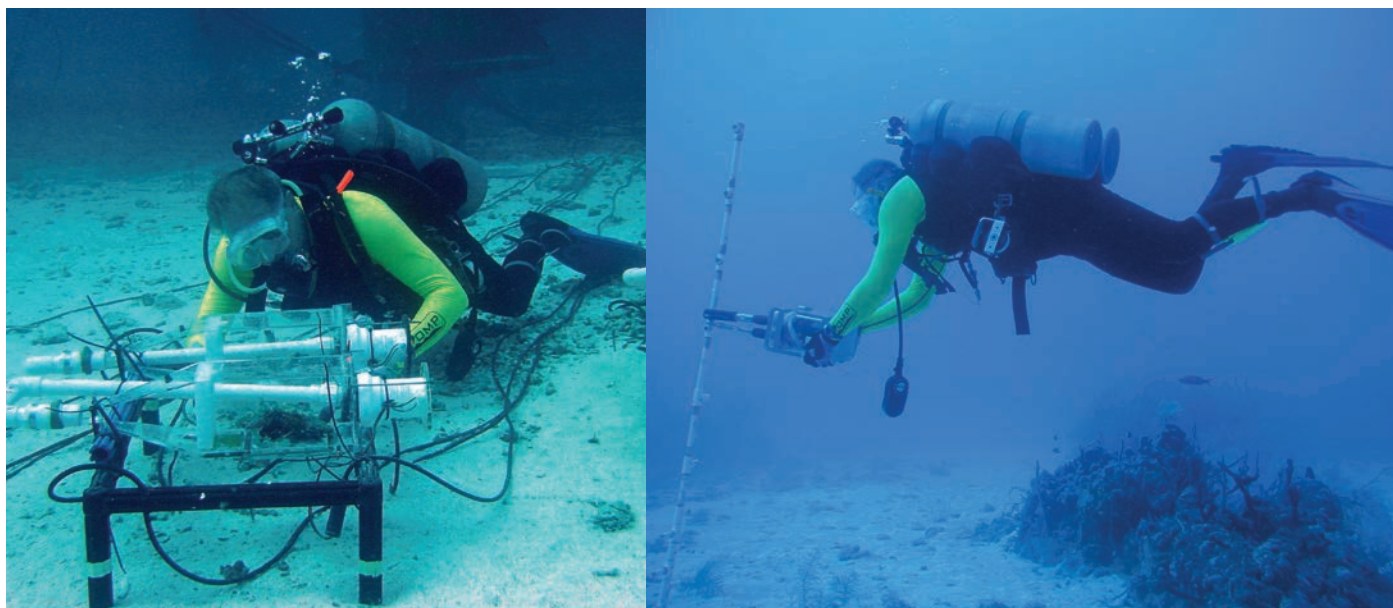

FIGURE 7. Mark Patterson investigates flow and temperature effects on reef benthos using the *Aquarius* underwater laboratory in 2002–2003. Heated metabolism chambers (left) and dissolved oxygen, pH, and temperature profiling apparatus (right). Photos by Janet Nestlerode.

reef, or left in place for 24 hours at a single location. This device has gathered valuable data on how a progression toward reef heterotrophy in the Florida Keys has impacted the geophysical boundary layer dynamics for dissolved oxygen, and how ocean acidification affects diurnal variation in pH. Both parameters have shown unexpected marked variation over short spatial distances (1 m).

Coral nutrition is another area of research that has benefited greatly from the extended time available to researchers using *Aquarius*, especially for field work at night when most corals are feeding on zooplankton. Sebens and Johnson (Johnson and Sebens, 1993; Sebens and Johnson, 1991) used *Aquarius* to study zooplankton availability using a new in situ pump developed for this work (Sebens and Maney, 1992; Graham and Sebens, 1996) to

monitor particle capture by several coral species, and to measure water flow at the height of corals on the reef over a broad depth range. Sebens and colleagues carried out similar studies of zooplankton feeding on a Jamaican reef using the methods developed in *Aquarius* (Sebens et al., 1996a, 1996b, 1997; Sebens, 1997), and

Mills and Sebens quantified sediment ingestion (Mills and Sebens, 1997, 2005; Mills et al., 2004). Apparatus developed for these studies of coral feeding and growth is illustrated in Figures 8–10.

