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SMITHSONIAN CONTRIBUTIONS TO THE MARINE SCIENCES • NUMBER 39

Research and Discoveries

The Revolution of Science through Scuba

Edited by
Michael A. Lang, Roberta L. Marinelli,
Susan J. Roberts, and Phillip R. Taylor

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ABSTRACT
Lang, Michael A., Roberta L. Marinelli, Susan J. Roberts, and Phillip R. Taylor, editors. Research and Discoveries: The Revolution of Science through Scuba. *Smithsonian Contributions to the Marine Sciences*, number 39, vi + 258 pages, 111 figures, 7 tables, 2013. The Smithsonian Institution, the National Science Foundation, and the Ocean Studies Board of the National Research Council convened the "Research and Discoveries: The Revolution of Science through Scuba" symposium on 24–25 May 2010 in Washington, D.C., to celebrate the advances and scientific contributions of research using self-contained underwater breathing apparatus (scuba). This volume presents 19 papers by 60 scholars of research findings, with particular focus on the scientific contributions accomplished using scuba. It is the first major effort to highlight and validate the use of scuba in science by evaluating the output of scientific research in high-impact journal publications. Thirteen papers report research findings and discoveries from around the world in environments such as coral reefs, oceanic blue water, under-ice polar habitats, and temperate kelp forests, providing perspectives on ecological scales and function, physiology, symbiosis and chemistry, biodiversity and behavior, and structured populations. The final six papers are illustrative of underwater research that was not only greatly facilitated by scuba, but could perhaps not have been accomplished without it. Topics range from biological studies on the coral holobiont to ecological roles of major algal groups on reefs and the functional role of small and cryptic metazoans. The research facilitated by scuba and reported in these papers focuses on the scientific results, not necessarily on the research methodologies using scuba to obtain those data and observations, and includes several case studies. Where appropriate, laboratory studies complementary to underwater field observations are referenced. The symposium showed the strong integration and validation of scientific diving within the overall science domain since the introduction of scuba to the science community in 1951. Overarching symposium themes celebrated past, present, and future scientific diving contributions, and evaluated the accomplishments and impact of underwater research on the overall understanding of nature and its processes. Enduring materials from the symposium, including abstracts, speaker biographies, and webcast videos of presentations, have been posted at www.si.edu/sds.

Cover images (left to right): *Pseudopterogorgia elisabethae* sea fan from Carrie Bow Cay, Belize (photo by Raphael Ritson-Williams); *Macrocystis pyrifera* kelp from San Diego, California (photo by Michael A. Lang); *Leptonychotes weddelli* seal from McMurdo Station, Antarctica (photo by Michael A. Lang).

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RESEARCH FACILITATED BY SCUBA

Executive Summary

The Smithsonian Institution, the National Science Foundation, and the Ocean Studies Board of the National Research Council convened a symposium in May 2010 in Washington, D.C., to celebrate the scientific contributions and value of scuba as a research methodology. The "Research and Discoveries: The Revolution of Science through Scuba" symposium presented research findings by U.S. scholars with particular focus on the scientific contributions accomplished using self-contained underwater breathing apparatus. This symposium was the first major effort to highlight and validate the use of scientific diving techniques by evaluating the output of scientific research that has been presented through high-impact journal publications.

During the two-day event, fifty scholars discussed their research findings and discoveries from around the world on coral reefs, blue-water environments, under-ice polar habitats, temperate kelp forests, and other systems of interest. This symposium showed the strong integration and validation of scientific diving within the overall science domain since the introduction of scuba to the science community in 1951. Overarching symposium themes celebrated past, present, and future scientific diving contributions, and evaluated the accomplishments and impact of underwater research on our overall understanding of nature and its processes. Exemplars of the first generation of scientific diving research include Paul Dayton's groundbreaking ecological work under Antarctic ice sheets; William Hamner's pioneering studies of gelatinous zooplankton in surficial blue waters of the open ocean; Mark and Diane Littler's multidisciplinary long-term phycological studies; William Herrnkind's crustacean behavioral ecology research; John Pearse and Michael Foster's kelp forest ecological work; and Ian Macintyre, Peter Glynn, and Chuck Birkeland's baseline-establishing coral reef research.

Approximately thirty years after the advent of scuba another research tool, molecular techniques, became more generally available to marine scientists. Together these two tools offer broad techniques to further our understanding of biodiversity, systematics, and genomics. The advances in biopharmaceutical work and the understanding of chemical defenses of marine organisms, harmful algal bloom outbreaks, and invasive species have encouraged more scientists to don scuba gear and conduct their research under water. In an era of increasing occurrences of multiple stressors on such systems as coral reefs, deep-time geological studies show patterns and trends of previous episodic events. It continues to be difficult to understand ecological processes and interactions and the functioning of nature itself in the underwater environment without actually immersing oneself in it to make firsthand observations and data collections.

Enduring materials from the symposium, including abstracts, speaker bios, and webcast videos of presentations, have been posted on the website www.si.edu/sds.

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The Revolution of Science through Scuba

Scuba Revolutionizes Marine Science

Jon D. Witman, Paul K. Dayton, Suzanne N. Arnold, Robert S. Steneck, and Charles Birkeland

ABSTRACT. Scuba provides scientists with the capacity for direct observation and experimental manipulation in underwater research. Technology allows broader-scale observations and measurements such as satellite detection of coral bleaching up to a global scale and LIDAR determination of reef-wide topographic complexity on landscape to regional scales. Scuba-based observations provide a means of ground truthing these broad-scale technologies. For example, ground truthing the readings on a scale as small as a video transect taken at 50 cm above the substratum can reveal that the previously confident interpretation of the transect data from the video analysis was inaccurate. At the opposite end of the spatial continuum, electron microscopy and DNA analysis provide the capacity to determine species traits at a scale too fine for direct observation, while observations made during the collection of samples by scuba can provide vital information on the context of the tissue sample collection. Using our hands and eyes to set up experiments under water is less expensive and more adaptable to the unexpected topographic complexities of hard substratum habitats than doing so with submersibles, robots, or via cables from ships. The most profound contribution of scuba to underwater science, however, is the otherwise unobtainable insights provided by direct observation. Ecology is not always predictable from species traits because the behavioral or interactive characteristics of marine organisms together cause them to function in surprising and often synergistic ways. Although our research is often framed around hypotheses developed by deductive reasoning, the solutions to research questions cannot always be found by deduction. Data taken by video or sensors from satellites, tow-boards, or other vehicles are all incomplete in their context evaluation in comparison to direct observation by the human brain. Scuba provides a unique ability to integrate detail with context across small and large scales. The history of marine research has provided numerous examples of mysteries that would have been unsolved and findings that would have been misinterpreted with confidence if not for direct observation on scuba. We illustrate this aspect of the utility of scuba for science with three examples of how direct observation of species in their natural habitats has furthered the development of ecological concepts.

INTRODUCTION

Since the ecological impacts of humans have become global (climate change, lowering of ocean pH, loss of one-third of global topsoil, deforestation, desertification, transport of invasive species, etc.), scientists have felt the necessity to measure ecological processes on larger spatial scales. The April 2004 issue of the journal *Coral Reefs* was devoted entirely to remote sensing of coral reefs, using sensors from satellites and aircraft to assess percentage of living coral cover, percentage of coral bleaching, biomass of fleshy algae, rugosity of substratum, transport of dissolved organic matter, transport of fine-sediment, and other variables on a large scale. While the focus on global and ecosystem processes is indeed imperative (Dayton and Tegner, 1984; Sala, 2001; Witman and Roy, 2009), controlled field experiments and carefully designed surveys and monitoring

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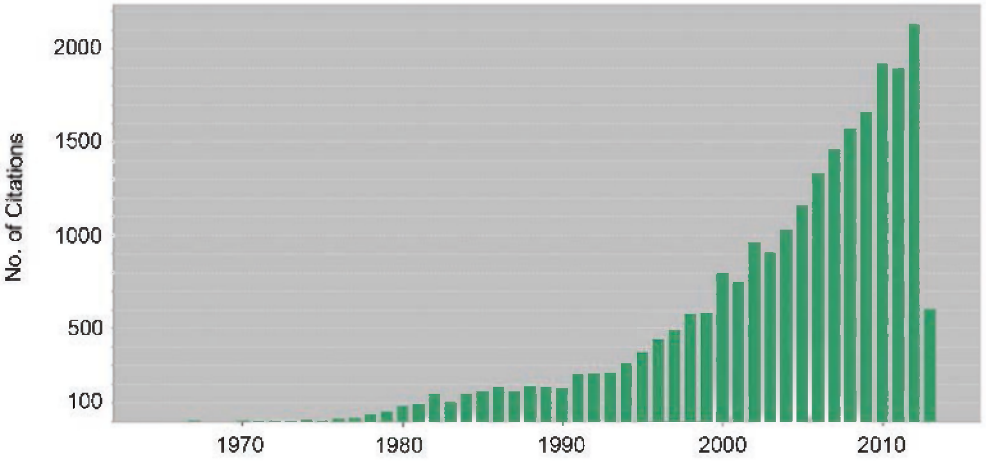

FIGURE 1. The use of scuba in the production of scientific papers in biology and oceanography has increased exponentially over the past few decades (data from ISI website).

programs could be completely misinterpreted if analysis of data obtained via scuba is not also incorporated.

Scuba created a scientific revolution by providing direct access to underwater habitats composing a large part of the biosphere. While there have been many important specific advances (noted in this volume), we believe that the overarching benefit of scuba for marine population, community, and ecosystem ecology has been to facilitate the direct observation and manipulations of individual organisms and their surrounding conditions. Prior to scuba, subtidal organisms were studied primarily by peering into the water on calm days (e.g., Darwin, 1909; Johnson and Skutch, 1928) and by analyzing specimens collected by fishing, dredging, or plankton nets (e.g., the HMS Challenger expedition). The invention of scuba enabled scientists to observe the behavior and ecology of organisms in their natural habitats, quantify patterns, study interactions, and conduct experiments to test hypotheses about ecological processes.

Scuba has been associated with an increasing number of scientific publications (Figure 1) and the rapid increase in our knowledge of marine biodiversity. One example: since the 1950s, there has been a consistent increase in the number of newly identified marine fish species per five-year period, from 305 in 1954–1958 to 846 in 2004–2008. Eschmeyer et al. (2010) documented this increase and emphasized the role of scuba.

DISCUSSION

Ground Truthing Theory and Ground-Breaking Findings

Hypotheses are tested by replicated, controlled, manipulative field or laboratory experiments, or by determining if the patterns discerned by surveys or monitoring programs correlate with the patterns predicted by the hypotheses. But the hypotheses to be tested are created by deductive reasoning of prior concepts. Without direct observation by scuba, models can lead to misconceptions. For example, in the 1960s, an unresolved issue in the data for coral reef ecosystems was that there was not nearly enough plankton to support the large biomass of suspension-feeding invertebrates and planktivorous fishes. Extensive and repeated surveys only reinforced the existence of this inconsistency in the models of required supply for the demand, until Bill Hamner and colleagues on scuba directly observed the behavioral and distributional characteristics of zooplankton on coral reefs (Hamner and Carleton, 1979). The behavior of the zooplankton indicated that the majority were resident and not drifting in from the surrounding waters. The scuba-based observations indicated that it was not possible for standard, surface-towed plankton nets to adequately quantify zooplankton on coral reefs. This led to the development of plankton traps that were more appropriate for assessing the zooplankton resident on coral reefs (Porter and Porter, 1977; Alldredge and King, 1977). The results of studies with demersal plankton traps developed and operated via scuba totally changed the understanding of the behavior and distribution of zooplankton and their role in coral reef ecosystem processes. Without scuba, the energy balance of coral ecosystems in the oligotrophic mid-ocean would still be a mystery.

Evolution of biotic characteristics is not entirely predictable by deductive reasoning, so knowledge of natural history cannot be complete without learning from direct observation in nature. Deductive reasoning provides a series of alternative hypotheses, but the truth might be in none of the hypotheses because we were not sufficiently circumspect of key aspects of natural history. We might have concluded the study with accepting that the results confirmed the best of the available hypotheses, even though the closest fit was false. Indeed, many models make the right predictions for the wrong reason because the modelers lack critical natural history (Dayton, 1973) available with scuba. For example, until the mid-1970s blue water oceanographers would bemoan the ubiquitous slime that fouled the inside of their nets during plankton tow surveys. Then, Hamner et al. (1975) published a landmark study showing that the slime was in fact a huge predator now categorized as gelatinous zooplankton.

Scuba allows a more panoramic, multi-dimensional, and unrestricted view than do cameras or other sensors that are developed for a subset of all signals characteristic of the underwater world. No instrumentation in the ocean has such detailed perception across large scales as humans with scuba. It is the capacity of scuba observers to integrate nearly simultaneous observations from the calices of corals to the presence of apex predators that makes it possible to verify our perceptions. Although satellites and LIDAR from aircraft generate information on a larger scale than humans, their perceptions are not fine enough to distinguish species. While DNA analysis and electron microscopy record information on a finer scale than possible by humans with scuba, the human observer has the essential ability to place the tissue or corallite sample in its natural context. It is this unique ability to integrate detail with context across small and large scales (e.g., from the details of the coral polyp to the community structure of apex predators) that makes the observer on scuba absolutely vital for the advancement of marine science.

On the finer scales of direct observation, the species identification of small individuals of corals such as mound-shaped *Porites* and encrusting *Montipora* in the central and western Pacific and Indian Oceans cannot be done reliably from video images or from submersibles. *Porites randalli*, a ubiquitous and often most abundant coral on American Samoan reefs (Forsman and Birkeland, 2009), is readily recognized by a scuba diver, but for decades (1917–1978), specimens of this species had been assumed to be an assortment of small individuals of other species. Although specimens can be collected by other means (e.g., hard-hat diving, submersibles, dredge, trawl, etc.) for genetic analyses of tissue samples and electron microscopy of corallite structure for final species descriptions, the awareness of the existence of the most abundant coral species would not have occurred without scuba. It is possible that once the distinction of this species was recognized by humans through the use of scuba, it might also be recognized by video or submersible. Without scuba, data analysis from surveys of American Samoan reefs might have failed to identify the most common species and mistakenly elevate the abundances of several other less common species of *Porites*. For example, in a 1995 survey that included 140 coral species, there were 2,289 recordings of *Porites randalli,* which composed 18% of the coral colonies; spreading these 2,289 data over several less common species would have given very misleading survey results (Forsman and Birkeland, 2009).

On the larger scales that apex predators occupy, observers with scuba are able to perceive potential biases of underwater imaging systems typically used in surveys. When surveying with video or other camera systems, the equipment is usually unidirectional with a fixed field of view and is not that sensitive to unexpected insights from other dimensions. For example, when doing tow-board surveys of large fishes, some species (e.g., the large jack *Caranx ignobilis* and the sharks *Carcharhinus amblyrhynchos* and *C. galapagensis*) show a tendency to aggregate behind towed divers (Benjamin Richards, NOAA Pacific Islands Fisheries Research Center, personal communication). On coral reefs, *Sphyraena barracuda* are known to swim above and behind divers—a commonly noted behavior (C. Birkeland, J. Witman, unpublished observations). These barracuda would not be recorded by a forward-facing camera system, which could lead to large underestimates of population densities.

Studies of predation on corals in Hawaii provide another example of how conclusions would have been very misleading without direct observations by scientists on scuba. The most common coral on the Hawaiian main islands, *Porites compressa,* receives an average of 69 fresh bites/m^2, and these bites were attributed to the common parrot fishes (Jayewardene et al., 2009). However, direct observations demonstrated that different corallivorous fishes have characteristically different bites (Jayewardene et al., 2009: fig. 2) and that these bites were made by puffers (*Arothron* spp.) that are relatively scarce. This was a conundrum until scuba divers observed that less than 2% of the bites of parrot fishes in Hawaii were on living corals and these few exceptions were at the edge of the coral where the coral contacted algae (Ong, 2007). Although the puffers rarely showed up on survey data, direct observations indicated that the puffers were common but were skittish in their behavior and darted for cover beneath large *Porites* colonies or other shelter. Fishes with such behavior are not adequately represented in survey data (Jennings and Polunin, 1995). It is the capacity of observers with scuba to integrate observations from small to large scales that provides us with the unique ability to verify our perceptions.

Scuba also provides insight into dimensions of topographically complex benthic habitats that might be missed by other survey methods. For example, coral planulae in shallow waters (<10 m depth) tend to settle and undergo metamorphosis on undersurfaces or on vertical surfaces, sometimes beneath algae (Birkeland, 1977). Studies with video transects might conclude that the broad spatial extent of the deterioration of the reef to rubble by *A. planci* and bioerosion might have reduced the larval supply, whereas scuba-based observations have suggested that diverse larval supply was sufficient and that survival of settled corals on unstable substrata was low or nonexistent. Subtidal surveys or experimental studies without direct observations by divers on scuba could render unwarranted conclusions.

In all of our examples above, breakthroughs resulted from applying scuba to key ecological questions. Note, however, that most of these scientific discoveries occurred around or before the late 1970s. Considering the accelerating rate of scientific publications that followed (Figure 1), it is clear that the early observations primed the pump of the scuba science revolution. In the remaining sections, we discuss applications of scuba to management, how it has promoted new insights into natural history, aided paradigm shifts, and contributed to ecological theory in a least three key areas of ecological research.

Revealing Heterogeneity for Improved Management

For decades, details of the life history of marine species were relatively unknown to biologists charged with managing economically important fisheries. Information was acquired primarily through catch data and trawl surveys. Discoveries made by scuba in temperate, tropical, and subarctic waters are now instrumental in managing fisheries and conserving ecosystems. For example, before scuba diving, American lobsters (*Homarus americanus*) in the Gulf of Maine were assumed to have a relatively homogenous population, and no one knew where lobsters recruited. Experiments via scuba allowed us to determine that this species selects cobblestone habitats as its nursery ground, and there it is safe from predators for the first few years of life (Wahle and Steneck, 1991, 1992). When the lobsters emerge from these early, benthic-phase refugia, they have outgrown their predators; thus this species has remarkably low post-settlement mortality (Butler et al., 2006; Steneck, 2006a). As a result, populations of this lobster have settlement-driven demography (Palma et al., 1999), with "hotspots" fueling high population densities (Steneck and Wilson, 2001) that drive intraspecific competition pressure (Steneck, 2006b). These experiments show that as population densities increase, competition increases and a counterintuitive thing happens: large, competitively dominant lobsters, which have no choice but to fight with every lobster within their range of detection, diffuse from the zones of competition to where population and trap densities are lower; thus, by default, the chance of being caught declines (Steneck, 2006b). This allows numbers of large reproductive lobsters to build up and serve as broodstock for future generations (Steneck, 2006a). Annual monitoring via scuba of lobster recruitment along the coast of Maine contributes to the American lobster fishery's status as one of the best managed fisheries in the world.

Decades of research via scuba have documented cascading processes and shifting baselines on coral and temperate reefs (Witman and Sebens, 1992; Dayton et al., 1998; Bellwood et al., 2004; Tittensor et al., 2009). Since the 1970s, diving scientists have documented the structuring dynamics of overfishing, declining herbivory, increasing algal biomass, and coral recruitment on coral reefs (reviewed in Sandin et al., 2010). The ramifications of overharvesting predators of sea urchins on coral and temperate reefs are now well known (Estes and Duggins 1995; McClanahan et al., 1999; reviewed in Steneck et al., 2002). In sum, this work has influenced the development of many marine protected areas, and the establishment of laws restricting fishing gear and the take of certain ecologically critical fish such as herbivores. Without spatially explicit scuba-generated data, this information would not be available for application to fisheries management and policy decisions.

Grasping Natural History

The ability to observe marine life in situ has fostered extensive research on intrinsic variables of organisms. While the observational–inductive approach to constructing general scientific theories suffers from the inability to falsify hypotheses (Popper, 1959), in situ observation nonetheless provides a valuable grounding in natural history that is required to understand the population biology of and interactions among organisms to gain a mechanistic understanding of the functioning of marine communities and ecosystems. Addressing many of the most pressing societal issues—such as how populations and communities will react to and recover from climate change and human-induced disturbances—requires a firm grasp of natural history (Dayton, 2003), without which ecologists may accept the right hypothesis for the wrong reason (Dayton, 1973), fail to recognize strong controlling interactions of consumer species, or oversimplify complex ecological communities, leading to inaccurate generalizations. Although investigations of climate change effects typically explain temporal population and community trends by physical factors extrinsic to local populations, substantial temporal variation may also be driven by intrinsic variables such as Allee effects, allocation tradeoffs, life history traits, behavior, and physiological limitations of organisms. The value of scuba lies in its ability to provide a window to view these fundamental attributes.

As we find ourselves in an age where people are increasingly disconnected from nature, scuba can also be a tool to attract young people to science. The sheer excitement of breathing under water and seeing a hidden world can inspire the next generation of scientists to take an interest in natural history, just as it inspired us.

Paradigm Shifts

The aquatic and marine sciences are relatively unique because most of what is studied is underwater and out of sight. Traditionally, this was handled by oceanographers measuring particles and concentrations to establish correlations and construct predictive models. In many cases, bottom-up (i.e., resource-driven) explanations prevailed when the organisms were treated as invisible components of the system.

G. E. Hutchinson (1959:147) pointed out that both Wallace (1858) and Elton (1927) asserted that food webs were constructed such that "the predator at each level is larger and rarer than its prey." This pattern became known as the Eltonian food pyramid and it developed into the field of trophic dynamics (sensu Lindeman, 1942). In this view, each trophic level is "successively dependent upon the preceding level as a source of energy" (Lindeman, 1942:415). In other words, the primary interactions resulted from lower trophic levels fueling those at the top. Today, this is called bottom-up control of community structure (sensu Power, 1992). Hairston et al. (1960) proposed a decidedly different interpretation of that pattern. Rather than resources at lower trophic levels fueling higher trophic levels (bottom-up), consumers at higher trophic levels limit the abundance of lower trophic levels (top-down) (sensu Power, 1992). This paradigm shift is much more than changing terminology. While predators had long been considered part of natural communities, they had been thought of as "passengers" carried by the resources available in the ecosystem. What had been underappreciated was that predators could be "drivers" of the system by limiting the abundance of their prey. This new way of thinking opened new avenues of ecological theory focused on the community-wide impacts of higher-order predators on organisms at lower trophic levels. This paradigm shift resonates today in high-impact scientific journals (Estes et al., 2011).

What scuba diving allowed marine ecologists to do was to test these differing world views by observing and manipulating direct ecological interactions such as predation and competition. With scuba, correlative studies could identify patterns but were no longer considered proof of what caused those patterns. Quantitative, experimental marine ecology in the broader ocean was possible primarily because in situ manipulations could be conducted by scuba diving (Witman and Dayton, 2001). In the sections below, we discuss how three ecological topics informed and enlightened by an in situ experimental approach taken by scuba diving ecologists have developed or broadened ecological concepts. This is not intended to be an inclusive discussion of the topic, but rather a means of illustrating the overarching scientific value of scuba.

Top-Down Regulation of Food Webs

The importance of both direct (consumptive) and non-consumptive (behavioral) trophic cascades is becoming well understood in ecology (Peckarsky et al., 2008). Scuba has made it possible to observe and understand both important consumptive effects and behavioral responses (Siddon and Witman, 2004) to predation that cascade down to lower trophic levels. While the sea otter–sea urchin–kelp trophic cascade is well known as a classic consumptive cascade (Estes and Palmisano, 1974; Estes and Duggins, 1995), behavioral interactions of urchins with their predators are sometimes overlooked despite the fact that early studies documented strong reactions. For example, escape behaviors from a sea star resulted in the urchins being an important part of the diet of anemones in Washington state (Dayton, 1973). Using scuba, Mauzey et al. (1968) and Dayton et al. (1977) found many examples of effective escape behaviors that critically modify our understanding of foraging biology because it forces a careful consideration of "catchability" into our interpretation of trophic dynamics.

In addition, perceptive observers are able to observe nuances of behavior that provide critical understanding to various patterns seen in nature. For instance, clear areas around foundation species (Dayton, 1975) were thought to result from allelopathic factors as in chaparral-dominated plant communities. However, Randall (1965) demonstrated that on coral reefs, they resulted from a zone of fear in which grazer foraging was restricted by the presence of predators, providing a mechanistic explanation for the commonly observed coral reef grazing halos. More recently, Siddon and Witman (2004) used scuba in the Gulf of Maine to examine variation in the strength of trophic cascades in different but common types of shallow subtidal habitats and found that the fear of lobsters prevented rock crabs from foraging on urchins, which caused less predation on mussels, providing the first example of a non-consumptive trophic cascade in subtidal ecosystems. Recent experiments in this system indicated that interspecific competition between the dominant lobster and subordinate crab caused crabs to escape vertically from lobsters by climbing up kelp stipes (Wells et al., 2010). Grabowski and colleagues have similarly found strong effects of predator avoidance behaviors on trophic cascades in subtidal habitats of Chesapeake Bay (Grabowski and Kimbro, 2005; Grabowski et al., 2008). It is clear that scuba-based research will continue to stimulate important insight into the role of behavior in driving trophic cascades.

Emergent Properties of Communities Revealed by Studying Functional Groupings and Guilds

The structure of ecosystems and communities is usually described from a simple tally of what is there. Terrestrial and aquatic ecologists were occupied with determining number of species, how biomass is distributed, and which species dominate for nearly a century before the new focus on ecological function emerged. Ecosystem function usually relates to driving processes such as reproduction, recruitment, growth, productivity, stress, competition, predation, and biodiversity.

In recent decades, several lines of research determined that functional attributes of organisms may be more important than their relatedness. For example, in the Gulf of Maine, the largest crab, *Cancer borealis,* forages bivalve prey in ways more similar to the lobster *Homarus americanus* than to its closely related congener *C. irroratus*. The latter crab forages identically to an unrelated non-native green crab, *Carcinus maenus* (Moody and Steneck, 1993). Similar shared functional attributes have been observed among herbivorous mollusks (Steneck and Watling, 1982), reef fishes (Hixon, 1997; Bellwood et al., 2004), and benthic marine algae (Steneck and Dethier, 1994). By observing behaviors in situ we come to develop new paradigms on how organisms use resources and interact. These new paradigms allows us to advance and test falsifiable hypotheses. As we do this we learn new things about these ecosystems, such as the new concept of sleeping functional groups (Bellwood et al., 2006).

Positive Effects of Associated Species on Habitat Stability and Biodiversity

Naturalists and early ecologists recognized that many species were associated with biogenic habitats such as forests and thickets of vegetation on land and beds of algae and mollusk and coral reefs in the sea (Elton, 1927; Thorson, 1957). Indeed, much early research in ecology described patterns of species associations. Decades of research since have concentrated on mechanistic explanations for patterns of species association and community assembly. Prominent research efforts were directed toward explaining the coexistence of species in these associations via competition (Connell, 1961), predation (Paine, 1966), and disturbance (Dayton, 1971). While there was a growing recognition of the role of mutualisms in population and community ecology, initial work on the subject was more focused on the role of coevolution in shaping mutualistic interactions and their geographic distribution (Boucher et al., 1982; Futuyma and Slatkin, 1983; Vermeij, 1983; Addicott, 1984) and the biology of individual mutualists than on their potential impact on communities and ecosystems. Mutualistic relationships were considered dynamically fragile and more prevalent in stable environments (May, 1981), an idea that is contradicted by recent research in environmentally stressful habitats (Bertness, 1985; Witman, 1987; Leonard et al., 1999). General predictive models for mutualistic interactions as a specific type of positive interaction were developed later (Bertness and Callaway, 1994) and have remained an influential component of theoretical ecology (Bruno et al., 2003, 2005).

Scuba-based observations and experiments helped promote the idea that positive interactions among species play key roles in the maintenance of biodiversity by facilitating the persistence of habitats created by foundation species (sensu Dayton, 1975), which are now often called physical ecosystem engineers (Jones et al., 1994). This critical role was demonstrated for Panamanian coral reefs in the early 1970s by elegant experiments following Peter Glynn's observation that *Trapezia* crabs and *Alpheus* snapping shrimp living within branching pocilloporid coral colonies prevented the crown of thorns starfish *Acanthaster planci* from feeding on the corals (Glynn, 1976; Figure 2A). Pocilloporid colonies where protective symbionts were experimentally removed suffered higher rates of destruction by *A. planci*, and coral diversity was higher where the crown of thorns starfish was prevented from foraging (Glynn, 1976). Another example of positive interactions affecting foundation species, and ultimately, species diversity, comes from the Caribbean forereef slope (Wulff and Buss, 1979). At a time when much of coral reef ecology was focused on the role of competition (Lang, 1973), Wulff and Buss (1979) hypothesized that sponges enhance the persistence of foliaceous corals on the steep forereef slope by binding the corals to the reef frame (Figure 2B). Corals fell off the reef slope on manipulated reefs where divers removed the sponges from the coral interstices, resulting in elevated (40% higher) coral mortality compared to controls. Later work in similar habitats showed that the underside of foliaceous corals supports an exceptionally high diversity of epifaunal invertebrates (Buss and Jackson, 1979). Thus, the positive effect of sponges on foliaceous corals enhances community-wide biodiversity. The last example comes from cold temperate waters where large beds of horse mussels (*Modiolus modiolus)* live on subtidal rocky substrata supporting an associated fauna of benthic invertebrates that Thorson (1971:175) called "the most luxuriant society cold temperate seas can offer." Scuba-based sampling and experiments indicated that the mussels were foundation species, supporting a highly diverse community of infaunal invertebrates by providing a refuge from predation in the mussel beds (Witman, 1985). The subtidal zonation at wave-exposed sites in the Gulf of Maine where this research was performed showed that the shallow subtidal was dominated by Laminarian kelp, giving way to a zone dominated by horse mussels at intermediate depths (Witman, 1987). The existence of some mussel beds in the shallow kelp zone was enigmatic, considering that dislodgement by kelp overgrowing the horse mussels during storms was the most significant source of mussel mortality, until divers observed that the mussel beds in the kelp zone were packed with green sea urchins (*Strongylocentrotus droebachiensis*) (Witman, 1987; Figure 2C). Subsequent manipulations demonstrated that the horse mussel–sea urchin relationship was a facultative mutualism, as mussel mortality from kelp-induced dislodgement was reduced by resident sea urchins grazing kelp off the mussels and, in turn, the sea urchins achieved a refuge from predation while in the beds (Witman, 1987).

Taken together, these three case studies clearly demonstrate that positive interactions are essential for the persistence of foundation species and for maintaining high levels of biodiversity, an area of recent emphasis in ecology (Thomsen et al., 2010). In all three cases, the integrity of the foundation species depended upon cryptic or semi-cryptic species. The positive feedback would not have been revealed without first-hand observations by scuba divers who detected positive interactions among the organisms because they studied them in their natural environments.

CONCLUSIONS

Scuba has stimulated a revolution in marine science analogous to manned space flight and the microscope. We have been able to more carefully construct and repair equipment in space since the development of manned space flight. Similarly, a diver's hands are more efficient, more adaptable, and less expensive for setting up experiments on a topographically and biologically complex substratum than arms from a submersible or a robot.

The invention of scuba was also a technological advance analogous to the invention of the microscope, an instrument that revolutionized our study of microbes from deductions to actually seeing how cells behave and are constructed. The most profound contribution of scuba is having the scientist set up the experiment and actually be present to observe any unexpected alternative hypotheses that were not available when the otherwise carefully designed monitoring program or controlled replicated manipulative experiment was designed (e.g., Dayton, 1973; Brandt et al., 2012). Experiments are designed to test specific alternative hypotheses we already have in mind by deductive reasoning ("all possible alternatives") when we conceive the experiment.

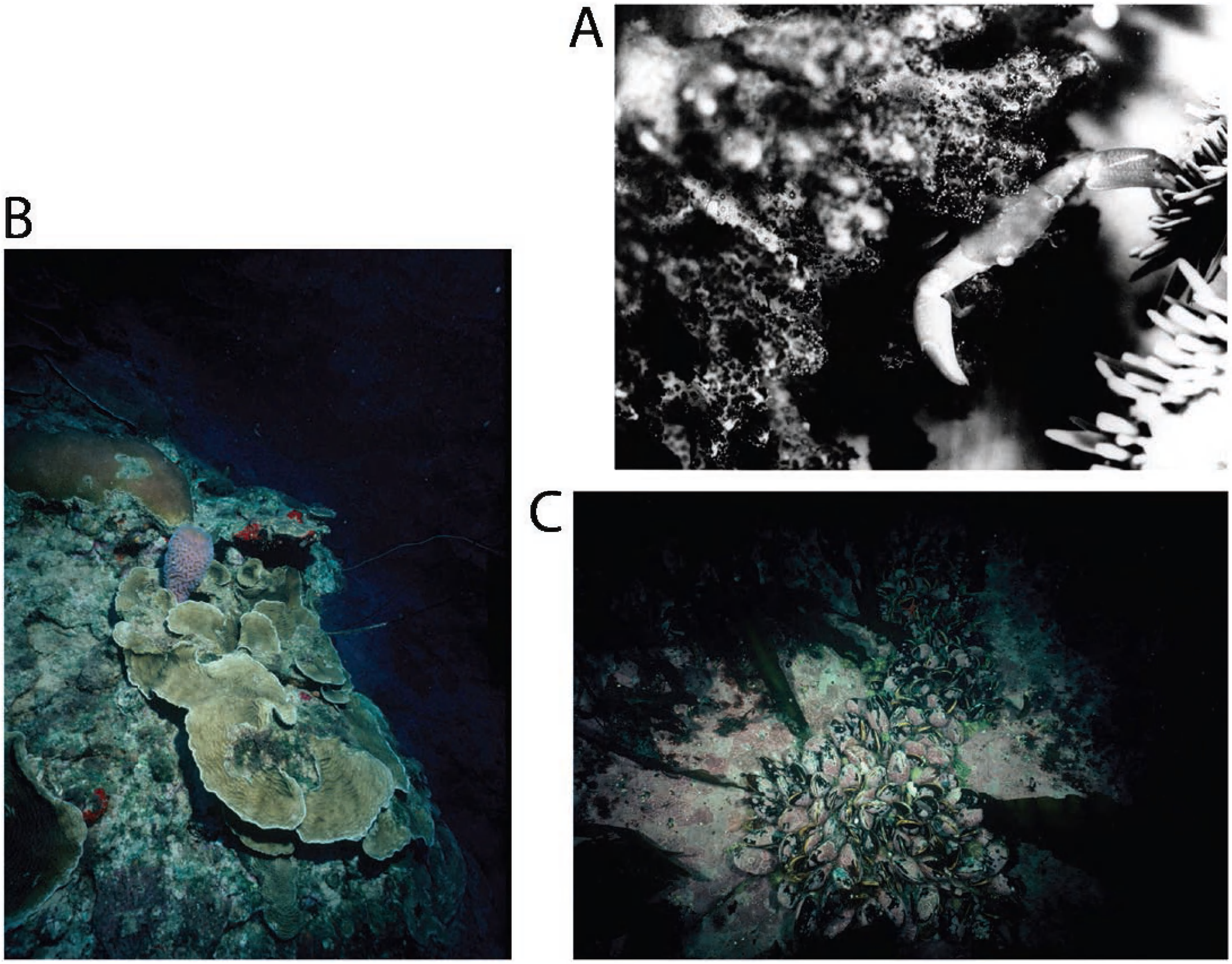

FIGURE 2. (A) *Trapezia* crab within a pocilloporid coral colony pinching a crown of thorns starfish *Acanthaster planci*, which deters it from consuming the coral. Red arrow points to chelae of *Trapezia* (photo from video by P. Glynn). (B) Foliose corals (*Agaricia* spp.) of the deep forereef slope in Jamaica. Sponges bind these corals to the reef frame to prevent them from falling off the slope (photo by J. Witman). (C) A mutualism between horse mussels (*Modiolus modiolus*) and green sea urchins (*Strongylocentrotus droebachiensis*) in the shallow kelp zone, Gulf of Maine. The sea urchins are grazing the kelp off the mussel shell, preventing high mussel mortality from kelp-induced dislodgement during storms. The sea urchins obtain a refuge from predation while in the mussel beds. The positive interaction enables mussel beds to persist, supporting diverse communities of associated invertebrates (photo by J. Witman).

An apparently successful experiment that “proves” one of the preconceived hypotheses might be hiding the truth of a third or fourth hypothesis that was not preconceived. However, a diver on hand might observe the true situation. One problem with deductive reasoning is that we are convinced that our experiment or survey has covered all possible alternative hypotheses. The value of observation is that discoveries of natural processes do not necessarily require deductive logic, and this is where scuba makes a fundamental contribution—providing the means to make novel, direct observations.

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Diving into the Past: Scuba and the Temporal Dimension of Coral Reefs

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ABSTRACT. A variety of sampling techniques afforded by scuba diving have made it possible to study the Holocene history of coral reefs in detail. This paper describes results of three geological techniques and illustrates them with examples from our own work in the Caribbean. First, cores extracted with a hydraulic drill from cemented reef frameworks provided the complete history of a fringing reef off the Caribbean coast of Panama and documented a relict reef stranded by rising sea level off St. Croix. Second, surface samples collected from a coral death-assemblage helped explain the demise of an algal-dominated reef off the southern coast of Barbados. Third, push-cores from uncemented reefs in the Belizean barrier-reef lagoon and a coastal lagoon in Panama revealed that 3,000 or more years of compositional stasis were followed in recent decades by precipitous turnover events, in which the previously dominant corals were replaced by a different species. Understanding the geological history of coral reefs over the last several thousand years is critical to predicting their response to climate change, alterations in land use, and other natural and anthropogenic perturbations.

INTRODUCTION

Among its many contributions to marine science, scuba diving has enabled researchers to collect vital information on the Holocene history of coral reefs. Historical information can be compared to the reefs' present-day status to explain current conditions and predict the future. In this paper we explore the contribution of scuba to the historical analysis of reefs by describing three methods of geological sampling. The geology of coral reefs has been reviewed in detail elsewhere (Aronson, 2007; Montaggioni and Braithwaite, 2009); here we focus on scuba-based techniques, which we illustrate with examples from our own research. The salient point is that without the technology of scuba diving much of this critical information would remain inaccessible.

ROTARY DRILLING

With the introduction of an underwater, hydraulically powered drill in the early 1970s (Macintyre, 1978), it became possible to collect cores from cemented frameworks across an entire reef, not only above water but underwater on scuba as well (Figure 1). Drilling revealed the complete Holocene history of a fringing reef off Galeta Point, Panama (Macintyre and Glynn, 1976). Cores collected at water depths of 0–10 m showed a reef about 14 m thick, with six distinct reef facies (Figure 2).

1. Back-reef sediment facies: This facies consists of skeletal debris composed mainly of *Acropora palmata*, *Acropora cervicornis*, *Porites furcata*, *Agaricia agaricites*, and

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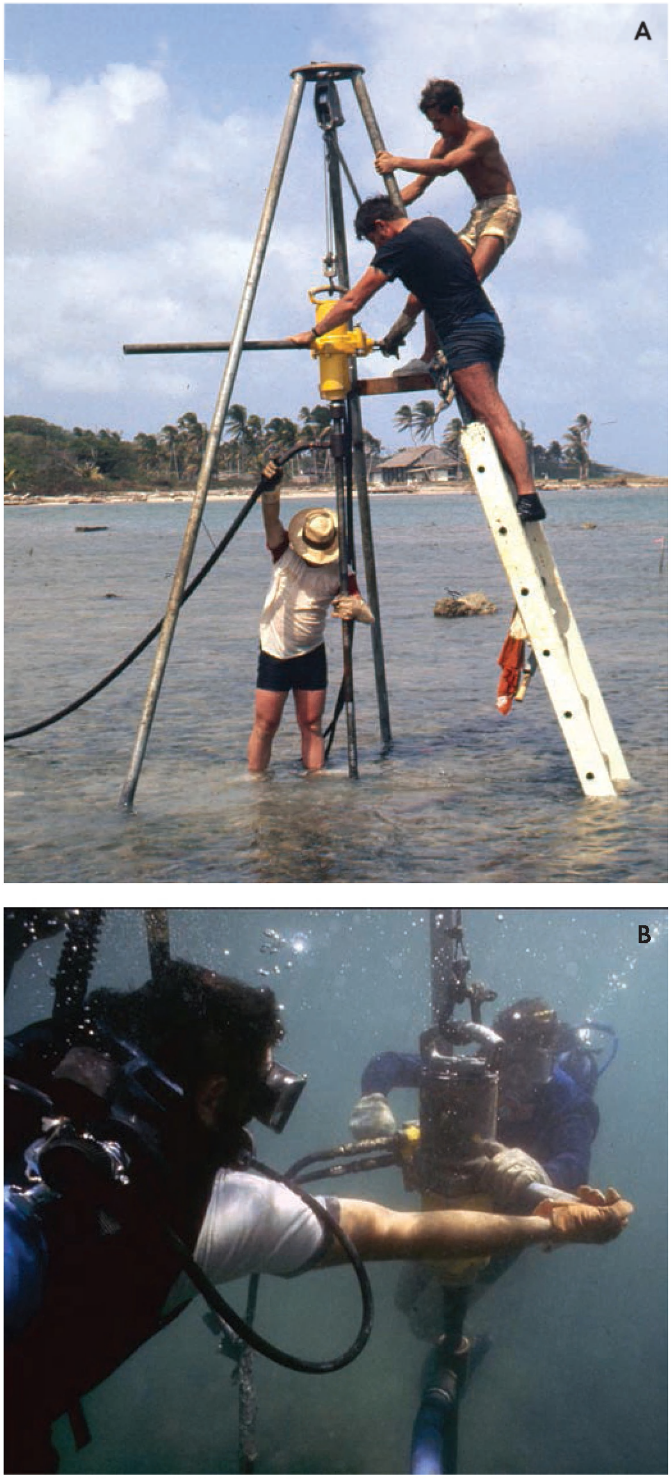

FIGURE 1. Collecting cores from Galeta Reef, Panama, above (A) and below (B) the sea surface with a hydraulically operated drill (photos courtesy of Ian G. Macintyre).

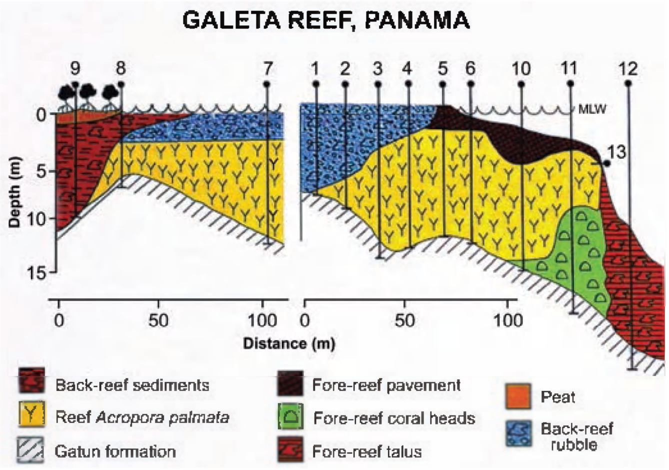

FIGURE 2. Transect across Galeta Reef showing the six reef facies and peat accumulation.

mollusks in a *Halimeda*-rich muddy sand. The top of this facies grades into a calcareous mangrove peat.

2. Reef-flat rubble facies: The rubble derives from a variety of coral species, including *Acropora palmata*, *Diploria* spp., *Agaricia agaricites*, *Millepora complanata*, and *Porites astreoides*. Most of this skeletal debris is water-worn, extensively bored, and encrusted.
3. Reef *Acropora palmata* facies: This main structural framework of Galeta Reef ranges from 3 to 11 m thick and consists primarily of well-preserved *Acropora palmata*. Growth patterns indicate that most of the *Acropora palmata* has not been overturned.
4. Fore-reef pavement facies: This facies is heavily indurated by submarine cement and extends from the reef crest to the drop-off at the outer edge of the reef. It contains a high-energy assemblage consisting of crustose coralline algae, *Millepora complanata*, *Agaricia agaricites*, and *Porites astreoides*. Much of this skeletal material has been obliterated by multicyclic boring and cementation.
5. Fore-reef coral-head facies: This facies occurs only at the base of the outer edge of the reef framework and consists of a mixed assemblage of massive corals, including *Dichocoenia stokesi*, *Siderastrea siderea*, *Porites astreoides*, and the *Orbicella annularis* species complex. Most of these corals show extensive bioerosion and are in-filled with submarine cement.
6. Fore-reef talus facies: The principal components here are fragments of coral, crustose coralline algae, bryozoans, mollusks, and *Millepora* spp. in a matrix of mud and sand.

As confirmed by eighteen radiocarbon dates, the Galeta Reef has gone through several stages of development (Figure 3):

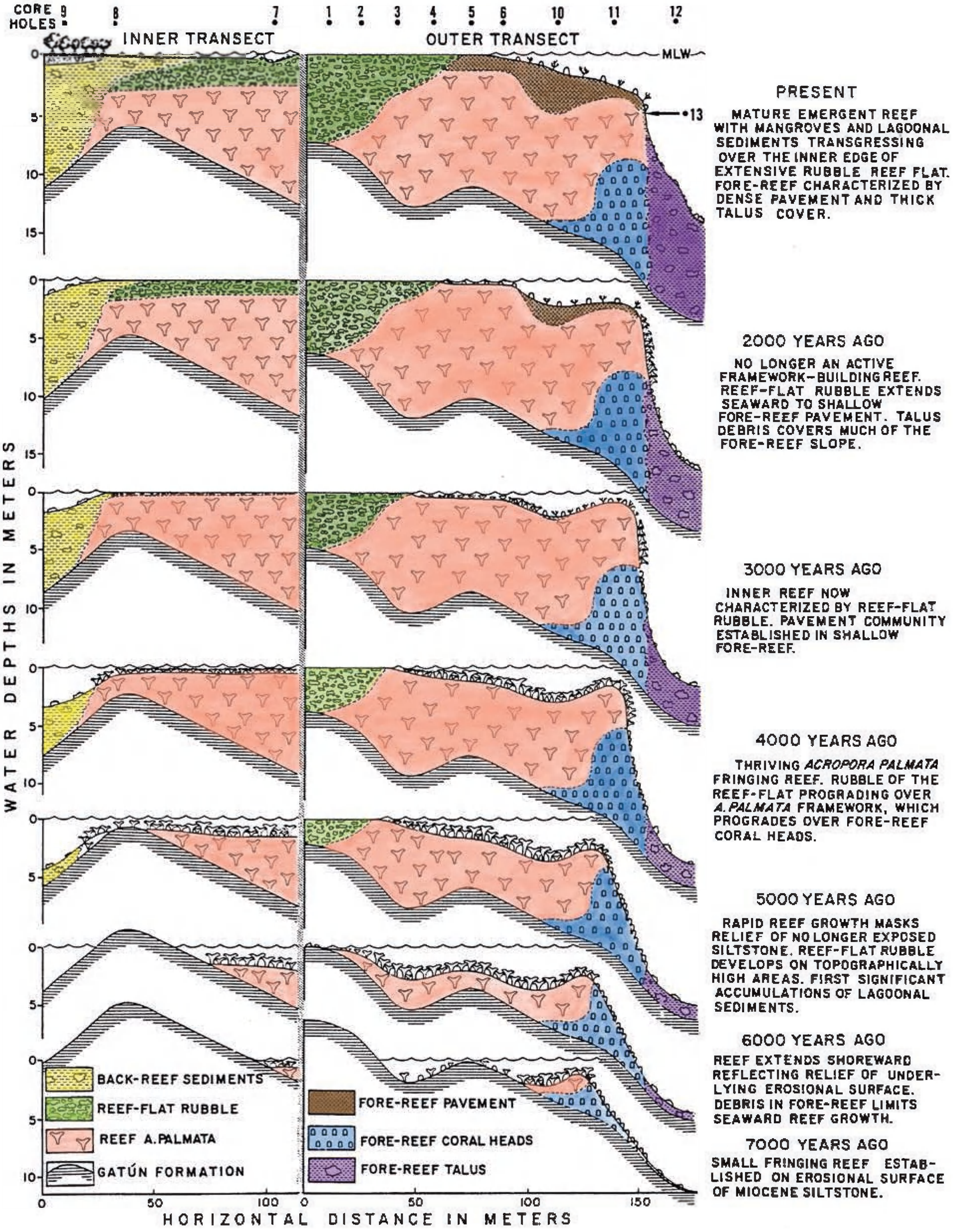

FIGURE 3. Stages of accumulation of Galeta Reef over the past 7,000 years in relation to the Western Atlantic sea-level curve (Lighty et al., 1982). Numbers at top indicate the core-hole locations.

- Beginning slightly more than 7,000 years ago, a small reef consisting of *Acropora palmata* and coral heads established on the mid-Miocene siltstone Gatun Formation.
- 6,000 years ago, the reef extended shoreward, taking on the relief of the underlying Gatun Formation.
- 5,000 years ago, rapid accumulation of *Acropora palmata* masked the substrate relief; the reef-flat rubble facies, back-reef sediment facies, and fore-reef talus facies began to form.
- 4,000 years ago, a mature reef with five facies had become well developed.
- 3,000 years ago, the reef continued to accumulate with the start of the formation of the fore-reef pavement facies.
- 2,000 years ago, all six facies were well developed, but the reef framework was no longer accumulating.
- At present, the mature, emergent reef has mangroves and lagoonal sediments transgressing over the reef-flat rubble, and the fore reef is characterized by dense pavement and a thick talus cover.

Galeta is a classic example of a catch-up reef (Neumann and Macintyre, 1985). It has reached sea level and any new vertical accretion will depend on the provision of new accommodation space through further sea-level rise.

In a subsequent project off the southeast coast of St. Croix (Adey et al., 1977), scuba made it possible to collect three cores from a shelf-edge system in water depths of 11–15 m (Figure 4). These cores all contained a deeper-water coral-head facies with radiocarbon dates ranging from 7,000 to 5,000 years BP (before present; see blue sections in Figure 5). The outermost core, however contained a section of shallow-water *Acropora palmata* below the coral heads, which yielded a date of 9,075 years BP.

When the date of this core was compared with the positions of rising sea level, it became apparent that the shallow-water *Acropora palmata* community died during flooding of the insular shelf about 7,000 years ago (Figure 5). Erosion of the sediment cover on the shelf likely produced turbid conditions at the shelf edge, which exceeded the tolerance of the sensitive *Acropora palmata*. Supporting evidence from X-ray diffraction analysis indicated a marked increase in terrigenous minerals trapped in the cement crusts of the coral-head facies, in contrast to the clean crusts of the *Acropora palmata* facies. By the time turbidity had declined and water quality had improved, sea level at the shelf edge had risen beyond the depth at which the shallow-water *Acropora palmata* could become reestablished. As a result, the massive-coral (or coral-head) assemblage became dominant on the outer shelf. The common occurrence of relict shelf-edge reefs in the Caribbean indicates that during the later stages of the Holocene Transgression most of these reefs succumbed to stress associated with shelf flooding and high turbidity.

The geological patterns illuminated by scuba-based studies in Panama and St. Croix hold lessons for the trajectory of reefs in our present era of rapid climate change. As rising sea levels associated with climate change flood terrestrial habitats, water quality will decline as it did off St. Croix 7,000 years ago and we can expect similar negative impacts on modern reefs. Continued sea-level rise, however, will provide the accommodation space necessary for reefs that have caught up with sea level to begin growing vertically again.

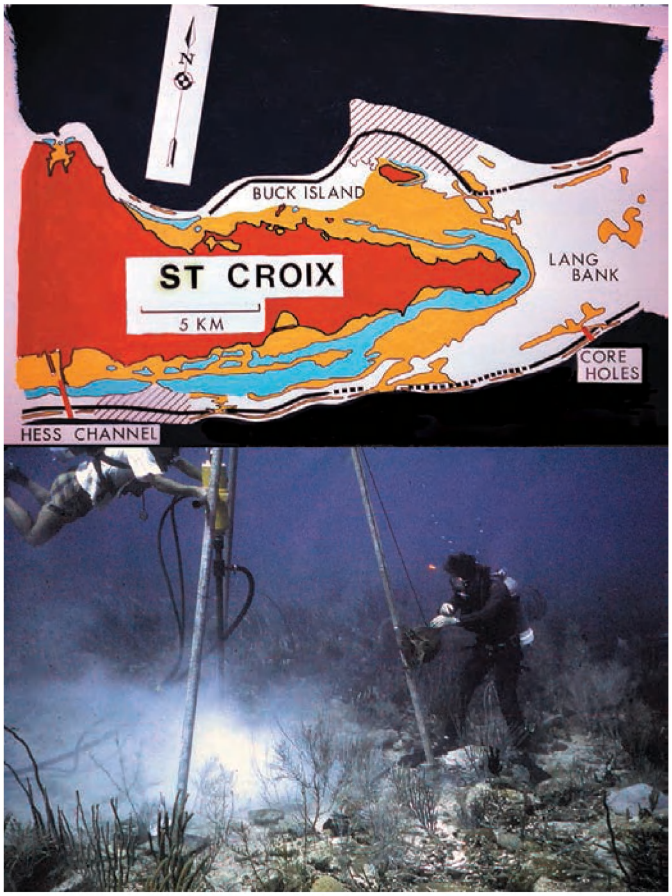

FIGURE 4. Map of the east end of St. Croix showing location of core-hole drilling on a bottom of scattered coral heads and octocorals (modified from Adey et al., 1977; photo courtesy of Ian G. Macintyre).

SURFACE SAMPLING

Geological samples collected from reef surfaces also provide valuable information on reef growth and the timing of inimical conditions that stop that growth. Another of our scuba-assisted studies took place on a "dead," algae-covered, bank-barrier reef off the southeast coast of Barbados (Figure 6). Because the reef lies in an area of constant and heavy wave energy driven by the trade winds, we could only work on it in September, a time of year when storm activity interrupts the otherwise persistent wind pattern (Macintyre et al., 2007).

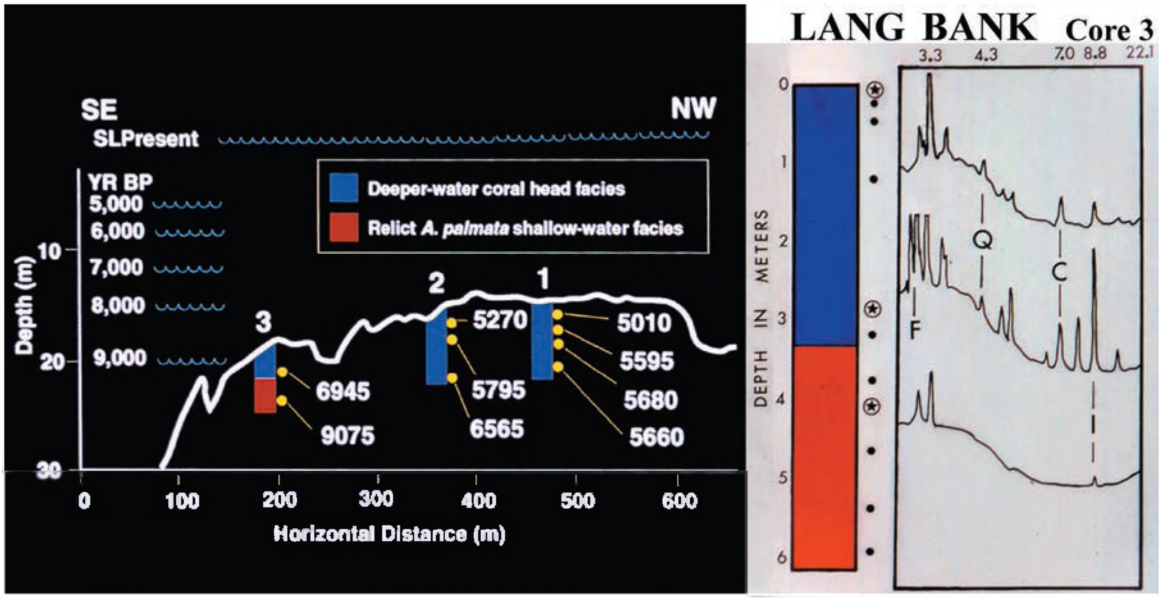

FIGURE 5. Transect of three core holes across the shelf edge off the south coast of St. Croix. Both coral-head and *Acropora palmata* facies are shown with radiocarbon dates. Note the relationship of the end of *Acropora palmata* accumulation to the flooding of the shelf 7,000 years ago. X-ray diffraction patterns of cement crusts from the outermost core show a marked increase in terrigenous material in the upper coral-head facies (modified from Adey et al., 1977).

FIGURE 6. Satellite photograph of Barbados showing Cobbler's Reef, a bank-barrier reef off the southeast coast (courtesy of DigitalGlobe).

We reached nine study sites along the 15-km crest of this bank-barrier reef (Figure 7). We completed ten-meter chain-transect surveys, along with digital photography, and collected samples of subfossil corals for radiocarbon dating. Although this was clearly a robust, *Acropora palmata*-dominated reef at one time, we found no living colonies. Instead, we encountered occasional small colonies of *Porites astreoides*, *Diploria* spp., and *Millepora complanata* (Figure 8). The substrate was dominated by macroalgae, crustose coralline algae, and turf algae on dead plates of *Acropora palmata*.

Although the demise of *Acropora palmata* populations in Barbados was previously thought to be partially related to human activity in the seventeenth century (Lewis, 1984), radiocarbon dates of 27 samples of *Acropora palmata* indicated that reef accumulation stopped 3,000 years ago, with 11 dates plotting above the sea-level curve (Figure 9). These dates, along with the taphonomic observation that the subfossil *Acropora palmata* was broken and flattened, indicate that severe storms around 4,000–3,000 years ago destroyed most of the reef. The few *Acropora palmata* colonies that survived until 400–300 years ago may have been killed off by the clearing of land for sugar cane in the late 1600s; however, there has been no reef-framework accumulation for the past 3,000 years. Apparently physical conditions, not human activity, were responsible for the demise of this bank-barrier reef.

Why did this reef not recover? There are at least two hypotheses, which are not mutually exclusive. One explanation is

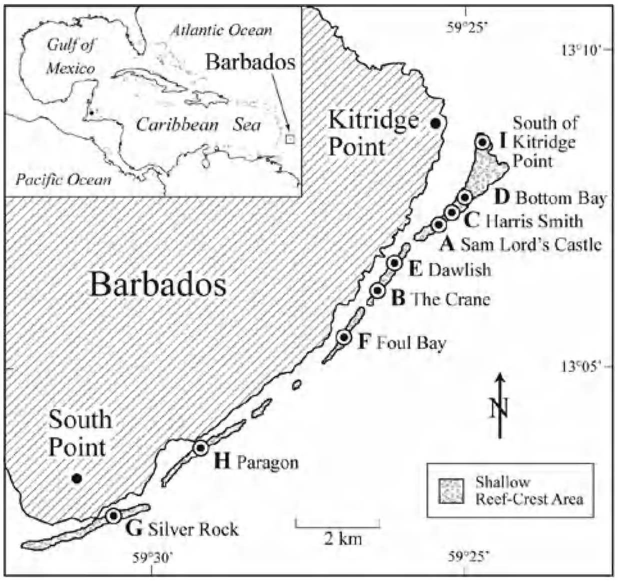

FIGURE 7. Index map showing the nine study sites (A–I) on Cobbler's Reef (Macintyre et al., 2007).

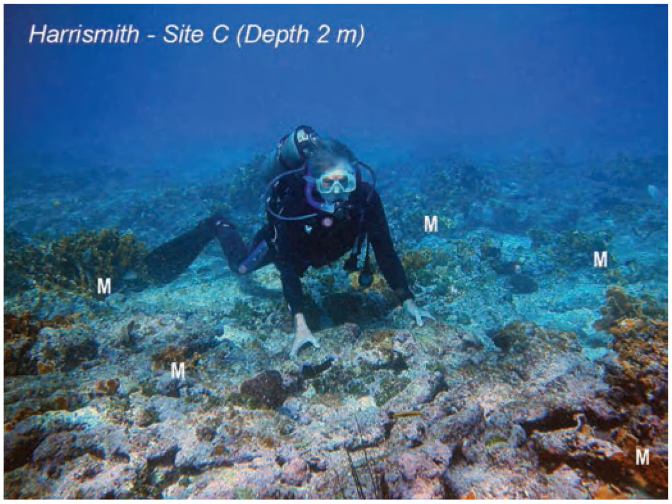

FIGURE 8. Harrismith site (site C) on Cobbler's Reef showing scattered and flattened *Acropora palmata* with a cover of crustose coralline algae, *Millepora complanata* (M), and macroalgae (modified from Macintyre et al., 2007; photo by Allan G. Macintyre).

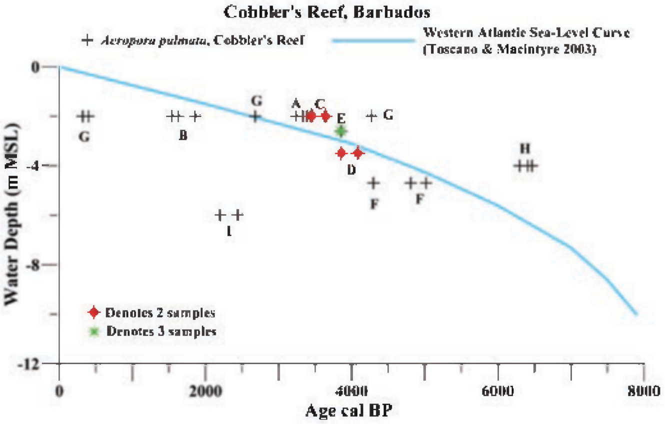

FIGURE 9. Radiocarbon dates of *Acropora palmata* from the crest of Cobbler's Reef plotted in relation to the Western Atlantic sea-level curve (Toscano and Macintyre, 2003). Note the samples that plot above the sea-level curve, which indicate storm damage. There has been no additional reef accumulation for the past 3,000 years (Macintyre et al., 2007). Letters refer to the sites in Figure 7.

that wave energy in this area may be too high and constant to allow herbivores to keep macroalgae in check (Steneck, 1988); once the corals died and the macroalgae rose to dominance, the macroalgae prevented corals from recruiting successfully. Alternatively, or in addition, the initial flattening of reef topography prevented recolonization by *Acropora palmata* (cf. Precht et al., 2001), due either to high turbulence or to the loss of sheltered microhabitat for herbivores (Szmant, 1997).

PUSH-CORING

Push-coring is an alternative to rotary drilling for reconstructing the Holocene history of coral reefs in lagoonal settings. The ribbon reefs, or rhomboid shoals, in the central shelf lagoon of the Belizean barrier reef; the patch and fringing reefs in Bahía Almirante, a coastal lagoon at Bocas del Toro in northwestern Panama; and certain lagoonal reefs elsewhere in the Caribbean and in the Indo-Pacific are uncemented, consisting essentially of accumulations of skeletal fragments of branching and foliose corals packed in an unconsolidated, sandy-mud to muddy-sand matrix (Aronson et al., 2002, 2004; Wapnick et al., 2004; Toth et al., 2012). Low-energy conditions and the abundant matrix are primarily responsible for the lack of submarine cementation on these reefs.

For the push-coring method, divers force a 5 to 6 m aluminum tube into the unconsolidated reef framework, rotating it in using adjustable core-slips with handles and pounding with a hammer-weight sleeved over the top of the tube (Figure 10). Once the tube has penetrated 4–5 m, the free end is sealed with a plastic cap and electrical tape. The core is then extracted from the reef. Its bottom is sealed and it is then brought to the surface for laboratory analysis. A team of three or four scuba divers can collect a core in a dive of 30–45 minutes. Push-coring is an inexpensive, highly portable alternative to drilling and other mechanized techniques such as percussion vibracoring (Dardeau et al., 2000). Expense and portability are not the sole reasons for

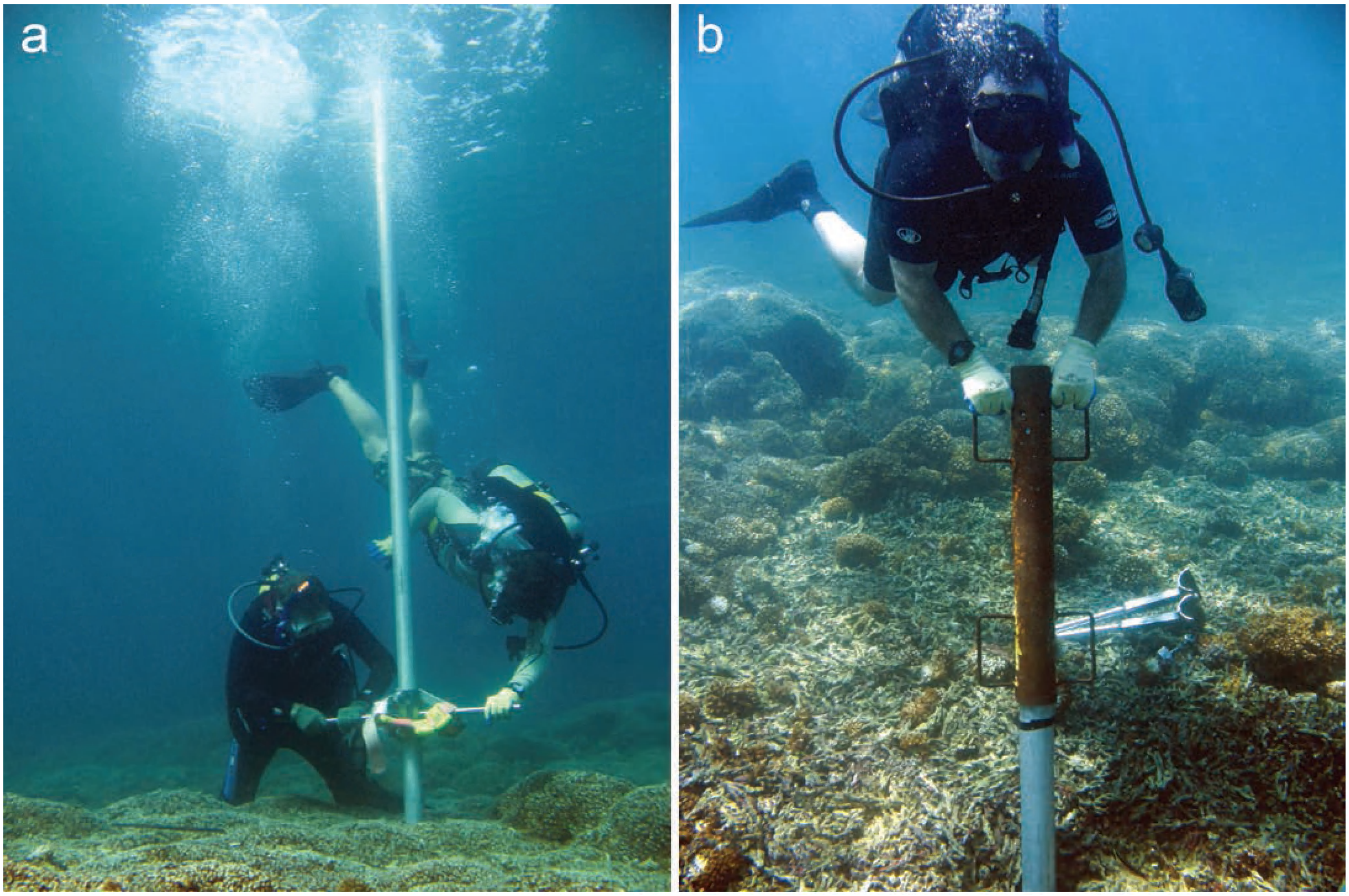

FIGURE 10. Push-coring technique: (a) two divers rotating a core tube into an uncemented reef, using adjustable core slips with handles (photo by Richard B. Aronson); (b) a diver pounding from the top of a core tube using a sliding hammer-weight (photo by Steven V. Vollmer, reproduced courtesy of Richard B. Aronson). Core slips are visible in the background (b), resting on dead coral on the reef surface below the diver.

the high value of push-coring in lagoonal environments. Drilling is inappropriate because the process itself pulverizes delicate corals and blows them and the unconsolidated fine sediments out of the core tube, destroying the very materials that are the focus of study.

Thirty-eight push-cores extracted from 20 sites in Belize at 3–12 m water depth, distributed over 375 km^2 of the central shelf lagoon, revealed a striking and remarkably consistent pattern of dominance and turnover during the past 3,000–4,000 years (as determined by radiocarbon dating). *Acropora cervicornis* dominated throughout the last several millennia until the late 1980s. Turnover events were highly localized in time and space, consisting of small-scale shifts in dominance between *Acropora cervicornis* and the lettuce coral *Agaricia tenuifolia* (Aronson et al., 2002). After 1986, virtually the entire population of *A. cervicornis* on the rhomboid shoals was wiped out by white-band disease, an infectious bacterial disease that killed acroporid populations throughout the Caribbean from the late 1970s through the early 1990s (Aronson and Precht, 2001). High levels of herbivory from the sea urchin *Echinometra viridis* controlled algal growth on the dead skeletons of *Acropora cervicornis* in the Belizean shelf lagoon, so that by the mid-1990s the reef surfaces at all 20 sites had switched to dominance by *Agaricia tenuifolia*. This large-scale, recent turnover event was recorded as a layer of *Agaricia* plates at the top of each of the cores (Figure 11, left).

The pattern of stasis and turnover was similar in Bahía Almirante in Panama, but the long-term dominant and the cause of turnover were different from the Belizean case. Thirty-six cores were extracted from 12 sites at 5–10 m water depth, distributed over an area of 128 km^2. In this case, branching *Porites* spp. were the continuously dominant corals for the last 3,000–4,000 years (Figure 11, right). Small-scale turnover events, localized in time and space as in Belize, consisted of transitions to *Agaricia tenuifolia* or *Acropora cervicornis*. Around 1970, the reefs of the Bahía switched to dominance by *Agaricia tenuifolia*. Aronson et al. (2004) attributed the transition in Bahía Almirante to deteriorating water quality from changing patterns of land use in Bocas del Toro and surmised that the turnover event was precipitated by massive flooding from unusually heavy rains in 1970. These hypotheses were corroborated by geochemical analysis (Hilbun, 2009). The convergence of lagoonal reef systems in Belize and Panama on dominance by *Agaricia tenuifolia* is a remarkable example of the biotic homogenization that is affecting marine ecosystems worldwide.

The push-cores from the Belizean lagoon and Bahía Almirante consisted of a sandy-mud to muddy-sand matrix containing up to 50% Mg-calcite in the clay-size fractions (<4 mm). The consistent mineralogy of 12–13 mole% $MgCO_3$ and the lack of significant Mg-calcite skeletal material in both the silt-size (4–63 mm) and sand-size (>63 mm) fractions indicate that most of the fine Mg-calcite is precipitated (Table 1). By contrast, authors of previous studies in Belize had speculated that the fine Mg-calcite had a skeletal source. Interestingly, the same Mg-calcite composition found in the lagoonal mud fraction was observed in lithified geopetal deposits on serpulid projections in a lagoonal cave in Belize (Figure 12). Lithification in the cave suggests that exposed sediments may become lithified, whereas the cores indicate that trapped sediments may not.

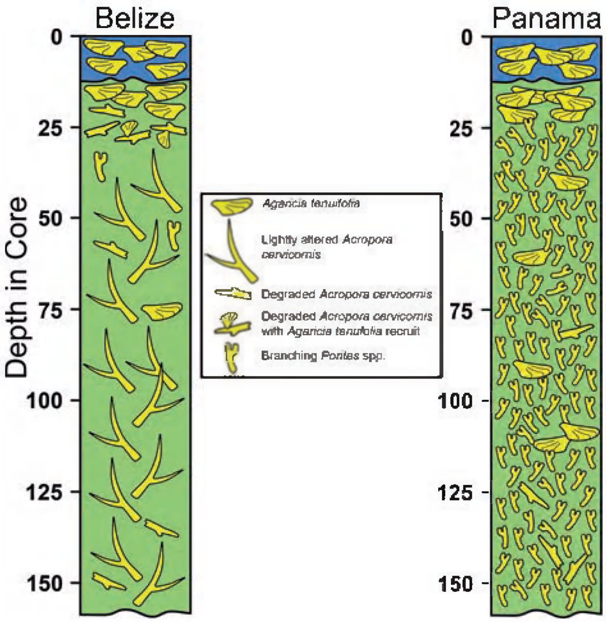

FIGURE 11. Generalized logs of push-cores from the central shelf lagoon of the Belizean barrier reef and Bahía Almirante, Bocas del Toro, Panama. Light green fill indicates a sandy-mud to muddy-sand matrix. Blue fill at the tops of the core logs indicates open framework that has not yet been in-filled with sediment (adapted from Aronson et al., 2002, 2005).

TABLE 1. Concentrations of magnesium calcite in three size fractions of the matrix in lagoonal cores from Belize and Panama (from Macintyre and Aronson, 2006). Note Mg-calcite values in the clay-size fractions. There was no evidence of a source of coarser skeletal Mg-calcite that could break down to form clay-size concentrations of Mg-calcite.

	Average percent Mg-calcite in substrate		
Lagoon location	Sand	Silt	Clay
Belize	9.4%	13.8%	38.2%
Panama	12.6%	16.0%	50.2%

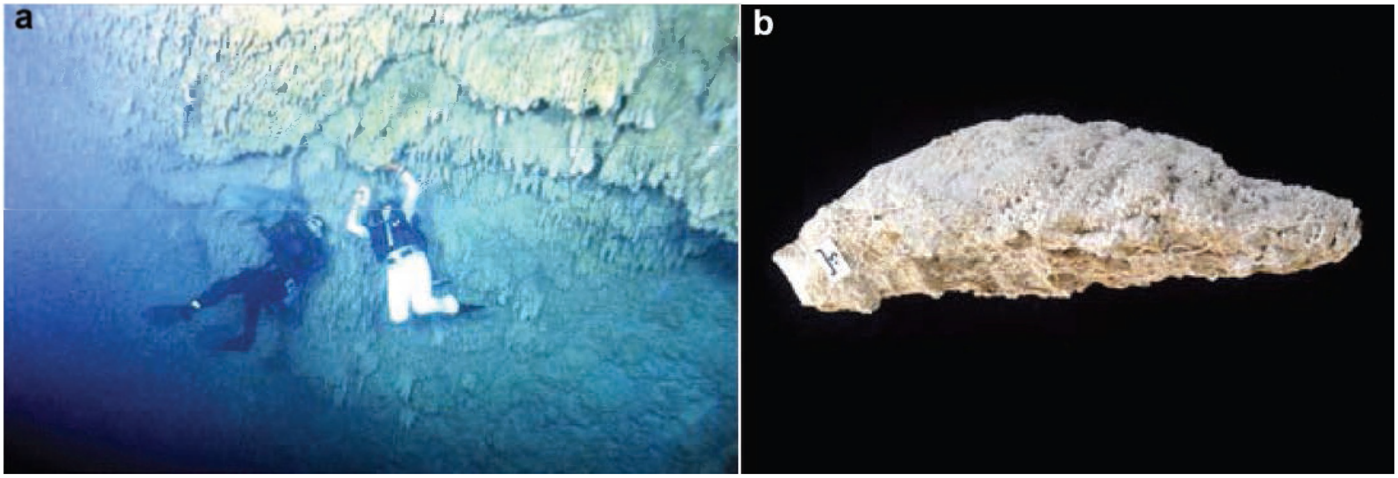

FIGURE 12. (a) Divers sampling serpulid projections on the ceiling of Columbus Cay cave, located in the Belizean barrier reef lagoon. (b) Sample of serpulid projection with thick surface deposit of lithified Mg-calcite (after Macintyre, 1984; photos courtesy of Ian G. Macintyre).

CONCLUSIONS

The ecological and geological responses of coral reefs to natural and human perturbations can only be understood in a historical context. We have presented examples of research on the Holocene history of Caribbean reefs that could not have been accomplished without scuba. The studies highlight the value of a millennial-scale perspective for distinguishing signal from noise in the trajectories of coral reefs. Predicting how reefs will grow and what they will look like in the future will continue to be both an ecological and a geological enterprise, with scuba-based methodologies figuring prominently.

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Diving Physiology and Decompression Sickness: Considerations from Humans and Marine Animals

Michael A. Lang, Jessica U. Meir, Tanya L. Streeter, and Karen B. Van Hoesen

ABSTRACT. The objective of scientific divers using scuba as a research tool is to be able to effectively work under pressure without incurring acute or chronic health effects. Chapters in this volume address underwater science results achieved through the use of scuba. This particular discussion considers physiological and decompression sickness parameters and effects that all humans and marine animals are subject to on a dive. We know that decompression sickness is triggered by a rapid reduction of ambient pressure that allows dissolved inert gas in the body to come out of solution in gas form (i.e., as bubbles.) Dive computers have been accepted as effective tools in assisting divers with the real-time monitoring of their decompression status. Oxygen-enriched air mixtures allow extensions of bottom times in certain depth ranges and optimize decompression on ascent. However, we continue to search for better tools and methods to take our science deeper. Since the publication of Haldane's "Prevention of Compressed-Air Illness" over 100 years ago, a variety of new research directions have attempted to further explain and reduce the occurrence of the decompression sickness syndrome. Humans have ventured under water for at least 2,000 years without the use of an external compressed air source. However, observations of physiological adaptations in breath-hold diving marine mammals and birds eclipse the capabilities of human breath-hold divers. Nitrogen narcosis and neurological decompression sickness on a single breath-hold dive can occur because of the depths and durations involved. The consummate divers, marine mammals and diving birds, have evolved numerous physiological and morphological adaptations that contribute to such remarkable diving capacity and obviate the two fundamental concerns of diving physiology: oxygen store management and the effects of pressure at depth. A more thorough understanding of the physiology underlying these phenomenal divers may also assist in preventing and treating diving-related pathologies in humans.

INTRODUCTION

Scuba diving conducted by scientists is an invaluable research tool. Since the advent of scuba in the 1950s, placing the trained scientific eye under water on compressed gas has provided research value and flexibility that unmanned systems often could not. One metric substantiating this value is provided by peer-reviewed scientific publications in high-impact journals of research that could not have been performed without the use of scientific diving techniques (Lang, 2007). For example, a recent computer search for the keyword "scuba" returned 671 articles from all 397 volumes published since 1967 of the *Journal of Experimental Marine Biology and Ecology* (JEMBE, Elsevier).

The purpose of a scientific diving project is the advancement of science requiring divers to use scientific expertise in studying the underwater environment. More often

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than not this research is conducted in challenging and remote environments such as under polar ice, from research vessels at sea, or at atolls far removed from immediate medical assistance. Yet exposure statistics document that these research activities are performed to a remarkable degree of safety and scientific productivity (Lang, 2009; Sayer et al., 2007).

Access to the underwater research site is provided by scuba, and we are in continuous pursuit of technology to expand our operational window within acceptable safety limits. Safety concerns, however, have gradually eroded our depth limit to what has become a 60 m compressed air scuba window for scientific diving in the United States with impacts on how and where research is conducted with diving. Our understanding of the ocean ecosystem in toto is therefore potentially impaired. For example, shallow-water coral reefs are well understood, as are the horizontal linkages between adjacent mangroves and sea grass beds and their contributions to the reef ecosystem. But diving limitations make vertical linkages and deep systems problematic to investigate. Akin to limiting a tropical rainforest biologist from climbing higher than 10 m (thereby missing the majority of biodiversity that resides in the canopy), a scientific diver cannot effectively study the biodiversity and contributions of the deep reef to the shallow-reef system because of current technology and training limitations. The U.S. Department of Labor's Occupational Safety and Health Administration does not restrict the scientific diving community with regard to technology, leaving the operational flexibility to utilize mixed gases, rebreathers, and saturation habitats in research methodology to meet the nation's marine science needs.

Physiological considerations and the probability of decompression sickness affect humans and marine animals on every dive. We know that decompression sickness is triggered by a rapid reduction of ambient pressure that allows dissolved inert gas in the body to come out of solution in gas form (i.e., as bubbles). Since the publication of Haldane's (1908) "Prevention of Compressed-Air Illness," a variety of new research directions have attempted to further explain and reduce the occurrence of the decompression sickness syndrome. Humans have ventured under water for at least two millennia without the use of an external compressed air source. However, observations of physiological adaptations in breath-hold diving marine mammals and birds eclipse the capabilities of human breath-hold divers. Even the current world-class human depth record of 214 m and breath-hold static apnea time of 11 minutes 35 seconds are orders of magnitude less than recorded marine mammal dives. Nitrogen narcosis and neurological decompression sickness on a single breath-hold dive can occur because of the depths and durations involved. The consummate divers, marine mammals and diving birds, have evolved numerous physiological and morphological adaptations that contribute to such remarkable diving capacity and obviate the two fundamental issues of diving physiology: oxygen store management and the effects of pressure at depth. A more thorough understanding of the physiology underlying these phenomenal divers may also assist in preventing and treating diving-related pathologies in humans.

Waking up the aquatic reflexes we harbor as infants is perhaps one of the most important elements of freediving, a 2,000-year-old diving technique still practiced today by the Ama of Korea and Japan. In 1967, Robert Croft was the first to practice 'lung packing,' the glossopharyngeal breathing technique. Today, extreme (No Limits) freediving prompts the question as to whether there is a finite limit to the depths a human can dive. Some contributing factors involve training and fitness regimen, mental strength, state of relaxation, chest (muscles/ribcage) elasticity, partial lung collapse to a residual volume of <0.5 L, possible pulmonary edema, glossopharyngeal insufflation that can increase pulmonary gas stores to >12 L, alternate equalization modes of sinuses and middle ears, dive times of about 4½ minutes, and a freediving decompression stop. Physiological phenomena such as nitrogen narcosis and neurological decompression sickness can affect freedivers on a single breath-hold dive due to the speed of descent, depths, and durations involved.

SCIENTIFIC DIVING SAFETY AND EDUCATION

Diving Safety Research

The scientific diving community has a traditionally proactive record of furthering diving safety to minimize the risk of harm to human health. The first scientific diving safety program was established at Scripps Institution of Oceanography in 1952, pre-dating the national recreational scuba training agencies. Diving safety programs can be generalized as fulfilling a twofold purpose. The first is a research-support function, which assists the diving scientist with specialized underwater equipment, advice, and diver support to assist in fulfilling the scientific objectives of the diving project. The second is a risk management function that protects the safety and health of the individual scientist and the liability exposure of the employing organization by providing state-of-the-art diving equipment, suitable breathing gases, and training and medical surveillance programs.

Scientific diving safety research by Lang and Hamilton (1989) considered a more effective means of decompression status monitoring using dive computers. Findings included the need for programs to approve specific makes and models of dive computers, training, and the operational consideration of the buddy pair to follow the most conservative dive computer profile. Initiation of appropriate surfacing procedures in case of dive computer failure, activation after previous use, and ensuring that complete outgassing has occurred were recommended as mitigation procedures. Careful consideration was advised for multiple deep dives. An evaluation of the future of dive computers was provided by Lang and Angelini (2009) reporting on functionality, features, and configurations. Lang and Egstrom (1990) investigated the slowing of ascent rates and performance of safety stops to provide scientific divers with a greater margin of decompression safety. Before certification, the diver must demonstrate proper buoyancy, weighting, and a controlled ascent, including a "hovering" stop. Ascent rates are controlled at a maximum of 10 m/min from 20 m and are not to exceed 20 m/min from depth, at the rate specified for the make and model of dive computer or table being used. Scientific diving programs and many dive computers usually require a stop in the 5 m depth range for 3–5 minutes on every dive. Scientific divers receive practical training in drysuits, which must have a hands-free exhaust valve. A buoyancy compensator, capable of horizontal deflation, is required with drysuit use for emergency flotation but should not be used under water to avoid uncontrolled buoyancy problems. In the case of any emergency ascent, breathing 100% oxygen above water is preferred to in-water air procedures for omitted decompression. The effects of multiday, repetitive diving on diver physiology were evaluated by Lang and Vann (1992), who estimated decompression sickness (DCS) incident rates in the USA to be 1 per 1,000 dives in the commercial diving sector, 2 per 10,000 dives for the recreational scuba community, and 1 per 100,000 dives in the scientific diving universe.

Scientific diving programs provide continuous training, recertification, and dive site supervision, which helps maintain established safe diving protocols. Making repetitive dives over multiple days may result in a higher risk of DCS. Increasing knowledge regarding the incidence of DCS indicates that the ability to predict the onset of DCS on multilevel, multiday diving is even less sensitive than the ability to predict DCS on single, square-wave-profile dives. There appears to be good evidence that there are many variables that can affect the probability of the occurrence of DCS symptoms. The ability to mitigate these variables through education, supervision, and training appears to be possible by promoting good levels of hydration, fitness, rate of ascent, and fatigue management. There is adequate technical support for the use of oxygen-enriched air (nitrox) and surface-oxygen breathing in scientific diving where higher gas loadings are anticipated in multilevel, multiday dives. Decompression sickness is generally recognized as a probabilistic event, which tends to steer the scientific diving community toward a more conservative approach to occupational diving.

The order of dive profiles was investigated by Lang and Lehner (2000), in part because of the difficulty for scientific divers to adhere to the "dive progressively shallower" rule while on projects investigating coral reefs at varying transect depths. More importantly, the genesis and physiological validity of the "dive deep first" rule was in need of examination. Historically, neither the U.S. Navy nor the commercial sector has prohibited reverse dive profiles. Reverse-dive profiles are acknowledged as being performed in recreational, scientific, commercial, and military diving. The prohibition of reverse-dive profiles by recreational training organizations cannot be traced to any definite diving experience that indicates an increased risk of DCS. There is no convincing evidence that reverse-dive profiles within the no-decompression limits lead to a measurable increase in the risk of DCS. This means that there may be no reason for the diving communities to prohibit reverse-dive profiles for no-decompression dives less than 40 m and with depth differentials less than 12 m.