Heidelberg and colleagues used *Aquarius* to examine behavior of zooplankton as they approach coral tentacles (Heidelberg
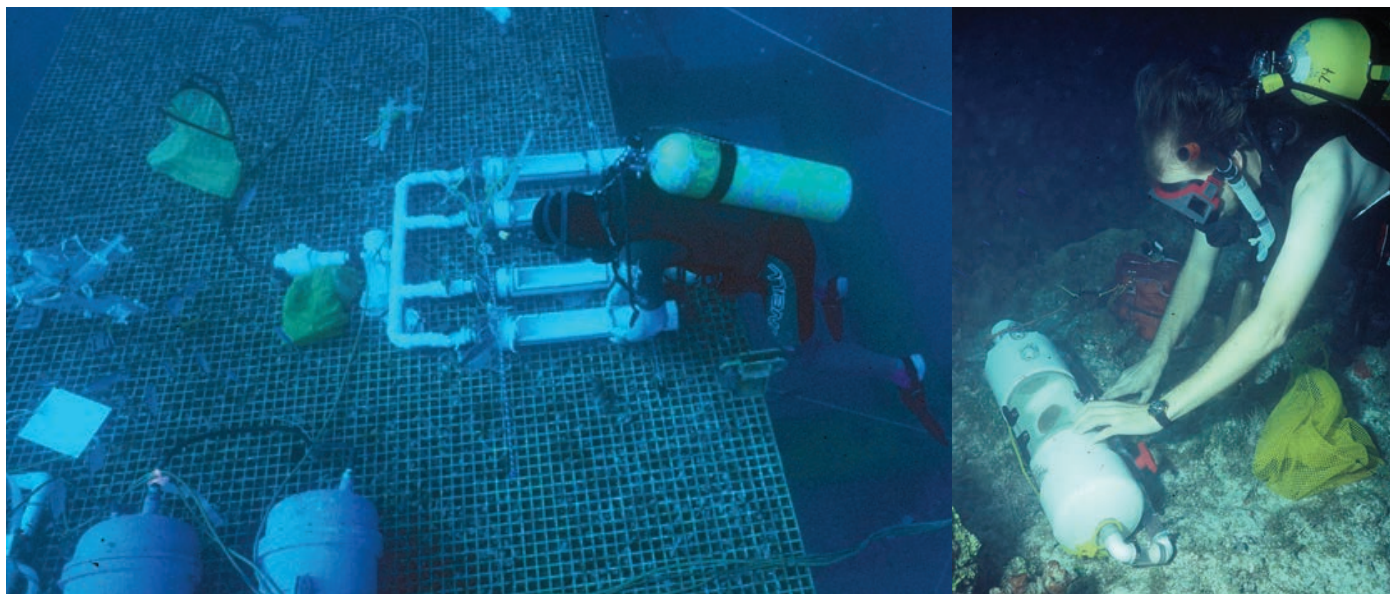

FIGURE 8. Experimental chambers used for coral feeding studies on top of *Aquarius*, and on Conch Reef near the underwater laboratory by J. Witting, K. Sebens, and colleagues (Witting, 1999; photos by Kenneth Sebens).
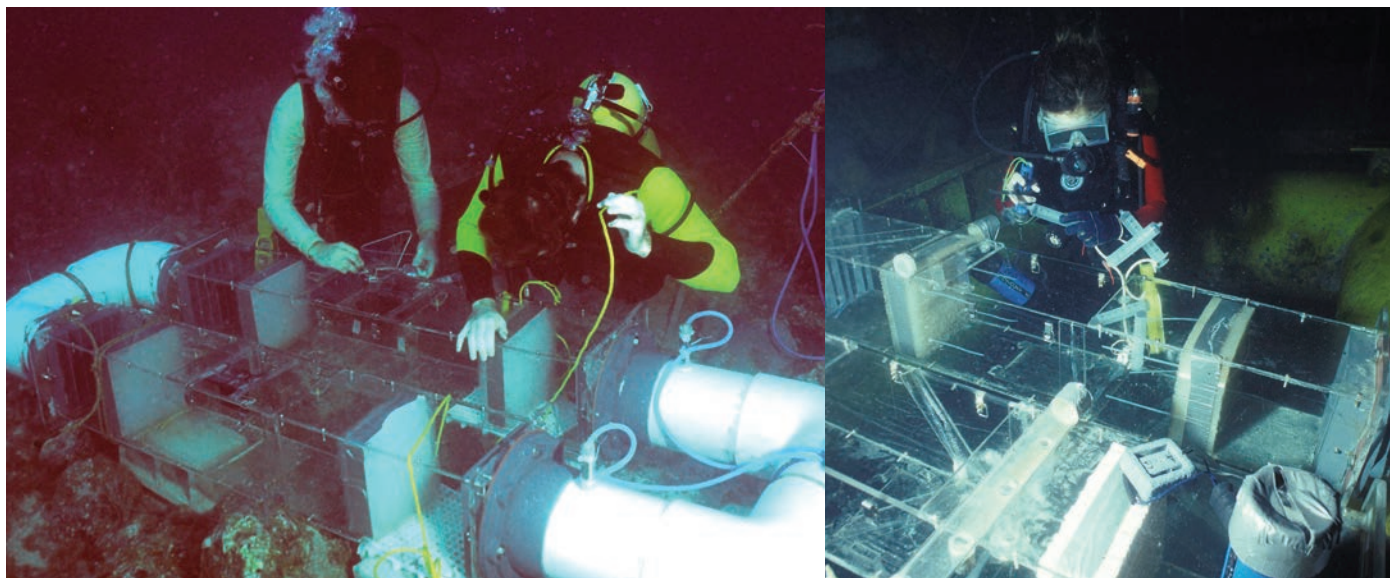

FIGURE 9. A large recirculating flume (left) on Conch Reef allowed flow studies of particle and zooplankton capture, and provided both unidirectional and bidirectional flow generated by two electric trolling motors inside the PVC sections. Zooplankton were attracted into the chambers using dive lights, then chambers were sealed. Screens prevented plankton from contacting propellors during bidirectional flow runs with live zooplankton (K. Sebens, unpublished). Detailed view of working area (right). Photos by Kenneth Sebens.
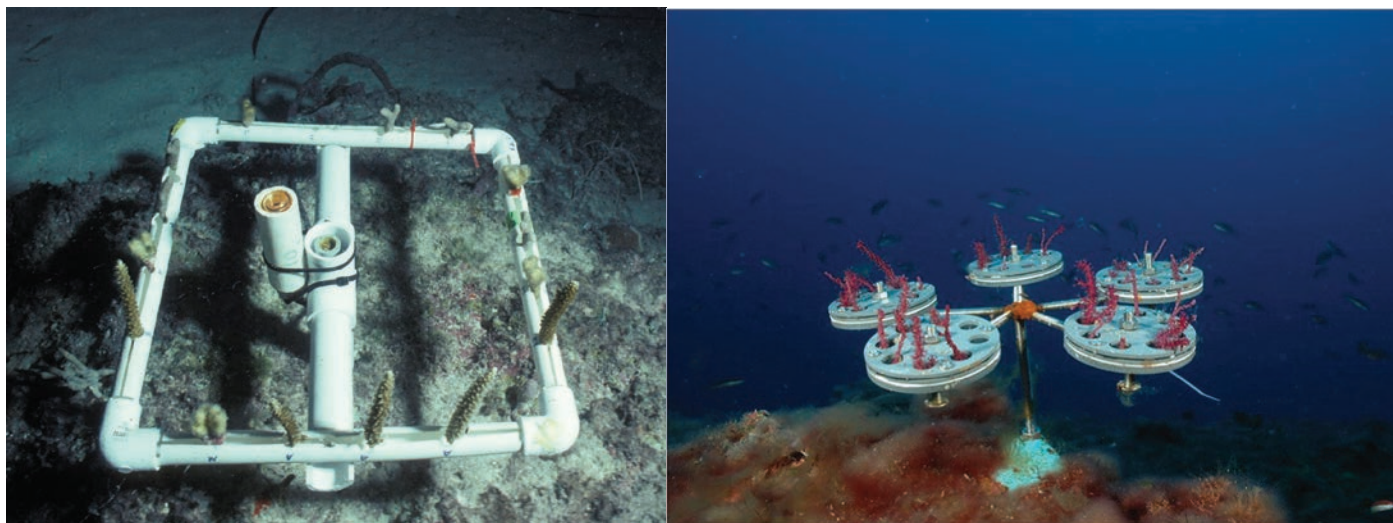
FIGURE 10. Transplant racks for coral growth studies at the *Aquarius* laboratory (left; Witting, 1999; photo by Kenneth Sebens) and in the Mediterranean (right; Cebrian et al., 2012; photo by Joaquim Garrabou). In the assembly at left, a cabled light was added to the center of half of the treatments to attract zooplankton at night and thus enhance capture rates by the corals on those racks.