Oxygen-enriched air (nitrox) has been used in the scientific diving community since the early 1970s. Lang (2001, 2006) reported that for entry-level, open-circuit nitrox diving there is no evidence that shows an increased risk of DCS with the use of oxygen-enriched air (nitrox) compared with compressed air. A maximum PO_2 of 1.6 atm is generally accepted based on the history of nitrox use and scientific studies. Routine CO_2 retention screening is not necessary for open-circuit nitrox divers. Oxygen analyzers should use a controlled flow-sampling device for accurate mix analysis, which should be performed by the blender and/or dispenser and verified by the end user. It is important to ensure that equipment used with oxygen or mixtures containing over 40% oxygen by volume are designed, dedicated, and maintained for oxygen service.

Operational Diving Procedures

Operational guidelines for remote scientific diving operations were promulgated on a consensual basis by the senior practicing scientific divers for blue-water diving by Heine (1986) and for polar diving by Lang and Stewart (1992) and Lang and Sayer (2007). A phased approach toward the expansion of the scientific diving operational window from 60 m to 90 m was published by Lang and Smith (2006), resulting in the evaluation of commercial and military diving methods for the science community through surface-supplied diving, rebreathers, mixed gas, and saturation techniques. The most immediately transferable method for access to 90 m is surface-supplied diving with mixed gas. This would allow for the dive profile management to occur topside, and for the scientist at the end of the hose to be able to focus on the scientific data collection. There are some disadvantages, such as limitations on horizontal mobility, that would make this method not applicable to all sites of scientific interest. However, surface-supplied training is not overly complicated and would allow for a quick transition from scuba to helmet-and-hose diving given the appropriate commercial diving equipment and topside management (Lang and Robbins, 2009). Deep-air diving for short-bottom durations under ideal conditions remains a possibility for very experienced divers who are cognizant of gas management, nitrogen narcosis, decompression strategies, and maximum operating depth limits of partial pressure of oxygen. Advanced tools such as rebreathers are not new technology, but with their surge in popularity in the technical diving community we are hopeful that with engineering solutions to support their increased reliability and reduce maintenance efforts they will evolve into a mainstream tool as well.

The U.S. scientific diving community has long adhered to a proven experience-accumulation schedule. Depth certifications provide a mechanism to gather diving experience incrementally, and scientific dives are planned around the competency of the least experienced diver. Diving with compressed air in scientific diving operations is not permitted beyond a depth of 58 m. The

100-hour scientific diver training course consists of theoretical training, practical skills training in confined water, and completion of 12 supervised open-water dives in a variety of dive sites for a minimum cumulative bottom time of 6 hours. Additional training is provided for diving specialties such as decompression diving, surface-supplied diving, mixed gas or oxygen-enriched air (nitrox) diving, semi- or closed-circuit rebreather diving, saturation diving, blue-water diving, drysuit diving, overhead environment (ice, cave, or wreck) diving, and altitude diving.

All scientific diving is planned and executed in such a manner as to ensure that every diver maintains constant, effective communication with at least one other comparably equipped, certified scientific diver in the water. This buddy system is based upon mutual assistance, especially in the case of an emergency. If loss of effective communication occurs within a buddy team, all divers surface and reestablish contact. A dive flag is displayed prominently whenever diving is conducted. Scientific diving is not conducted unless procedures have been established for emergency evacuation of the divers to a hyperbaric chamber or appropriate medical facility and these procedures have been approved by the Diving Officer. Diving first aid training is a requisite for scientific diver certification and emergency oxygen kits are present at the dive location. Hyperbaric chambers, as a rule, are not required to be on site. In the case of an asymptomatic diver diving within the dive computer no-decompression limits during the previous 48 hours, there should be a minimum 12-hour delay period with no diving prior to flying. The longer the diver delays an ascent to altitude, the lower the probability of onset of decompression sickness symptoms.

Diving Medical Surveillance

Scientific divers who are exposed to hyperbaric conditions must possess a current diving medical certification. In passing that examination the diver will have been declared by the physician to be medically fit to engage in diving activities as may be limited or restricted in the scientific diver medical certification. All medical evaluations are performed by, or under the direction of, a licensed physician of the applicant diver's choice, but preferably one trained in diving/undersea medicine. The diver must be free of any acute or chronic disabling disease or conditions contained in the list of conditions by Bove (1998) for which restriction from diving may be recommended. There are currently no fitness standards per se for scientific divers other than during the initial scientific diver training course, which includes in-water time and distance challenges for swimming. A stress tolerance test can be prescribed by a physician based on preliminary screening that indicates the potential of a higher than normal risk of coronary artery disease. Cardiac events are the proximate cause of more than 30% of diving fatalities in the recreational diving community (Vann and Lang, 2011). Medical evaluations are completed before a diver may begin diving and thereafter at five-year intervals up to age 40, three-year intervals after the age of 40, and two year-intervals after age 60. Any major injury or illness or any condition requiring hospital care requires diving medical clearance. If the injury or illness is pressure-related, then the clearance to return to diving must be performed by a physician trained in diving medicine.

DECOMPRESSION SICKNESS

Breathing and Inert Gas

The increased pressure gradient between inspired gas and the dissolved gas tension in the body at depth results in an equilibration of the pressure differential leading to saturation. The composition of the air we breathe consists of nitrogen (79%), an inert gas that is absorbed and dissolved in the bloodstream and tissues. The nitrogen partial pressure (PN_2) at sea level in the lungs and surrounding tissues is in equilibrium. Ambient pressure increase (on descent) causes denser air in the lungs to be driven into the tissues to maintain this equilibrium, a process termed ongassing. Ambient pressure decrease (on ascent) causes the increased PN_2 in the tissues to be driven into the lungs, called offgassing.

It takes time for nitrogen to enter and to leave the body. Upon ascent the body begins to eliminate N_2. If too much N_2 is still present after surfacing, the excess nitrogen forms bubbles in the body, creating microscopic clots that impair circulation and can damage endothelial linings of vessels. Decompression sickness symptoms range from skin rash, extreme fatigue, coughing, and painful joints to paralysis and unconsciousness. Commonly accepted prevention is to stay within dive computer no-decompression limits, maintain slow ascent rates (<10 m/min), perform safety stops, and not run out of breathing gas.

Haldane and Prevention of "The Bends"

Our fundamental knowledge of decompression was provided by Boycott, Damant, and Haldane (1908) in their paper "The Prevention of Compressed Air Illness." Haldane initially used goats and later divers in his decompression experiments to validate his dive tables and make some important observations and findings: no diver had the bends after rapid decompression from 12.8 m (42 ft) to the surface; the general principle that a 2:1 pressure difference could be tolerated; the concept of staged decompression; a model using six compartments with different half times; and deep compressed-air test dives to 64 m. The tables describing uptake and elimination of nitrogen were developed by Haldane's son Jack, aged 13 at the time, who with Ronald Fisher and Sewall Wright later became the founder of population genetics (Lang and Brubakk, 2009). Validation of Haldane's tables was followed by the Royal and U.S. navies' adoption of their use in 1908 and 1912, respectively. They were revised in 1957 and became the diving guide for military, commercial, scientific, and recreational diving for decades. Subsequently, decompression physiologists and modelers modified surfacing ratios, ascent rules, Workman's M-values, Thalmann's algorithm, probabilistic models, bubble models, and deep stops. Despite these efforts, gas content models that are direct descendants of Haldane's model remain the most prevalent approach to decompression (Doolette, 2009).

Decompression Sickness and Bubbles

Decompression sickness is a syndrome caused by a reduction of absolute pressure and a separation of gas in body tissues due to inadequate decompression leading to an excessive degree of gas supersaturation. In 1879, Paul Bert (1978) demonstrated that decompression of animals after a hyperbaric exposure produced bubbles in the blood. The signs and symptoms of DCS and treatment with oxygen and recompression are well described. However, other aspects of DCS are poorly understood, such as the relationship between gas phase separation and DCS injury and the large variation in individual susceptibility to DCS.

Bubbles within the blood and tissues cause vascular obstruction leading to hypoxic tissue damage. Bubbles activate various plasma proteins including the coagulation cascade, complement, and kinins (Ward et al., 1987), and are associated with aggregation of platelets. Vascular endothelium is a monolayer of cells lining blood vessels. The endothelium senses stimuli and triggers release of vasoactive substances including nitric oxide (NO), which can inhibit adhesion of platelets and leukocytes. In response to inflammatory signals initiated by bubbles, endothelial cells become activated, generating endothelial microparticles (EMP), which in turn may reduce endothelial function. Vascular bubbles can injure endothelium and reduce the vasoactive effects of other compounds such as substance P and acetylcholine (Nossum et al., 1999). There is growing evidence that the endothelium may play a key role in the development of DCS.

Venous gas bubbles (VGB) are found in the vasculature and right heart after recreational and professional dives and can be monitored and documented with the use of ultrasound by either Doppler or echocardiography (Eftedal and Brubakk, 1997). There is a statistical relationship between detectable bubbles and the risk of DCS (Eftedal et al., 2007). Doppler-detected VGB is a useful method of measuring decompression stress and the absence of VGB is a good indicator of decompression safety.

Exercise has long been thought to be a risk factor for the development of DCS. However, more recent studies have revealed that pre-dive exercise and exercise performed during a decompression stop may significantly reduce bubble formation. Wisløff and Brubakk (2001) serendipitously found that aerobic endurance exercise training reduced bubble formation in rats exposed to hyperbaric pressures. In follow-up studies, an acute bout of exercise produced the same protective effect against DCS. Rats that were exercised 20 hours prior to a 60 m dive for 45 minutes had protection from bubble formation and improved survival (Wisløff et al., 2004). Survival time was lengthened even with exercise at 48 hours prior to diving. Dujić et al. (2004) found that a single bout of high-intensity exercise in humans 24 hours prior to a dive significantly reduced the number of bubbles in the right heart. In humans, the optimum time to exercise appears to be shorter; exercise just 2 hours prior to a dive provides a protective effect (Blatteau et al., 2005).

Mild exercise during decompression decreases the number of bubbles, most likely due to increased gas elimination from increased alveolar (lung air sacs) ventilation (Dujić et al., 2005). In follow-up studies, post-dive exercise caused an eightfold reduction in gas bubbles, presumably due to increased blood flow causing a depletion of bubble nuclei at the blood vessel lining surface (Dujic, 2009). Hence, exercise performed 24 hours prior to decompression, during decompression stops, and after a dive is not harmful as previously thought, but appears to protect from DCS. The mechanism responsible for these interactions may be related to nitric oxide (NO).

There is growing evidence that the endothelium may play a role in the development of DCS. Endothelial nitric oxide (NO) is an important vasodilator and can attenuate bubble formation and incidence of DCS. Rats that are given an NO blocker exhibit far greater bubble formation and minimal survival following a dive compared to controls (Wisløff et al., 2003, 2004). Møllerløkken et al. (2006) demonstrated similar findings in a pig model, as did Dujić et al. (2006) in humans; pre-dive administration of nitroglycerin to humans results in a reduction of bubble formation after diving. Thus, administration of an NO donor (such as nitroglycerine) may be a reasonable alternative to exercise and may protect against DCS.

Heat stress is a nonpharmacological preconditioning strategy that can lead to protection against various types of insults such as ischemia, hypoxia, inflammation, and bubble-induced injury. Activation of the heat shock protein HSP70 by mild hyperthermia allows cells to resist subsequent insults that would otherwise result in death. This response is referred to as preconditioning. Blatteau et al. (2009) showed that a single pre-dive sauna session significantly increased HSP70 and decreased circulating bubbles after a chamber dive. Previous work by the same group showed that moderate dehydration and hypovolemia induced by pre-dive exercise could decrease VGB in divers (Blatteau et al., 2007). They hypothesize that heat-exposure-induced dehydration and NO pathway could be involved in this protective effect, but further investigation is needed to understand the heat-exposure-induced reduction in bubble formation. The role of HSP may be more related to the attenuation of tissue reaction to vascular bubbles than to direct reduction of bubble formation.

Diving in cold water tends to increase the risk for DCS. Previous studies in the 1960s showed that reduced blood flow caused by vasoconstriction and the resultant reduction in inert gas washout from tissues caused symptoms of DCS. However, more recent work by the U.S. Navy (Ruterbusch et al., 2004, 2005) showed that the risk of DCS could be lowered by keeping the diver warm during decompression. It may be beneficial for the diver to be cold during the bottom phase of the dive but not during decompression. Vasoconstriction can hinder the uptake of gas during the dive while increased peripheral tissue perfusion from being warm during decompression may result in a greater elimination of inert gas (Mueller, 2007).

In a recent article, Møllerløkken and Eftedal (2009) suggested that genetic and epigenetic makeup of individual divers may play a role in the variable susceptibility to DCS. Could there be genetic links between endothelial dysfunction and DCS? Genes involved in NO homeostasis display individual differences in activity. Since NO is an important mechanism in bubble formation, genetic links between endothelial dysfunction and DCS may be possible. Hence, genetic variations in humans may explain the variable susceptibility to DCS. Møllerløkken and Eftedal (2009) proposed to study alterations in genetic expression profiles of RNA in vascular endothelium following decompression using rat models, which may provide further knowledge of genetic variability in the physical and biochemical changes experienced in diving. By understanding the genetic basis of individual responses to diving, we may be better able to predict individual risk of developing DCS with the potential to prevent or relieve disease by preconditioning or pharmacological interventions.

FREEDIVING

Decompression Sickness in Breath-Hold Divers

Breath-hold diving (freediving) is also a method utilized in underwater research and can also subject scientists to decompression sickness. Unlike scuba divers, breath-hold divers do not breathe compressed gas; hence the nitrogen that remains in the lungs after the last breath before diving is the only inert gas that could accumulate in tissues. During a breath-hold dive, compression of the chest increases the nitrogen partial pressure in the alveoli, which causes nitrogen to be taken up by the blood. It was previously assumed that a breath-hold diver could not accumulate enough nitrogen concentration in the tissues to cause the supersaturation that results in decompression sickness. However, reports from the 1960s from the Ama divers in Japan describe symptoms of decompression sickness in these pearl divers, including partial or complete paralysis, vertigo, and loss of consciousness. Cross (1965) described a syndrome in pearl divers called "Taravana," which means to "fall crazily" and most likely represented decompression sickness. These divers performed frequent dives to over 30 msw (100 fsw) with bottom times of 30–60 seconds. They repeated these dives with short surface intervals for 6 hours per day. Cross (1965) also reported another group of divers who had surface intervals twice as long as the Tuamotu divers and did not get DCS. Other reports have described decompression sickness in breath-hold divers. Schipke et al. (2006) reported 90 cases of decompression sickness after repetitive breath-hold dives. In a recent review of the literature and breath-hold diving, Lemaitre et al. (2009) reported 141 cases of DCS in 447 divers.

Lanphier (1965) proposed that repeated deep breath-hold dives separated by short intervals at the surface could lead to progressive accumulation of enough nitrogen to cause decompression sickness. Short surface intervals do not allow tissue nitrogen to be eliminated. Hence, nitrogen can accumulate in the tissues during repeated breath-hold dives equal to the amount found in scuba divers. As in scuba diving, repetitive breath-hold diving has been reported to produce venous gas emboli detectable with ultrasound Doppler (Spencer and Okino, 1972). A single deep breath-hold dive is much less likely to lead to decompression sickness; however, two reports of neurologic symptoms occurring after a single deep breath-hold dive may represent DCS (Magno et al., 1999; Desola et al., 2000).

Repeated breath-hold dives and short surface intervals are factors that predispose to decompression sickness. Fahlman and Bostrom (2006) have suggested that increasing the surface interval to at least twice the duration of the dive may help reduce accumulated tissue nitrogen and reduce the incidence of DCS in breath-hold divers. Understanding how marine mammals avoid excessive nitrogen tissue concentrations could help reduce decompression sickness in human breath-hold divers and scuba divers.

Freediving History

For the first nine months of their lives, humans exist in an aquatic environment very similar to sea water. If an infant is submerged, it instinctively holds its breath for up to 40 seconds while swimming breast strokes. It appears that we seem to lose this innate diving ability as soon as we commence walking. Waking up these reflexes is one of the most important elements of freediving, thus giving humans better abilities to be protected at greater depths. Relevant adaptations for freedivers would include reflex bradycardia, blood shifts, vasoconstriction, and splenic contraction.

The Ama of Japan and Korea are female pearl divers who still use a diving technique at least 2,000 years old. Women older than 17 years of age use rocks to descend to the bottom where they pick up shells and sea weeds; they dive naked 8–10 hours per day in water barely over 10°C. Rahn and Yokoyama (1965) reviewed the diving physiology of the Ama, which remains the baseline of our knowledge of breath-hold diving physiology.

Chatzistathis, a leading sponge diver from Symi, Greece, was 1.70 m tall and weighed 65 kg. He suffered from remarkable lung emphysema, smoked tobacco extensively, and was part deaf from a life of diving without proper equalization. In 1913, at age 35, Chatzistathis salvaged an anchor from estimated 88 m depth, freediving up to three minutes at a time. He was carried down by a heavy stone, a primitive diving technique as old as the Greek civilization itself. In 1962, Enzo Maiorca was the first to reach the fateful 50 m barrier unassisted, despite predictions from scientists that beyond 50 m the human lungs would collapse from the pressure. Jacques Mayol was introduced in 1966 and revolutionized freediving with his use of Eastern yoga and meditation traditions, rather than the previous norm of heavy hyperventilation.

In 1967, Robert Croft of the U.S. Navy was the first to freedive beyond 70 m and his achievements were important in establishing most modern scientific conclusions about freediving, among them the mammalian diving reflex and the blood shift phenomenon. He was the first record breaker to use "lung packing," the glossopharyngeal breathing technique first described in polio patients by Dail (1951). Loring et al. (2007) measured results of glossopharyngeal insufflations and found maximal lung volume was increased by 0.13–2.84 L, resulting in volumes 1.5–7.9 SD above predicted values. The increased circumference of the thorax and a downward shift of the diaphragm enable a larger filling of the lungs through chest expansion. The amount of gas in the lungs after packing increased by 0.59–4.16 L, largely due to elevated intrapulmonary pressures of 52–109 cmH$_2$O that compress gas in the lungs to 100 cmH$_2$0 (=10 kPa or 10% more air compared to 0 kPa).

By 1999, Francisco Rodriguez (aka Pipin Ferreras) and Umberto Pelizzari pushed each other competitively to 150 m depth records in No-Limits. By 2003, Tanya Streeter mirrored Angela Bandini's 1989 feat by breaking the intergender No-Limits world record, reaching 160 m depth.

Germonpré et al. (2010) described a technique by Patrick Musimu who, by training, was capable of allowing passive flooding of the sinuses and middle ear with sea water during descent by suppressing protective reflexes during this process. Musimu attempted to breach 200 m in No-Limits, but outside the supervision of any diving federation. On one last training attempt he reached 209 m depth with his sled and successfully returned to the surface. Minutes after surfacing, he suffered symptoms of decompression sickness and received hyperbaric treatment, which canceled the public attempt scheduled a few days later.

MODERN-DAY FREEDIVING LIMITS

Herbert Nitsch currently dominates deep freediving and aimed to surpass Musimu's unofficial but widely acknowledged 209 m dive in this increasingly challenging discipline. On his 4½ minute 214 m record deep dive, Nitsch used deep-water breath-hold decompression by ascending very slowly and making a stop to avoid decompression sickness (Figure 1). Table 1 lists current

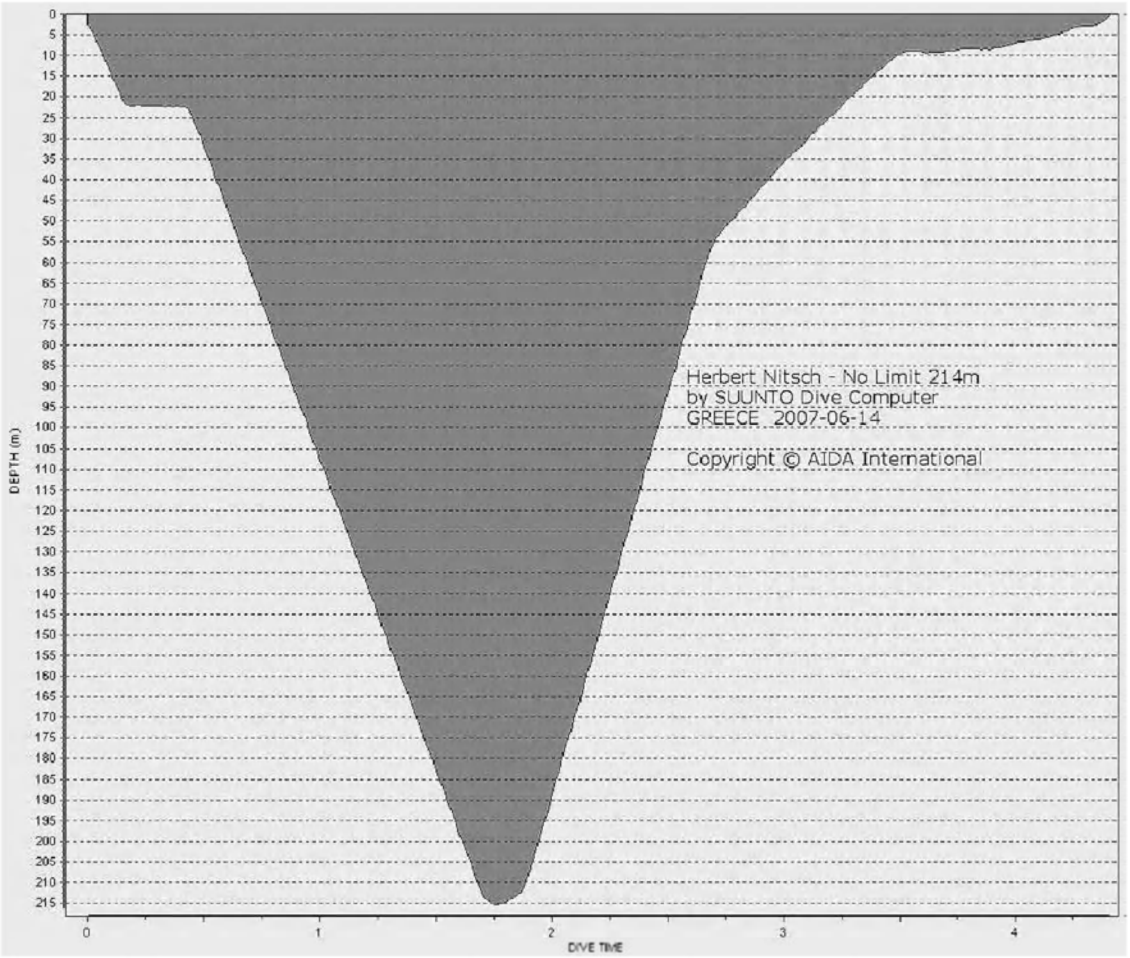

FIGURE 1. Profile of Herbert Nitsch's record no-limit freedive to 214 m in 4½ min, Spetses, Greece, 2007 (from Lindholm, 2009, courtesy AIDA International, with permission).

TABLE 1. Current open water and pool world records.

	Depth or time: Record holder (date)	
Record type	**Male divers**	**Female divers**
Open water		
No limits	214 m: Herbert Nitsch (06/07)	160 m: Tanya Streeter (08/02)
Variable weight	142 m: Herbert Nitsch (12/09)	122 m: Tanya Streeter (07/03)
Constant weight	124 m: Herbert Nitsch (04/10)	101 m: Natalia Molchanova (09/09)
Free immersion	116 m: William Trubridge (04/10)	90 m: Natalia Molchanova (09/09)
Constant weight without fins	92 m: William Trubridge (04/10)	62 m: Natalia Molchanova (12/09)
Pool		
Static apnea	11 min, 35 s: Stephane Mifsud (06/09)	08 min, 23 s: Natalia Molchanova (08/09)
Dynamic apnea	250 m: Alexey Molchanov (10/08)	214 m: Natalia Molchanova (10/08)
Dynamic without fins	213 m: Tom Sietas (07/08); 213 m: Dave Mullins (08/08)	160 m: Natalia Molchanova (08/09)

world men and women records in eight competitive disciplines. Streeter (2006) described her training, work-up dives, narcosis symptoms, operational logistics, and actual freedive for the 2002 No-Limits record to 160 m. She utilized a weighted sled for the descent and an inflated lift bag for the ascent. Approximate travel speeds were 1.5–2 m s^{-1} round trip with a total dive time of 3 min, 32 s. Competition freedivers are athletes first with performance being the main objective, but they obviously wish to perform safely.

We stand to improve freediving performances and learn from clinical research on the physiological aspects of breath-hold diving and from marine mammal and bird studies.

Considerations

The nitrogen that is available during diving is compressed in the lungs and would potentially be the cause of narcosis. This amount of nitrogen is not likely to be evenly distributed to the body tissues in the short period of freedive time. The body's diving response vasoconstricts the periphery, forcing the nitrogen to go mostly to the brain, which potentially results in an elevated brain PN_2. It may not be possible to absorb a significant amount of nitrogen from a lung that is severely compressed. The lung tissue follows the compression of the air, so that the exchange surface area (normally about 70 m^2 between the lung blood and the gas space) is reduced to an extremely small area. That could support the high-pressure nervous syndrome (HPNS) theory. In freedives, nitrogen is being taken up on the way down, but very rapidly through a severely shrinking exchange area. It is also possible that nitrogen narcosis may be limited due to reduction in gas uptake through atelectasis (lung collapse).

Nitrogen is soluble, allowing pressures to build up substantially, and it is possible that a level of hypoxia exists. The loss of lung volume at depth could allow for mixing venous oxygen levels. The sensations of nitrogen narcosis and reduced oxygen saturations can be quite similar, with increased susceptibility potentially aided by higher CO_2 levels. Comparative physiological knowledge seems to indicate that elephant seals' pre-dive exhalation strategy occurs, in part, to reduce susceptibility to decompression sickness, shallow-water blackout, and nitrogen narcosis. Observations of many more dives to these depth ranges would be needed to form a more conclusive opinion on nitrogen narcosis and decompression sickness in extreme freedivers. Diving physiology in the twilight zone is complicated. There may also be a transient hypovolemic (decreased blood volume) effect from significant blood pooling, which may interfere with adequate perfusion in the tissues for a short period.

PHYSIOLOGY OF THE CONSUMMATE DIVERS: MARINE MAMMALS AND DIVING BIRDS

The freediving depth records described above are impressive, yet even these extreme human performances hardly compare to the capabilities of the true consummate divers, marine mammals and diving birds. These animals routinely plummet to great depths for extended durations (Table 2), yet emerge unscathed by the myriad physiological conditions with which human divers must contend. Historical studies on diving animals revealed basic physiological and morphological adaptations (e.g., "armored" airways, air sinus modifications, thermoregulatory features, enhanced oxygen stores) that contributed toward this aptitude, and recent studies have shed further light on the remarkable capacity and mechanisms underlying this behavior. Advances in technology, remote monitoring, and advanced modeling have provided significant insight into the two fundamental issues of diving physiology: oxygen store management and the effects of pressure at depth.

TABLE 2. Maximum dive depth and duration records for various diving species (Association Internationale pour le Développement de l'Apnée [AIDA International]; Norris and Harvey, 1972; Watkins et al., 1985; Ridgway, 1986; Le Boeuf et al., 1988; Eckert et al., 1989; Lutcavage et al., 1990, 1992; Thorson and Le Boeuf, 1994; Kooyman and Kooyman, 1995; Mate et al., 1995; Stewart and DeLong, 1995; Ponganis et al., 1997; Kooyman and Ponganis, 1998; Kooyman et al., 1999; Southwood et al., 1999; Noren and Williams, 2000; Ponganis et al., 2003; Hays et al., 2004; Tyack et al., 2006; Ponganis et al., 2007).

Species, record type (holder: year)	Depth (m)	Duration (min:s)
Human *Homo sapiens*		
Men: No Limits (Nitsch: 2007)	214	4:30
Women: No Limits (Streeter: 2002)	160	3:32
Men: Apnea in pool (Mifsud: 2009)	Surface	11:35
Women: Apnea in pool (Molchanova: 2009)	Surface	8:23
Leatherback turtle *Dermochelys coriacea*	1230	67:18
Bottlenose dolphin *Tursiops truncatus*	390	8
Emperor penguin *Aptenodytes forsteri*	564	23:06
Northern elephant seal *Mirounga angustirostris*	1581	119
Beaked whale *Ziphius cavirostris*	1888	85
Sperm whale *Physeter macrocephalus*	2250	138

The diving performance of humans is significantly impacted by the effects of pressure, namely via decompression sickness (DCS), N_2 narcosis, and high-pressure nervous syndrome (HPNS). Although more commonly associated with breathing compressed air, DCS has been reported in human breath-hold divers, as discussed above. How, then, do the elite divers of the animal kingdom escape the deleterious effects of pressure during their frequent, repetitive, and very deep dives? Several recent reviews detail the morphological and experimental evidence of the adaptations of diving animals to the pressures of diving (Fahlman, 2009; Lemaitre et al., 2009; Ponganis, 2011) with modifications such as the absence of air-filled cranial sinuses in seals, middle ear cavities lined with venous plexuses that may engorge with blood at depth, anatomical modifications of the airways and their responses to compression, and enhanced lung surfactants. Scholander's original model of lung collapse and the cessation of gas exchange at depth has been particularly well supported by both anatomical and experimental evidence in marine mammals; lung collapse undoubtedly plays a role in limiting the accumulation of nitrogen at depth, though the degree and depth of collapse are likely variable and dependent on a variety of factors (Scholander, 1940; Fahlman, 2009; Ponganis, 2011).

Cardiovascular adjustments such as reduced heart rates and decreased cardiac outputs that occur during diving serve not only to conserve oxygen, as discussed below, but also to reduce the accumulation of nitrogen. Theoretical and modeling studies have demonstrated that such responses may play a large role in limiting the accumulation of nitrogen, at least in certain tissues (Fahlman et al., 2006; Lemaitre et al., 2009). Dive patterns (depths, durations, and ascent rates) and dive behavior will also dictate the accumulation of nitrogen at depth, though no data exist as to how animals might sense or cognitively influence these types of parameters.

Despite the protective adaptations of diving animals, relatively recent strandings of beaked whales associated with naval sonar exercises and accounts of dysbaric osteonecrosis in sperm whales have heightened interest regarding the effects of pressure on diving animals, as these findings are consistent with, though not diagnostic of, DCS and N_2 absorption at depth (Jepson et al., 2003; Moore and Early, 2004; Fernandez et al., 2005). If nitrogen loads do reach high levels in diving animals, novel means of dealing with this gas burden may exist in the animal kingdom. Because of the few actual studies of nitrogen pressures in diving animals, more biological data are necessary to further elucidate these adaptations.

Oxygen stores in animals are distributed between the respiratory system, blood, and muscle. It is well documented in the field of diving physiology that accomplished divers have enhanced oxygen stores, mainly attributed to increased blood volumes and increased hemoglobin and myoglobin concentrations. For example, an elephant seal has almost twice the hemoglobin concentration, three times the mass-specific blood volume (Simpson et al., 1970), and 10 to 15 times the myoglobin concentration (Thorson and Le Boeuf, 1994) as compared to a human. Equally as important as these increased oxygen stores, however, are the rate at which oxygen is depleted and hypoxemic tolerance, or lowest level of oxygen that an animal can tolerate. Despite the importance of these latter two parameters, few studies have addressed the rate and magnitude of oxygen depletion while diving.

Another hallmark of diving animals is a redistribution of oxygen stores among the three compartments (Figure 2). Compared to humans, phocid seals have minimized the percentage of oxygen located in the respiratory store, likely an advantage toward the avoidance of nitrogen accumulation and decompression sickness. This fits with the fact that phocids dive upon expiration and undergo lung collapse at depth, as reviewed previously (Fahlman, 2009). Penguins, otariid seals, and cetaceans, however, are thought to dive upon inspiration, and correspondingly have a higher percentage of oxygen stores in the respiratory system (Kooyman and Sinnett, 1982; Ponganis et al., 2010; Skrovan et al., 1999). In line with their increased oxygen stores, diving animals have large percentages of their total oxygen within the blood and muscle (Figure 2).

In discussing the management of oxygen stores in diving animals, specific examples from the literature highlight three central themes: (1) cardiovascular responses, (2) hypoxemic tolerance and the rate of oxygen depletion, and (3) energy saving mechanisms such as a hydrodynamic shape and locomotive strategies.

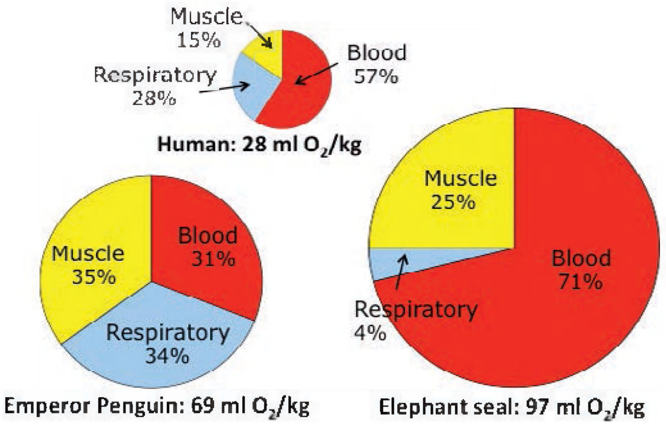

FIGURE 2. The distribution of oxygen stores in humans, elephant seals, and emperor penguins (Kooyman, 1989; Kooyman and Ponganis, 1998; Kooyman et al., 1999; Ponganis et al., 2003, 2007, 2009).

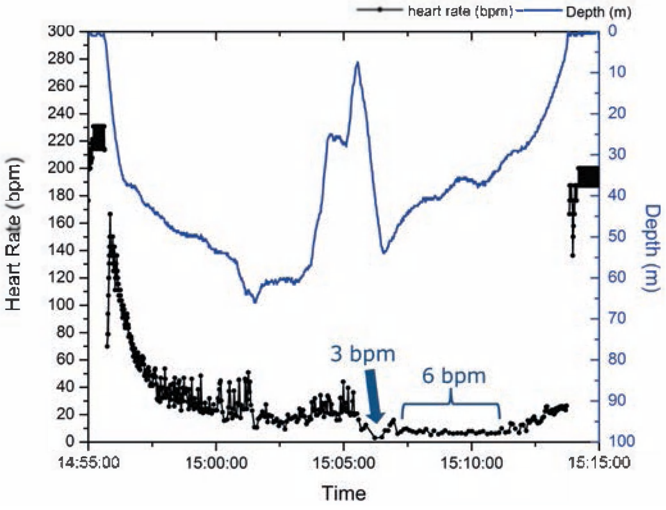

FIGURE 3. Heart rate and dive profile of an 18.2 min dive of an emperor penguin (modified from Meir et al., 2008).

CARDIOVASCULAR RESPONSES

Since Scholander's and Irving's classic findings during forced submersion studies, it has been suggested that reductions in heart rate and peripheral perfusion are the principal determinants of oxygen depletion (Scholander, 1940; Irving et al., 1941; Scholander et al., 1942). This follows from the fact that the organs accounting for approximately half of O_2 consumption at rest are either perfusion dependent or directly related to heart rate (Schmidt-Nielsen, 1983; Butler and Jones, 1997; Davis and Kanatous, 1999). Pre- and postdive tachycardias provide optimal loading of O_2 before the dive, and heart rate alterations can result in a reduction and redistribution of blood flow during the dive. Most diving animals experience a decrease in heart rate upon submersion, the degree varying with species and dive duration (Scholander, 1940; Irving et al., 1941; Butler and Jones, 1997). This can be thought of in terms of an energy conservation strategy, as a reduced heart rate will result in a slower rate of oxygen depletion, consequently yielding increased aerobic dive duration.

A recent investigation that deployed digital electrocardiogram (ECG) recorders on diving emperor penguins has revealed a particularly extreme heart rate response in this elite avian diver, documenting the highest and lowest measured heart rates for the emperor penguin (Meir et al., 2008). Heart rate decreased to as low as 3 bpm during diving, with periods of bradycardia near 5–6 bpm sustained for over five-minute intervals (Figure 3).

Despite these extreme reductions in heart rate, this diver remains capable of propulsion for active maneuvering and pursuit of prey. The mean heart rate during diving was significantly lower than the ~70 bpm heart rate of a penguin at rest (heart rates of penguins at rest are in the same range as those of humans at rest, with these extreme decreases occurring routinely) (Meir et al., 2008). In contrast, although other diving birds show decreases in heart rate upon submersion, this is only relative to their predive tachycardic values (i.e., not lower than resting heart rate) (Millard et al., 1973; Butler and Woakes, 1984; Enstipp et al., 2001; Froget et al., 2004). Heart rates as high as 256 bpm, the highest value ever measured in this species, were also measured during pre- and post-dive periods (Meir et al., 2008). These extreme highs and lows show the dramatic range of physiological responses of which this animal is capable, while its heart rate at rest hovers around 70 bpm, not unlike that of our own. In all diving animals, heart rate responses can be quite variable, demonstrating the plasticity of oxygen management strategies during diving (Thompson and Fedak, 1993; Andrews et al., 1997; Meir et al., 2008).

OXYGEN DEPLETION

Although heart rate responses are indicative of overall oxygen consumption, a more direct approach to understanding the management of oxygen stores is to measure oxygen directly during the dive. Miniaturized microprocessors, biologging instrumentation, and the novel use of an oxygen electrode have recently allowed researchers to document hypoxemic tolerance (the lowest tolerable level of oxygen) and oxygen depletion in this manner in freely diving emperor penguins and elephant seals. This PO_2 (partial pressure of oxygen) electrode has been successfully deployed in air sacs and blood vessels in the emperor penguin (Stockard et al., 2005; Ponganis et al., 2007; 2009), and in blood vessels in the elephant seal (Meir et al., 2009). With the recent characterization of the oxygen–hemoglobin dissociation curve for these species (Meir et al., 2009; Meir and Ponganis, 2009), the PO_2 profiles can be converted to hemoglobin (Hb)

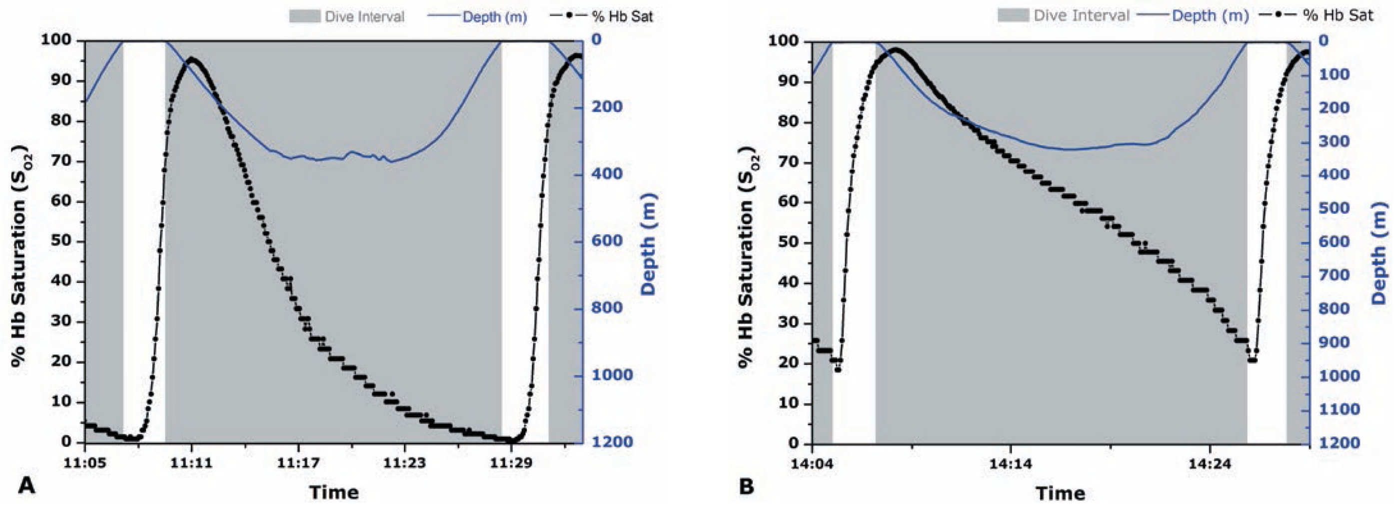

FIGURE 4. (A) Venous percent hemoglobin (Hb) saturation and (B) arterial percent Hb saturation and dive profiles for an elephant seal (modified from Meir et al., 2009). In A (venous profile), note the very high % Hb saturation value at the start of the dive (arterialization) and the near complete depletion at the end of the dive.

saturation profiles, providing values for the amount of oxygen present in the system at the start of, throughout, and after the dive.

These studies have demonstrated exceptional hypoxemic tolerance in these species, particularly in the elephant seal. Arterial PO$_2$ values as low as 12 mmHg (6–8% Hb saturation) at the end of the dive were measured in the elephant seal, the lowest PO$_2$ ever measured in a freely diving seal (Meir et al., 2009). This is well below the limits of most other mammals, including those of mountaineers at the brink of human tolerance at the summit of Mt. Everest (Grocott et al., 2009). This value, obtained in a voluntary diving setting with unrestricted access to the surface in the open ocean, is even nearly equivalent to the critical arterial PO$_2$ of seals in forced submersion studies, as defined by EEG criteria marking the threshold of cerebral dysfunction. Venous saturation values at the end of the dive were routinely as low as 2–10 mmHg (0–4% Hb saturation) in these seals (Figure 4A; Meir et al., 2009), and as low as 2–6 mmHg in emperor penguins (Ponganis et al., 2007). Again, these values are well below the limits of humans or mammals at maximal exercise, and even lower than those of the well-documented hypoxemic extremes of horses performing strenuous exercise (Taylor et al., 1987; Bayly et al., 1989; Roca et al., 1989; Manohar et al., 2001). Both species demonstrated an arterialization of the venous oxygen store (Hb saturations > 90%) (Figure 4A). Combined with the near-complete depletion of the venous oxygen store, this illustrates highly efficient optimization of the venous oxygen reserves.

Adaptation at the biochemical level relevant to oxygen management has also been recently revealed in the emperor penguin. The hemoglobin of the emperor penguin has a higher affinity for oxygen than that of other birds (Meir and Ponganis, 2009), similar to that which has been reported for other penguin species and the high-flying bar-headed goose (Lenfant et al., 1969; Milsom et al., 1973; Petschow et al., 1977; Black and Tenney, 1980). This is particularly advantageous for a diving animal that experiences low levels of oxygen while diving, as it implies that more oxygen is available at any given PO$_2$. It also allows for more complete depletion of the significant respiratory oxygen store in this diving bird.

An analysis of results from these studies further highlights the differences in the distribution of oxygen stores in different species. For example, oxygen profiles of diving emperor penguins illustrate that arterial hemoglobin saturation is maintained near 100% throughout most of the dive, declining only in the final portion of the dive when the bird makes its ascent, when ambient pressure also declines (Meir and Ponganis, 2009) (Figure 5). This keeps oxygen levels high for critical organs like the heart and brain, and is consistent with the large respiratory oxygen store in this species, the high-affinity hemoglobin of this species, and ongoing gas exchange from the lungs to the blood. In contrast, arterial hemoglobin saturation values of elephant seals show a continuous decline after the start of the dive, often to lower final values than those of the emperor penguin at the end of dives (Figure 4B; Meir et al., 2009). This is consistent with the fact that the elephant seal has only about 4% of its total oxygen stores in the respiratory system (Figure 2), undergoes lung collapse, and dives upon expiration.

Oxygen depletion patterns in both arterial and venous compartments are highly variable, even for dives of the same duration. As discussed in relation to heart responses, these investigations further support the plasticity of oxygen management strategies during diving.

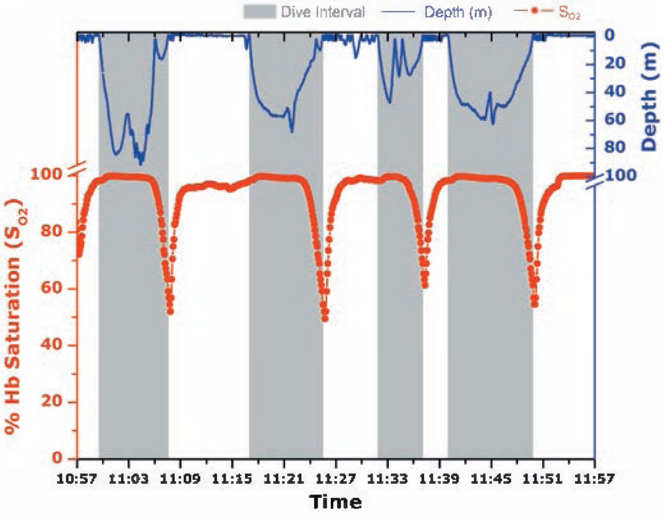

FIGURE 5. Arterial percent hemoglobin (Hb) saturation and dive profile of four dives of an emperor penguin (modified from Meir and Ponganis, 2009).

Energy-Saving Mechanisms

In addition to physiological adaptations and responses, the hydrodynamic shape of marine mammals and diving birds (Fish, 1994) coupled with various locomotor strategies also allows for significant energy and oxygen conservation in these animals. Investigations of various species have shown that diving animals routinely employ efficient swimming speeds (consistently around $1–2\ m\ s^{-1}$) and optimal stroke frequencies while maneuvering through their aquatic habitat (Ponganis et al., 1990; Sato et al., 2007). Burst and glide swimming strategies and the exploitation of buoyancy changes can also result in considerable oxygen savings. It has been estimated that gliding alone could reduce the cost of diving by an average of approximately 28% (Williams et al., 2000).

DISCUSSION

Given our current operational framework and knowledge of human physiology and decompression sickness, we would expect the following elements to receive further consideration: a 90 m for 30 min operational scientific diving window within acceptable risk parameters; rebreather development with a goal toward providing engineering solutions to minimize investment of training time and pre-and post-dive maintenance requirements while enhancing reliability through mass production; replacement of passive thermal protection strategies with the advent of electrically heated gloves, socks, and undergarments; portable diving saturation system development, attainable within the constraints of scientific resources, with advantages that outweigh the lower cost and relative simplicity of bell diving/surface-supplied systems; and operational and physiological limits of wet diving using scuba versus one-man atmospheric diving systems.

Further development of dive computers will better approximate inert gas loads in the diver. Most current units have a dive-profile logging function, downloading capabilities for paperless databases, ascent rate monitors, an air-integration mode, and gas programmability. Benefits from advances in consumer electronics technology could bring the next generation of dive computers high resolution color displays, rechargeable batteries, GPS receivers, underwater communication and navigation, and emergency position-indicating radio beacons (EPIRB). Benefits from monitoring technology integrated into the dive computer algorithm could provide heart rate monitoring, skin temperature and oxygen saturation measurements, and possibly even inert gas bubble detection. Dive computers have for all practical purposes replaced dive tables in scientific diving and it would not be unreasonable to state that regardless of the number of algorithm variations incorporated within them, they all appear to fall within an acceptable window of effectiveness based on available databases of pressure-related injuries. It is also clear that neither tables nor dive computers can eliminate all decompression problems, but when utilized conservatively computers have emerged as an important tool for the improvement of scientific diver safety.

In a recent review of DCS in breath-hold diving, Lemaitre et al (2009) proposed that if marine mammals could sense low levels of bubbles, they could possibly use behavioral or physiological means to reduce the inert gas burden. The future of human diving might entail some type of device that allows for measurement of our own tissue supersaturation and bubble formation. Understanding the specialized adaptations that reduce decompression sickness in marine mammals and how they avoid excessive blood and tissue PN_2 and prevent bubble formation may improve our knowledge of reducing the risk of DCS in human breath-hold divers and scuba divers.

How deep can a human go? Avoiding barotrauma of descent and decompression illness and managing nitrogen narcosis are critical in attaining extreme breath-hold depths. Mental strength, fitness, and exercise to increase elasticity of the ribcage, muscles, and diaphragm are important. Trachea and lungs must be able to withstand a collapse to a residual volume of < 0.5 L. Lindholm (2009) concludes that it is possible for (some) humans to hold their breath for more than 10 minutes or to dive to more than 200 m. Special lenses in fluid-filled goggles can be used instead of a mask to reduce the non-collapsible air spaces, and glossopharyngeal insufflations (lung packing) may be used to increase pulmonary gas stores to over 12 L. Water equalization of the sinuses and middle ear, while painful, is a useful adjunct. Pulmonary edema and partial lung collapse will likely occur. Currently, the limits of deep breath-hold diving seem to be pulmonary barotrauma of descent causing pulmonary edema and nitrogen narcosis incapacitating the diver at depth or causing decompression sickness on ascent.

Recent advances in technology and continued effort in the arena of the diving physiology of marine mammals and birds have been fruitful, documenting extreme responses beyond what has been traditionally hypothesized for these divers. These insights have implications for a wide variety of topics in diving physiology and physiological ecology, with the potential to redefine previous efforts of estimating oxygen utilization, which depend on accurate assessments of oxygen storage capacity and the extent of depletion while diving. Future work remains in further elucidating the mysteries of the management and exchange of gases in marine mammals and diving birds. A complete understanding of the physiology underlying these phenomenal divers and the mechanisms behind these abilities may also assist in preventing and treating diving-related pathologies in humans, as well as human medical situations involving hypoxic damage including heart attack, stroke, organ transplant, and reperfusion energy.

CONCLUSIONS

The U.S. scientific diving regulatory, medical, training, and operational framework has resulted in a remarkably low decompression sickness incidence rate. In this particular segment of the diving community, diving safety research on dive computers, ascent rates, multiday repetitive diving, polar diving, reverse-dive profiles, oxygen-enriched air, and advanced scientific diving contributes to the conservative risk-management approach of scientific diving. Advances in diving medicine allow for mitigation of additional risk while pursuing further understanding of the mechanisms of decompression disease. Freediving sheds light on the extreme capabilities of human performance, approximating the outer limit. Physiological considerations, such as morphological adaptations, and processes, such as management of oxygen stores in diving animals, shed light on the remarkable capacity and mechanisms that enhance diving capabilities in diving animals. Investigations of cardiovascular responses, oxygen depletion, and energy-saving mechanisms have found further evidence in support of the phenomenal capabilities of the consummate divers. The importance of scientific diving as a valuable research tool that places the trained scientist's eye under water is illustrated by the quantity of research projects reported in this volume that could otherwise not have been performed, with results published in the scientific literature. The peer-review publication process validates the viability and effectiveness of scuba as a research methodology.

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

Kenneth P. Sebens, Giacomo Bernardi,
Mark R. Patterson, and Deron Burkepile

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

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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

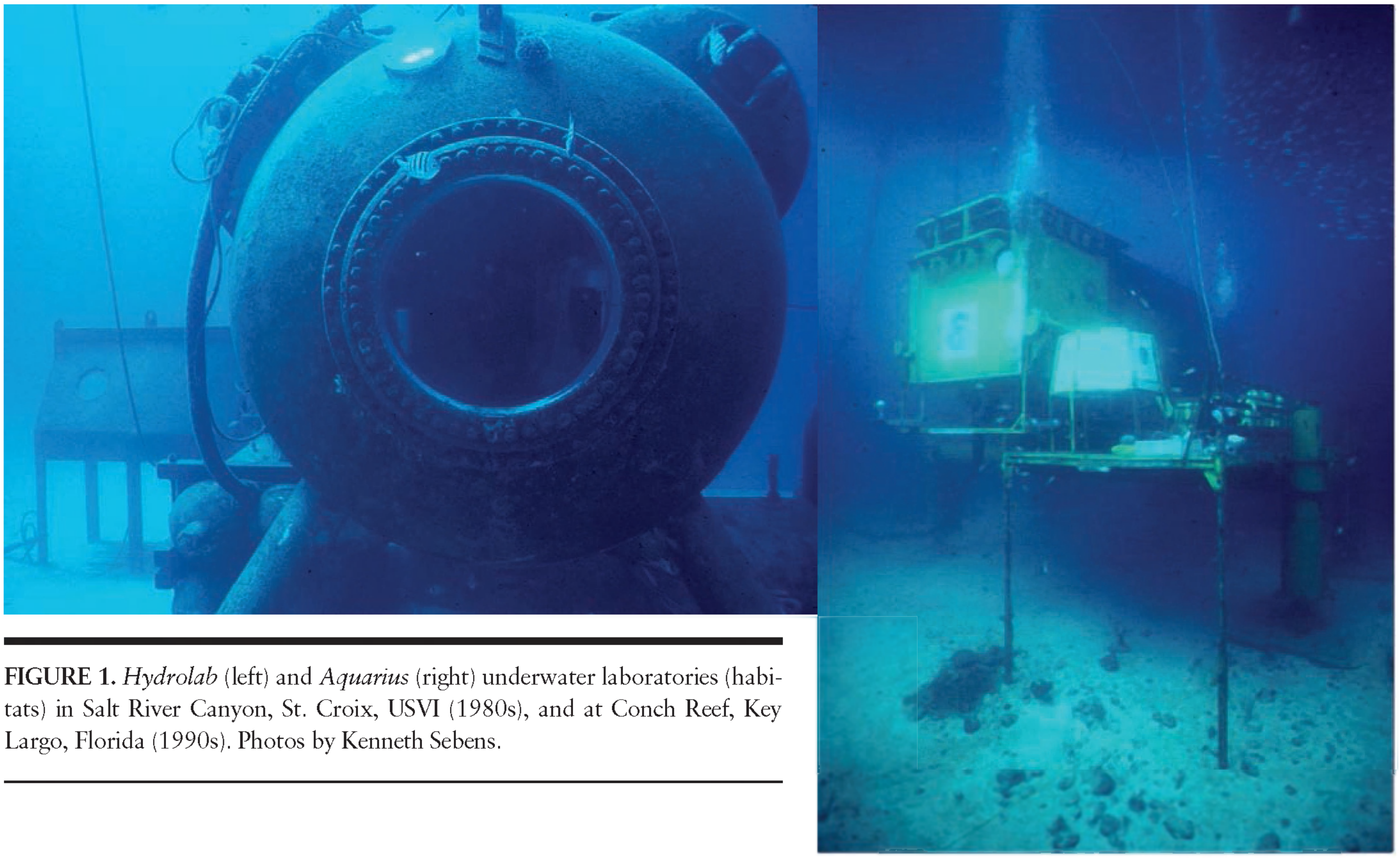

FIGURE 1. *Hydrolab* (left) and *Aquarius* (right) underwater laboratories (habitats) in Salt River Canyon, St. Croix, USVI (1980s), and at Conch Reef, Key Largo, Florida (1990s). Photos by Kenneth Sebens.

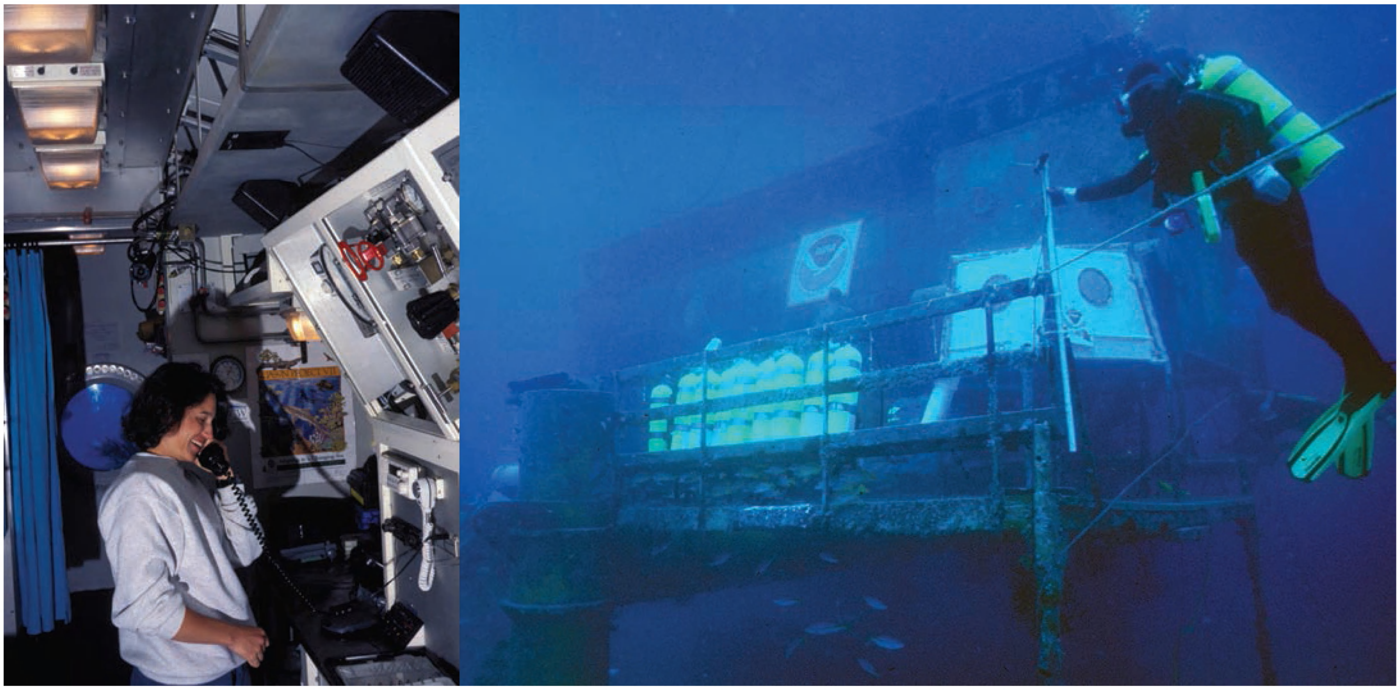

FIGURE 2. The *Aquarius* underwater laboratory (right) at Conch Reef, Florida, and the communications and data center inside the habitat during the Jason Project (1996, with A. Grottoli). Photos by Kenneth Sebens.

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

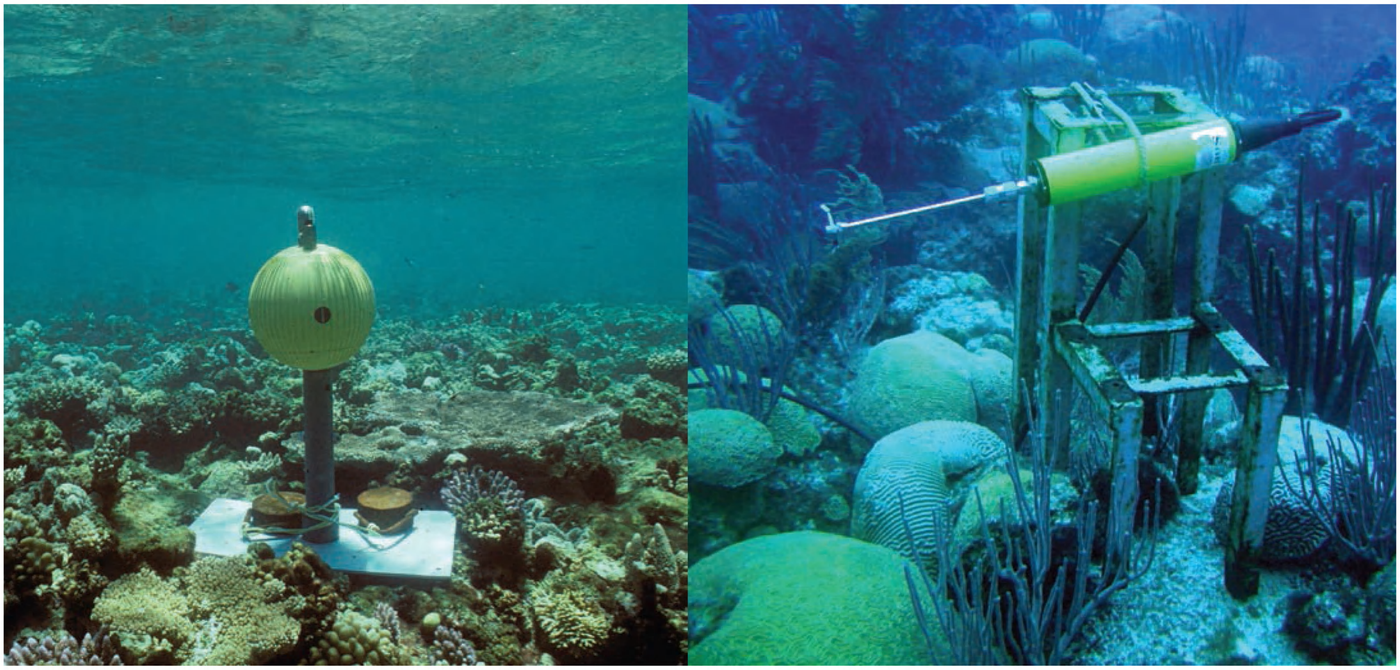

FIGURE 4. An InterOcean S4 electromagnetic current meter in place on a shallow reef, and a Sontek ADV flow meter on a stand that allows vertical profiling from just above coral tentacles to 2 m above the bottom. These and several other recently developed instruments have been used to characterize flow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

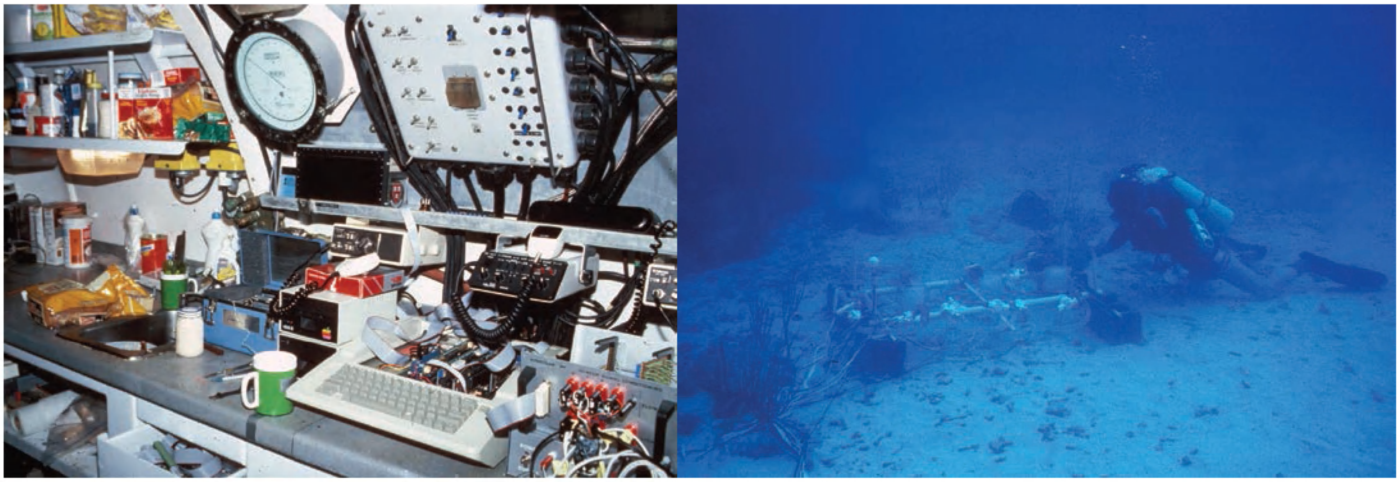

FIGURE 5. The first computer (Apple II) used in *Hydrolab* (by M. Patterson and colleagues), including a prototype flat-screen monitor on loan from the manufacturer (1984) (left). Chambers used for respirometry and flow studies, deployed adjacent to the reef at *Hydrolab* (1984) (right). Photos by Kenneth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

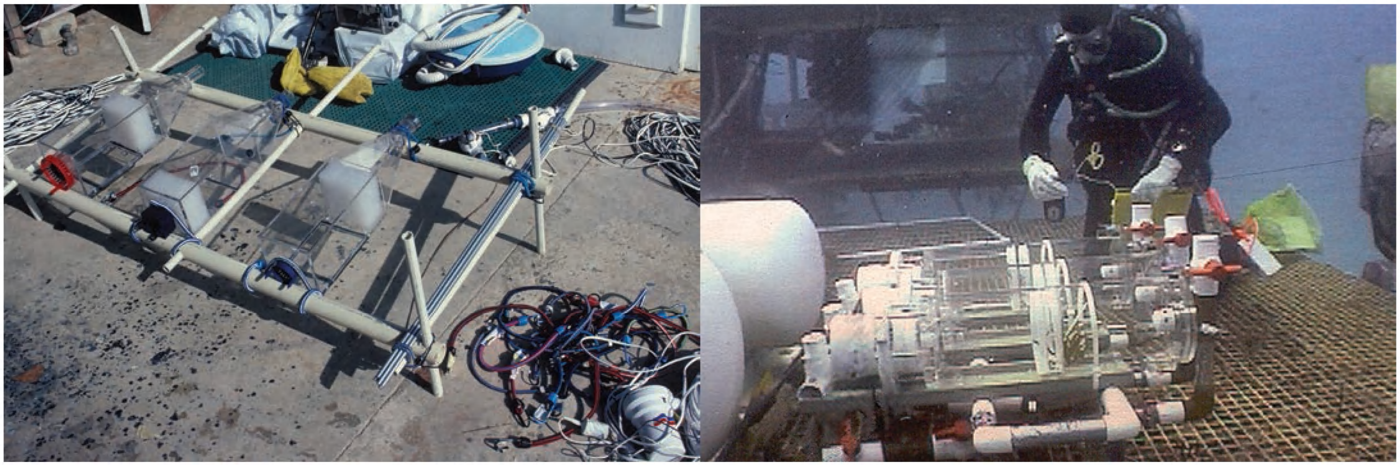

FIGURE 6. Respirometry chambers used for coral production and respiration measurements at a range of flow speeds being prepared for use in *Hydrolab* by M. Patterson and colleagues (left) (Patterson et al., 1991; photo by Kenneth Sebens), and similar chambers being used for nutrient uptake studies (right)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

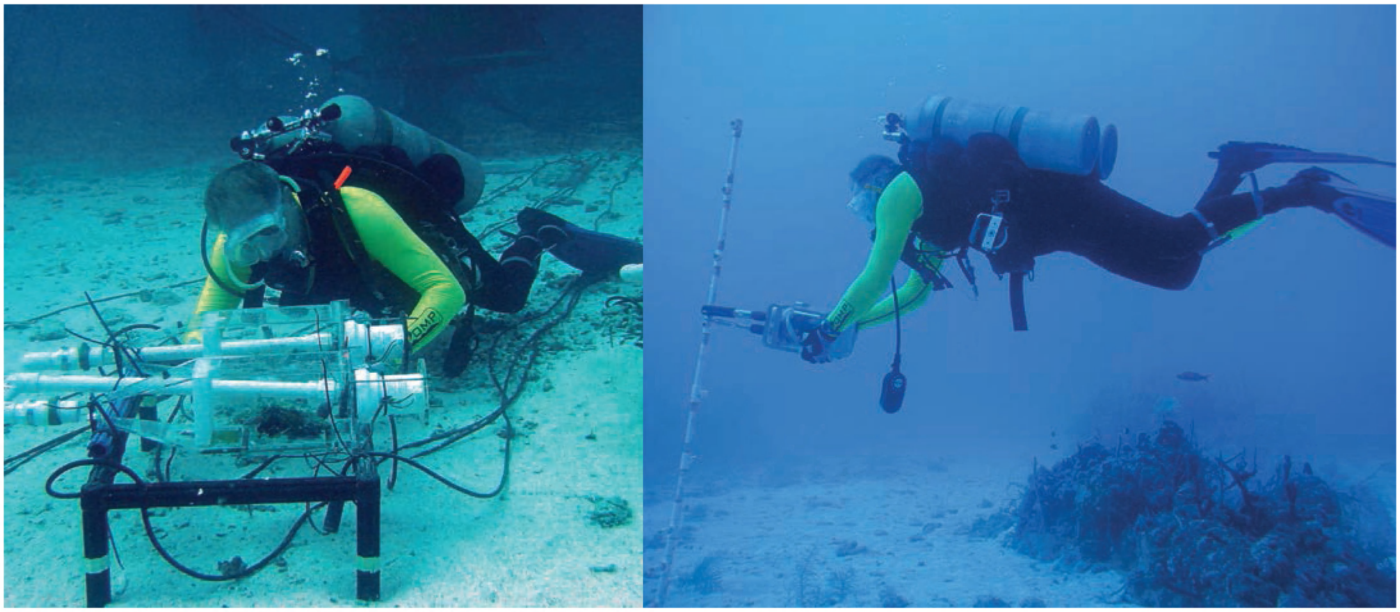

FIGURE 7. Mark Patterson investigates flow and temperature effects on reef benthos using the *Aquarius* underwater laboratory in 2002–2003. Heated metabolism chambers (left) and dissolved oxygen, pH, and temperature profiling apparatus (right). Photos by Janet Nestlerode.

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

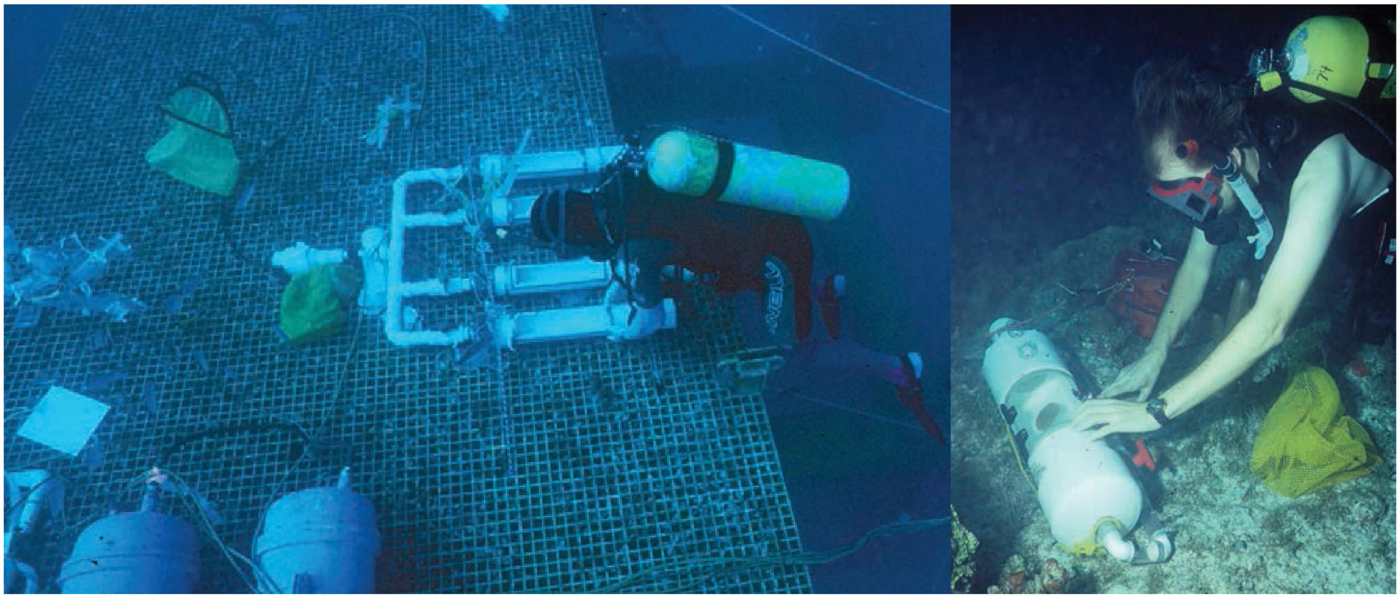

FIGURE 8. Experimental chambers used for coral feeding studies on top of *Aquarius*, and on Conch Reef near the underwater laboratory by J. Witting, K. Sebens, and colleagues (Witting, 1999; photos by Kenneth Sebens).

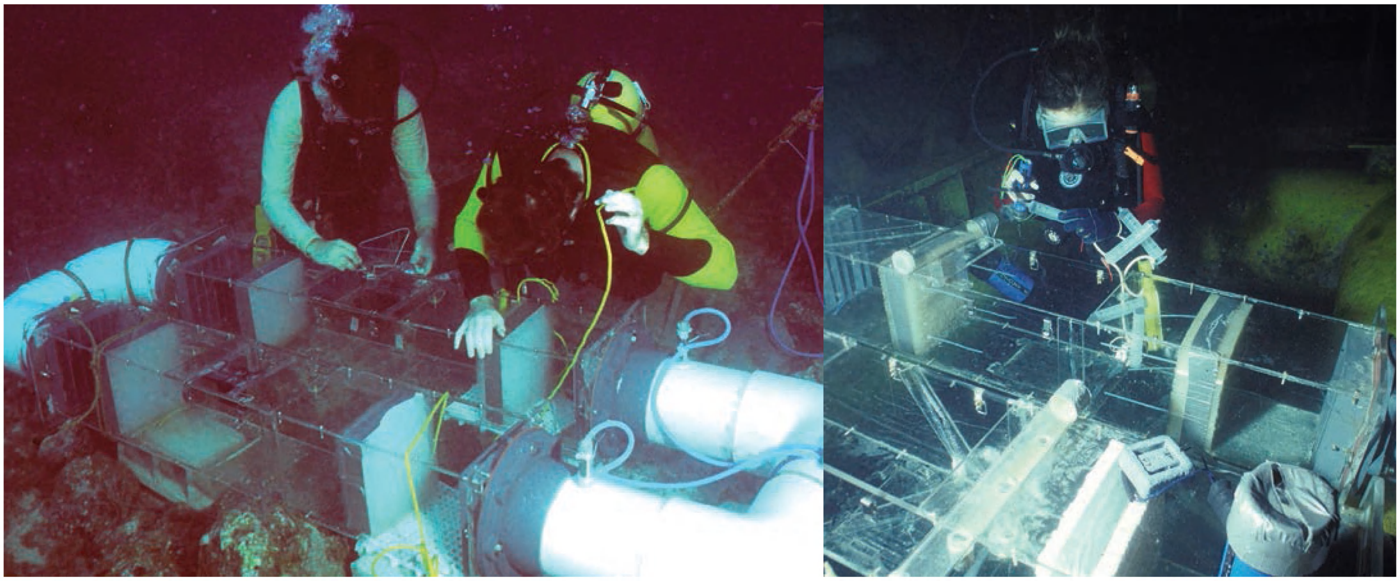

FIGURE 9. A large recirculating flume (left) on Conch Reef allowed flow studies of particle and zooplankton capture, and provided both unidirectional and bidirectional flow generated by two electric trolling motors inside the PVC sections. Zooplankton were attracted into the chambers using dive lights, 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.

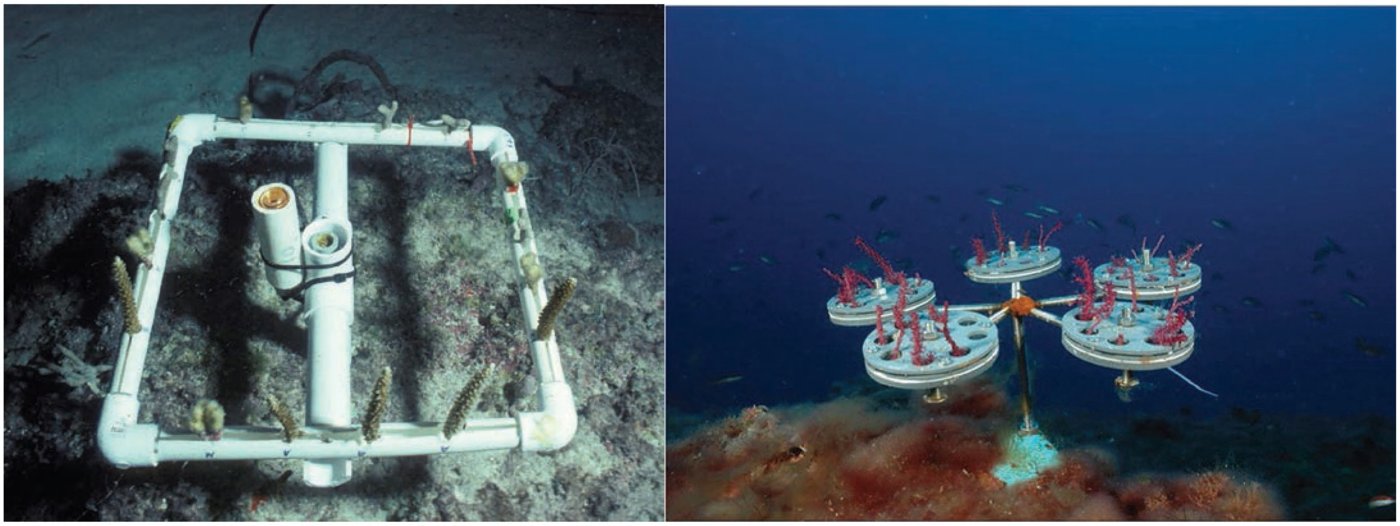

FIGURE 10. Transplant racks for coral growth studies at the *Aquarius* laboratory (left; Witting, 1999; photo by Kenneth Sebens) and in the Mediterranean (right; Cebrian et al., 2012; photo by Joaquim Garrabou). In the assembly at left, a cabled light was added to the center of half of the treatments 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.

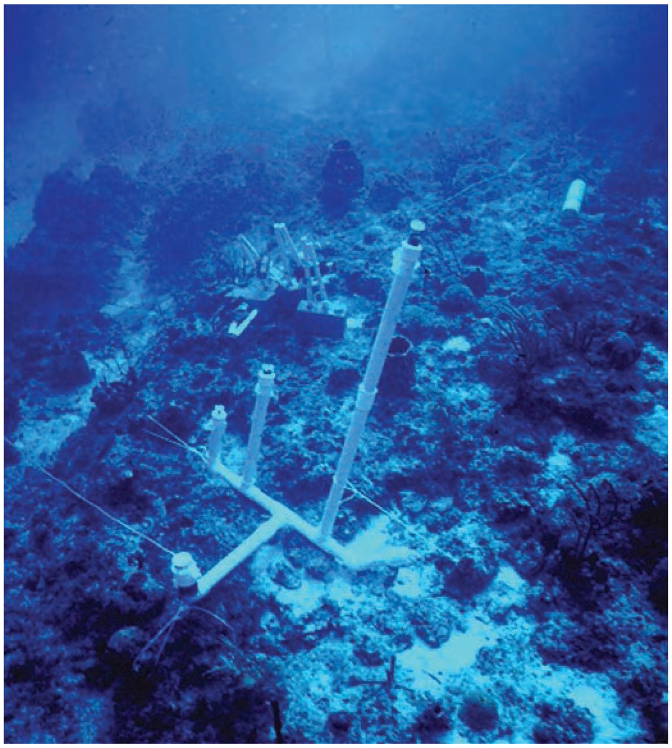

FIGURE 11. A plankton sampling array in place near the *Aquarius* laboratory on Conch Reef, Florida, used to examine zooplankton distribution above the bottom. The center section is 2 m tall and all four inlets, at four different heights, are powered by a single large submersible pump at bottom left (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 m^2 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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Marine Chemical Ecology: A Science Born of Scuba

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ABSTRACT. For more than 50 years, organic chemists have been interested in the novel chemical structures and biological activities of marine natural products, which are organic compounds that can be used for chemical defense and chemical communication by diverse marine organisms. Chemical ecology, the study of the natural ecological functions of these compounds, is an interdisciplinary field involving chemistry, biology, and ecology. Examples of ecological functions of marine natural products include distastefulness that inhibits feeding by predators, settlement cues for larvae, allelopathic effects that prevent fouling by epiphytes and overgrowth by competitors, and pheromones for mate-searching behavior. Much of the research in marine natural products and marine chemical ecology has used scuba diving and related undersea technologies as necessary tools. The breadth of marine organisms studied and the types of experiments conducted under water have expanded with technological developments, especially scuba diving. In this paper, we highlight the importance of scuba and related technologies as tools for advancing marine chemical ecology by using examples from some of our own research and other selected studies. We trace the origins of marine chemical ecology on the heels of marine natural products chemistry in the 1970s and 1980s, followed by the development of increasingly sophisticated ecological studies of marine algae and invertebrates in Caribbean, tropical Pacific, and Antarctic waters.

INTRODUCTION

Natural products are chemical compounds derived from natural sources, including plants, animals, fungi, and bacteria. Marine natural products research involves determining the structure, function, and biosynthesis of these compounds from marine microbes, phytoplankton, macroalgae, sponges, tunicates, and corals, among others. Natural products are also called secondary metabolites because they are small molecules with no known function in the primary metabolism of the organisms that produce them. As a scientific discipline, marine natural products research is an offshoot of the much older study of terrestrial secondary metabolites found primarily in vascular plants, insects, bacteria, and fungi. Many marine natural products possess novel functional groups and molecular structures compared to those from terrestrial sources. To date, 21,800 natural products have been described from marine organisms (MarinLit, 2011; Blunt et al., 2011).

Marine natural products include diverse classes of compounds, such as terpenes, phenols, polyphenolics, acetogenins, peptides, alkaloids, and others. Most research on marine natural products focuses on their potential biomedical uses. Metabolites from marine organisms have shown antitumor, antiviral, and anti-inflammatory activities, and several of these are currently in clinical trials to establish their effectiveness as new drugs, or are in clinical use (Newman and Cragg, 2004; Molinski et al., 2009; Villa and

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Gerwick, 2010). In addition, some marine natural products may realize their biomedical potential by becoming useful molecular or biochemical probes (Mayer et al., 2010, 2011). Through detailed mechanistic studies, these biochemical probes may lead to the discovery of receptor proteins, enzymes, or other macromolecular targets. The improved understanding of biochemistry and cell and molecular biology that has resulted from these studies may ultimately lead to the discovery of new drugs (Mayer et al., 2010).

The study of the ecological functions of natural products is termed "chemical ecology." While the roles of natural products in terrestrial plants and insects are relatively well studied, much less is known for marine natural products. Examples of ecological functions of natural products include distastefulness that inhibits feeding by predators, settlement cues for larvae, allelopathic effects that prevent fouling by epiphytes and overgrowth by competitors, and pheromones for mate searching behavior. Marine chemical ecology relies on chemical and ecological experimentation to determine the individual or suite of compounds responsible for driving the observed interactions. Determining the compounds responsible for ecological interactions can open a window into other interdisciplinary fields that contribute to ecology, including studies of animal behavior, neurobiology, sensory ecology, reproduction, predator–prey and plant–herbivore interactions, competition, symbiosis, and dispersal and recruitment.

Much of the research in marine natural products and marine chemical ecology has used scuba diving and related undersea technologies as necessary tools. Until the invention of scuba diving, most of the ocean depths were obscured from basic observation, and many marine organisms could not be readily collected. Sampling of the benthos at depths greater than a few meters was carried out using nets and dredges; this was often compared to collecting rainforest insects by pulling a butterfly net behind a low-flying plane. Beginning in the 1960s and 1970s, scuba diving became an essential tool for the collection of benthic marine organisms, particularly macroalgae and invertebrates, for studies of their natural products chemistry (Scheuer, 1990). Also, it was not until scientists could use scuba that they could begin to observe ecological and behavioral interactions in situ and also conduct manipulative experiments to better understand the mechanisms underlying marine behavioral and ecological interactions. Marine chemical ecology has now developed into a broad research area encompassing studies of the chemical mediation of a variety of ecological interactions among marine organisms. The field has been comprehensively reviewed on a regular basis (Paul, 1992; McClintock and Baker, 2001; Paul and Puglisi, 2004; Paul et al., 2006, 2007, 2011b; Amsler, 2008; Paul and Ritson-Williams, 2008; Hay, 2009; Pawlik, 2011), and it is not our intention to duplicate these reviews. Instead, we will highlight the importance of scuba and related technologies as tools for advancing marine chemical ecology by using examples from some of our own research and other selected studies.

HUMBLE BEGINNINGS: TOXICITY ASSAYS TO MORE RELEVANT TECHNIQUES

The field of marine natural products chemistry experienced a "gold rush" in the 1970s and 1980s, when organic chemists took advantage of two emerging technologies: scuba diving and rapidly advancing spectroscopic methods (mostly nuclear magnetic resonance, or NMR, spectroscopy). The result was a rapid increase in the number of publications describing novel metabolites from benthic marine invertebrates and algae (reviewed by Faulkner and Fenical, 1977; Scheuer, 1978–1983). Relying on the assumption that secondary metabolites must serve some function for the organism that produces them, many of these publications ascribed ecologically important properties to new compounds without empirical evidence; in fact, whole reviews of chemical ecology from this period were compiled of references with little or no experimental data to support an ecological function for secondary metabolites (Karuso, 1987).

At about the same time, ecologists were also taking advantage of the advent of scuba diving and describing the distributions and abundances of benthic animals and plants previously known only from much less effective sampling methods, such as dredging (see other contributions in this volume). The assumption of many of these researchers was that anything sessile and soft-bodied must be chemically defended to avoid consumption by abundant and ever-present predators (Randall and Hartman, 1968; Bakus and Green, 1974). In an effort to introduce empiricism to what was otherwise descriptive work on species abundances, some ecologists began extrapolating chemical defenses from toxicity assays in which fish (usually goldfish or mosquito fish) or invertebrates were exposed to aqueous suspensions of crude organic extracts of invertebrate tissues (Bakus and Green, 1974; Jackson and Buss, 1975). Subsequent studies that have compared data from these types of toxicity assays with more relevant feeding experiments have found no relationship between them (Schulte and Bakus, 1992; Pawlik et al., 1995; Tarjuelo et al., 2002).

Beginning in the mid to late 1980s, the first publications began to appear that employed more ecologically relevant techniques for addressing the biological functions of secondary metabolites from marine animals and plants. These were born of collaborations between students and young faculty primarily educated in marine biology and ecology and established natural products chemists who had developed an interest in the ecological functions of secondary metabolites. Some of this work began in the rocky intertidal of Southern California, with members of John Faulkner's natural products group at Scripps Institution of Oceanography collaborating with graduate-student marine ecologists to produce some of the first studies of chemical defenses of sponges (Thompson, 1985; Walker et al., 1985) and intertidal snails (Albizati et al., 1985; Pawlik et al., 1986). However, it was scuba diving that allowed these and other researchers unprecedented access to marine organisms in the subtidal environment, where the vast majority of marine biodiversity is found, permitting the collection of rare organisms and large quantities of patchily distributed organisms, comparative collections across broad geographic regions, and most importantly, manipulative experiments to test hypotheses about the functions of secondary metabolites in the field. The following provides a regional glimpse of a variety of important chemical ecological studies that elucidated the diverse role of secondary metabolites in population and community structure.