et al., 1997), and later to quantify the zooplankton resource available to corals (Heidelberg et al., 2010). In a related set of experiments, Witting (1999) demonstrated experimentally (Figure 10) that coral growth can be enhanced by added capture of zooplankton (attracted by lights directed away from coral transplants), a finding that was later supported by laboratory research by Witting and colleagues (Ferrier-Pagès et al., 2003; Houlbrèque and Ferrier-Pagès, 2008). The importance of inorganic nutrients to reefs and reef corals has also been a focus of research using *Aquarius* (Szmant-Froelich, 1983; Leichter et al., 2003).

ZOOPLANKTON ON REEFS

Zooplankton are important prey for coral reef fish, corals, and other zooplanktivores living on or near reefs. The composition and dynamics of the reef plankton community are interesting in their own right, and zooplankton provide a link between primary production in the water column and the reef community. Observation of plankton swarms near reefs and some in situ sampling suggested that zooplankton are not homogeneously distributed over reefs and do not all originate from offshore water flowing over reefs (i.e., some are reef residents). When researchers needed to quantify the plankton resource available to near-reef fish, for example, they used divers to swim plankton nets along the reef as close as they could maneuver near the reef surface (Hobson and Chess, 1976) because they were aware that zooplankton assemblages differed nearer to and farther from the substratum.

Observations of crustaceans swimming upward from reef surfaces led to the design of emergence traps to quantify those demersal plankton that migrate off the reef at dusk (Hobson and

Chess, 1979; Ohlhorst and Liddell, 1984; Ohlhorst et al., 1985 [using *Hydrolab*]; Alldredge and King, 1985) and may return to the reef at some later time. These zooplankton provide a link between benthic productivity, by reef microalgae for example, and both reef fish and sessile invertebrate predators. They are, however, a very small fraction of the reef plankton in most places (Heidelberg et al., 2003, 2010). The majority of the zooplankton over reefs are either open-water plankton advected onto the reef or reef-resident plankton that do not live on the reef surfaces but maintain themselves near the reef and migrate vertically (Heidelberg et al., 2003, 2010).