INTO THE FIELD

Chemical Ecology in the Caribbean

The transition from toxicity screening to more ecologically relevant studies of secondary metabolites from marine organisms began with studies of the chemical defenses of macroalgae from Caribbean coral reefs (Paul and Fenical, 1983, 1986; Paul and Hay, 1986). At first, these studies relied on research scuba diving for collecting alone; not only were ample volumes of algae needed for the isolation of secondary metabolites, but these collections had to be separated by species, as in the case of the common calcareous algae in the genus *Halimeda* (Paul and Fenical, 1983). Algae of this genus yielded halimedatrial, a diterpenoid trialdehyde that was active in a series of antimicrobial, antimitotic, and toxicity assays, but was also tested in artificial foods as a feeding deterrent against damselfishes and herbivorous mollusks (Paul and Fenical, 1983, 1986). The geographically extensive collections of algae, gathered by diving from a research vessel as a mobile diving platform, combined with chemical analysis of the concentrations of the metabolites, allowed the authors to determine that higher levels of defensive metabolites were correlated with higher levels of herbivory (Paul and Fenical, 1986). Field assay methods were developed to survey interspecific differences in chemical and morphological defenses in Caribbean macroalgae (Paul and Hay, 1986). In what is perhaps the first use of saturation diving in the service of marine chemical ecology, researchers using the *Hydrolab*, then in St. Croix, U.S. Virgin Islands, monitored levels of secondary metabolites in *Halimeda* over the course of the night and day (Hay et al., 1988b). Saturation diving from the *Hydrolab,* and later the *Aquarius* habitat on Conch Reef, near Key Largo, Florida, has proven to be a particularly useful technology for time-intensive research. Saturation divers live for a week or more at 15 m depth in the habitat, essentially a stationary submarine, and can use standard scuba diving gear to perform research dives of 6 hours or longer per day at the same depth as the habitat. This allows research divers to carry out time-consuming observations or manipulations that could never be accomplished by diving from the surface. Night- and day-long studies of *Halimeda* living on the coral reef resulted in the discovery that these algae invest high concentrations of chemical defenses in the new, unpigmented, soft, and nutritionally valuable tissues that grow rapidly at night, with a subsequent reduction in chemical defenses in these tissues as they turn green and become photosynthetic, age, and become protected from herbivores by calcification (Hay et al., 1988b).

Research on the chemical ecology of macroalgae in the Caribbean accelerated rapidly, with defensive roles assigned to metabolites from several species in different taxonomic groups (Hay et al., 1987, 1988a, 1990; Paul et al., 1987). Again, this research required geographically extensive collections using scuba, but also included field observations of species abundances and herbivory. Many of these studies introduced novel field and laboratory experiments to assess chemical defenses by using diverse consumers, including fishes, sea urchins, sea slugs, polychaete worms, and amphipod crustaceans (Hay et al., 1987, 1988a, 1988c; Hay and Fenical, 1988). These studies tested fundamental hypotheses about plant–herbivore interactions that had previously only been applied to terrestrial systems.

Scores of papers were published over the ensuing two decades that further refined our understanding of the chemical ecology of macroalgae on Caribbean reefs (reviews in Hay and Steinberg, 1992; Hay, 1997, 2009; Duffy and Hay, 2001; Paul et al., 2001, 2006, 2007, 2011a; Paul and Puglisi, 2004; Amsler, 2008). This knowledge came with new developments in laboratory and field assays designed to test algal chemical defenses against a variety of potential threats, including grazers, competitors, and fouling organisms (Hay et al., 1998). Diving technologies were fundamental to the collection of subject and assay organisms (Figure 1a), as well as to the field assays themselves (Figures. 1b–d). Some recent studies have focused on the antimicrobial and allelopathic effects of Caribbean macroalgae, including the negative effects of macroalgal extracts on adult corals (Rasher and Hay, 2010) and settlement of coral larvae (Kuffner et al., 2006; Paul et al., 2011a), antimicrobial effects of macroalgal extracts and compounds (Kubanek et al., 2003; Engel et al., 2006), and both inhibitive and stimulative effects of algal extracts on bacteria cultured from the surfaces of Caribbean corals and macroalgae (Morrow et al., 2011). Recently, saturation diving has again been employed to study plant–herbivore interactions at the ecosystem level, with the *Aquarius* habitat off Key Largo, Florida, serving as a base for saturation dives to nearby Conch Reef (Burkepile and Hay, 2008, 2010). Large-scale caging studies that require long-term saturation dives have revealed that the abundance and diversity of herbivores dramatically affects macroalgal cover on reefs, with indirect effects on the survival of reef-building corals (Burkepile and Hay, 2010).

Investigations of the chemical ecology of Caribbean coral reef invertebrates tracked that of macroalgae, with studies focusing on gorgonian corals among the earliest (Gerhart, 1984; Pawlik et al., 1987; Harvell et al., 1988; Harvell and Fenical, 1989; Pawlik and Fenical, 1989; Van Alstyne and Paul, 1992; Slattery, 1999). The technical requirements for these studies were the same as for those focused on macroalgae, with scuba diving figuring prominently in the collection of both subject and assay

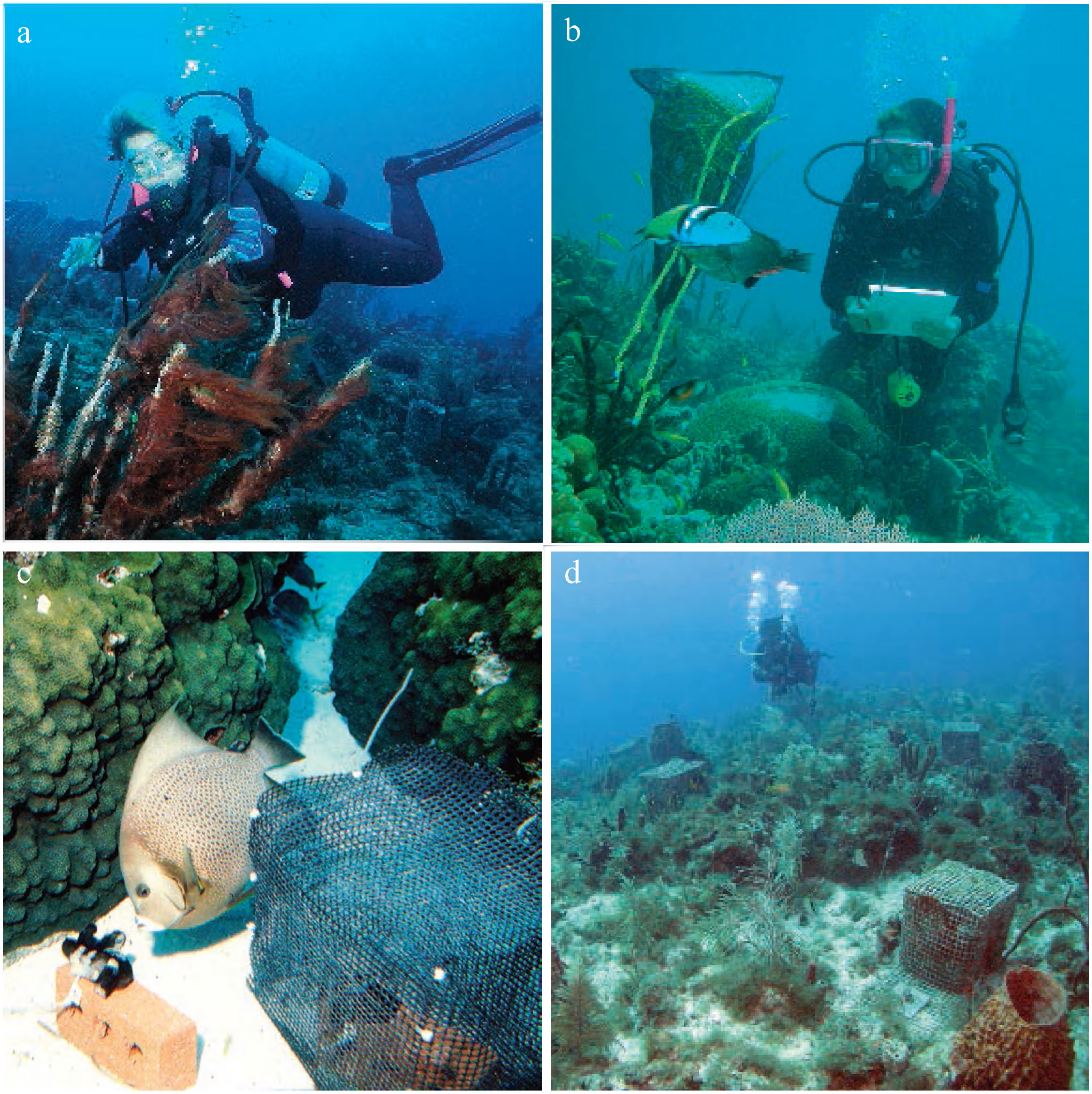

FIGURE 1. Photographs illustrating various field methods that use scuba diving for studies of marine chemical ecology in the Caribbean. (a) A diver examines and prepares to collect marine cyanobacteria, *Lyngbya* spp., that are overgrowing a gorgonian (photo by Karen Lane Schroeder); (b) A diver observes fishes feeding during an underwater feeding assay. Paired feeding assays are commonly used to test the palatability of algal extracts and natural products. Artificial food made with palatable algae is attached to polypropylene lines, with one line containing control food cubes and one containing food with extracts or pure compounds at their natural concentrations (photo by R. Ritson-Williams); (c) Gray angelfish, *Pomacanthus arcuatus*, feeds on the palatable sponge *Chondrosia collectrix* attached to a brick. Angelfishes are major consumers of some species of Caribbean sponges (photo by J. Pawlik); (d) Predator exclusion ("caging") experiment set-up on Conch Reef, Florida. In this case, replicate sponge pieces are placed inside and outside of cages to observe net differences in growth after one year for species that are protected by chemical defenses and those that are not (photo by J. Pawlik).

organisms and in field experiments. Initial surveys of the chemical defenses of gorgonians against generalist predatory fishes suggested that there was some interspecific variation in the levels of defense (Pawlik et al., 1987), but subsequent experiments after assay techniques had been refined revealed that gorgonians were broadly defended by secondary metabolites, and that structural defenses in the form of small calcareous spicules were likely not effective defenses against coral reef consumers that are accustomed to eating limestone when grazing on calcified macroalgae and reef-building corals (O'Neal and Pawlik, 2002).

The chemical ecology of a variety of less sedentary Caribbean marine invertebrates, ranging from planktonic larvae (Lindquist and Hay, 1996; Bullard and Hay, 2002) to hydroids on floating mats of *Sargassum* seaweed (Stachowicz and Lindquist, 1997) to crustaceans that co-opt defended algae or invertebrates to protect themselves by association (Stachowicz and Hay, 2000; Stachowicz, 2001), has been studied. For the beautiful feather-duster worms (Sabellidae) that are common to some Caribbean reefs, the relative speed with which these tube-dwelling worms retract their feeding radioles correlated to chemical defense, with those that retracted more slowly having more potent defenses (Kicklighter and Hay, 2007), with the trade-off between defense and escape speed extending to spaghetti worms (Terebellidae) and others as well (Kicklighter et al., 2003; Kicklighter and Hay, 2006).

Caribbean sponges are perhaps the best-understood aquatic organisms in terms of their chemical ecology, from the level of molecule to ecosystem (Pawlik, 2011), again thanks to the various diving technologies that have contributed to their study. Sponges are now the dominant habitat-forming organisms on many Caribbean reefs, and their populations are increasing (Maliao et al., 2008; McMurray et al., 2010). The earliest studies of Caribbean sponge ecology suggested that fish predators had little impact on sponge distributions (Randall and Hartman, 1968), an idea that was subsequently overturned (Pawlik, 1997). A survey approach that considered secondary metabolites as well as structural and nutritional defenses was used to investigate defenses against fish predators (Chanas and Pawlik, 1995, 1996; Pawlik et al., 1995), with chemical defense clearly playing the dominant role (Jones et al., 2005). The secondary metabolites responsible for chemical defense were isolated and identified using laboratory and field experiments for most of the common sponge species on Caribbean reefs (Albrizio et al., 1995; Wilson et al., 1999; Kubanek et al., 2001; Pawlik et al., 2002); for the oroidin class of compounds of the genus *Agelas*, the molecular basis for chemical defense was explored using both natural and synthetic metabolites (Assmann et al., 2000; Lindel et al., 2000). At the same time, studies of chemical defenses of Caribbean sponges against other potential threats were proceeding, including defenses against invertebrate predators (Waddell and Pawlik, 2000a, 2000b), invertebrate and coral competitors (Engel and Pawlik, 2000; Pawlik et al., 2007), fouling (Kubanek et al., 2002), and microbial pathogenesis (Newbold et al., 1999; Kelly et al., 2005).

Technologies more advanced than simple scuba diving, including saturation and technical diving, have contributed to research into the chemical ecology of Caribbean sponges, and these studies have advanced our understanding of how secondary metabolites influence the entire reef community (Pawlik, 2011). A novel use of the *Aquarius* habitat on Conch Reef, off Key Largo, Florida, was as a platform for long-term videography of fish and sea turtle behavior in response to an array of reef, seagrass bed, and mangrove sponges (Dunlap and Pawlik, 1996). It was discovered not only that angelfishes and turtles preferred to eat sponges that were chemically undefended in feeding experiments with generalist fish predators, such as bluehead wrasses (Pawlik et al., 1995) (Figure 1c), but also that parrotfishes, long thought of as grazers on only algae and corals, were voracious sponge predators (Dunlap and Pawlik, 1996, 1998). These studies led to the determination that sponges on Caribbean reefs could be placed into three categories: (1) chemically defended species that are left alone by predators, (2) palatable species that are consumed by sponge-eating fishes, and (3) preferred species that are removed from the reef and persist only in refuge habitats, such as the interstices of the reef or seagrass or mangrove habitats where predators do not forage (Pawlik, 1997). Resource trade-offs between investment in chemical defenses and reproduction or growth are responsible for the presence of both defended and palatable sponge species on Caribbean reefs, a concept that was tested by observing the healing rates of defended and palatable sponges (Walters and Pawlik, 2005) by conducting long-term growth experiments with sponges inside and outside of cages (Leong and Pawlik, 2010) (Figures 1c–d), and by using diving to survey patterns of sponge recruitment to a shipwreck adjacent to a reef off Key Largo, Florida (Pawlik et al., 2008). These studies provide strong evidence that fish predation is the dominant force structuring sponge communities in the Caribbean, and that the secondary metabolites produced by chemically defended sponges come at a cost to reproduction, growth, or both of these life functions (Pawlik, 2011).

CHEMICAL ECOLOGY IN THE TROPICAL PACIFIC

The earliest investigations of chemical ecology in the tropical Pacific were studies of the comparative toxicities of extracts of sponges, sea cucumbers, and soft corals (Bakus and Green, 1974; Bakus, 1981; Coll et al., 1982). Natural products chemist John Coll and ecologist Paul Sammarco developed a collaboration that led to some of the earliest field studies of allelopathy and antifouling in marine chemical ecology. Focusing on the taxonomically diverse and chemically rich alcyonarians (soft corals) of the Great Barrier Reef, this research team discovered that some species of soft corals were competitively dominant over both soft and hard corals (Labarre et al., 1986; Alino et al., 1992). Subsequent work demonstrated that the allelopathic effects of soft corals against each other extended to the inhibition of settlement of hard corals (Maida et al., 1995), and evidence of toxic effects of specific metabolites from soft corals on hard corals (Aceret et al., 1995). More recently, this group has developed more effective methods of assessing antifouling activity in the field (Maida et al., 2006).

Studies of the chemical ecology of macroalgae in the tropical Pacific followed those done in the Caribbean by Valerie Paul and coworkers. Observations of macroalgal blooms and the persistence of macroalgae in the presence of herbivorous fishes were made by scuba divers in the field (Figure 2a), suggesting that these algae were defended from grazers. Experiments were conducted to determine palatability of the natural compounds with and without confounding factors of food quality or structural defenses (Paul et al., 1990; Van Alstyne and Paul, 1990; Duffy and Paul, 1992; Schupp and Paul, 1994). Often potential herbivores had species-specific preferences that allowed them to specialize on otherwise chemically defended algae (Hay and Steinberg, 1992; Paul et al., 2001). As experiments progressed, researchers found that the concept of algal chemical defense was more complex. Some algae had variable concentrations or different compounds across space and time (Steinberg and Paul, 1990; Meyer and Paul, 1992; Paul and Van Alstyne, 1992; Puglisi and Paul, 1997; Van Alstyne et al., 2001). Other compounds found in marine algae inhibited the growth of pathogens, suggesting that some natural products are important for other functions that contribute to survival, such as reducing disease (Puglisi et al., 2007; Lane et al., 2009). Extensive research has shown that natural products from algae inhibit biofouling on their surfaces (reviewed in Fusetani, 2004, 2011; Lane and Kubanek, 2008). Halogenated furanones produced by the red alga *Delisea pulchra* in Australia inhibited herbivory and also the growth of algae on its surface (Wright et al., 2004; Dworjanyn et al., 2006). Chemically rich macroalgae can negatively affect corals through allelopathic interactions when they are in contact (Rasher and Hay, 2010; Rasher et al., 2011). These types of studies continue today and are important for defining how algae can persist in herbivore-rich habitats and compete with other benthic organisms.

Although benthic blue-green algae (Cyanobacteria) are not related to eukaryotic macroalgae, they fill a similar ecological role. Extensive work on the Pacific island of Guam was conducted to study the chemical ecology of marine benthic cyanobacteria, and also to determine which factors might affect their growth and persistence in coral reef habitats (Figure 2b). Cyanobacteria are prolific producers of natural products (Tan, 2010), some of which have been tested for their feeding deterrent properties (Paul and Pennings, 1991; Pennings et al., 1996, 1997; Thacker et al., 1997; Nagle and Paul, 1998, 1999). In situ manipulations, including caging experiments, showed that the exclusion of herbivores can sometimes contribute to macroalgal and cyanobacterial bloom formation and growth (Thacker et al., 2001). Benthic surveys using scuba showed that some blooms of cyanobacteria were regulated by large storms that produced heavy wave action that dislodged the cyanobacteria (Becerro et al., 2006). Research on benthic cyanobacteria is ongoing around the world, as these organisms can form large-scale blooms that kill many benthic organisms (Paul et al., 2005, 2007; Watkinson et al., 2005).

Studies of specialist consumers, especially herbivores that specialize on chemically defended algae or cyanobacteria, are revealing much about how natural products can influence trophic interactions. Saccoglossans, a group of opisthobranch mollusks, often specialize on green algae, and they can sequester algal secondary metabolites, which are then used for their own defense against predators (Paul and Van Alstyne, 1988; Hay et al., 1990; Becerro et al., 2001). By stealing defensive compounds from their food sources, these soft-bodied slugs avoid the costs of making chemical defenses. Possibly the best-studied specialists are sea hares, which sequester dietary-derived natural products primarily in the digestive gland (Pennings and Paul, 1993; de Nys et al., 1996; Ginsburg and Paul, 2001). Some sea hares, such as species of *Dollabela* and *Stylocheilus*, bioaccumulate natural products from cyanobacteria (Pennings and Paul, 1993; Pennings et al., 1996, 1999, 2001). Demonstrating the potential for studies of chemical ecology to generate possible new drugs, the sea hare *Dolabella auricularia* was discovered to contain natural products with anticancer properties (Flahive and Srirangam, 2005; Sato et al., 2007). Subsequent collection and isolation required huge numbers of sea hares, until it was discovered that the animals were sequestering the compounds from their cyanobacterial food (Luesch et al., 2002), illustrating the importance of in situ observations of species interactions for discovering the dietary source of a natural product.

A variety of sessile benthic invertebrates from the tropical Pacific have been the focus of chemical ecology research. Chemical defenses of Pacific soft corals and gorgonians were studied on the reefs of Guam for many years (Wylie and Paul, 1989; Van Alstyne et al., 1994; Puglisi et al., 2000, 2002). Slattery and coworkers characterized changes in steroids and secondary metabolites over the reproductive period of *Sinularia polydactyla*, and determined that chemical defenses of this soft coral were transferred to its eggs and larvae (Slattery et al., 1999). Considerable variation was observed in concentrations of defensive terpenes in *S. polydactyla* and *S. maxima* at different reefs on Guam. Scuba was used to conduct transplant studies and video transects that linked higher levels of defensive compounds in soft corals that lived on reefs with higher levels of predation by butterflyfishes, suggesting that predation induced greater production of the defensive compound pukalide in the corals (Slattery et al., 2001). The soft coral *S. maxima* was further studied to determine how bleaching might influence its production of defensive compounds. During a natural bleaching event of soft coral colonies in the field, concentrations of a defensive compound decreased but recovered again after several months. Predation rates increased on bleached colonies, and extracts of bleached colonies did not deter predation (Slattery and Paul, 2008). Most recently, studies of hybridization within the genus *Sinularia* have revealed that hybrid soft corals exhibited greater fitness than the parental species, including stronger allelopathic effects against one parental species and stronger antipredatory defenses than either parental species (Slattery et al., 2008).

Sponge chemical defenses have also been investigated in the Pacific. One sponge, *Dysidea* sp., overgrew and killed another

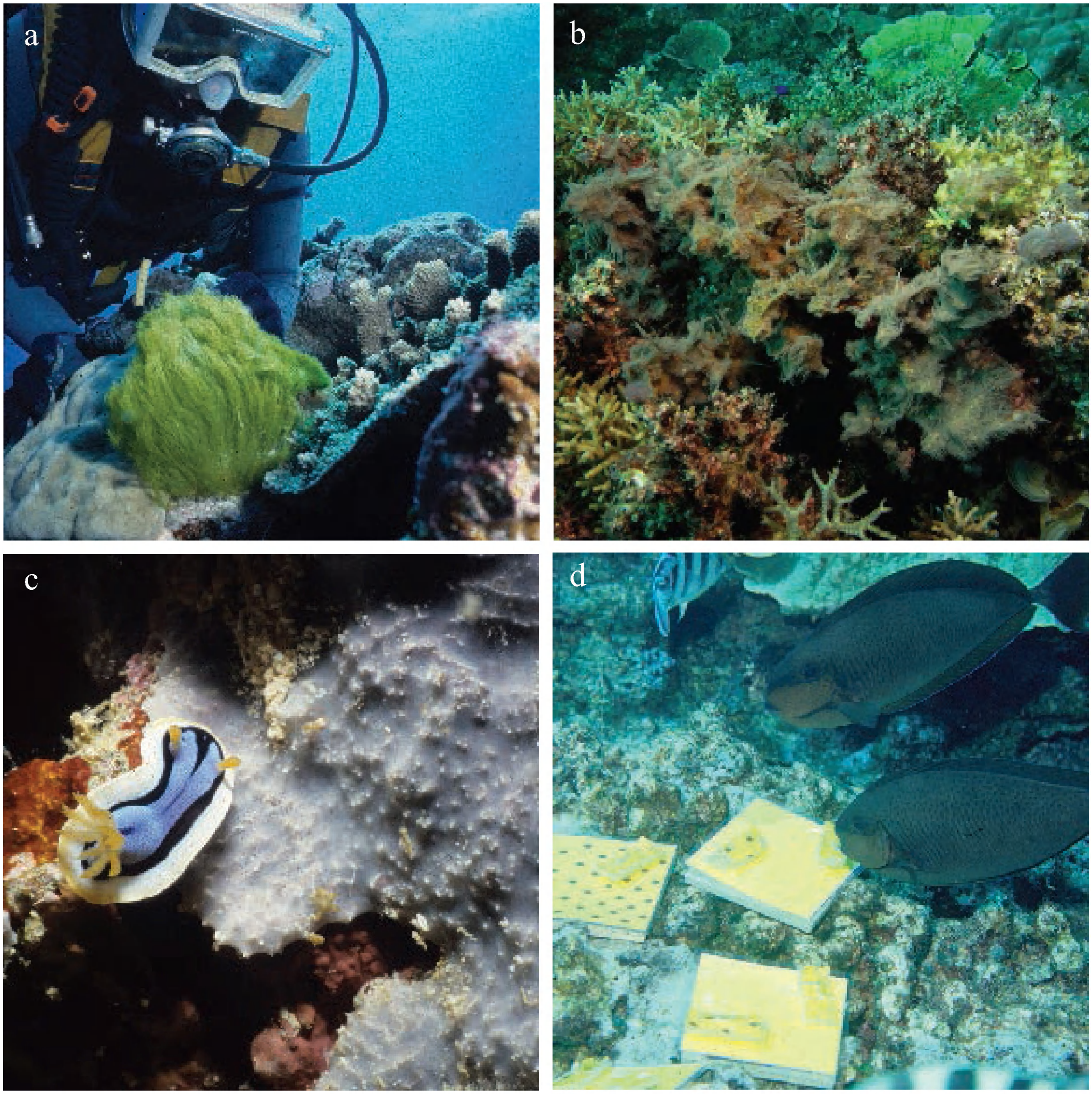

FIGURE 2. Photographs illustrating various field methods that use scuba diving for studies of marine chemical ecology in the tropical Pacific. (a) A diver examines the chemically rich green alga *Chlorodesmis fastigiata* before collection (photo by V. Paul); (b) Mixed assemblages of cyanobacteria overgrow corals (photo by R. Ritson-Williams); (c) The dorid nudibranch *Chromodoris lochi* eats an unidentified sponge (photo by V. Paul); (d) A feeding assay examines chemical defenses and the role of aposematic coloration in phyllidid nudibranchs (photo by R. Ritson-Williams).

sponge, *Cacospongia* sp., on Guam. The sponge *Dysidea* sp. contained the compound 7-deacetoxyolepupuane, which deterred fish predators in situ (Thacker et al., 1998). Using scuba, these researchers also tested for allelopathic effects of this compound by attaching agar strips containing natural concentrations of 7-deacetoxyolepupuane onto the co-occurring sponge *Cacospongia* sp. After seven days, the presence of this compound alone caused sponge tissue necrosis similar to that observed in the sponge–sponge interactions. This chemically mediated competition was first observed by divers in the field, and through extensive field-based ecology using scuba it was shown that the isolated sponge compound had multiple ecological functions in competition and predator defense (Thacker et al., 1998).

As in the Caribbean, sponge consumers have also been studied in the tropical Pacific, and again, underwater observations were critical to understanding predator–prey interactions. Dorid nudibranchs are specialized predators on sponges (Figure 2c), but in the tropical Pacific sponge diversity is so large that it would be impossible to test every possible combination of nudibranch and prey. Perhaps the earliest investigation linking a nudibranch to its prey did so by demonstrating the presence of structurally complex natural products called macrolides in the dorsal tissues of the large Spanish Dancer nudibranch, *Hexabranchus sanguineus*, and in the sponge *Halichondria* sp., collected by night diving on Kwajalein atoll in the Marshall Islands (Pawlik et al., 1988). This study went on to demonstrate that the macrolides were "stolen" by the nudibranch from its sponge diet and passed on to the egg masses of the slug, and that these metabolites were highly effective chemical defenses against co-occurring fish and crab species (Pawlik et al., 1988). Observations of another dorid nudibranch, *Glossidoris palida,* determined that the nudibranch was eating the sponge *Cacospongia* sp., from which it would sequester compounds for defense (Avila and Paul, 1997; Becerro et al., 1998). Many brightly colored nudibranchs can be observed by divers during the day, which appears to be a strategy to advertise their chemical defense. The phyllidiid nudibranch *Phyllidiella granulatus* was frequently seen in Guam, and when the nudibranchs were offered alive to fish they were never eaten (Ritson-Williams and Paul, 2007). Underwater observations showed that *P. granulatus* was eating the sponge *Acanthella cavernosa,* and laboratory analyses found that these two organisms had many of the same natural products. In situ feeding assays with the sponge compounds showed that they inhibited fish predation at levels below natural concentrations (Figure 2d). Using an underwater video camera, fish predators were found to avoid these sponge compounds without tasting them, demonstrating modification of fish behavior by chemical defenses in the field (Ritson-Williams and Paul, 2007). This study illustrates not only the potency of marine chemical defenses but also the complexity of ecological interactions that can only be observed by conducting research under water.

Often, marine natural products from soft bodied invertebrates are assumed to be defensive compounds. While this is certainly the best-studied ecological role of natural products, it is not their only function. Tetrodotoxin and its analogs are potent neurotoxins that have been found in a wide variety of marine and terrestrial organisms (Zimmer and Ferrer, 2007), and these compounds are typically assumed to have a defensive function. Tetrodotoxin and several analogs were found in a planocerid flatworm species that eats mobile snails. In situ experiments were conducted to see if a natural assemblage of reef fish would eat whole live flatworms (Ritson-Williams et al., 2006). Reef fish ate almost all of the flatworms offered, suggesting that tetrodotoxin is either not defensive or not detected by these predators and providing further evidence that toxicity is not the same as antipredatory defense. Further investigation showed that tetrodotoxin was actually used by the flatworm to kill prey items, which are mostly gastropod mollusks (Ritson-Williams et al., 2006). These experiments show the importance of field experiments using scuba to elucidate the function of a secondary metabolite.

Chemical Ecology in Antarctic Waters

The history of chemical ecology in Antarctica is more recent than at lower latitudes. The first scientist to use scuba diving as a research tool in Antarctica was Michael Neushul in 1958 (Neushul, 1959, 1961). Neushul described the benthic marine communities along the western Antarctic Peninsula currently being studied by chemical ecologists, particularly the macroalgal flora (Neushul, 1965, 1968). Since Neushul's time, it has become known that chemical defenses against predation are widespread in the Antarctic marine flora and fauna (reviewed by Amsler et al., 2001a, 2001b, 2008, 2009a; Avila et al., 2008; McClintock et al., 2005, 2010; McClintock and Baker, 1997, 1998), which is in contrast to predictions made before field studies were initiated in Antarctica that included scuba diving (cf. Amsler et al., 2000). Diving collections have also facilitated the elucidation of many of the secondary metabolites that mediate these ecological interactions (Figures 3a–d; Amsler et al., 2001a, 2001b; Lebar et al., 2007).

A majority of the diving-based studies of Antarctic marine chemical ecology have been conducted from the United States Antarctic Program (USAP) facilities at Palmer Station (64°46′S, 64°03′W) off the western Antarctic Peninsula and at McMurdo Station (77°51′S, 164°40′E) in McMurdo Sound, the southernmost extension of the Ross Sea that abuts land. The communities in these two areas differ markedly. Like at other sites along the northern half of the western Antarctic Peninsula, at Palmer Station qualitative and quantitative diving observations reveal that the communities are dominated by forests of large brown macroalgae to depths of 30–40 m or greater (Amsler et al., 1995; DeLaca and Lipps, 1976). The algal biomass in these communities rivals that in temperate kelp forests, particularly in the upper 20–30 m (Amsler et al., 1995). At greater depths or, beginning at approximately 30 m on vertical rock walls, sessile invertebrates dominate the benthos, including sponges, tunicates,

FIGURE 3. Marine chemical ecology research in Antarctic waters. (a) Diving through a natural crack next to a small, grounded iceberg in McMurdo Sound (photo by C. Amsler); (b) A diver returning to the surface in a melted dive hole within a McMurdo Sound dive hut (photo by C. Amsler); (c) A diver collecting amphipods from macroalgae near Palmer Station (photo by B. Baker); (d) A diver collecting the sponge *Haliclonissa verucossa* near Palmer Station (photo by B. Baker).

soft corals, and bryozoans (Figure 3d; C. Amsler and B. Baker, personal observations). At McMurdo Station, smaller red macroalgae are present at some but not most dive sites in the 2–20 m depth range (Miller and Pearse, 1991). Otherwise, sessile, benthic organisms are sparse down to approximately 33 m depth due to the formation of anchor ice, which disrupts communities by ripping objects, including benthic organisms, from the bottom (Dayton et al., 1969, 1970). However, below 33 m qualitative and quantitative diving observations have revealed rich benthic invertebrate communities dominated by sponges (Dayton, 1979; Dayton et al., 1974).

Most current benthic marine research, including chemical ecology, at Palmer Station and other sites along the western Antarctic Peninsula is carried out in open water without solid overhead ice cover, and the equipment and techniques are very much like those used in colder temperate waters. Scientific diving in McMurdo Sound is primarily carried out through land-fast sea ice. Divers gain access by drilling, melting, or blasting holes through the ice or by diving through naturally occurring cracks (Figures 3a–b; Lang and Robbins, 2009). Because water visibility is commonly in the 100–200 m range in McMurdo Sound, USAP regulations do not require divers to be tethered to the surface in this overhead diving environment so long as the bottom is within the depth limits for the dive, a down-line with strobe lights and flags extends from the dive hole all the way to the bottom, and water currents are negligible (Lang and Robbins, 2009). In both regions, variable volume drysuits with thick undergarments are used for thermal protection. Water temperatures along the western Antarctic Peninsula range from approximately −1.5°C to +2.0°C and the water temperature in McMurdo Sound is typically −1.8°C during the diving season, so regulator freeze-up is a concern, particularly when temperatures are below 0°C. "Slingshot" ("Y") or "H" valves can be used to allow a diver to mount two completely independent regulators on a single tank so that the primary regulator can be turned off if it freezes-up and free-flows, thereby allowing the diver to make a controlled ascent with the remaining gas. United States Antarctic Program regulations require such a valve system in overhead environments such as that in McMurdo Sound (Lang and Robbins, 2009), and these are also commonly used along the Antarctic Peninsula as an extra safety precaution.

At Palmer Station, a majority of the macroalgal flora is unpalatable to common sympatric animals that include algae in their diet (Amsler et al., 2005; Aumack et al., 2010; Huang et al., 2006). Overall, nearly half of the macroalgal species have been shown to be unpalatable because they produce chemical defenses, including all of the large brown macroalgae that dominate the community in terms of biomass, as well as most of the more common red macroalgae (Amsler et al., 2005; Aumack et al., 2010). Hence, on a biomass basis, well over 90% of the macroalgal flora resists herbivory using chemical defenses. A number of the specific secondary metabolites responsible for this bioactivity have been identified (Ankisetty et al., 2004).

Early in these studies of macroalgal chemical ecology at Palmer Station, divers recognized that the dominant macroalgae were supporting very dense assemblages of amphipods. Subsequent quantitative diving collections of the amphipods along with their host algae revealed densities of 2–20 amphipods g^{-1} algal wet weight (Figure 3c; Huang et al., 2007), which when combined with algal biomass data from this community (Amsler et al., 1995) resulted in estimated amphipod densities ranging from approximately 30,000 to 300,000 amphipods m^2 of the benthos in solid stands of the dominant macroalgae (Amsler et al., 2008). These amphipods appear to benefit the macroalgae by keeping them relatively clean of epiphytic microalgae and filamentous algae, which otherwise would heavily foul them (Aumack et al., 2011). The amphipods also benefit from the association by gaining a refuge from omnivorous fish predators (Zamzow et al., 2010). Consequently, these two numerically dominant components of the benthic flora and fauna appear to exist in a community-wide, mutualistic relationship with its basis in the widespread occurrence of chemical defenses in the dominant macroalgae.

On a species-by-species basis, an even higher percentage of the sponge species (Figure 3d) at Palmer Station are unpalatable to the dominant sea star predator in the community, *Odontaster validus*. Peters et al. (2009) found that 78% of the 27 species examined were unpalatable to the sea star, and in all cases tested the unpalatability could be explained by the production of defensive metabolites. This prevalence of chemical defense against macropredators is comparable to that observed in Caribbean sponges (Pawlik et al., 1995). However, amphipods were deterred from feeding by extracts of only 2 of 12 randomly chosen demosponge species (Amsler et al., 2009b). With tunicates from this community, even though 100% of 12 species were unpalatable to omnivorous fish and 58% were unpalatable to sea stars, chemical defenses explained the unpalatability to fish in only one tunicate species (Koplovitz et al., 2009). Either secondary metabolites or low tunic pH could explain the unpalatability in five of the seven tunicate species unpalatable to sea stars (Koplovitz et al., 2009). Similar to sponges, only one of ten tunicate species' extracts deterred amphipods from feeding (Koplovitz et al., 2009).

In McMurdo Sound, only two species of fleshy macroalgae occur throughout most of the year and both are unpalatable to sympatric sea urchins because they produce defensive secondary metabolites (Amsler et al., 1998). Divers commonly observe the sea urchins covered with these chemically defended red algae (Amsler et al., 1999; Miller and Pearse, 1991). Laboratory studies motivated by these diving observations demonstrated that although the urchins do not eat the chemically defended algae, they preferentially chose these algae to cover themselves with over other available objects. The algae provide urchins with a physical defensive barrier against their main predators, two large species of sea anemones (Amsler et al., 1999). Moreover, the chemically defended algae benefit because the urchins hold large amounts of drift algae in the photic zone where they can still photosynthesize (Schwarz et al., 2003) and produce spores for the next algal generation (Amsler et al., 1999). Consequently, this is a second mutualistic relationship between Antarctic macroalgae and potential herbivores that is based on the common occurrence of chemical defenses in Antarctic macroalgae.

Although no comprehensive or randomized-sampling survey of the palatability of sponge species has been completed in McMurdo Sound, divers have observed that only relatively few sponge species are commonly preyed on by sea stars (Dayton et al., 1974; Amsler, Baker, and J. McClintock, pers. obs.). All such species for which chemical defenses have been examined were undefended (McClintock et al., 1994, 2000) while most other sponge species in the community have been shown to elaborate defensive metabolites (reviewed by Amsler et al., 2001b). Unlike at Palmer Station, divers do not observe high densities of amphipods associated with benthic organisms in this community (Amsler, Baker, McClintock, pers. obs.). Sea stars are clearly the dominant predators of sponges, although some nudibranchs also specialize on sponges (Dayton et al., 1974; Dearborn, 1977; McClintock, 1994). Unlike lower-latitude communities, there are no vertebrate or other important visual predators of sponges and they have likely been absent for millions of years (Aronson et al., 2007). Because the sponges do not occur shallower than approximately 30 m depth, sponges are unlikely to be subjected to damaging levels of ultraviolet radiation (Karentz and Lutze, 1990). At lower latitudes, sponge pigmentation has been hypothesized to be involved in aposematism (warning coloration) (Harrison and Cowden, 1976; but see Pawlik et al., 1995) and photoprotection against ultraviolet radiation (Bergquist, 1978; Harrison and Cowden, 1976). Neither of these roles would appear to be of selective advantage in Antarctica, at least at locations other than the western Antarctic Peninsula, particularly if one assumes some metabolic cost to production of the pigments (McClintock and Baker, 1998). However, all pigments so far identified from Antarctic sponges have been found to have chemical defensive properties against potential predators, pathogens, or biofoulers (McClintock et al., 2005). It has been hypothesized that these pigments may originally have been of selective value because of other roles but have been maintained in Antarctic sponges because they secondarily took on defensive functions that remain advantageous in the modern Antarctic environment (McClintock et al., 2005).

Diving observations in McMurdo Sound also revealed a unique symbiotic relationship in the plankton that is mediated by chemical defenses. Divers ascending from the benthos noticed a pteropod (pelagic mollusk), *Clione antarctica,* being carried on the backs of the amphipod *Hyperiella dilatata* (McClintock and Janssen, 1990). The pteropods are chemically defended from fish predation by the polyketide pteroenone (Bryan et al., 1995; Yoshida et al., 1995), whereas the amphipods are readily consumed. However, when the amphipods are carrying a captured pteropod, they too are rejected as food by the fish (McClintock and Janssen, 1990). This is likely detrimental for the pteropods, which apparently are unable to feed while being carried by the amphipods, and this relationship has been referred to as an "antagonistic symbiosis" by McClintock and Baker (1997). Dead pteropods were never detected being carried in situ by amphipods, suggesting that they are periodically released and replaced with a fresh individual (McClintock, pers. obs.).

CONCLUSIONS

Scuba diving and other undersea exploration technologies have played a fundamental role in the birth and development of both marine natural products research and marine chemical ecology. Again, the purpose of this contribution has not been to exhaustively review marine chemical ecology, but rather to provide insight into the development of this scientific subdiscipline in response to the rise of undersea technologies. Research boundaries continue to be expanded, with increasing reliance on scuba diving using nitrox mixtures for safer dives and longer bottom times, and mixed-gas technical diving to reach even greater depths (Lesser et al., 2009). Moreover, researchers interested in marine chemical ecology are now using scuba for field studies around the world, including in the North Sea (Toth and Pavia, 2002), Mediterranean (Tarjuelo et al., 2002; Becerro et al., 2003; Haber et al., 2011; Noyer et al., 2011), Red Sea (Ilan, 1995; Kelman et al., 2000; Burns et al., 2003), mid-Atlantic (Ruzicka and Gleason, 2009), and temperate South Pacific (Wright et al., 2000; Duckworth and Battershill, 2001). This discipline is only a few decades old, and vast undersea habitats remain poorly studied in terms of the chemical defenses and signals involved in their ecology, particularly the open-water plankton, the meiofauna and infauna of sandy and muddy benthic habitats, and the deep-sea benthos, including hydrothermal vent and seep communities. Perhaps new undersea technologies will expand ecological and chemical studies to these habitats as well.

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We dedicate this chapter to the memory of two pioneers in marine natural products chemistry, Paul J. Scheuer and D. John Faulkner, who collaborated with and inspired marine biologists and ecologists to investigate the ecological roles of marine natural products.

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Scuba Diving in Blue Water: A Window on Ecology and Evolution in the Epipelagic Ocean

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ABSTRACT. Conventional methods of zooplankton sampling have serious limitations for the study of soft-bodied gelatinous animals, which are easily damaged or destroyed in nets and trawls. An alternative approach is scuba diving in the upper waters of the open ocean to make observations, measurements, and collections in situ. With appropriate safety measures, this method has proved highly effective in revealing natural behavior of a variety of animals, as well as in allowing collection of live specimens for experimental work or detailed taxonomic examination. Simple precautions and protocols have allowed blue-water diving to be conducted safely and productively for the last 40 years. It has provided insight into both the biology of individual species and the structure and functioning of epipelagic communities in tropical, temperate, and polar oceans. It has further revealed the occurrence and effects of nonliving material like marine snow, as well as the microstructure created by density layers and convergences. The direct experience of the water column environment that blue-water diving can provide is a valuable key to understanding the lives of its inhabitants.

INTRODUCTION

The study of zooplankton has been based historically on the results of pulling nets of various configurations through the water column and taking what was collected as representative of the zooplankton community. It is obvious, though frequently ignored, that different nets capture different categories of organisms depending on their mouth diameter, mesh size, bridle configuration, and towing speed. Crustaceans are usually well represented in net samples, along with other small- to medium-sized animals with hard bodies and slow swimming speeds. Trawls with very large mouth openings and coarse mesh size capture faster and larger epipelagic animals, such as fish and squid. Other sampling devices, like Niskin bottles, retrieve an intact water sample with everything in it, and in principle provide a comprehensive picture of all planktonic organisms present. But the necessarily small sample size of a water bottle (typically 1–30 L) with its small opening (centimeters in diameter) makes it unlikely to catch anything that is rare or large, or that would avoid a bottle moving through the water on a wire. With nets or water samplers, it is possible to get a fairly representative sample of small organisms ranging from microbes, phytoplankton, and protozoa up through the smaller crustaceans and other mesozooplankton. What is typically missing from these samples are alert, fast-swimming animals like euphausiid and decapod crustaceans, squid, and fish, and also the

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gelatinous animals that are often sparsely distributed, relatively large and fragile, and usually damaged or destroyed by plankton nets and trawls.