Living on the reef for many days and nights by scientist aquanauts using underwater laboratories has allowed the extensive observation necessary to adequately ascertain zooplankton behavior, and the interaction of predators with the plankton resource. One recent investigation to quantify zooplankton above a coral reef was conducted using *Aquarius* (Heidelberg et al., 2010). This team designed a four-inlet plankton sampler made of PVC pipe and powered by a large bilge pump (Figure 11). The pumps are also inexpensive enough to replace quickly when they fail. Each intake pipe, located at 2 m, 1 m, 50 cm, and 5 cm off the reef surface, respectively, had a conical plankton net inside the PVC pipe end that could be changed easily by divers. There was also a separate pump sampler taking zooplankton from 1 m below the water surface. Divers were thus able to take samples every three hours for 24 hours per day for seven days in a row, illustrating how zooplankton assemblages are structured above the reef, and thus what type and amount of plankton are available to zooplanktivores on the reef or in the water column near the reef. While theoretically possible, this task would have been much more difficult, and less safe, working from surface vessels.
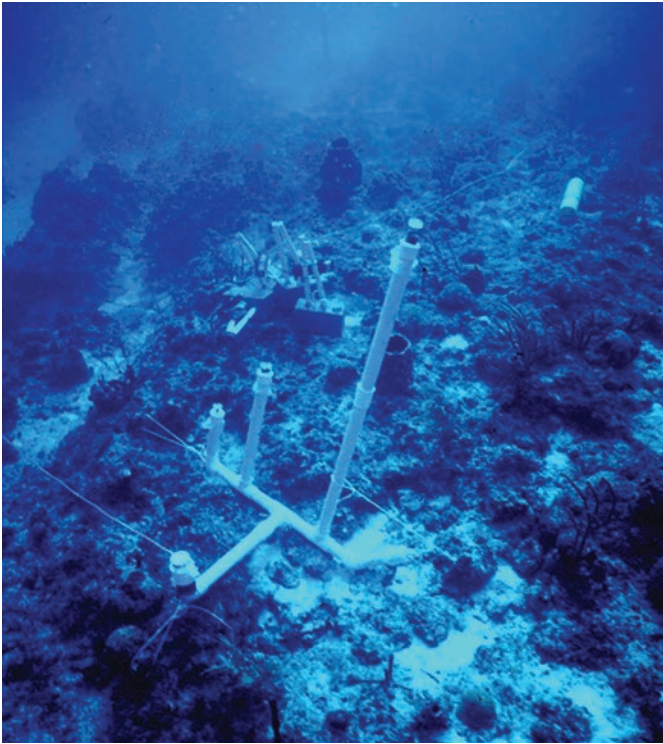
FIGURE 11. A plankton sampling array in place near the *Aquarius* laboratory on Conch Reef, Florida, used to examine zooplankton distribution above the bottom. The center section is 2 m tall and all four inlets, at four different heights, are powered by a single large submersible pump at bottom left (Heidelberg et al., 2010). Photo by Kenneth Sebens.

Another excellent example comes from the work of Leichter and colleagues, whose observations and measurements using *Aquarius* led to the discovery that internal waves deliver zooplankton (as well as nutrients) from deeper water masses up to depths where reef organisms can make use of them (Leichter et al., 1998, 2003, 2005, 2007).

Reef Fish Behavior and Ecology

In the 1980s, the National Oceanic and Atmospheric Administration's (NOAA) National Undersea Research Program had a surface-supplied, hot-water-suit research platform at the University of Southern California's Catalina Marine Science Center on Santa Catalina Island. Schmitt used this facility extensively for a shallow subtidal project on fish and other predators that could not have been done in any practical way using regular scuba. The experiment tested for predator-mediated, apparent competition between two prey types (snail and bivalve) and involved daily censuses of large subtidal areas for the two prey types that had been eaten in the previous 24 hours; dead prey

were removed and replaced daily. The results were the first experimental test of apparent competition (Schmitt, 1987), a process wherein two species affect each other negatively because of higher trophic-level influences (i.e., predator effects). It is also the project for which Schmitt was awarded the 1989 George Mercer Award for Distinguished Research by the Ecological Society of America.

The Schmitt project was important as well in highlighting the power (albeit with challenges) of achieving long observation times through saturation diving (Schmitt, 1987). Schmitt's project required six-hour or longer dives to 10 m (33 ft) every day for about six weeks; divers used U.S. Navy extreme exposure decompression tables, and each six-hour dive included a decompression stop of at least one hour. When a diver reached the limit of multiple days of extreme exposures (i.e., after six consecutive dive days), the diver had to stay out of the water for a full day. Obviously this study needed the hot-water suits (with water pumped through suits from the surface) to do six-hour dives daily in the (cold) summer water temperatures of Catalina Island.

Underwater saturation facilities have greatly facilitated further research on fish ecology and behavior. For example, Levitan and Petersen (1995) used a saturation mission in *Aquarius* to investigate fish spawning and fertilization rates under natural conditions. Over many years, these researchers collected data from 3–12 m using NOAA's day-boat operation, but the use of extended saturation diving allowed them to examine species that spawn at greater depths (20–30 m). These were long dives during which they examined spawning behavior and then sampled eggs after release to obtain an estimate of female fertilization success. This team also used *Aquarius* itself as their working laboratory so that they could use a microscope to rapidly score eggs for fertilization without the necessity of bringing them to the surface and transporting them to shore.

During 2003–2005, Hay and Burkpile used *Aquarius* to establish 32 in situ mesocosms (4 m² each) where they manipulated herbivorous fish species richness to establish the links between herbivore identity and richness and benthic community structure on this coral reef. The saturation capabilities of *Aquarius* allowed them to perform a labor-intensive study that would have taken weeks to accomplish via other means in nine days. The amount of time needed at 16–18 m would not have been logistically or financially possible without the capabilities of saturation diving. Consequently, they were able to do some of the first direct, long-term assessments of the role of herbivore richness on the health of coral reef communities (Burkepile and Hay, 2007, 2008, 2009, 2010, 2011). For example, Burkepile and Hay (2008, 2010) showed that herbivore species richness and identity are both important for facilitating the removal of seaweeds and the growth of corals. When compared with single-species treatments, mixed-species treatments lowered macroalgal abundance by 54%–76%, enhanced cover of crustose coralline algae (preferred recruitment sites for corals) by 52%–64%, increased coral cover by 22%, and prevented coral mortality. Complementary feeding by different herbivorous fish species drove the herbivore

richness effects because macroalgae were unable to effectively deter fishes with disparate feeding strategies. Ultimately, their work suggests that maintaining herbivore species richness appears critical for preserving coral reefs, because complementary feeding by diverse herbivores produces positive, but indirect, effects on corals, the foundation species for the ecosystem.

In general, studying fish behavior requires very long observation times. This is why most studies are done in aquaria. Research has demonstrated that saturation diving allows for observation times long enough to make more complete and ecologically meaningful observations. Dunlap and Pawlik (1996), for example, using the *Aquarius* habitat as their base, were able to observe and video fish feeding on several species of reef sponges for several consecutive hours. These observations allowed inference of predatory mechanisms structuring the reef by spongivorous fishes such as trunkfishes and angelfishes. There are many other examples where the extended dive times and depths afforded by saturation diving have led to major findings in fish ecology and behavior, many more than can be cited here.

OTHER BIOLOGICAL AND ECOLOGICAL INSIGHTS ABOUT REEFS AND THEIR INHABITANTS

Underwater habitats and saturation diving have made it possible to follow the behavior of marine animals that must be studied in situ. An early example comes from the work of William Herrnkind (1974). Around 1970, it was thought that spiny lobsters were randomly nomadic scavengers with a limited social repertoire. Based on his observation of mass migration by queuing and reports from initial telemetry studies by others, he suspected far more complex behavior and sophisticated social and navigational abilities. However, these animals are largely nocturnal and adults often occur at depths of ~20 m, at considerable distances from shore. In addition, they walk at near-swimming pace and roam widely, making it a challenge to observe them by standard scuba; their large size and spatial range made it unreasonable to infer natural behavior from even large aquaria. *Tektite*, in particular, and *Hydrolab* manned undersea habitats provided means to substantially overcome these logistical hurdles.

At *Tektite I* and *Tektite II,* with successive, lengthy missions (three 3-week missions in *Tektite II*), Herrnkind and colleagues were able to daily and repeatedly access the numerous resident lobsters within a kilometer of the facility to tag them and identify their den sites (Herrnkind, 1974). Ultrasonic telemetry, then in its infancy, allowed them to locate individuals during nocturnal foraging and document movement from dens to feeding areas throughout the night. The initial data suggested homing to particular favored dens, necessitating accurate orientation by non-visual cues. Displacement experiments, sometimes with night-long tracking by aquanauts, on telemetered and simple color-coded, tagged individuals established that spiny lobsters do indeed exhibit accurate non-visual homing from distances of at least one kilometer. Further research demonstrated remarkable orientation by hydrodynamic, chemical, and geomagnetic senses.

The previous, inaccurate conceptual premise of lobster natural history was replaced as an outcome of that underwater-habitat-facilitated work. The manned habitats enormously facilitated access and logistics over standard scuba for this work on the typical lifestyle of spiny lobster. In addition, the researchers were able to witness behaviors unlikely to occur in captivity, from which they developed new hypotheses.