Many oceanographers and marine biologists unfortunately still think of the upper water column of the open ocean as a biological desert, a misconception related to the fact that most epipelagic zooplankton are effectively invisible, either transparent or too small to be seen. Nonetheless, net zooplankton are always present in blue, seemingly empty surface waters. One need only tow a net for five to ten minutes to collect a valid sample of net zooplankton, but short net tows grossly undersample rare species, and small-diameter nets underestimate the abundance of larger taxa, most of which are gelatinous and transparent. As blue-water diving research has shown, epipelagic waters contain a rich spectrum of larger gelatinous zooplankton that is rarely represented in net collections.

BLUE-WATER SCUBA DIVING

We know now that many aspects of animal biology are best understood by observing undisturbed animals in the environments where they live and evolve. Terrestrial biologists are not constrained physiologically from conducting most field investigations, but comparable field studies of undisturbed oceanic animals are surprisingly recent because humans are not adapted for underwater work. William Beebe used hard-hat surface-supplied air to observe fish and zooplankton under water in 1926 (Beebe, 1926), and he later used a bathysphere a half-mile down (Beebe, 1935) to observe midwater fish and invertebrates. Although the aqualung was invented in 1943, publications about underwater behavior of fish did not appear until the 1960s (Randall and Randall, 1960; Hobson, 1963, 1965). Use of scuba to investigate demersal fish and invertebrates is now routine (see other chapters herein), with long-term in situ investigations possible under water day after day at the exact same site, often on the same individual organisms. In the open sea, however, one cannot return day after day to investigate the same individuals or population of pelagic animals because zooplankton drift and pelagic fishes swim away. According to Haddock (2004:553), "With the exception of pioneers like Bieri (1966) and Ceccaldi (1972), few people attempted to observe plankton in their natural environment before Hamner and students pioneered the technique of blue-water scuba diving (Hamner, 1975; Hamner et al., 1975)." Subsequently, many biologists have spent thousands of hours using scuba in blue water to observe undisturbed, mostly gelatinous animals in their own environment. It is important to emphasize that our review of discoveries about epipelagic animals via use of scuba since 1972 is concerned with only those creatures that are found routinely in the upper 40 m of the water column. Many gelatinous animals occur also in much deeper water where they have been investigated via bathysphere, research submersible, and remotely operated vehicles (ROVs) (Beebe, 1935; Nishizawa et al., 1954; Mills et al., 1996; Johnsen, 2001; Haddock, 2004; Robison, 2004).

Blue-water scuba diving was formalized during a research program in 1971–1972 in the Florida Current near Bimini in the Bahamas (Hamner, 1974; Hamner et al., 1975). Although primarily a scuba-oriented exercise, the work also included sampling of zooplankton with 30-cm-diameter nets every month for 15 months. Specimens of only the most common gelatinous species were captured with nets, although gelatinous animals were clearly present in the water column because they were observed almost every day by scuba divers. Ctenophores were often strained through the mesh of the net or damaged almost beyond recognition. Other gelatinous taxa, delicate but also fast-swimming, actively avoided nets. For example, the pseudothecosome mollusks *Gleba*, *Corolla*, and *Cymbulia* are especially sensitive to turbulence. They are vulnerable to predators when feeding motionless with mucus structures, and they swim away rapidly when disturbed by the bridle of a plankton net (Gilmer, 1972). Planktonic mollusks sometimes even evade capture by divers and it is not surprising that they had not been collected previously in large numbers (Gilmer, 1974). However, given good visibility, a group of divers can examine thousands of cubic meters during a dive, locating individuals of many of the larger gelatinous animals within that volume.

The gelatinous zooplankton studied via scuba in the Florida Current were, at that time, poorly known taxa such as foraminifera, radiolarians, hydromedusae, siphonophores, scyphomedusae, ctenophores, heteropods, pteropods, salps, and appendicularians (Hamner et al., 1975). Most of these gelatinous zooplankton have evolved convergent attributes: they are all mostly transparent, delicate, relatively large (>1 cm), neutrally buoyant, slow-swimming, tactile, and nonvisual. Most do not react to scuba divers unless physically disturbed, enabling scuba divers to observe undisturbed, undamaged specimens from all these taxonomic groups at very close range in the upper sunlit regions of tropical seas. Though many gelatinous taxa are transparent and hard to see against a uniform blue background, there are ways to enhance their contrast by looking at them from certain angles relative to down-welling sunlight and, with practice, divers sometimes can spot and identify species from meters away. Like birdwatchers who recognize a species from a flash of color or movement, experienced blue-water divers can often identify animals by their characteristic swimming attitudes or motions or a gestalt impression, even without a clear, close-up view.

Plankton nets and trawls damage or destroy gelatinous zooplankton, so scuba divers collect individual, undamaged animals by hand in wide-mouthed jars for subsequent identification and laboratory study. Oceanic zooplankton live in the water column away from the sea floor, rarely encounter the seabed or shallow reefs, and have not evolved behavioral responses for avoiding rigid surfaces. In standard rectangular laboratory aquaria, therefore, these animals often sink to the bottom and become trapped in the corners, or are embolized by air bubbles. Some taxa can be cultured or maintained in the laboratory via use of circular planktonkreisels (Hamner, 1990) or other taxon-specific aquaria (Raskoff et al., 2003), but it is difficult to know how much physical confinement alters their behavior. Blue-water diving is without question the best way to learn how undisturbed pelagic animals behave naturally (Hamner, 1985; Haddock, 2004).

Different sampling procedures can mislead, but they can also corroborate and confirm the nature of biodiversity in a marine community. Thus, in a study of the western Mediterranean Sea (Mills et al., 1996), use of scuba in blue water generated a list of gelatinous organisms that was as rich in species as the taxa collected with the *Johnson Sea Link* submersible, yet few of these species are ever present in plankton tows in the same waters. Many new gelatinous species are yet to be described; some, such as the ctenophores *Tinerfe cyanea* (Chun, 1889) and *Deiopea kaloktenota* (Chun, 1879), not seen since the nineteenth century, were recently "rediscovered" in the Mediterranean by blue-water divers.

Studies of bio-optical properties of open-ocean animals have benefitted greatly from blue-water collections by scuba divers. Blue-water collections of individual, undamaged, hand-collected specimens are especially critical for studies of physiology and bioluminescence. A series of recent papers has cataloged the distribution and physical properties of transparency of scuba-collected specimens (e.g., Johnsen and Widder, 1998, 1999, 2001; Johnsen, 2001). Examinations of bio-optical properties of these species have included luminescence spectra (Haddock and Case, 1999) and the discovery and cloning of a green-fluorescent protein from a ctenophore (Haddock et al., 2010).

LOGISTICS AND SAFETY AT SEA

Blue-water divers are neutrally buoyant in a featureless open sea. There are no landmarks for orientation, the sea floor is far below and out of sight, and it is possible to become disoriented and drift too far from other divers or descend too deep. To avoid these potential hazards and ensure the safety and productivity of blue-water diving, simple operational procedures for use of scuba at sea have been employed (Hamner, 1975; Haddock and Heine, 2005).

Blue-water divers usually work at sea from a small boat launched from a mother ship or driven offshore from a marine lab. At the research location, the divers tie a surface float to the boat with a 10 m line. A weighted (1–2 kg) 30–40 m down-line with a small trapeze is suspended from the surface float. One person acts as a safety diver and stays close to the trapeze, which is a central hub for organizing the divers' lines. Lightly weighted 10 m safety lines (tethers) slide up and down through clips on the trapeze, and each diver attaches the free end of a tether to his or her buoyancy vest. With tethers attached to the trapeze, the divers descend, moving the trapeze to the desired working depth, where they are then free to search for animals within a 10 m radius from the down-line without danger of drifting away or going too deep.

Blue-water dives typically last from 30 to 60 minutes. Maximum dive depths depend on the certification levels of the divers but rarely exceed 40 m (130 ft), with dive time dependent on water temperature, the depth at which the divers work, and how hard they swim. Usually no-decompression diving is practiced, with mandatory safety stops as the divers ascend. As with other types of scuba diving, dive computers help determine dive parameters. Enriched air nitrox gas has been used, and GPS technology allows divers to make accurate records of their dive location and drift rate when landmarks are not available. Specialized blue-water diving methods have been adapted for use at night and also for operations under Antarctic ice (Hamner, 1982).

TROPICAL AND TEMPORATE EPIPELAGIC ECOLOGY

Physical Characteristics of a Liquid Three-Dimensional World

The waters of the world's oceans are the largest known living space in the solar system: at over 1.37 billion km^3 and extending to an average depth of 3.7 km, they comprise 98% of all the water on Earth. The open ocean stretches from the surface to the bottom—a vast, three-dimensional, fluid environment that presents some extreme challenges for all inhabitants. The organisms that occupy this vast space are among the most numerous of Earth's creatures but also some of the most unfamiliar to us land-dwellers; they are sometimes called "aliens from inner space." This liquid environment has permitted the evolution of organisms quite unlike any terrestrial species, which are restricted by gravity to life primarily in two dimensions. Blue-water diving allows humans to briefly experience what life in the upper waters of the largest biome of Earth is like, enhancing our understanding of the open ocean environment and the daily lives of its inhabitants.

The liquid, three-dimensional nature of the water column is perhaps its most significant difference from terrestrial environments. Reduced gravity has allowed for the evolution of the largest animal on Earth, the blue whale, and gelatinous zooplankton with bizarre shapes and without rigid support structures. Pelagic organisms are released from the physical constraints imposed by gravity on terrestrial animals, swimming or floating neutrally buoyant in the ocean. The opportunity to observe the beauty and grace of gelatinous invertebrates is a splendid reward for those scientists fortunate enough to have dived in blue water.

The water column is divided by subtle yet important vertical gradients and discontinuities that affect the distribution, behavior, and life histories of the organisms that inhabit it. Temperature is an important structuring gradient in the open ocean. In the blue water of the tropics and subtropics, heating from the sun often creates a thin, very warm layer of water just below the surface, which can be a unique habitat for small animals like radiolarians, ctenophores, and calycophoran siphonophores. An upper, mixed layer of uniform temperature is usually bounded by a lower thermocline where temperature changes several degrees over a few meters or less. This sharp boundary creates a density difference, or pycnocline, that often is within diving range. Organisms sensitive to the temperature difference may be restricted to above or below the thermocline. Food particles, grazers, and their predators often accumulate at the pycnocline between lighter and denser water masses (Hamner et al., 1987). Particulates like marine snow and clumps of inorganic and organic materials are also sometimes trapped within density layers. Sometimes multiple layers of water with different densities can occur within the top tens of meters, creating a layer-cake structure that sorts organisms according to size, density, and behavior. These discontinuities can be visible to divers, whether through a difference in refractive index, which is seen as a shimmering or hazy layer, or through the presence of dense phytoplankton layers that visually indicate the subsurface chlorophyll maximum, which is typically measured by oceanographers through its fluorescence.

A second pervasive gradient throughout the water column is hydrostatic pressure. The monotonic increase in pressure with depth is almost certainly of ecological significance to organisms in the water column and may be an important sensory cue regulating depth distributions and diel or ontogenetic migrations, but little is known about mechanisms of pressure sensitivity in zooplankton.

Light is strongest at the surface and the photosynthetic zone typically extends to about 200 m. However, some light penetrates to about 1,000 m at intensities that allow animals to detect the difference between day and night. This mesopelagic zone is home to a wide variety of predatory and scavenging animals, most of them bioluminescent, and with many that make daily vertical migrations. At night in the open ocean the gradients of temperature, density, and pressure remain, but light is gone and the composition and activity of the biological community in the epipelagic zone often change dramatically, with the arrival of diel migrators and an increased level of feeding. Use of scuba at night in the open sea has begun to provide insight into the behavior and ecology of midwater migratory animals (Graham et al., 2009).

The movement of water in the open ocean also creates horizontal as well as vertical discontinuities and boundaries. Fronts between water masses, such as the west wall of the Gulf Stream, can create distinct barriers that separate adjacent horizontal water masses and accumulate large and small organisms at the interface. Wind-driven down-welling structures like Langmuir cells can also concentrate passively and actively swimming organisms, as can areas of shear at the boundaries between different currents (Rakow and Graham, 2006). The scale of these discontinuities is sometimes small enough to be observable by divers.

The Nature of Cover in Open Water

Recent textbooks on biological oceanography assume that pelagic ecosystems are controlled almost exclusively by the flow of materials and energy and microbial processes. Alternately, 40 years of blue-water diving have shown us that although epipelagic communities are affected on a daily and seasonal basis by flows of energy and materials and by microbial processes, over geological time these communities have been shaped primarily by convergent evolution related to the attenuation and diurnal pattern of sunlight, an absence of cover in the open sea, and predation.

Charles Elton (1939:336) noted that terrestrial animals use the presence of cover on land as a refuge from predators, but that refuge can be achieved also through the "influence of the physical qualities and behavior of the prey, such as size, speed, color, and quickness of sense," as well as nocturnal behavior, camouflage, running, and flying. Thus, according to Elton (1939), there are a limited number of broad but nonetheless discrete categories of terrestrial animals that hide, burrow, fly, or run quickly; that are large, aggressive, nocturnal, small, or dangerous; or that aggregate for protection as in herds, flocks, and schools. All of these attributes are part of Elton's (1939:334) "protective system of the prey." We recognize a similar ecological taxonomy for the creatures of the surface of the sea (Hamner et al., 1975; Hamner, 1995; see also Zaret, 1975, for freshwater). Epipelagic animals cluster due to convergent evolution into seven major oceanic assemblages based on the absence of cover at sea and the necessity for refuge from predators. We describe these categories of adaptation below.

Plants on land are large and rooted in the soil, they structure the ambient light environment through foliage density and shade, and they provide lots of cover where animals can hide from predators. In the epipelagic ocean, however, the primary producers are phytoplankton, single-celled algae. Phytoplankton cannot provide cover for oceanic animals because they are too small, and in the water column there are no rocks beneath which animals can hide nor soils into which they can burrow. In the epipelagic zone light is attenuated primarily by the absorption spectrum of water rather than by shade from the primary producers. In the open ocean, quite simply, there is no place to hide from predators.

In the absence of cover, species interactions are governed dramatically by predators, as we learned for ourselves when our University of California (UC), Davis, research group began blue-water diving in Bimini, Bahamas, in 1972. As we observed and collected many types of gelatinous zooplankton in the surface waters of the Gulf Stream, suspended in clear blue water over a sea floor thousands of feet below, we felt vulnerable to large predators. Our first three weeks of blue-water diving were uneventful, but then one morning a large shark suddenly appeared. None of the scuba divers reacted calmly, but instead everyone tried unsuccessfully to get into the boat at once. We subsequently developed better protocols for responding to the presence of sharks.

Just as noted by Elton (1939) for terrestrial animals, a surprisingly limited number of effective antipredatory evolutionary options are also available for oceanic animals. In the open sea there has been convergent evolution for

1. transparency: relatively large (0.5–20 cm), slow, nonvisual, gelatinous animals (e.g., medusae, ctenophores, siphonophores, salps, and pteropods);

2. small size: below visual resolution of the vertebrate eye (less than 0.2 mm; e.g., copepods, appendicularians, fish eggs, and invertebrate larvae);
3. schooling behavior: individuals identical in size and color (2–20 cm, fast and silvery) in schools (e.g., clupeid fishes, small squid, and krill);
4. nekton: fast swimming, large size(20 cm–20 m), and aggressive (e.g., tuna, billfish, sharks, penguins, and seals and other mammals);
5. vertical diurnal migration: relatively fast swimmers, micronekton, intermediate in size (2–10 cm; e.g., euphausiids, midwater fish, and squid);
6. neuston: sea-surface dwellers (e.g., *Physalia* and *Velella*); and
7. "cheaters": 20–200 cm, slow, conspicuous, armored or tricky (e.g., turtles, *Mola mola*, remoras, and flying fish).

The epipelagic ocean is therefore a rich mixture of transparent zooplankton, microplankton, schooling species, nekton, vertical diurnal migrators, and neuston, but transparent gelatinous animals are by far the easiest group of animals for blue-water divers to study because humans are poorly designed to keep pace with faster swimming animals. Many taxa of relatively large, slow, gelatinous invertebrates are almost always present in blue water near the sea surface. They are protected from fast-swimming predators during the day because most visual predators cannot see them. Blue-water scuba divers can see these creatures by hovering in place, focusing for close-up vision, and looking upward to enhance side- and back-lighting of the organisms against the sea surface. Excellent vision is required to collect effectively in blue-water research. Since many gelatinous zooplankton are unrelated genetically, it is certain that tissue transparency is a highly selected feature and has evolved quite independently in many taxonomic groups via convergent evolution. In the future, we anticipate that additional cladograms similar to that constructed by Johnsen (2001) for tissue transparency will demonstrate that epipelagic transparent animals also have converged evolutionarily for relatively large body size, slow swimming speeds, and reduction of sense organs.

Food Resources and Trophic Structures

In situ scuba observations of feeding behavior and mechanisms have provided many new insights into how epipelagic animals obtain food. Some animals such as thecosome and pseudothecosome pteropods (Gilmer, 1972, 1974) and some medusae, siphonophores, and ctenophores (Swanberg, 1974; Harbison et al., 1978; Matsumoto and Hamner, 1988; Haddock, 2007) can be observed only in situ because they do not behave normally in captivity. Even animals that can be used in lab experiments, such as salps and some medusae and ctenophores, give the best results when collected by divers (Madin, 1974; Hamner et al., 1975 [for prey selection and avoidance], 1987 [for ctenophores]; Matsumoto and Harbison, 1993; Madin and Deibel, 1998). Information on the potentially important role that the "jelly web" might play in oceanic trophic structure was provided by Robison (2004) and Condon et al. (2011). It should be noted that both laboratory and in situ observations are often required to determine the full suite of feeding behavior. There are behaviors observed in the field that are not typically seen in the laboratory, and if actually observed in the laboratory, they could not have been understood without corroborative field evidence (e.g., foraging behavior); but there also are behaviors observed in the laboratory that are never or infrequently observed in open sea. Recent advances in technology have elicited some very detailed water flow mechanics used for feeding both in the field (Dabiri et al., 2005) and in the laboratory (Colin et al., 2010).

Our observations of epipelagic gelatinous zooplankton using blue-water scuba in the Florida Current and the Gulf of California showed us three trophic levels: grazer-herbivores, primary carnivores, and secondary carnivores (Hamner et al., 1975). These zooplankton constitute a distinct evolutionary assemblage based on shared, convergent attributes of large size, neutral buoyancy, tissue transparency, slow swimming speeds, and tactile sensory abilities, but they also constitute an ecological assemblage that exchanges nutrient resources via competition and predation (Alldredge and Madin, 1982). One of our most unexpected early findings regarding trophic relationships was that, in contrast to a rigidly layered trophic pyramid wherein small herbivorous crustaceans use tiny appendages and fine setae to select and capture a narrowly restricted size of phytoplankton, large gelatinous grazers instead use mucus structures to capture and consume a broad range of sizes and types of food particles across different trophic levels, including algae, live net zooplankton, and detritus. We observed for the first time how mucus sheets, nets, and strands were used to collect, concentrate, and transport food particles by pteropods (Gilmer, 1972, 1974; Lalli and Gilmer, 1989), thaliaceans (salps, doliolids, and pyrosomes; Madin, 1974), prosobranch veliger larvae (R. Gilmer, UCLA, unpub. observation), polychaete larvae (Hamner et al., 1975), and free-swimming appendicularians (Alldredge, 1972, 1976a). These large gelatinous grazers filter commensurately large volumes of water. For example, a single chain of a large oceanic salp, *Pegea confoederata*, composed of 200 individual zooids filters as much water per minute as 90,000 copepods/1,000 m^3 (Harbison and Gilmer, 1976). Thus, although not nearly as abundant numerically as net zooplankton, large gelatinous animals are disproportionately effective grazers and predators in the water column.

The use of mucus for food capture by epipelagic grazers, along with phytoplankton aggregations, produces copious quantities of marine snow, a primary mechanism for carbon flux (Alldredge, 1972; Wangersky, 1974; Hamner et al., 1975; Silver et al., 1978; Alldredge and Silver, 1988). Feeding filters and mucus webs become clogged, discarded, and heavy with unwanted materials and feeding wastes, and this material sinks rapidly away from surface waters. These macroparticles can be collected by hand in syringes by divers and used in a variety of studies (Silver et al., 1978; Villareal et al., 1999). The constituents of the marine snow and associated microbial or invertebrate populations may also be observed. During the 38 years since our description of marine snow in the blue waters of the Florida Current, we have learned much about how microbes process particulate and dissolved organic carbon and transparent exopolymer particles (Alldredge, 1989; Alldredge et al., 1993). There are more than 1,600 literature entries for marine snow in ISI Web of Science since 1975, but none prior to this, not even the unfortunately ignored initial description of marine snow by Nishizawa et al. (1954).

Recently we have learned that salp-mucus feeding webs can capture an even greater size-range of particulates than we thought initially, including submicrometer particles. According to Sutherland et al. (2010:15129), "Although particles larger than 1 µm (e.g., flagellates, small diatoms) represent a larger carbon pool, smaller particles in the 0.1- to 1-µm range (e.g., bacteria, *Prochlorococcus*) may be more quickly digestible because they present more surface area, and we find that particles smaller than the mesh size (1.4 µm) can fully satisfy salp energetic needs" (see Figure 1). Epipelagic offshore waters are frequently dominated by microplankton that are too small to be captured by mechanical sieving (Riisgård and Larsen, 2010), yet salps apparently can fulfill their entire energetic requirements through an exclusive diet of submicrometer particles, including viruses, bacteria, and colloids. It was known that small copepods are size-specific herbivores, and we knew from observations made while blue-water diving (Hamner et al., 1975) that the much larger salps and pteropods were generalized grazers that fed on particulates that sometimes differed in size by two to three orders of magnitude, thereby blurring the distinctiveness of discrete trophic levels. We learn now, however, from controlled laboratory and field experiments that "salps and other pelagic tunicates remove particles that are four to five orders of magnitude smaller than themselves, thereby bypassing several trophic levels" (Sutherland et al., 2010:15132).

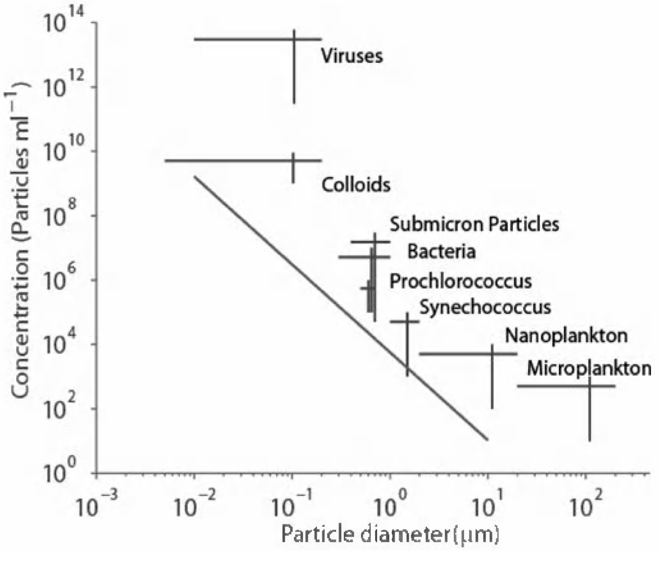

FIGURE 1. Size distribution of living and nonliving particles in the upper ocean, including viruses, colloids, submicron particles, bacteria, *Prochlorococcus*, *Synechococcus*, nanoplankton, and microplankton. Diagonal line is regression of microphytoplankton concentration versus cell diameter.

Direct observations under water have provided exciting and previously unknown details of parasitic or commensal relationships. One of the most common involves hyperiid amphipods and some copepods living on or in a variety of gelatinous hosts (Harbison et al., 1977; Madin and Harbison, 1977; Laval, 1980), and that often rear their broods on the bodies of gelatinous animals (Gasca and Haddock, 2004). These associations rarely are apparent in net-collected samples, yet constitute an important ecological niche occupied by major groups of otherwise nonpelagic crustaceans. Similar behavior is also seen in some juvenile cephalopods and fishes.

There are also many kinds of predatory gelatinous zooplankton in the water column. In our initial blue-water publications from Bimini we described predation by medusae, siphonophores, ctenophores, heteropods, pteropods, and chaetognaths (Hamner et al., 1975). Medusae, siphonophores, and ctenophores feed directly on small copepods via tentacles with nematocysts and colloblasts; some siphonophores consume surprisingly large prey (Pagès and Madin, 2010). Narcomedusae and ctenophores can also specialize, capturing specific types of gelatinous prey, including other ctenophores, medusae, appendicularians, or salps (Harbison et al., 1978; Madin, 1988; Haddock, 2007). In many simple oceanic food pyramids or linear food chains, herbivorous copepods are directly preyed upon by primary carnivores. But chaetognaths also eat copepods, and many medusae, siphonophores, and ctenophores eat chaetognaths, thus feeding as secondary carnivores higher on the food chain. Tuna, flying fish, cod, sea turtles, and albatross (Madin, 1974) sometimes eat salps, and salps capture and consume copepods along with diatoms, yet salps apparently can also consume viruses, colloids, and bacteria (Sutherland et al., 2010). Consequently it is often difficult to assess trophic status at any given time without simultaneous analysis of gut contents.

During the past 38 years we have learned an enormous amount about predatory relationships within the gelatinous epipelagic assemblage beyond our initial observations in the Gulf Stream and Gulf of California (Madin, 1988). It is now clear that the gelatinous assemblage of blue-water zooplankton is not a "dead end" to the flow of energy and materials in the open sea, but instead is a complex, often-changing food web, with surprising and strange trophic interactions and links to everything from the microbial web to fish, whales, turtles, and birds. Gelatinous grazers and predators can sometimes unexpectedly overwhelm entire pelagic ecosystems and become keystone species, such as when a single species of introduced ctenophore ate all the fish larvae in the Black Sea, eliminating most commercial fishing (Kideys, 2002; Ghabooli et al., 2011). Recently it has been shown that blooms of medusa and ctenophores also produce large quantities of dissolved and colloidal organic material that both stimulates and alters the composition of the microbial community, potentially with broad consequences for the biogeochemistry of entire habitats (Condon et al., 2011).

BEHAVIOR

Blue-water diving allows observation of many aspects of behavior, one of the most obvious of which is locomotion. Although the word plankton means "drifting," in fact zooplankton, including most gelatinous taxa, can swim by various means. Swimming behavior can be difficult to study in the laboratory because confined tank volumes and the delicate construction of many species often lead to artifacts of behavior and misleading observations or measurements. Constraining animals with tethers and other devices to restrict their movements, while effective for small, hard-bodied forms like copepods, is usually impractical with larger gelatinous animals and can create problems with natural fluid flow. Tanks large enough to minimize these effects make it hard to observe animals closely.

Direct observations by divers at sea are preferred to ensure accurate documentation of swimming behavior, but these can be difficult to obtain under uncontrolled field conditions. The tethered-diver safety system for blue-water scuba allows divers to maintain good visual distance and continuous visual contact with a subject animal without disturbing them, but this is only effective for fairly large and slow-swimming species. Besides by direct visual observation, behavior can be recorded on video and fluid flow visualized with dye tracers (Madin, 1990; Sutherland and Madin, 2010). Estimates of swimming speed in situ have been made by timing the transit of animals over known distances, measured with depth gauges or by marking start and end points with dye and measuring distance (Madin, 1990); fluid flow patterns and rates can be measured from video of dye traces (Sutherland and Madin, 2010). Recently the development of a Self-Contained Underwater Velocimetry Apparatus (SCUVA; Katija and Dabiri, 2008) makes possible in situ digital particle image velocimetry measurements that provide information on swimming energetics.

Medusae were thought to swim by jet propulsion but work by Costello, Colin, and colleagues (Colin et al., 2003; Costello et al., 2008) has shown that there are different modes of fluid manipulation by different species that combine jetting with swimming and feeding currents created by the "rowing" action of the bell margin. Early studies of siphonophore locomotion (Mackie, 1964) were made in aquaria, with subsequent lab and field studies by Purcell (1980, 1981). Swimming of ctenophores has also been studied in tanks, but the size and fragility of many lobates and cestids makes in situ observations critical (Harbison et al., 1978; Matsumoto and Hamner, 1988; Matsumoto and Harbison, 1993). While some early studies of swimming by salps were done only in lab tanks (Bone, 1984), later studies combined lab and field observations and measurements to observe both small- and large-scale aspects of swimming behavior by single salps and chains of various species (Madin, 1990; Sutherland and Madin, 2010). Blue-water diving also enables study of complex swimming behavior of animals relative to their environment or in schools or swarms.

Complex behavior of the moon jellyfish (*Aurelia aurita*) was investigated using scuba in Saanich Inlet, Vancouver Island, British Columbia, Canada (Strand and Hamner, 1988; Hamner et al., 1994). Dense swarms of *Aurelia* can be found in Saanich Inlet in late summer. Jellyfish dispersed across Saanich Inlet at night via tidal currents, but when direct sunlight hit the water in the morning the medusae began to swim horizontally at the surface and directionally to the southeast, producing massive swarms along the southeastern sides of the fjord in the afternoon. Jellyfish that had greater distances to swim also swam directionally southeast in the afternoon, demonstrating that horizontal navigation is controlled by a time-compensated sun compass. When the jellyfish reached the sides of the fjord, they ceased swimming horizontally and instead swam vertically, and thereafter male medusae released sperm strands into the water column. The dense swarms of *Aurelia* in Saanich Inlet, therefore, are breeding aggregations, something that could only have been determined from direct observations via use of scuba. Similar swarms of moon jellies with trailing sperm strands have been seen in the waters off California (G. Matsumoto, Monterey Bay Aquarium Research Institute, pers. obs.).

TAXON-SPECIFIC OBSERVATIONS

A broad diversity of organisms have become gelatinous as they evolved to live suspended in the water column. These span a taxonomic range from single-celled organisms to large jellies and colonies of tunicates. Many larvae of fish, worms, mollusks, and others also spend a portion of the life cycle as semitransparent meroplankton.

Macroscopic protists, such as radiolarians and foraminifera, and other protists, such as the giant dinoflagellate *Noctiluca*, can reach high numbers in surface waters. Radiolarians and foraminifera are amoeboid but bear siliceous (radiolaria) or calcareous (foraminifera) "shells" or spicules. Some of these feed by snagging marine snow on spicule tips, where it is enveloped by the cell membrane. Inactive particles and live microzooplankton also adhere to the sticky surface of the cell membrane. *Noctiluca* feeds with an external mucus web (Omori and Hamner, 1982). Shallow polycystine radiolarians contain algal symbionts, and while their molecular phylogeny has been examined (Amaral Zettler et al., 1997), little is known of their ecological impact (Swanberg, 1983). Some species are small enough to be collected with syringes, while other colonial forms (often mistaken for egg masses) may reach a meter in length. These gelatinous colonies trap small zooplankton like copepods on their surfaces, and digest them within vacuoles. Yet at the same time, hyperiid amphipods of similar size roam freely over the colonies as commensals. The observation and collection of these colonial radiolarian in situ has only been possible with blue-water diving. Foraminifera are important indicators of past climate change. Their shells hold a record of the isotopic composition of the seawater in which they were formed, and thus they are of great interest to paleo-oceanographers. Divers have collected live forams in snap-cap vials so they can be cultured and studied in the laboratory (Spero et al., 1997).

Many planktonic cnidarians, principally hydromedusae, have been investigated in the field, collected using scuba, and studied further in the laboratory (Colin et al., 2003; Costello et al., 2008). Siphonophores, fragile colonial forms that are rarely seen intact, are especially suitable for blue-water collection (Biggs et al., 1986) and have contributed to a recent molecular phylogeny of this group (Dunn et al., 2005). Hydromedusae, smaller scyphomedusae, and cubozoans are all readily collected in jars; larval anemones (particularly cerianthid larvae) and larval corals may be encountered.

Comb jellies are among the most fragile gelatinous zooplankton. Only the hardiest species, such as *Pleurobrachia* and *Beroe*, could be found in plankton net collections or were figured in older textbooks. Scuba divers, however, now collect even the most fragile of lobate and cestid ctenophores by hand in individual jars, and ctenophores collected through blue-water diving have revealed new facets of their ecology (Swanberg, 1974; Harbison et al., 1978) and molecular phylogenetics (Podar et al., 2001). Rarely seen forms sometimes appear common to blue-water divers; many new species have been discovered in surface waters (Madin and Harbison, 1978; Matsumoto, 1988).

Pelagic tunicates (salps, doliolids, pyrosomes, and appendicularians) feed directly at low trophic levels, demonstrate rapid population explosions, and form an important component of many highly productive food webs (Madin, 1974; Alldredge, 1977). While many salps are hardy enough to be enumerated from plankton tows, their physiology and ecology is difficult to study without in situ observation and hand-collected live specimens for laboratory experiments. Doliolids are even more fragile and difficult to maintain in the laboratory (Madin and Deibel, 1998). Appendicularians (also called larvaceans) build elaborate feeding webs (or "houses") that, until recently, could only be observed in situ (Alldredge, 1976b; Deibel, 1986). A few species of appendicularians have been successfully cultured (Paffenhöfer, 1973; Fenaux et al., 1986), but the great majority of species are poorly known and not amenable to laboratory observation.

Pelagic mollusks, such as pteropods, heteropods, and nudibranchs, have been investigated using blue-water scuba techniques. Pteropods (*Limacina*, *Corolla*, and *Clione*) may occur in large numbers, along with diverse species of heteropods and other pelagic mollusks (Lalli and Gilmer, 1989). Holoplanktonic nudibranchs such as *Phylliroe* prey on planktonic cnidaria. Ommastrephid squid may occasionally be observed with their large gelatinous egg masses (Staaf et al., 2008).

Arrow worms (phylum Chaetognatha) are sometimes large enough to be observed by divers. They are among the most important net zooplankton predators, feeding particularly on copepods. A diverse array of polychaetes are found both free-living and in association with other gelatinous plankton. Alciopid polychaetes, for example, are often predators or parasites of ctenophores.

Open-ocean adult fish, such as the sunfish *Mola mola*, as well as sharks, billfish, and some schooling pelagic species, can be occasional, charismatic visitors during scuba dives in blue water; larval fish are frequently encountered at night. In addition, some pelagic fish hide behind the veil of large gelatinous species such as scyphomedusae or the siphonophore *Physalia*.

EPIPELAGIC POLAR OCEANS

In polar regions, the light regime of the epipelagic zone differs from that in all other parts of the ocean. Instead of experiencing a diurnal light/dark regime, surface waters at high latitudes remain sunlit for most or all of a 24-hour day in summer, and the opposite in winter. Polar oceans are also unique in that sea ice provides cover for epipelagic organisms, year-round in the Arctic and seasonally in the Antarctic. We have used blue-water scuba extensively in the open sea in the Antarctic, Arctic, and subpolar oceans to investigate epipelagic euphausiids, salps, ctenophores, and medusae, but we have been able to study euphausiids near the sea surface during the day only in polar oceans. "In polar oceans in summer, diurnal vertical migration [is not necessarily advantageous] . . . for an herbivore such as *Euphausia superba* because all phytoplankton production occurs quite near the surface and pelagic herbivores either feed there or they starve. Rather than swimming down into deep water to evade predators, *Euphausia superba* engages in schooling behavior in the epipelagic zone, . . . electing a modal survival strategy that is quite different from the diurnal vertical migratory solution so effective for most tropical euphausiids. Thus, when the temporal periodicity of the 24-hour light environment changes, so must the nature of the convergent adaptive solutions change to permit survival in an illuminated, three-dimensional environment devoid of cover" (Hamner, 1995:75).

For behavioral research on Antarctic krill *Euphausia superba* near the Antarctic Peninsula, we used tethered, blue-water scuba protocols modified for dry-suit diving (Hamner, 1982). In most parts of the world euphausiids are vertical diurnal migrators, near the surface only at night, but surface schools of Antarctic krill had been seen previously in summer at the surface by Hardy and Gunther (1935) around the docks at South Georgia Island and by Marr (1962) from aboard ship; density of krill in schools was estimated at about 64,000/m^3 (1 krill/in^3), which was later confirmed photographically under water via scuba by Ragulin (1969), Hamner and colleagues (Hamner et al., 1983; Hamner, 1984a), and O'Brien (1987). These observations of schooling behavior by Antarctic krill are of central importance for understanding the ecology of the entire Antarctic water column (Hamner et al., 1983; Hamner, 1984b; Hamner and Hamner, 2000).

The behavior of *Euphausia superba* changes during ontogeny from a dispersed solitary larva to larvae clumped within swarms and then to uniformly polarized furciliae close-packed into schools. We directly observed this behavioral transition for krill larvae in the Gerlache Strait, Antarctica, while blue-water diving (Hamner et al., 1989). In open ocean without sea ice, isolated furciliae at the surface were at very low densities (0.003/m^3). In the presence of sea ice, individual, free-swimming furciliae were more abundant (0.3/m^3), but tiny schools of furciliae also were found below the sea ice at densities of about 3×10^9/m^3. Sea ice provides larval krill with concentrated epontic algal food and protection from predators, and it facilitates formation first of swarms of nonpolarized individuals and then of small, ice-oriented polarized schools. "*Euphausia superba* makes an abrupt behavioral transition after the last larval molt from an individualistic, planktonic lifestyle to that of a highly social, nektonic juvenile. Then and throughout the rest of its life, most aspects of krill behavior are expressed within the context of highly organized, polarized schools" (Hamner and Hamner, 2000:192).

The large cydippid Antarctic ctenophore *Callianira antarctica* captures and digests Antarctic krill. Near the Antarctic Peninsula we saw ctenophores with feeding tentacles fully extended and with partly digested krill in their guts, but only when there were no krill schools in the immediate vicinity, although krill were clearly nearby as evidenced by krill acoustic signatures and krill fecal pellets and molts in the water column (Hamner and Hamner, 2000). When *C. antarctica* was seen within krill schools, ctenophore guts were empty and fishing tentacles were completely retracted. *Callianira antarctica* captures prey with colloblasts and stretchy tentacles that reel in prey one at a time, which often takes several minutes. Schooling, therefore, protects most krill from *C. antarctica* because it is physically impossible for cydippid ctenophores to fish with delicate, extended tentacles within schools of tens of thousands of krill/m^3.

At least one large lobate ctenophore, probably a new species in the genus *Eurhamphaea*, has been observed and collected by blue-water divers in the Antarctic. This species also appears to be a predator on krill or their larvae. Also present is *Beroe cucumis*, the species that preys on other ctenophores and attains a size of 25 cm in the Antarctic. In the Arctic, the cydippid *Mertensia ovum* occupies a similar niche to *Eurhamphaea*'s, but preys on large copepods as well as krill (e.g., Matsumoto, 1991; Swanberg and Bamstedt, 1991). *Mertensia ovum* appears to store lipids derived from crustacean prey in numerous droplets contained within the mesoglea, presumably as an energy store (Larson and Harbison, 1989). Other ctenophores observed by diving in the Arctic include *Bolinopsis infundibulum*, which attains a size of 20 cm or more, *Beroe cucumis*, and *Dryodora* (Purcell et al., 2010).

Pelagic tunicates have an unusual asymmetric distribution in polar seas. While appendicularians are common in the Arctic, salps are absent (Deibel and Daly, 2007), yet salps are extremely abundant in the Southern Ocean where they often alternate with krill as the dominant grazing species (Loeb et al., 1997; Atkinson et al., 2004). The dominant species of salps in most of the Southern Ocean is *Salpa thompsoni*, with smaller populations of the very similar *S. gerlachei* reported nearer the Antarctic continent. Two other species, *Ihlea racovitzai* and *I. magalhanica* also occur in the region, but usually in smaller numbers. Three of these species appear restricted in distribution to south of the Antarctic Convergence, with *I. magalhanica* found in the vicinity of the Falkland Islands. Blue-water divers have provided material for studies of salp energetics and fecal pellet production (Phillips et al., 2009).

CONCLUSIONS

Although study of gelatinous animals of the plankton began in the nineteenth century when naturalists like Chun, Mayer, and Bigelow dipped specimens from the sea, major progress in understanding the functional morphology, behavior, and ecological roles of these organisms has depended on the ability afforded by blue-water diving to observe and collect gelatinous fauna from their natural oceanic environment. Blue-water diving is simply field biology carried out in a field that has become accessible with scuba in the last four decades. It has allowed biologists to do the kind of research that was done a century ago on land, but in one of the largest and least known habitats on Earth, populated by diverse, abundant, and largely unknown animals. While the method has clear limitations, it is a powerful complement to other approaches to the study of open-ocean organisms, and deserves to be more widely used by a new generation of oceanographers. In addition to its value as a means of observing, collecting, and experimenting with planktonic animals in situ, blue-water diving gives oceanographers and marine biologists a personal, immersive experience of the nature of the open ocean environment that cannot be achieved by towing nets, looking at instrument readouts, or even watching video from an ROV. We believe this is a valuable experience for all ocean scientists.

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Scientific Polar Ice Diving

Adam G. Marsh, Amy L. Moran, and James B. McClintock

ABSTRACT. Early ecological descriptions of under-ice benthic communities in McMurdo Sound were made over 40 years ago by wetsuit divers Paul Dayton and John Pearse, resulting in seminal papers. Polar diving equipment has evolved since then in areas of life-support breathing apparatus and thermal protection. Scientific polar ice diving has developed into a research tool for intensive sampling and experimental programs by marine ecologists describing under-ice ecosystem structure, and provided insights into how benthic communities respond to disturbance. Direct scuba observations have established the remarkable continuity that exists in species distribution and abundances. The ability to scuba dive in a stable, marine benthic community in polar habitats provides researchers with a unique opportunity to understand the structuring forces at a population level and selective adaptations at an organismal level. Research by Moran and Woods using cutting-edge methods in underwater environmental measurement developed and tested a sophisticated model for metabolic regulation in embryos developing on the sea floor. Work by Marsh in understanding energy utilization during development in an Antarctic sea urchin highlighted a novel mechanism of metabolic energy conservation associated with protein metabolism. A current research focus is on environmental imprinting via epigenetic modifications to genomic DNA, which could have a large impact on cellular physiological activities. This could possibly function as a mechanism for regulating large-scale shifts in cellular energy utilization, perhaps serving as the key mechanism by which organisms have adapted to polar life in the cold and dark. McClintock and coworkers' discovery regarding feeding deterrents in an Antarctic sponge has fueled an extraordinary understanding of chemically mediated defense in polar benthic communities.