Sessile reef fauna other than corals have also been the target of extended saturation diving research. One example is from the work of Pawlik (1997, 2011), who used the *Aquarius* habitat to study the demographics of giant barrel sponges, their growth rates, re-attachment of sponges after disturbance, and species preferences of spongivorous fishes using underwater videography. Sponges as competitors for space on reefs were described by Suchanek et al. (1983) for the St. Croix sites. Sponge feeding biology and physiology was also examined by Patterson and colleagues using chambers designed specifically for this purpose (Trussell et al., 2006). Gorgonian corals have been studied in terms of their reproductive biology (West et al., 1993), effects of predators (Harvell and Suchanek, 1987; Ruesink and Harvell, 1990), chemical defenses against predators (Harvell et al., 1993), primary production (Miles and Harvell, 1990), and nutrition (Lasker et al., 1983).

Algal biology has also been an important focus of research using underwater habitats and laboratories. Using *Aquarius*, James Coyer and colleagues studied the mode of propagation of the alga *Halimeda*, a major carbonate producer in reef system. This work was important in understanding the overall dynamics of the algal population on the entire reef (Vroom et al., 2003). This research required long observation times both for the team that studied the algae and for the team that studied the impact of fish on the algae. With long observation times, the algae team was able to observe *Halimeda* "spawning," an event that was later described very precisely in *Halimeda* and other green algae by Clifton (1997).

Earlier work by Hay et al. (1988) using *Hydrolab* showed how diel patterns of growth in *Halimeda* was an effective strategy to minimize losses to herbivores. They performed essentially round-the-clock dives over the course of their saturation mission to show that *Halimeda* produces new, uncalcified tissues that are susceptible to herbivores only at night when herbivore activity is low, rather than during the day when herbivory is intense. These new, nutrient-rich tissues are flushed with photosynthetic pigments only just before sunrise, but they are also increasingly resistant to herbivores as the tissues age and become calcified. These diel patterns in growth and deployment of energy to constituents of the algal thallus (pigments, carbonate) are cued primarily by the timing of light and dark cycles rather than diel changes in seawater chemistry.

Halimeda produces a toxin that mildly affects fishes. Hay et al. (1988) observed a number of fishes feeding on *Halimeda*, but invariably they would take just a few bites until finding it distasteful. On several occasions, they saw fishes, particularly porkfish, *Anisostremus virginicus*, grab bites of *Halimeda,* then

swim off and spit out a few morsels. These morsels were then recovered and analyzed to determine if they could reattach and regrow, which they did. Thus long observation times afforded by saturation diving allowed them to discover sexual and asexual propagation of *Halimeda* at Conch Reef (Walters et al., 2002; Herren et al., 2006), and to document variability in ecophysiology of these algae (Beach et al., 2003). Disturbance effects on *Caulerpa* spp. were also examined earlier in deep reef sites at St. Croix (Williams et al., 1985), as were disturbances in deep seagrass beds (Williams, 1988) and seagrass detritus as a source of nutrition in deep habitats (Suchanek et al., 1985).

CONCLUSION

Underwater laboratories and saturation diving techniques have also been instrumental, if not transformative, in defining the ecosystem parameters of reefs, including their physical oceanography (Shepard and Dill, 1977; Sebens and Johnson, 1991; Leichter et al., 1998), effects of extreme storms (Hubbard, 1992; Aronson et al., 1994), and geology (Adey and Steneck, 1985; Hubbard et al., 1985; Hubbard and Scaturo, 1985). In addition, via the longevity of deployment and support, *Aquarius* and its base station on Key Largo have afforded an opportunity for long-term research in the Florida Keys that would otherwise have been unlikely (Aronson and Swanson, 1997; Miller et al., 2000). The overall effect of the various underwater habitat programs (along with associated technology they have driven) on our understanding of coral reefs and other subtidal habitats has been enormous. With the rapidity of changes in oceans, particularly in shallow coastal systems, these technological assets and their development will continue to be needed for deriving a greater understanding of how best to manage these valuable ecological assets.

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