INTRODUCTION

Polar marine ecosystems are vastly understudied. In general, they possess unique features related to extremes of temperature, photoperiod, and the frequent occurrence of a sea ice layer at the ocean–atmosphere boundary. It is this latter feature of sea ice dynamics that makes these habitats particularly challenging for studying benthic macroorganisms (both animals and plants). Surface ice conditions confound the collection of living specimens and constrain logistics for in situ experimental manipulations. Consequently, scientific research activities in polar coastal margins focusing on benthic organisms require well-organized and -trained scuba diving teams for direct observations, collections, and experiments. Scientific research on polar marine organisms poses many challenges. In areas where sea ice coverage is significant in terms of either a solid layer or high ice floe densities, great skill and caution must be exercised by dive teams engaged in scuba diving activities. Scientific ice diving in polar regions has yielded a wealth of information that could not have been obtained by any other sampling methods. The ability of a diver to make direct under-ice observations and the delicate skill with which critical samples can be collected or experimental arrays handled have yielded critical new knowledge of the richly diverse and ecologically complex polar habitats. In short, polar ice diving

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has developed as a mature branch of scientific diving that is irreplaceable in terms of the discoveries that have been made and will continue to be made.

DIVING

Techniques and strategies for diving in polar ice environments have received considerable expert attention in recent years (Lang and Sayer, 2007; Lang, 2009). Local dive-site conditions can be variable and require unique solutions to mitigate risk. However, there are some aspects to polar ice diving that all scientific divers face, which we briefly summarize below to provide an overview of the challenges that are involved with scientific ice diving in polar coastal zones. Readers should consult Lang and Sayer (2007) and Krupnik et al. (2009) for more details specific to ice diving research activities.

The biggest challenge to ice diving can be limited options for water entry and exit. In floe environments, dynamic interactions of winds and currents can establish significant risks for the ability of a diver under water to navigate back to a safe exit point. In conditions with a solid sea ice surface, divers operate as if in an underwater cavern with restricted access. Diving is not conducted under conditions where there is any doubt about the ability to return to the exit location. Once all the risk factors have been identified and mitigated, then underwater work can commence. A second significant challenge is thermal protection for the diver while under water. Drysuits are standard equipment now and there are a variety of commercial designs using heavy-duty, tear-resistant outer-layer materials to make the suits durable under harsh field conditions. Drysuits need to be fitted to the diver's body, with sufficient extra space to allow for several layers of insulating undergarments. A third challenge for working in water under ice is buoyancy control. Maintaining a larger air volume in the drysuit to accommodate the insulating undergarments results in more potential for large air pockets to move around within the suit and cause sudden shifts in balance points and trim levels. More air necessitates more lead weight, and so a larger total mass of the diver plus equipment requires greater attention to suit-volume regulation for maintaining neutral buoyancy. A fourth challenge is ensuring that the diver has the appropriate equipment for a safe dive. This mostly means that divers must have first- and second-stage regulators that are designed for use in sea water at -2°C without developing internal ice crystals that could result in a free-flow event. A great deal of scrutiny must be exerted to ensure that any regulator used under the ice is not prone to free-flow events.

SCIENCE

Some of the most important work involving early ecological descriptions of under-ice benthic communities in McMurdo Sound were made by wetsuit divers in the mid-sixties and resulted in seminal papers by Paul Dayton and John Pearse (Pearse, 1966, 1967; Dayton et al., 1969, 1974). Dayton and Pearse were pioneers in making detailed underwater observations and experiments, and continued productive Antarctic research careers with their students by utilizing scuba as the first tool for observation and collection (Dayton and Oliver, 1977; Oliver, 1984; McClintock and Pearse, 1986, 1987; Pearse et al., 1991; Pearse and Lockhart, 2004). Scientific ice diving became the primary mechanism for intensive sampling and experimental programs by marine ecologists describing under-ice ecosystem structure (Slattery and Oliver, 1986; Brey et al., 1995; Slattery and McClintock, 1995; Blight et al., 2010). The ability to perform direct experimentation under the ice has provided many insights into how benthic communities respond to disturbance (Lenihan et al., 2003; Conlan et al., 2004; Kim et al., 2007; Conlan et al., 2010; Kim et al., 2010) and the delicate balance that exists between abiotic selection pressures and population survival (growth, reproduction, and recruitment) in marine communities subjected to continuous harsh environmental conditions.

We now have a much better understanding of the longevity of polar benthic communities and how shifts in trophic organization may proceed over much more gradual time scales than in other marine ecosystems (Brey et al., 1995; McClintock and Pearse, 1986, 1987). Direct scuba observations and research diving activities for the last 40 years have established the remarkable continuity that exists over this time frame in species distribution and abundances. This level of system equilibrium is only possible because of the seasonally and annually stable ecosystem structure. The only other comparable marine ecosystems are the abyssal plains of the deep oceans, where direct observations are only possible via deep submergence vehicles. The ability to scuba dive and directly observe, collect, and manipulate a stable marine benthic community in polar habitats provides researchers with a unique opportunity to understand the structuring forces at a population level and selective adaptations at an organismal level. The majority of the biosphere on this planet, 75% by volume, consists of a single habitat type: cold (~2°C), dark sea water. One of the few places where this habitat type is accessible by scuba is along the coastal margins of Antarctica.

Ongoing research by the coauthors of this paper continues a tradition of strong scientific diving programs in coastal Antarctic habitats. The observation, collection, and experimentation that is afforded from a first-person perspective by actively engaging in under-ice research constantly fuels new discoveries and new questions (McClintock et al., 2010b). As the field of biology has been moving more and more toward molecular-level understandings based on increasingly sophisticated technologies, scientific diving remains an important tool for collecting organisms necessary for physiological, biochemical, and molecular genetic research.

Work by Amy Moran, in collaboration with Art Woods, has used cutting-edge methods in underwater environmental measurement to develop and test a sophisticated model for metabolic regulation in embryos developing on the sea floor (Woods and Moran, 2008a, 2008b; Woods et al., 2009; Moran and

Woods, 2010). In general, the availability of oxygen in seawater and the rate of oxygen consumption by an organism is a critical balance (supply versus demand) that is unique in polar environments. One facet where this is particularly important is for the egg capsules of nudibranchs (Mollusca). Here, the deposition of numerous embryos into a single capsule is under a tight selective constraint of ensuring that sufficient oxygen is available in the center of the capsule so that all embryos can survive through development. The research of Woods and Moran has made many interesting discoveries of embryo size, egg-capsule size, capsule density, and capsule geometry that are associated with adaptations for survival of nudibranch embryos in polar habitats. Questions of oxygen transport, growth regulation, metabolic energy utilization, and developmental period remain key questions for understanding the life-history adaptations of many polar marine invertebrate species. Pursuing this work will require additional in situ work under the ice.

Work by Adam Marsh has focused on understanding energy utilization during development in an Antarctic sea urchin (Marsh and Manahan, 1999; Marsh et al., 1999; Marsh and Manahan, 2000; Marsh et al., 2001). Metabolic efficiency is an overriding feature of many species in polar ecosystems where primary production is severely limited to only a small portion of each year. Many invertebrate larval forms have feeding structures and rely on the capture of exogenous food for their nutrition. However, in polar ecosystems, there is very little food available in the water column throughout most of the austral spring and summer developmental periods. Work in the Manahan laboratory has demonstrated a fascinating and novel mechanism of metabolic energy conservation associated with protein metabolism: the net cost of protein accumulation (net of synthesis and degradation) is much less in the embryos of the Antarctic sea urchin than in any other known marine organism (Marsh et al., 2001).

Recent work by Marsh is delving into genomic-level responses to temperature stress (Fielman and Marsh, 2005; Ulrich and Marsh, 2009) and the potential for salinity stress to become an important selection force in the future (Cowart et al., 2009). We are now focusing on environmental imprinting via epigenetic modifications to genomic DNA, which could have a large impact on cellular physiological activities. This would function as a major mechanism for regulating large-scale shifts in cellular energy utilization, perhaps serving as the key mechanism by which organisms have adapted to polar life in the cold and dark. Despite the molecular focus of ongoing studies, diving operations under the ice for collections and observations remain an important component of this field work.

Work by Jim McClintock has been prolific, particularly in collaboration with marine natural products chemist Bill Baker and phycologist Charles Amsler. A simple discovery regarding feeding deterrents in an Antarctic sponge has fueled an extraordinary understanding of chemically mediated defense in polar benthic communities (McClintock and Vernon, 1990; McClintock and Gauthier, 1992; Peters et al., 2009, 2010; Aumack et al., 2010). The revolutionary discovery here was McClintock's shattering of a paradigm that asserted that chemical defense in polar environments was not important because of the lack of predation pressures in comparison to tropical coral reefs (where chemical defense was well documented; Slattery and McClintock, 1995). This work completely shifted our perspective of the role of predation in shaping polar benthic communities. Subsequent work on identifying chemical deterrents that exist in polar organisms (both plants and animals) has led to a better understanding of the precarious balance in oligotrophic systems that exists among predators and their sessile prey or herbage. Knowing about these biochemical-level interactions that exist among species has led to a much broader understanding of processes that shape polar benthic community structure, particularly in terms of the interactions between consumers and producers (Amsler et al., 2009a, 2009b; McClintock et al., 2010a).

SUMMARY

There is no substitute for direct observation. Much of what we know today about polar benthic communities was derived from questions that scientific divers asked based on their own observations. In truth, we know much less about benthic coastal habitats below polar sea ice than other marine systems (perhaps with the exception of the deep sea). Even after 50 years of scuba exploration there remains a host of research questions to ponder. The limited access to the environment imposed by sea ice coverage substantially reduces the observation time often taken for granted when exploring a rocky intertidal pool or snorkeling on a coral reef. Scientific diving by principal investigators is an essential component of establishing a working knowledge of what "normal" looks like under the ice in Antarctica, and a key focus of future polar diving is to provide basic information that will help to identify and evaluate the impact of environmental change on these unique habitats.

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The Use of Scuba to Study Early Life Histories of Marine Invertebrates

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ABSTRACT. Scuba has permitted in situ research of the early life histories of subtidal marine invertebrates, limited only by the small size of early stages. Investigators have used scuba to observe, among other things, coral spawning, including the spectacular mass spawns on the Great Barrier Reef, which established that most corals are hermaphroditic broadcast spawners. Observations and experiments have been conducted to measure fertilization rates of free-spawning species, such as octocorals, sea cucumbers, sea urchins, and sea stars. Experiments have measured relative male reproductive success and the gamete traits that influence it in sea urchins. Finally, in tunicates, which produce larvae large enough to be seen by the naked eye and short-lived enough to be followed on a single dive, scuba has allowed direct observation from release to settlement, thus helping to shed some light on this process, which otherwise can only be studied indirectly.

INTRODUCTION

The reproductive biology of marine organisms was, during the nineteenth century, the realm of zoologists and embryologists. Dissection and histological analysis of adults identified reproductive cycles, and careful study of the morphology of embryos and their metamorphoses into adults was a hallmark of "nineteenth century biology." The products of those efforts—expansive, often beautifully illustrated monographs—form the basis of our understanding of the reproductive biology of many marine invertebrates. This foundation was skewed toward taxa that could be studied in the laboratory or could be readily collected and observed. Entering the water and finding out what these organisms do in nature is an essential additional component to this foundation. If the American baseball player Yogi Berra's dictum, "You can observe a lot by watching," is correct, then it is scuba that has allowed researchers to "watch."

For over a century it has been recognized that understanding the early life history stages of marine organisms is critical to understanding their population dynamics. Yet it was only in the 1980s that researchers took to the field to observe these stages. With the advent of scuba, investigators were able to conduct careful observations on the relative importance of different life stages and determine what traits made individuals more or less likely to survive through these transitions. Observations and experiments took time, patience, and a careful hand, requirements that provided an excellent match between the research question and the use of scuba.

In this chapter we consider how in situ observations and experiments have provided information on spawning behavior, fertilization, larval survivorship, and settlement of several marine invertebrates. Our aim is to illustrate how the use of scuba has permitted the acquisition of critical knowledge connected to early life histories in the natural environment.

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THE USE OF SCUBA TO STUDY THE REPRODUCTIVE BIOLOGY OF MARINE INVERTEBRATES

SPAWNING OBSERVATIONS

A striking example of the role of scuba in facilitating new knowledge is the reproductive biology of corals. At the start of the twentieth century, few data were available about coral reproductive biology. Reports characterized scleractinians as brooders that released fully developed planula larvae. Although there were data indicating that some species broadcast gametes (see references in Fadlallah and Pearse, 1982), the suggestion that scleractinians were primarily brooders (Marshall and Stephenson, 1933; Yonge, 1940) persisted until the 1980s.

This perception was corrected when a group of researchers from James Cook University discovered a mass spawning event on the Great Barrier Reef (Harrison et al., 1984). In that first publication on the mass spawning, the number of scleractinians known to broadcast spawn grew from eight to over sixty. The in situ observations of spawning behavior and characterizations of the extent and timing of the event were the product of scuba use. Similarly, the microscopic examination of tissue and the laboratory observations, which were also an important component of the research, were dependent on scuba for the collection of specimens. Scuba allowed the study of reproductive biology to expand from those species that could be readily collected in shallow pools and exposed tidal flats to species in the full extent of the reef. The images of the spawning event electrified a generation of researchers who proceeded to search for similar events at other locations. The data from the Great Barrier Reef mass spawning continued to grow (Babcock et al., 1986), and additional reports from the Pacific and the Caribbean (Szmant, 1986; Van Veghel, 1993) led to the conclusion that the majority of scleractinian taxa are hermaphroditic and broadcast spawners (Richmond and Hunter, 1990; Carlon, 1999). The most recent review of the literature (Harrison, 2011) identifies 367 broadcast-spawning species compared to 75 that brood planulae. It is difficult to imagine that our understanding would be as complete without the use of scuba.

Although many species exhibit some degree of synchrony among individuals, observations of spawning are rare. An event that lasts minutes to hours and occurs on only a few days each year is not readily observed. Perhaps the greatest contribution of scuba to increasing our knowledge of spawning is that it enables researchers to spend large amounts of time in the water and serendipitously observe spawning events. For instance, Hendler and Meyer (1982), Lessios (1984), Pearse et al. (1988), McEuen (1988), Lamare and Stewart (1998), and Himmelmann et al. (2008) all report observations of spawning events in a variety of echinoderms. In a study of reproduction of *Strongylocentrotus* spp., Levitan (2002a) twice observed natural spawning by *S. franciscanus*, and was able to incorporate data from these events into a study that otherwise relied on induced spawning. Serendipity is a key factor in discovering spawning events, but the good fortune in all of these studies was facilitated by many hours of diving.

The discovery of the mass spawning event on the Great Barrier Reef led to observations of other taxa (Babcock et al., 1986; Alino and Coll, 1989; Babcock et al., 1992) and inspired efforts to discover similar events in the Caribbean (Gittings et al., 1992; Van Veghel, 1993; de Graaf et al., 1999). Other studies in which divers have identified spawning times and patterns have their origins in observations of tissue samples that indicate the general timing of spawning. For instance, observations of tissue samples led Lindquist et al. (1997) to place covers over colonies of two species of Caribbean sponges to collect their gametes and characterize the timing of their spawning. While scuba provides a window on spawning events, it does not always produce dramatic results. For instance, Beiring and Lasker (2000) used the presence of gonad in collected specimens to predict spawning of *Eunicea (Plexaura) flexuosa* in Panama, but were able to observe spawning in only a small number of colonies relative to the number of colonies that were believed to spawn over the weeks of their observations. Similarly, many of the spawning events reported by Babcock et al. (1992) involved only small numbers of individuals.

Species with well-synchronized and predictable spawning events have been particularly amenable to study using scuba. Once the basic information on spawning has been elucidated, scuba has provided researchers with the ability to make detailed observations and conduct elaborate experiments to study various aspects of reproductive biology. For instance, a variety of studies have investigated the role of the timing of spawning in reproductive isolation of closely related species with both intraspecific and interspecific differences being observed (Van Veghel, 1993; Sanchez et al., 1999; Van Oppen et al., 2002; Levitan et al., 2004).

FERTILIZATION SUCCESS

Mortensen (1938) considered fertilization to be a significant obstacle in the life history of broadcast spawners. In contrast, in a paper that for decades was one of the guiding forces of benthic ecology, Thorson (1946) considered and rejected the likelihood of variation in successful production of embryos. These hypotheses were examined in a series of experiments by Pennington (1985). Working with the sea urchin *Strongylocentrotus droebachiensis*, Pennington was able to show that in natural settings sperm released by males in induced spawning events were rapidly diluted. As sperm were advected, the probability of fertilization decreased dramatically within meters of the spawning male. These experiments, which were conducted by scuba divers in 10 m depths, were followed by theoretical papers (Denny, 1988; Denny and Shibata, 1989) that underscored the difficulty of achieving high fertilization rates in some environments. Subsequent work with sea urchins has raised a number of methodological questions about the appropriate manner to assess fertilization success (Thomas, 1994; Yund and Meidel, 2003;

Yund et al., 2005). However, regardless of the precise values of fertilization rates, Pennington's study changed the paradigm to one in which fertilization success was not necessarily high. Where, when, and how marine species achieve high fertilization success is a fundamental question in their reproductive biology that relates to the fitness of individuals, the sustenance of populations, and even the efficacy of such conservation approaches as marine protected areas.

Assessing fertilization rates in the field requires access to benthic organisms as they spawn, which (with the exception of intertidal or very shallow habitats) requires the use of scuba. Fertilization probabilities measured in the field vary widely among studies. While cases of sperm limitation have been reported, most studies include at least some examples of high probabilities of fertilization. This may reflect the importance of fertilization rates and thus of strong selection for mechanisms that enhance fertilization, or alternately it may be a reflection of the life history of organisms that have been studied.

The first series of reports of in situ measurements of fertilization rates appeared in 1992 (Babcock and Mundy, 1992; Babcock et al., 1992; Brazeau and Lasker, 1992; Oliver and Babcock, 1992; Sewell and Levitan, 1992). Babcock et al. (1992) based their estimates of fertilization success on collections of eggs from the water column following their release from several Great Barrier Reef holothurians. They reported fertilization success ranging from 0% to 96%. The proportion of eggs fertilized in the spawning events varied among species, by day, time of day, and number and proximity of spawning individuals. Most of the values were well over 50%, with the sea cucumber *Bohadshia argus* having fertilization success ranging from 86% to 96% during the same night. Most studies suggest eggs are fertilized at the peak of spawning events: eggs spawned early in the event, late in the event, or by relatively isolated individuals can have low, sometimes near-zero fertilization rates. Sewell and Levitan (1992) found high fertilization success in a spawning sea cucumber. The octocoral *Plexaura kuna* exhibits fertilization success that varies with day of the spawning event and current speed (Lasker et al., 1996). Individual samples had fertilization success ranging from 0% to 100%, and the monthly means for the multi-day synchronous spawning events ranged from 0% to 60.4%. Similarly collected data for *Pseudoplexaura porosa* found overall fertilization success to be 67%, but the rates varied with day and position on the reef (Coma and Lasker, 1997). Up to 83% of *Acanthaster planci* eggs were fertilized (Babcock and Mundy, 1992). Eggs released by individuals that were over 60 m from the nearest male still had fertilization success rates of 23%. All of the eggs collected in these studies were obtained using scuba. Eggs of octocorals (which are large and positively buoyant) could possibly have been collected on the surface downstream of the spawning colonies, but counting the numbers of colonies spawning and characterizing the fine-scale variation that was observed would have been impossible without scuba.

Fertilization success has also been measured in several species that brood. Brazeau and Lasker (1992) estimated fertilization rates of the octocoral *Briareum asbestinum* on two reefs in the San Blas Islands, Panama. The estimates of Brazeau and Lasker (1990) were based on comparisons between the number of mature eggs present in the polyps and the numbers of embryos produced by the colonies. Values of fertilization success on reefs that had relatively low abundances of *B. asbestinum* are among the lowest reported in natural spawning events. In many instances none of the eggs were fertilized, and in the best of three years the average success was only 20%. As might be expected in a system with low fertilization success, colonies with nearby males did better. In contrast, estimates of fertilization success are markedly higher for *Pseudopterogorgia elisabethae,* a Caribbean octocoral that also surface broods (Lasker, 2006), and for the scleractinian *Goniastrea favulus* (Miller and Mundy, 2005). Fertilization occurs on the colony surface in both of these species and in both, the fertilization of released eggs approached 100% in some samples.

ESTIMATING MALE REPRODUCTIVE SUCCESS

Most work on fertilization ecology has focused on the percentage of eggs that are fertilized. Female success provides key information on the demographic effects of sperm availability and how females with different traits might be under differential selection. Estimates of male fertilization success are also critical for understanding selection on male traits and for determining the relative intensity of sexual selection between males and females. Measures of male reproductive success have lagged behind female estimates because they are more difficult to obtain. As the use of genetic markers has become more efficient, more affordable, and possible with tiny embryos, estimates of male reproductive success have started to emerge.

The first estimates of male reproductive success focused on species that brood offspring. In these species, females retain eggs and collect sperm for fertilization from the water column. Estimating parentage from brooders is somewhat simplified because maternity is known and only paternity must be estimated. In addition, embryos can be collected more simply from the brood chamber. Divers do not need to be on hand during the moment of spawning to collect eggs and embryos in the sea during brief and often unpredictable spawning events. The first study of male success was conducted on the ascidian *Botryllus schlosseri* (Grosberg, 1991). Colonies bred to be homozygous for rare alleles were explanted, and their sperm were allowed to disperse. After two weeks, samples from adult colonies at marked distances from these source colonies were collected, and embryos were analyzed for these rare alleles. The results showed that paternity rapidly diminished over the first 50 cm from the focal colony, suggesting that effects of sperm on gene flow are highly localized. Further experimental work with brooding species of both *Botryllus* and the bryozoan *Celleporella hyalina* has investigated how the presence of nearby mates influences the likelihood of mating with more distant mates and also the likelihood of selfing versus outcrossing (Yund and McCartney, 1994).

Work using scuba to place and retrieve experimental arrays of sessile brooding invertebrates examined the consequences of egg versus sperm allocation on reproductive success in hermaphroditic species. The hypothesis was that hermaphrodites should allocate much more energy toward eggs than sperm if fertilization requires a one to one interaction between sperm and egg, and if sperm are smaller than eggs. Empirical data, however, indicated that energy allocation was much more even between the male and female gametes than predicted. Subtidal experiments showed that under conditions of competition, individuals allocating more energy to sperm garnered higher success (McCartney, 1997; Yund, 1998). More recent work also demonstrated that even in the absence of competition, increased allocation to sperm allowed individuals to overcome sperm limitation when mates were distantly located (Johnson and Yund, 2009). Combined, these findings provide a potential explanation for similar levels of investment to male and female gametes in hermaphrodites.

Patterns of paternity, and multiple parentage in natural populations of brooding invertebrates, has also been explored using scuba. Studies on both ascidians (Johnson and Yund, 2007) and soft corals (Lasker et al., 2008) suggest that multiple paternity is common, and that patterns of paternity are not clearly related to mate distance, body size, or density. It may be that the timing of release of sperm may influence paternity more than differences in mate distance; nearby mates have no chance at fertilization if they release sperm when eggs are not available. Experiments conducted on broadcast-spawning individuals indicate that male timing is critical to fertilization and paternal success (Levitan, 2005). In addition to timing effects, there is some evidence indicating that increases in the number of males contributing sperm can influence the fraction of fertilized eggs (Purchase et al., 2007), presumably because eggs vary in their compatibility with different kinds of sperm. High multiple paternity across gradients of adult density (Johnson and Yund, 2007) or distance (Lasker et al., 2008) may reflect the importance of both timing and gametic compatibility that results in genetic variation within a brood across these demographic conditions.

Paternity from natural spawning has been measured in one system of a broadcasting marine invertebrate. Coffroth and Lasker (1998) established long-term studies of male and female reproductive success in the broadcast spawning soft coral *Plexaura kuna*. This species often fragments asexually. Male reproductive success was examined as a function of distance from a focal female to each male genotype and the number of colonies that belonged to each genotype (clone size). *Plexaura kuna* predictably broadcasts gametes 3 to 9 days following the full moon, releasing eggs large enough to be seen by divers. Egg samples were collected into syringes by divers located downstream of spawning female colonies. Embryos were reared for several days and then frozen for genetic analysis using RAPD markers. Most variation in male reproductive success could be attributed to their distance from the female. In addition, clone size might indirectly influence paternal success by spreading individuals across a larger area, thus decreasing the distance to potential mates.

The Use of Scuba to Determine if Gamete Traits Influence Fertilization in the Sea

Gamete interactions have been studied in the laboratory for the past hundred years (e.g., Lillie, 1915). Gamete traits such as egg size (Levitan, 1993; Marshall et al., 2002), egg accessory structures (Podolsky, 2002; Farley and Levitan, 2001), chemical attractants (Miller, 1966; Riffell et al., 2004), sperm velocity (Levitan, 2000a; Kupriyanova and Havenhand, 2002), and sperm-egg compatibility (Hagström and Lönning, 1967; Evans and Marshall, 2005) have been shown in the laboratory to influence the rate of fertilization within species and the likelihood of hybridization across species. However, to understand the fitness consequences of variation in sperm and egg traits it is necessary to study it in the sea. There is reason to doubt the importance of variation in these traits because the velocity of water flow (cm to m per second; Denny, 1988) can be orders of magnitude greater than sperm velocity (~200 micrometers per second; Levitan et al., 1991), and because mate density and distance exert large effects on the local concentration of sperm (Pennington, 1985; Levitan, 2002a). These variables could perhaps swamp the consequences of subtle variation in traits such as sperm velocity or egg receptivity. Determining how gamete traits influence reproductive success in the sea provides support for the numerous theories on how sperm availability influences gamete morphology (Levitan, 2000b; Podolsky, 2004; Luttikhuizen et al., 2004) and compatibility (Swanson and Vacquier, 2002; Zigler et al., 2005).

Field studies conducted along the shores of Vancouver Island, British Columbia have investigated the influence of sperm availability and gamete traits on fertilization in three congeneric subtidal sea urchins: *Strongylocentrotus droebachiensis*, *S. franciscanus*, and *S. purpuratus*. Gamete traits vary in these three species. *Strongylocentrotus purpuratus* has the smallest eggs and requires the highest sperm concentrations to achieve fertilization; it is also the species with eggs most resistant to polyspermy and has the fastest, but shortest-lived sperm. *Strongylocentrotus droebachiensis* has the opposite traits: large eggs that require the least amount of sperm to achieve fertilization but are the most susceptible to polyspermy, and the slowest, but longest-lived sperm. *Strongylocentrotus franciscanus* is intermediate in all these traits (Levitan, 1993; Levitan et al., 2007). This gradient in gamete traits is consistent with *S. purpuratus* having gamete traits best adapted to high levels of sperm availability and *S. droebachiensis* having traits best adapted to low levels of sperm availability. Field surveys using scuba documented that along the outer west coast of Vancouver Island these traits match the level of aggregation and population density seen among these three species; average nearest-neighbor distances (Levitan, 2002b) and local densities (Levitan, 2002a) indicate that *S. purpuratus* lives in the most crowded populations and *S. droebachiensis* lives in the most sparse ones.

Subtidal field experiments have examined how gametes from these three species perform under a range of conditions of sperm availability. The first set of experiments was intended to isolate gametes from the adults to see how within- and among-species variation in gamete performance in the field could be predicted by how well they performed in the laboratory. The protocol was to induce sea urchins to spawn in the laboratory and measure gamete traits and gamete performance. Then the protocol was to bring these gametes into the field and release them, wait for fertilization to occur, and then collect eggs with a subtidal plankton pump. Collected eggs were then brought back to the laboratory to determine the fertilized fraction. The results of these studies documented that individuals that produced gametes that performed well in the laboratory also produced gametes that performed well in the ocean; the subtle differences in gamete traits noted in the laboratory translated into fitness differences in the ocean (Levitan, 1996). The results also documented that each species produced gametes that performed best under conditions of sperm availability that were typical for that species (Levitan, 1998).

A second set of field experiments attempted to reflect spawning in nature more accurately. Sea urchins were induced to spawn in situ via an injection of 0.55 mol/L KCl solution and then placed back into their natural locations across a range of population densities and flow conditions (Levitan, 2002a). In these experiments, a 5 × 5 meter grid was established on the bottom over a range of sea urchin abundances. All the sea urchins from one species within the grid were injected with KCl to induce spawning. After 30 minutes, the position of all individuals was mapped and a sample of eggs was collected above each female with a subtidal plankton pump. Patterns of water flow and depth were measured with a S4 current meter, which recorded flow and water depth every 0.5 s. The results indicated strong effects of population density and abundance, but also revealed species differences as suggested by the previous study, which had examined gamete traits independently of adult spawning behavior; *S. purpuratus* performed best at high population densities, but *S. droebachiensis* performed best at low densities (Levitan, 2002a). Manipulation of *S. purpuratus* to lower densities than typical resulted in that species doing poorly relative to the other two species (Levitan, 2002a). Further tests, examining how *S. franciscanus* performed at higher densities, indicated that this species was much more susceptible to embryo death caused by polyspermy compared to *S. purpuratus* (Levitan, 2004). In sum, the field studies suggest that these species have gamete traits that perform best under typical conditions and also suggest density-dependent selection of gamete traits based on levels of sperm availability.

Investigations of patterns of sexual selection and the influence of selection on gamete traits (specifically on gamete recognition proteins) used the same field protocols as above, with the addition that the developing embryos were cultured for three days, and then frozen for parentage analysis (Levitan, 2004; 2008). In addition, tube foot samples were collected from all adults in the experiment for genetic analysis to determine their reproductive success, but also to sequence sperm bindin, a protein on the head of the sperm that binds to a receptor on the surface of the egg (Levitan and Ferrell, 2006; Levitan and Stapper, 2010). These experiments were conducted with *S. franciscanus* and *S. purpuratus*, species that differ in their susceptibility to polyspermy. The results of the parentage analysis indicated that in *S. franciscanus* the level of male competition for eggs was similar across male densities. Across densities ranging from sperm limitation to polyspermic conditions the variance in reproductive success was relatively high and constant; there were male winners and losers at all densities.

The pattern in females was more complex. At low sperm densities, there was high variance in female success caused by sperm limitation. As male density increased, female fertilization success increased to the point where all females were saturated with sperm and the variance among females was very low; all females were successful. However, as densities increased further, variance in female reproductive success increased again, driven by variation in polyspermy among eggs produced by different females. These results suggest very different selective pressures at high and low sperm densities. At low densities both males and females are selected to produce gametes with the capacity for a high rate of fertilization. However, at high densities, eggs suffer from polyspermy, so that females producing eggs less compatible with sperm avoid embryo death. Males, on the other hand, should compete for fertilization and be selected for higher fertilization rates. This produces sexual conflict over fertilization rate (and gametic compatibility) at high densities (Levitan, 2004).

Individuals from this same experiment were then sequenced to determine their sperm bindin genotype. The results indicated that males with a common form of the protein had a fertilization advantage over males with a rarer form of the protein, while females with the rarer genotypes were more successful. Further analysis indicated that males that matched females at the sperm bindin locus were most successful at low densities when sperm were limited, while mismatched individuals had higher success at high densities when polyspermy was common (Levitan and Ferrell, 2006). These findings and similar results noted in *S. purpuratus* (Levitan, 2008; Levitan and Stapper, 2010) suggest that, in spite of the large influences of water flow and distance on reproductive success, subtle within-species differences in gametic compatibility can be important in determining fertilization success in the sea.

The Use of Scuba to Follow the Fate of Planktonic Larvae

Many benthic marine organisms display dual life cycles. The adults are sessile or sedentary, but they produce planktonic larvae that are released in the water column, where they stay for different lengths of time ranging from a few minutes to several months, and travel with the currents to distant locations (Scheltema, 1988) where they settle to complete the life cycle. The fate of such larvae is an important parameter, both in the study of the life history of particular species (Stearns, 1977) and in our understanding of the factors that affect marine community composition (Lewin, 1986; Underwood and Fairweather, 1989; Grosberg and Levitan, 1992; Roughgarden et al., 1994). However, given their microscopic size, often unpredictable release, and frequently long planktonic stages, larvae are difficult or impossible to observe directly in nature. Thus in most instances investigators have had to rely on indirect methods of assessing the mode and rate of larval influx into benthic ecosystems. Such methods include radioactive labeling and release of larvae into their native habitat (Arnold et al., 2005); comparison of larval supply (determined by plankton sampling) to quantities of metamorphosing juveniles (Grosberg, 1982; Yoshioka, 1982; Lamare, 1998; Lamare and Barker, 1999; Doherty et al., 2004; Mariani et al., 2005; Pineda et al., 2010); or identification of paternity using genetic markers (Grosberg and Quinn, 1986; Mackie et al., 2006). Though the study of the larval lives of most organisms has necessarily relied on such indirect methods or on laboratory observations, the larvae of a few organisms are large enough to be seen with the naked eye, and the planktonic phase is short enough to be followed by divers on a single tank of air. Through the use of scuba, a handful of studies have taken advantage of these properties to elucidate important aspects of larval behavior and their consequences for successful establishment events.

Olson (1983; 1985) was able to follow the larval fate of the ascidian *Diademnum molle* at Lizard Island, Australia. Diademnid larvae remain in the plankton for a matter of minutes or hours and are large enough to be seen by the naked eye. Species of the family Diademnidae also release their larvae at a predictable time every day of the year. Variation in the timing of release among species appears to depend on whether a species contains symbiotic algae. Species that lack algae release larvae around dawn, whereas those that possess algae release larvae near the middle of the day. *Diademnum molle* larvae are 2.5 mm long and contain algae of the genus *Prochloron* sufficient to add color and thus be visible under water. Olson (1983) was able to track 89 larvae, 14 of them from release to settlement. Newly released larvae displayed positive phototaxis and swam toward the surface. After one to ten minutes, the phototaxis was reversed, and the larvae appeared to be attracted by dark surfaces, including divers' wetsuits. The planktonic stage of the 14 larvae that could be followed from release to settlement ranged from 40 seconds to 6 minutes. Larvae that swam longer were often lost from observation before they settled, but laboratory experiments showed that in general they settle 20 minutes to 2 hours after release, with 90% settling within 30 minutes. When a patch reef was denuded of adult colonies, recruitment ceased on a downstream reef that the larvae could reach within these times, but continued almost unaffected on a more distant downstream reef (Olson, 1985).

Monitoring of settling panels showed that the larvae overwhelmingly preferred to settle in dark spaces, and that the newly formed colonies died if exposed to bright light. Given that light appears to be lethal to the newly settled juveniles, a larval release in the middle of the day appears paradoxical, but it may well be an adaptation for allowing the larvae to choose spaces appropriate for adult growth by avoiding overly bright spots. The best time to choose a spot likely to remain shady for most of the day is during the period of most abundant light. Even though adult colonies can move over small distances, there is a clear advantage in choosing the proper habitat during the larval stage.

Davis (1987) also took advantage of the large size of ascidian larvae to perform direct observations of their behavior. He studied the settlement preferences of the colonial ascidian *Podoclavella cylindrica*, which releases 4 mm long larvae with easily observed bright blue coloration. Monitoring of natural recruitment showed that it was higher than expected by chance on bare space and on the sponge *Euryspongia*, but lower than expected on three other genera of sponges. Davis observed larvae approaching bare space and four kinds of sponges and scored how many settled on each substratum versus how many touched it and then released. Eighty four larvae could be followed from release to settlement. They showed a preference for settling on bare space or on unfouled surfaces of *Euryspongia*, with a high percentage of rejection of three other sponges. Davis also quantified post-settlement survival of recruits for 30 days, and found a tight correlation between larval substrate preference and juvenile survivorship. In a different study, Davis and Butler (1989) followed 100 larvae of *Podoclavella moluccensis* to assess how far they traveled before settlement. The distance ranged from 5 cm to 13.4 m, with nearly 80% settling within 2.5 m of the point of release.

Potential sources of mortality could also be determined by following the larvae of both *Diademnum molle* (Olson 1983) and of *Podoclavella moluccensis* (Davis and Butler, 1989). Stony corals and hydroids often entangled the ascidian larvae. Entangled larvae usually were able to break free, but in some cases were ingested. Fishes that put the larvae in their mouth invariably spit them out, presumably because they are unpalatable. Such high rejection rates were not observed in a study conducted by Stoner (1990; 1994) in Hawaii on the larvae of the ascidian *Diplosoma similis*.

In Stoner's (1990; 1994) study, 259 larvae of *Diplosoma similis* were followed in Kaneohe Bay, at the island of Oahu in Hawaii. Like *Diademnum molle, Diplosoma similis* is host to algal cells of the genus *Prochloron*. Larvae are approximately 2 mm long and are released predictably in the morning hours, so they could be followed by divers. Stoner found that larvae swim for an average of 3.8 minutes and disperse at an average distance of 2.2 m from the parental colony. At approximately 42 seconds after release, the larvae swam down toward the substratum, maintaining a distance of a few centimeters from it. At a mean time of approximately two minutes after release, they contacted the surface of the reef. Dead coral, an unidentified sponge, and the green algae *Dictyosphaeria* were preferred points of contact. After contact, they moved along the bottom for a distance of 20 cm before losing their tails and settling to form new colonies (Stoner, 1994). Of the total number of larvae that were followed by divers, 34% were lost from observation. Of the remaining 171 larvae, 71% settled successfully, and 49% were either eaten by planktivores or became ensnared in mucus sheaths of coral and the larvacean *Oikopleura*, an important difference from the larvae of *Diademnum molle* observed by Olson (1983) and of *Podoclavella cylindrica* observed by Davis (1987).

Predation by pomacentrids and coral was also high on another ascidian, *Lissoclinum patella* (Olson and McPherson, 1987). Post-settlement mortality of *Diplosoma similis* was much higher than mortality in the larval stage: 50% of the newly metamorphosed individuals perished within one day of metamorphosis, and none survived longer than a month (Stoner, 1990).

These studies, along with a few others (e.g., Young and Chia, 1984) have greatly increased our knowledge of events that occur in the larval life stage of ascidians and of the factors that influence their rate of entering benthic communities. The extent to which information from ascidians can be generalized to other organisms with much longer periods in the plankton, particularly planktotrophic ones, remains to be determined. Scuba cannot be used for direct observations of larvae that measure less than 1 mm or that stay in the water column for long periods of time, but it is still useful in documenting the beginning of their lives (i.e., their release) and the stage at which they are transformed to their sedentary stage (i.e., settlement).

The Use of Scuba to Determine Larval Settlement

Settlement, the selection of substrate and metamorphosis into the sedentary phase, is a critical phase in the lives of many marine organisms. However, it can be observed only when larvae are large enough to be seen as they settle (see section on larval observations). For most organisms we can study only recruitment, the addition of individuals to an arbitrary age class as they grow. Each study of recruitment attempts to concentrate on recruitment to the smallest size that can be observed within sampling intervals (dictated by logistic considerations) in order to deduce as accurately as possible the processes that affect settlement. Stoner's (1990) finding that 50% of newly metamorphosed ascidian colonies perished within a day after larval settlement suggests that the window provided by recruitment for a realistic view of settlement may be very narrow. Although this is expected to vary with the type of organism (Hunt and Scheibling, 1997), 30 studies on bivalves, gastropods, barnacles, ascidians, bryozoans and echinoderms, reviewed by Gosselin and Qian (1997), all suggest that juvenile mortality is generally quite high. High mortality before the first observation of recruiting juveniles can lead to erroneous estimates of settlement, particularly if mortality is not random, though the unknowable distortions do not necessarily affect all studies. For example, studies that seek to quantify the number of juveniles of a particular species that enter the benthic community at a given time can accommodate net recruitment without knowledge of pre- versus post-settlement mortality.

Without scuba, recruitment of juvenile marine organisms can be studied in only the intertidal (e.g., Crisp, 1961; Connell, 1972; Strathmann et al., 1981; Grosberg, 1982; Connell, 1985) or on panels that can be suspended in the water and then retrieved (e.g., Osman and Whitlatch, 1995). With the ability of divers to remain under water for long periods of time, the study of recruitment of both sessile and mobile juvenile marine organisms has blossomed and has resulted in more studies than can be reviewed here. Scuba has allowed non-destructive quantification of organisms that appear on a given natural or artificial substrate in pre-determined intervals, as well as comparisons and manipulations intended to uncover factors that affect the entrance of juveniles into benthic communities as the result of larval settling preferences (Highsmith, 1982; Snelgrove et al., 1999; Mariani et al., 2005), oceanographic conditions (Stoner et al., 1997), predation (Sammarco, 1980; 1982; Yoshioka, 1982; Doherty et al., 2004), depth (Hurlbut, 1991), and other physical parameters (Yoshioka, 1982).

Occasionally, the fortuitous occurrence of a major ecological shift during the period of monitoring has resulted in the opportunity to study a phenomenon of even wider importance than recruitment itself. An example of such a case has been the study of Bak (1985) of recruitment of the sea urchin *Diadema antillarum* during mass mortality suffered by this species. Bak (1985) studied the recruitment of juvenile *Diadema* to plastic grates suspended over the reef in Curaçao from 1982 to 1984. *Diadema antillarum* was, until 1983, a dominant component of Caribbean coral reefs, affecting community composition through its grazing of algae (Sammarco, 1982; Carpenter, 1986), predation on live coral (Bak and van Eys, 1975; Sammarco, 1980), and bioerosion of the calcium carbonate substrate (Scoffin et al., 1980). Starting in April 1983, *D. antillarum* suffered mass mortality, which was first noticed on the Caribbean coast of Panama, and was then followed as it affected all populations in the Caribbean and the western Atlantic (Lessios et al., 1984) one by one. Population densities in all studied localities were reduced by more than 97% (Lessios, 1988). The mass mortality front, traveling along coastal currents, reached Curaçao in October 1983 (Bak et al., 1984).

In Bak's (1985) study, divers examined the small cells of the plastic grates similar to the ones shown in Figure 1 every two weeks and were able to locate juvenile sea urchins 1–3 mm in diameter. The number of recruits at each plate over time established that (1) recruitment was higher where the resident adult populations of the species were dense; (2) there were seasonal peaks of recruitment; and (3) a certain amount of growth of coralline algae on the grates was necessary for sea urchin recruitment, but excessive fouling of the plastic by algae depressed the number of juveniles observed by the divers. The number of small *Diadema* located by Bak at each sampling interval between June 1982 and February 1984 was impressive. Maximum densities of juveniles were 102–188/m^2 recruited in a fortnight in June 1983. After February 1984, practically no juveniles recruited on the plastic grates through December 1984, when monitoring stopped. Thus, *Diadema* larvae were arriving at Curaçao for four months following the decimation of the adult populations on this island in October 1983. These larvae could have only come from other populations that had not yet been affected by the mass mortality. Indeed, *D. antillarum* populations on the coast of Venezuela died off in late November 1983 and at Barbados, upstream of Curaçao on the Caribbean Current, in early December 1983 (Lessios et al., 1984). In the laboratory, larvae of this species settle 34 to 90 days after fertilization (Carpenter, 1997; Eckert, 1998), so the

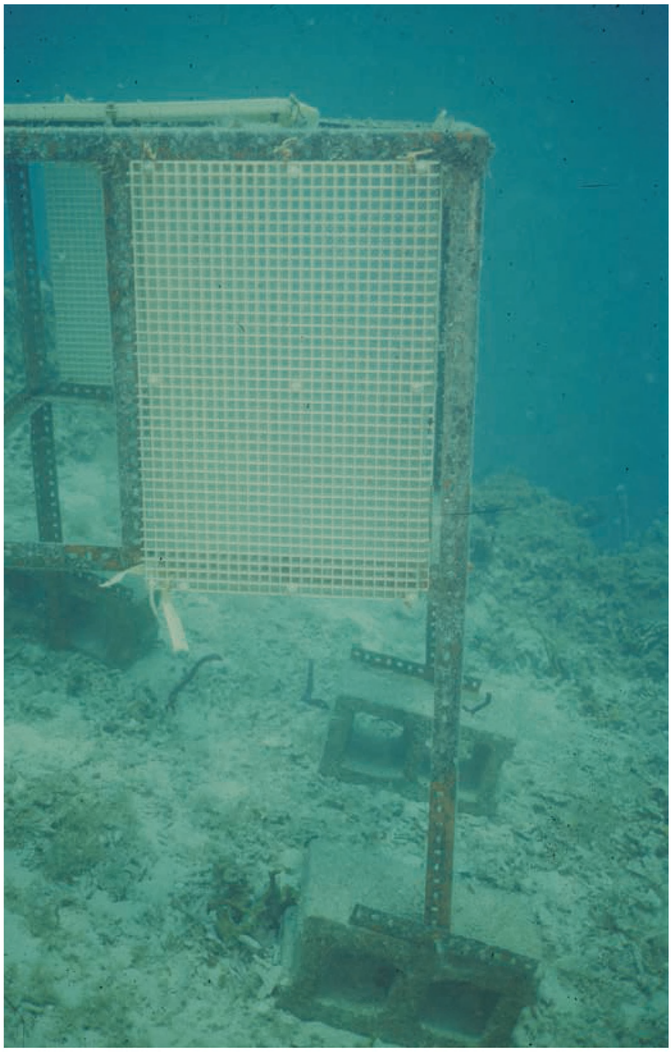

FIGURE 1. Larval collector similar to the one used in Bak's (1985) study of *Diadema* recruitment (photo by H. Lessios).

cessation of recruitment in Curaçao in March 1984 is consistent with the hypothesis that larvae continued to arrive from as far as Barbados, then stopped after the Barbados populations were decimated. Bak's study thus demonstrated not only factors that are important for eliciting settlement, but also the geographical extent of linkages between populations and the significance of events at distant places for settlement of a prominent component of the coral reef community.

Diadema antillarum populations in the Caribbean continued to remain low for the next quarter of a century (Lessios, 2005; Chiappone et al., 2008; Miller et al., 2009). Vermeij et al. (2010) followed up on Bak's (1985) study by setting up the same plastic grates on leeward reefs at Curaçao and monitoring recruitment from March to July 2005. They found that 22 years after the decimation of resident populations, the recruitment rate had increased by a factor of 56 relative to what it was immediately after the mass mortality, but was still half of what it was before this event. Despite this increase in recruitment, adult populations around the island remained low, indicating that settlement and recruitment are necessary but not sufficient causes for population recovery.

CONCLUSIONS

As the examples we presented in this chapter indicate (and they are only a small part of underwater research), much has been accomplished through scuba to study reproductive biology and early life histories of marine invertebrates. Some of the data that have been gathered have been the result of systematic or serendipitous observations, but a large part of marine research involves actual experimentation that was probably never envisioned in the days before autonomous diving became a reality. The study of biology will never be as easy under water as it is on land, but technological advancements that permit longer, deeper dives with less need for infrastructural support will, in the future, provide new insights into the life histories of marine organisms.

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Behavioral Ecology of Mobile Animals: Insights from In Situ Observations

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ABSTRACT. We draw on three primary examples from our collective work on mobile decapod crustaceans, fish, and humans, as well as the work by others on fish and invertebrates, to illustrate the beneficial influence of in situ observations on behavioral ecology, marine conservation, and education. Diver observations of mass migration and gregarious behavior in Caribbean spiny lobster (*Panulirus argus*) in the 1960s led to over 40 years of experimentation that identified (1) the environmental factors driving the mass migration of lobsters each fall, (2) queues of migrating lobsters that afforded them the benefits of reduced hydrodynamic drag and predation, (3) the body-odor attractant underlying gregarious behavior, and (4) the use of gregariousness as a type of "guidepost effect" that minimizes search time for shelter. In situ observation of spider crabs in kelp forests off central California showed complex resource partitioning along multiple niche dimensions in a guild of five species, driven by intense predation pressure by an array of fish and sea otters. Ultrasonic telemetry and innovative tagging studies, as well as diver-deployed experiments, revealed blue crab movement and behavior in murky estuarine waters of the Chesapeake Bay where direct visual observation is impossible. Over three decades, these studies showed mechanisms of dispersal and migration, foraging behavior in response to patchily distributed prey, and habitat selection for molting and minimization of intense cannibalism of juveniles by adults. We also highlight how in situ observations helped to refine behavioral ecological theory by testing whether humans display a relatively simple or sophisticated predatory response to varying densities of spiny lobster prey. Knowledge of human predatory behavior can identify how effective certain fishery management policies will be in sustaining the spiny lobster fishery. Improved conservation is also afforded by the knowledge about the novel responses of these mobile organisms to both the fishery disturbance and the nondisturbed habitats via lobster spill-in to marine protected areas (MPAs). The results also have value in improved diver education relating to reducing injury to sublegal lobsters. In situ observations have also contributed to our knowledge of differential reproductive strategies, species invasions, and range extensions, as well as novel behaviors. While no single research tool is or will be capable of addressing the entirety of these behavioral scales, it is clear that in situ observations have made, are making, and will continue to make profound contributions to the field of behavioral ecology.

INTRODUCTION

> *"Now I had become an amphibious being and could go along in the same way as the fish. I could hover, sit, turn, kneel or lie down. I could even have stood on my head. We could study the animals in their natural world as we swam like fishes amongst them. And then this slimy body glided with its long tentacles over the sea floor, obviously seeking to find a protective hole."* —Hans Hass, 1942

Hans Hass, a biologist and one of the pioneers of the development of scuba and its scientific use expressed the potential and discovery of direct observation in the description of his first experience using a rebreather (from the film *Menschen unter Haien* [Men among Sharks]).

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In situ behavioral observations of mobile benthic animals have helped to inform, refine, and test ecological theory, support conservation measures, and enhance education. Previous in situ observations of animal behavior in the marine realm have used direct observations including (1) submersibles, (2) remotely operated vehicles (ROVs), (3) time-lapse video recording from stationary platforms, (4) animal-borne video recordings, (5) hydroacoustic methods paired with scuba, and (6) scuba. Given that diver observations by snorkeling and scuba are limited primarily to 30 m depths, the use of manned research submersibles and unmanned ROVs has greatly extended the depth range and physical conditions under which scientists can study the natural history of marine organisms, particularly deep sea organisms and their behaviors (e.g., Cohen, 1977; Mackie and Miller, 1983; Hamner and Robison, 1992; Spanier et al., 1994; Gebruk et al., 2000; Drazen et al., 2003; Uiblein et al., 2003).

There are three major advantages to studying animal behavior in situ for natural history observations and subsequent experimentation: (1) mesocosms necessarily oversimplify the environment and may inhibit certain behaviors or produce behavioral artifacts; (2) natural conditions in situ can act as a control on experimental factors imposed on a particular community or system and can reveal unanticipated ecological synergisms; (3) field observations can reveal novel behaviors and ecological processes that would never be revealed in confined experimental conditions. For example, interactions of deep-sea organisms with their environment have been documented from videotapes taken from submersibles and ROVs, providing insight into the environmental variables that affect the distribution of these animals and their key habitats for spawning and feeding (Drazen et al., 2003; Uiblein et al., 2003). In situ diver observations have often been paired with hydroacoustic surveys capable of sampling in conditions beyond diver capabilities and over relatively large areas (MacLennan and Simmonds, 1992; Starr et al., 1996; Taylor et al., 2006). Hydroacoustics, defined as measurement of active sound in water (sonar), is used to study mobile organisms, typically fish. Hydroacoustic assessments have traditionally employed either mobile surveys from boats to evaluate fish biomass and spatial distributions, or use of fixed locations that use stationary transducers to monitor fish passing an area. Hydroacoustics provide a method of noninvasive sampling of animal assemblages, collecting spatially continuous data in three dimensions on submeter to kilometer scales and rapidly assessing animal distribution, abundance, and movement over large spatial scales. For example, using hydroacoustic surveys off Little Cayman, British West Indies, Taylor et al. (2006) found that spawning aggregations of Nassau grouper (*Epinephelus striatus*) were three times larger in population size than diver estimates, remained near bottom along the reef edge during the day, formed a massive cone-shaped aggregation of fish near dusk that was punctuated by upward-swimming spawning rushes of four to eight individual fish, and moved as an aggregation just off the reef wall at night. These types of behavioral observations at night would not have been possible by diver surveys.

In contrast, there are also research examples in which diver observations have proven critical to ground-truthing hydroacoustic surveys. In one example, a recent stock assessment for Nassau grouper in the Bahamas (Ehrhardt and Deleveaux, 1999), acoustic sampling of possible grouper aggregations without visual ground truthing, suggested that “exploitation levels of Nassau grouper were still acceptable from a biological standpoint.” There was concern, however, that this acoustically based stock assessment, along with other assumptions, overestimated the population size of Nassau grouper. Subsequent hydroacoustic surveys of Nassau grouper populations in the Bahamas in 1999–2001, coupled with ground truthing by scuba divers, found that both Nassau grouper and Bermuda chub (*Kyphosus sectatrix*) have nearly identical acoustic signatures, that many of the putative grouper spawning aggregations were actually aggregations of Bermuda chub, and that many of the grouper aggregations identified by diver observations in the mid-1980s (Colin, 1992) were extinct (Eggleston et al., 2003; Taylor et al., 2006). Thus, the sampling methods highlighted above, when coupled with diver observations as appropriate, provide a comprehensive suite of in situ research tools for studying behavior of mobile animals in the marine realm with important applications to fisheries management.

Ultrasonic biotelemetry, in which a sonic transmitter is attached to an animal and emits a unique frequency pulse that is detected with hydrophones, can provide detailed measures of location, behaviors, and environmental variables encountered by the organism (Wolcott and Hines, 1996). These data can be transmitted more or less continuously or stored by the tag for periods of time before transmission at intervals. Ultrasonic biotelemetry can thus keep up with moving organisms for long periods, at great speeds, and in low visibility or darkness, which cannot be achieved by direct observation. When paired with direct observations and experiments conducted by cameras, submersibles, and scuba, this is a powerful approach to determine in situ behavior.

WHY STUDY BEHAVIOR IN SITU?

There are three general areas of behavioral ecological theory where in situ observations in marine systems have been especially important: (1) optimization theory, (2) differential reproductive success, and (3) evolutionary stable strategies. The behavior of organisms in response to their environment is a central theme of ecology, since these traits are adaptive through natural selection to optimize ecological trade-offs, maximize efficiencies, and ultimately enhance fitness (Krebs and Davies, 1993; Begon et al., 2005; Cooper and Frederick, 2010; Webb et al., 2010). An inductive and deductive scientific approach, whereby behavioral observations lead to experimentation, often followed by more detailed observations of behavior and more refined experiments, has facilitated the rapid growth of the field of behavioral ecology (Herrnkind, 1974; Begon et al., 2005). Along with this progress, the urgency of understanding the evolutionary basis of behavioral ecology increases concomitant with the environmental changes in earth systems in which organisms exist (e.g., Parsons and Eggleston, 2006; Zeidberg and Robison, 2007; Albins and Hixon, 2008).

The behavior of marine animals is especially interesting because of their phylogenetic and biological diversity, but also because many of their behavioral adaptations cannot be found in other environments (Herrnkind, 1974). For example, specially adapted animals not only tolerate but often thrive in deep-sea hydrothermal vent regions characterized by extremes in pressure and temperature, low oxygen, and the presence of toxic hydrogen sulfide and heavy metals. In most cases, this tolerance is due to a combination of physiological and behavioral adaptations that allow animals to avoid the extremes of their habitats and yet benefit from the chemoautotrophic production characteristic of these environments (McMullin et al., 2000).

In addition to environments and behaviors characteristic of marine organisms and ecosystems, there are numerous examples of behavioral strategies that optimize ecological trade-offs or maximize efficiencies that can be compared and contrasted across marine, terrestrial, and aerial systems. These examples have helped to refine ecological theory and supported conservation measures. In many instances, these studies have benefited from direct, in situ observation by humans (Herrnkind, 1974; Begon et al., 2005). For example, in situ feeding observations by divers on 1,420 pelagic salps representing six species showed that feeding rates described from aquarium observations were much lower than in situ rates, therefore increasing former estimates of the trophic impact of salps (Madin, 1974). In situ observations provided important insights concerning the significance of salps as an important direct trophic link from nano–1-mm-particulate food to higher trophic levels, as well as the role of their fecal pellets in concentrating food and delivering it to the benthos (Madin, 1974).

Direct observations by humans can also provide numerous distinct advantages over unmanned systems such as remotely operated vehicles, submersibles, gliders, and acoustic surveys (Taylor et al., 2006; Bellingham and Rajan, 2007). For example, humans are capable of rapid integration of and adjustment to changing circumstances under water, peripheral vision and use of multiple senses that are beyond the ability of unmanned systems, and adjusting swimming speed, buoyancy, and other behaviors in an interactive manner so as to maximize natural behaviors by the target organism(s) (Herrnkind, 1974). Moreover, unmanned systems can be prohibitively expensive (Starck, 1968; Herrnkind, 1974). While much has changed in terms of underwater technological advances since the application of scuba to behavioral ecology in the 1960s and 1970s (Miller et al., 1971; Herrnkind, 1974), much has remained the same in terms of the need for in situ observations by humans as a key component of research, outreach, and educational capabilities in marine systems.

In this paper, we draw on our collective expertise and experiences, as well as the scientific literature, to illustrate how in situ behavioral observations of mobile animals (including humans) made by scuba divers, underwater video, and biotelemetry has tested and refined our understanding of how animals optimize trade-offs and maximize efficiencies, and how such an understanding is contributing to the conservation of these species in a rapidly changing ocean system. We build on previous comprehensive reviews on this topic by Miller et al. (1971) and Herrnkind (1974), and reassess the contribution of in situ behavioral observations of mobile animals to testing and refining behavioral ecological theory, conservation, and education/outreach.

BEHAVIORAL ECOLOGICAL THEORY

Behavioral ecology is the study of the ecological and evolutionary basis for animal behavior, and the roles of behavior in enabling an animal to adapt to its environment and maximize its lifetime fitness or reproductive success (Krebs and Davies, 1993). In addition to identifying novel behaviors and unanticipated ecological processes, there are three general areas of behavioral ecological theory where in situ observations in marine systems have been especially important: optimization theory, differential reproductive success, and evolutionary stable strategies. Optimization theory stipulates strategies that offer the highest return (e.g., caloric intake) to an animal given the various factors (e.g., prey availability or predatory abundance) and constraints (e.g., prey-handling time) facing the animal (Stephens and Krebs, 1986). Cost–benefit analyses and optimization models can help to identify environmental and biological conditions that drive behavioral decisions by mobile animals, such as when to mate or change habitats so as to maximize fitness (Stephens and Krebs, 1986). For mobile animals that must make decisions about balancing conflicting demands associated with foraging and avoiding predators, simple optimality models predict that animals should respond to changes in mortality risk (u) and growth rate (g) by shifting habitats in a way that maximizes net benefits (McNamara and Houston, 1986). Minimizing the ratio of mortality risk to growth rate, also known as the minimize u/g rule, has been a useful construct for addressing ecological processes underlying ontogenetic habitat shifts in fish (Werner and Gilliam, 1984; Dahlgren and Eggleston, 2000).

As one example, field caging and tethering experiments conducted by scuba divers quantified habitat-specific growth rates and mortality risk, respectively, for three size classes of coral reef fish (*E. striatus*) during their tenure in off-reef nursery habitats (Dahlgren and Eggleston, 2000). These size classes bracketed the size at which this species undergoes an ontogenetic habitat shift from the interstices of macroalgal clumps (algal habitat) to areas outside, or adjacent to, macroalgae and other physically complex microhabitats (postalgal habitats; Eggleston, 1995). Results indicated that small fish trade off living in relatively safe algal habitat with achieving high growth rates in postalgal habitats—the value of u/g was significantly lower in algal habitats than in postalgal habitats for small fish, which typically reside in the algal habitat, and significantly lower in postalgal habitats for medium and large fish that reside in postalgal habitats (Dahlgren and Eggleston, 2000). These results suggest that ontogenetic habitat shifts by juvenile *E. striatus* are consistent with the minimize *u/g* rule, and highlight how behavioral responses to ecological processes, such as changing predation risk with body size, determine distribution patterns of mobile animals.

Ultimately, however, behavior is subject to natural selection just as any other trait, resulting in differential reproductive success. For example, animals that employ optimal behavioral strategies specific to their environment will generally leave greater numbers of offspring than their suboptimal conspecifics, and greater numbers of offspring generally lead to greater fitness (Krebs and Davies, 1993). Given that environments change over time, and at an ever-increasing rate due to anthropogenic factors, an optimal behavior now may not be optimal in the future. In situ observations may provide great insight into evolved behavioral changes that come about because of environmental changes.

Behavioral patterns among interacting individuals can sometimes result in evolutionary stable strategies (ESS; Maynard Smith, 1982). For example, the more likely a rival male is to back down from a threat, the more value a male gets out of making the threat. The more likely, however, that a rival will attack if threatened, the less useful it is to threaten other males. ESS is considered to be the evolutionary end point selected for by these social interactions, and the fitness conveyed by a strategy is influenced by what other individuals are doing (Krebs and Davies, 1993). Thus, animal behavior can be governed not only by optimality, but by the frequencies of strategies adopted by others. Behavioral evolution is therefore influenced by both the physical environment and interactions between other individuals. The latter line of research has particularly benefited from in situ observations, especially in observations of mating systems in fish.

EXAMPLES OF IN SITU OBSERVATIONS, HYPOTHESES, AND KEY FINDINGS

Case Study: Mass Migration and Gregarious Behavior in Caribbean Spiny Lobster

We begin our examples by continuing a line of observation and subsequent research that was first highlighted in Herrnkind's (1974) review on this topic: a chance encounter by scientists using scuba with thousands of Caribbean spiny lobster (*Panulirus argus*) migrating in head-to-tail queues off the coast of Bimini, Bahamas (Figure 1; Herrnkind and Cummings, 1964; Herrnkind, 1969). The repeated observations of mass migrations, coupled with observations of gregarious den sharing by lobsters during the day and homing by lobsters back to specific dens after nighttime foraging (Herrnkind et al., 1975), hinted at a far more sophisticated and complex behavioral repertoire and lifestyle than previously considered for marine crustaceans.

FIGURE 1. A queue of migrating spiny lobsters (*Panulirus argus*) crosses long stretches of shelterless sand substrate in daylight near Bimini, Bahamas. All queues orient southward parallel to the edge of the Great Bahama Bank following late fall bouts of stormy weather. Photo by W. Herrnkind.

These scuba observations of spiny lobster migratory behavior, first described in the scientific literature by Herrnkind and Cummings (1964), Herrnkind (1969), and Herrnkind et al. (1975), triggered an iterative process of laboratory experiments, field experiments, more field observations, and more refined experimentation that continues today. The initial migration research is reviewed by Herrnkind (1980, 1983) but described briefly here to demonstrate specific examples of the reciprocal interplay of scuba-mediated field insights with lab and semifield studies (see Herrnkind, 1980, 1983, 1985, and references therein for details). The first encounters by diving scientists with mass-migrating lobsters at Bimini in 1961 and 1963 were brief, fortuitous, and involved no quantitative data recording. However, they revealed distinctive features: lobsters moved in daytime across atypical habitat (open sand), all migrants moved in single file (queues), most migrants were adult males and nongravid females, all observed queues moved in similar directional headings, and the mass migration event followed several days of autumnal squalls (late October). This latter coincidence was confirmed in the first planned field study in 1969 (and seasons thereafter), which tested the hypothesis that some component or combination of storm-caused environmental changes stimulated the mass migration. Since captive migrant lobsters were found to spontaneously queue around the periphery of outside circular pools, it was possible to set up replicated experiments under controlled conditions.

Based on field measures of storm-linked thermal and hydrodynamic changes, a series of indoor controlled pool experiments simulating storm levels showed that a sharp increase of current or turbulence induced day-long queuing, sometimes enhanced by combining a temperature decrease with shelter removal. While storm stimuli triggered mass movement, additional results under artificial fall photoperiod hinted at both a preliminary shift in internal state—probably hormonal—that increased susceptibility to a migratory response, and a lingering poststimulation effect of gradual cessation of queuing hours or days after ambient conditions were restored. The underlying physiological mechanism remains to be fully investigated.

The striking and unique queuing formations begged functional explanation. Quantitative ethological studies revealed that queuing involved nearly continuous tactile (and probably chemotactile) contact by lobster followers using inner-antennular rami and anterior walking legs. Constraining any of these appendages induced more contact by the others. In this way, migrants are able to queue in complete darkness or high turbidity, as well as after severe appendage loss. Several hypotheses regarding how this queuing behavior may enhance lobster efficiency, survival, and, ultimately, fitness were then tested. Observations of lobsters walking in circular tanks in the laboratory provided weak evidence that queuing behavior enhanced directional orientation by lobsters. However, the most compelling evidence was for enhanced hydrodynamic efficiency. By placing lobsters into laboratory tow tanks, researchers determined that individuals in a queue benefit from reduced hydrodynamic drag via drafting in a manner similar to cyclists drafting (Bill and Herrnkind, 1976). At migratory pace, nonleaders in a queue experience only about one-half the drag of solitary lobsters. Further tow tank data suggested that drag reduction was enhanced as the antennal angle was reduced (antennae brought closer together) as speed increased. This behavior was confirmed by time-lapse field photography under different walking speeds. Field observations of moving queues also revealed that the high-drag position of lead lobster spontaneously changed as queues joined or the lead individual briefly stopped to forage. Despite this strong behavioral evidence, no one has, as yet, tried to measure improved metabolic efficiency theorized to underlie functional drag reduction.

Mass migrants generally assembled in relatively large groups exceeding 20 individuals. Migrants rarely traveled or rested solitarily in the open (<2%; Herrnkind et al., 2001). Divers occasionally witnessed attacks by queen triggerfish (*Balistes vetula*) on isolated lobsters encountered over shelterless substrate that was characteristic of the migratory pathway. By contrast, threatened queues as long as ~50 migrants reassembled in a remarkable manner. The lead lobster pirouetted as the followers wound into a radial array, forming within minutes into a closely packed pod with all individuals facing outward or upward (Figure 2). We hypothesized that queues and the formations served as an antipredation strategy (Herrnkind et al., 2001).

Although divers witnessed too few natural predatory attacks on migrants to test the antipredation hypothesis, they took extensive data on group and queue numbers during migrations in 1969–1975. Notably, these data were prescient, taken well

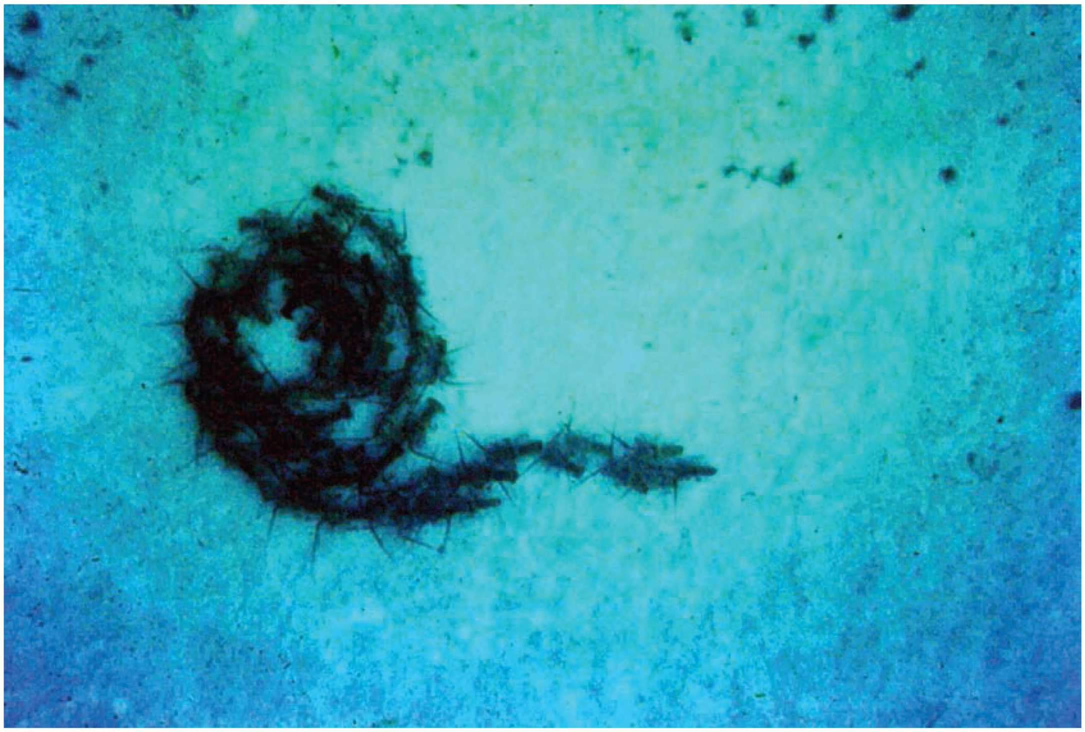

FIGURE 2. When threatened by predators (a descending diver in this case), a queue winds around the pirouetting lead lobster, quickly forming a stationary pod, all members directing their defensive antennae outward to confront attackers. Photo by W. Herrnkind.

before socio-biological research emerged to focus on the evolution of cooperative behavior. Spiny lobster gregariousness serves as a useful model because their life cycle (six-month free-drifting larval period) and sometimes nomadic benthic nature obviate cooperation based on kinship or long-term, interindividual reciprocity (Herrnkind et al., 2001).

Lobster group-size frequencies under field conditions were compared to hypothetical optimal distributions for particular functions. For example, a dilution benefit (safety in numbers) predicts large, amorphous groups of migrants moving along close together whereas antipredatory vigilance predicts lines of relatively small numbers of individuals for rapid warning communication. Group numbers were evaluated for chance, crypticity, dilution, drag reduction, vigilance, and combined defense in behavioral categories of nonmigratory denning, migratory denning, movement from dens, movement in the open, and resting in the open (Herrnkind et al., 2001). The group distributions of lobsters differed statistically among categories and the distributions for each behavior supported two or more hypothetical functions. All migratory group types hypothetically benefit from antipredation. Strong cohesion among migrants is reflected by their migratory behavior in which lobsters initially leave crowded dens as small, loosely arranged groups, moving slowly, but thereafter join other groups as they are encountered, then move swiftly as queues. Queues predictably benefit from vigilance and drag reduction but, as they form pods to rest or to confront predators, also potentially benefit from both dilution and combined defense (Herrnkind et al., 2001).

The dilution and combined defense hypotheses were experimentally tested by pitting gray triggerfish (*Balistes capriscus*) against tethered lobsters in the field, as well as against free-moving lobsters in large, seminatural enclosures (~40 m^2) (Lavalli and Herrnkind, 2009). During field encounters, lobsters attached by swivel and cable ties to dive weights were alternately set out solitarily or in groups of five near reefs with 1–23 wild gray triggerfish. The lobsters defended by antennal points, whips, and lunges, rarely attempting tail-flip escape. After 90 minutes, ~40% of solitary lobsters were killed or debilitated while none of the lobsters in the quintets were seriously wounded. Lobsters in a group were formidable defenders even with multiple attackers (Lavalli and Herrnkind, 2009).

The semifield encounters pitted 1, 3, 5, 10, and 20 lobsters against 1, 2, 5, and 10 triggerfish (Lavalli and Herrnkind, 2009). All the test triggerfish were initially observed to kill and devour a lobster and were not fed during the 24 hours before a trial. Captive lobsters confronted by triggerfish subsequently assembled into pods or phalanxes or queued around the pool periphery. Lobster group cohesion and assembly into a pod increased after a nearby lobster was bitten by an attacker. Lobster survival rate sharply improved as the number in the group increased. Solitary lobsters suffered ~70% mortality compared to ~80% survival among quintets. All debilitated lobsters were outside the pod, either having defected from the group or the group having moved away, isolating the attacked individual. However, five attacking triggerfish were no more effective than two attackers either in debilitating a lobster or in the time taken to do so. Competition or aggression among the triggerfish often interfered with the effectiveness of the attacks. When confronted by triggerfish during migration it is best for a lobster to stay amidst a large queue that quickly forms a pod, and for the attackers to be inexperienced. Simply expressing strongly cohesive behavior, especially during mass migration, provides antipredatory benefits to spiny lobsters approximating that achieved via kinship and reciprocal sociality in social mammals, birds, and insects (Lavalli and Herrnkind, 2009).

Scuba and the advent of manned undersea habitats (late 1960s) contributed to understanding the mechanisms and benefits of spiny lobster gregariousness, particularly sharing of selected shelters—a hallmark of many spiny lobster species throughout benthic life. Until then, spiny lobsters were known to aggregate in dens and traps but it was not clear whether this was social attraction or merely attraction of many individuals to a common food source or sheltering structure. *Tektite* aquanauts/scientists in saturation mode, using visible coded tags and ultrasonic transmitters, discovered that lobsters homed over kilometers to specific dens for periods of weeks, often with the same den mates (Clifton et al., 1970; Herrnkind and McLean, 1971; Herrnkind et al., 1975). This raised questions of the fitness consequences of den quality, co-occupancy, and homing mechanisms.

Subsequent scuba research revealed that shelter was vital to survival of small, newly settled juvenile lobsters. Caribbean spiny lobsters were discovered to settle, reside, and feed within complex macroalgae attached to hard substrate (Marx and Herrnkind, 1985), with an eventual ontogenetic habitat shift to crevice dwelling. Field tethering experiments showed that juvenile lobsters suffer relatively high daily mortality in the absence of macroalgal shelter prior to crevice dwelling (Butler et al., 2006). A series of elegant field experiments (Eggleston et al., 1990; Eggleston and Lipcius, 1992) using artificial dens ("casitas") revealed that there is a trade-off between predation risk, choosing a shelter scaled to your body size, and gregariousness. Under high predation risk, relatively small lobsters chose small shelters scaled to their body size in the absence of conspecifics, but chose to reside with larger conspecifics rather than shelters scaled to their body size when given a choice (Eggleston and Lipcius, 1992). Above a certain lobster size, the presence of conspecific coresidents also reduces the risk of predation (Mintz et al., 1994; Butler et al., 1999).

Shelter choice and sharing by adult lobsters (*Panulirus interruptus*) was found by both lab and field studies to be facilitated by chemical odor attraction over meters to one or more conspecific individuals already in residence(Zimmer-Faust et al., 1985). Conspecific odor of sufficient intensity also attracts juvenile Caribbean spiny lobsters as they become socially gregarious crevice dwellers, a response termed "guide effect" (Ratchford and Eggleston, 1998; Childress and Herrnkind, 2001). This odor-mediated attraction over distance reduces the time to locate a suitable den in a new foraging range as well as providing the added benefit of a codefender once there.

Recently, scuba-mediated field observations and follow-up lab experiments by Behringer (2003) showed that healthy juveniles avoid denning with conspecifics infected by a lethal virus, probably by chemo-sensing. Bouwma (2006) experimentally demonstrated rapid departure from a den, even by an individual lobster in daylight, cued by the body fluids of a recently killed conspecific. Based largely on insights from scuba observations in nature, research continues to reveal a complex and sophisticated behavioral, sensory, and ecological repertoire for spiny lobsters.

Conclusion

In the case study of the behavioral ecology of Caribbean spiny lobster, we have highlighted how in situ observations first identified mass migration and gregarious sheltering behavior in lobsters, and how a subsequent reciprocal interplay of scuba-mediated field insights with lab and semifield studies identified the mechanisms underlying these behaviors. The initiation of mass migrations of lobster queues in fall was driven by a combination of a shifting hormonal state of lobsters due to fall photoperiod and a sharp increase in current-speed characteristics of the first fall storms in the Caribbean. Queues of migrating lobsters were afforded the benefits of reduced hydrodynamic drag and predation. Lobsters exhibited a body odor attractant underlying their gregarious sheltering behavior, and this gregarious behavior served as a type of guidepost effect that minimized search time for shelter.

Case Study: Behavior and Ecology of Crabs

How does one make observations of animal behavior when the animals cannot be seen? In this case study, we compare and contrast in situ observations of crabs in two distinctly challenging circumstances. In one, niche partitioning and its underlying mechanisms were analyzed for a guild of five species of spider crabs (*Loxorhynchus crispatus*, *Pugettia producta*, *Pugettia richii*, *Mimulus foliatus*, *Scyra acutifrons*) in kelp forests off central California. While the water in this ecosystem is relatively clear, most of the crabs are small and extremely cryptic, requiring long hours of painstaking direct observations on scuba. In the other, the behavioral ecology of blue crabs (*Callinectes sapidus*) in soft-bottom communities was advanced in the turbid waters of Chesapeake Bay, where direct visual observation is impossible.

A Guild of Spider Crabs in Kelp Forests

Direct observations and collections on scuba allowed analysis of population dynamics and niche partitioning in a guild of spider crabs in giant kelp (*Macrocystis pyrifera*) forests of central California (Hines, 1982). All five species are highly cryptic and utilize dense cover of algal-invertebrate turf of the kelp forest, often residing in crevices and interstices. All of the crabs exhibit different color morphs, color change (due to algal diet), and decorating behavior. Observations of these morphologies and behaviors generated the hypothesis that they are adaptive for concealment from predators (Palma and Steneck, 2002; Todd et al., 2006). Consistent with the hypothesis, the diversity of predators that take spider crabs as a major portion of their diets indicated that predation pressure is high and may limit overall population levels of the crabs. Predation by sea otters (*Enhydra lutris*) probably limits the density of *P. producta*, and fish predation, especially by sculpins and rockfish species (*Sebastes*), probably limits abundance of the other four species.

Diver counts and size-frequency measures of crabs in plots along a transect from the intertidal shoreline through the kelp forest out to a deep reef offshore showed that each species had zones of abundance. *Pugettia richii* was the most abundant species, with peaks in the inner and middle zone of the kelp forest. *Mimulus foliatus* was second most abundant, with peaks in the middle and outer zones of the kelp forest. Abundance of *S. acutifrons* had peak densities in the outer edge of the kelp. Fourth in abundance, *P. producta* had highest densities in the intertidal zone; juveniles recruit into the intertidal and shallow eelgrass zones and migrate out into the kelp forest as they grow. However, the other species did not have zones of recruitment separate from adult distribution. *Loxorhynchus crispatus* was present in low densities from the middle of the kelp forest to the deep reef. The greatest combined density of spider crabs (11 crabs/m^2) occurred in the middle of the kelp forest (Hines, 1982).

Body size at maturity of the five species varied an order of magnitude in carapace width from 1 cm for *S. acutifrons* to 10 cm for *L. crispatus*. Mean size of mature females and mean body size of the entire population of all pairs of species except *M. foliates* and *P. richii* had ratios greater than Hutchinson's (1959) predicted value of 1.28 for niche separation. Body size likely limits crabs' use of crevice refuge in the microhabitat.

The cryptic morphology and behavior of the spider crabs required painstaking quantification of microhabitat use by substrate type. *Mimulus foliatus* had the largest microhabitat breadth and was found on most substrate types, with an important refuge in kelp holdfasts. *Pugettia richii* was found mainly on the alga *Cystoseira* and in coralline algal mats. *Scyra acutifrons* occurred mainly in interstices of algal-invertebrate turf, and *L. crispatus* was found on top of the turf. *Pugettia producta* occurred on kelp plants and had the narrowest microhabitat niche breadth.

Stomach contents of diver-collected crabs also showed partitioning of food resources. *Pugettia producta* was a strict specialist grazing on giant kelp. *Mimulus foliatus* and *P. richii* also had narrow diets of mostly drift kelp. *Scyra acutifrons* had main food categories of detritus, sponge, and pieces of kelp trapped in the algal-invertebrate turf. *Loxorhynchus crispatus* was a dietary generalist on a broad range of invertebrates and kelp.

Niche separation in the guild is multidimensional, and similar use of one resource is generally complemented by dissimilar use in another resource. Niche analysis for three dimensions of microhabitat, food, and body size showed *P. producta* is an overall specialist, and *L. crispatus* is a generalist. *Scyra acutifrons* also has a distinct niche within the algal-invertebrate turf, but *M. foliatus* and *P. richii* exhibit extensive overlap in all of the variables measured. However, the degree to which a species is a specialist versus a generalist for a resource did not relate to the amount of niche overlap with the rest of the guild. Microhabitat resources appeared to be the most important for niche separation and may also be explained as adaptations for minimizing predation.

Blue Crabs in Chesapeake Bay

Blue crabs (*Callinectes sapidus*) are dominant benthic predators in estuaries of the U.S. East and Gulf coasts, and the ecology of juvenile and adult blue crabs has been reviewed recently by Hines (2007). Their distribution and abundance patterns vary as a function of their migratory life cycle using a diverse array of estuarine habitats. Newly settled blue crabs generally grow through a series of early juvenile instars (developmental stages punctuated by ecdysis) within seagrass and other settlement habitats of lower estuaries (Orth and van Montfrans, 1987; Pile et al., 1996; Pardieck et al., 1999). Upon attaining the fifth to seventh crab instar and ~20 mm carapace width (cw), juveniles typically disperse from their settlement site to exploit an array of habitats throughout the estuary (Pile et al., 1996; Etherington and Eggleston, 2003). However, dispersal may occur as early as the first crab instar shortly after settlement in some estuaries, such as in North Carolina (Reyns and Eggleston, 2004). Dispersed juveniles use a variety of microhabitats where they forage and grow for 6–18 months (depending on temperature and food availability) until they reach sexual maturity in the sixteenth to twentieth crab instar at ~110–180 mm cw (Van Engel, 1958; Tagatz, 1968). After mating, inseminated mature females cease molting and migrate back to the lower estuary, produce broods, and incubate eggs until larvae are released and transported out of the estuary onto the continental shelf. By contrast, mature males may continue to molt and grow for one to three additional instars (typical large size is 180–200 mm). Unlike females, mature males tend to remain dispersed in the upper estuary without migrating directionally along the salinity gradient (Van Engel, 1958; Hines et al., 1990, 1995).

Blue crab movement varies with life stage and molt stage, and depends on habitat and geographic region, as well as on tidal and seasonal cycles (Gillanders et al., 2003), as seen from spatially or temporally disjunct distributions of life stages, as when immature females molt to maturity and mate in upper estuarine zones but ovigerous females later occur primarily near the mouth of estuaries (e.g., Van Engel, 1958). Movement between points (without knowing the route traveled) can be estimated directly by mark-recapture studies involving large numbers (thousands) of crabs marked with inexpensive external or internal tags (reviewed by Hines, 2007). External tags are readily visible to fishers and typically cause little harm to crabs, but they are lost during molting. As a result, external tags usually have been applied to large mature crabs that do not molt (females) or molt only infrequently (males). Internal tags that are retained during molting also have been used, but these may require expensive equipment for insertion (e.g., microwire tags; Davis et al., 2004a, 2004b) and detection (e.g., "pit tags"; Wolcott and Hines, 1996). Internal tags are often not seen by fishers, and also may cause significant mortality (e.g., dart tags; A. H. Hines, personal observation) or induce limb autotomy (e.g., elastomer injection; Davis et al., 2004a, 2004b). However, some forms of internal tags (especially microwire or coded wire tags and elastomer injection) work well for juveniles as small as 10 mm cw (Davis et al., 2004a, 2004b).

External ultrasonic telemetry tags, which are expensive and usually applied to small numbers of crabs >60 mm cw, allow acquisition of detailed data on the path of movement and other selected aspects of behavior and physiological functions (Figure

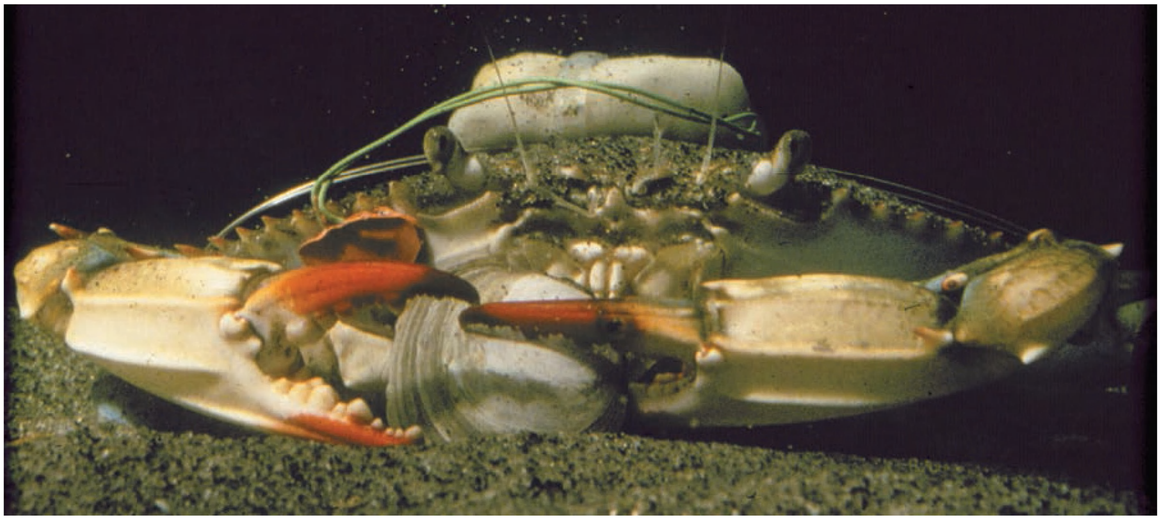

FIGURE 3. Biotelemetry tag attached to blue crab (*Callinectes sapidus*) eating a clam prey item. Photo by A. Hines.

3; Wolcott and Hines, 1989, 1990, 1996; Hines et al., 1995; Clark et al., 1999a, 1999b, 2000; Bell et al., 2003a, 2003b). Ultrasonic tags may also be used to transmit data on environmental variables (temperature, conductivity, depth, light) that crabs encounter, and they have been developed to signal physiological variables (muscle action potentials, posture, suture breaks of the exoskeleton) that are integral components of crab behaviors (locomotion, feeding, fighting, mating, molting) in relation to location and time (Wolcott, 1995; Wolcott and Hines, 1996). Electronic tags that record data about environmental variables on microchips and that can be downloaded to a computer when the tag is recaptured have been applied recently to blue crabs to deduce movement and behavior (Wolcott and Hines, 2004).

In subestuaries of the upper Chesapeake Bay, telemetry studies showed that juveniles (60–80 mm cw) move along shorelines within subestuaries, with a typical pattern of periods of meandering slowly (2 m h^{-1}) in shallow (<1 m) water interspersed with rapid (>50 m h^{-1}) directional movement to a new meandering area (Hines et al., 1995). Juveniles tend to move rather directly and rapidly across channels, and not meander in deeper water where they are most vulnerable to cannibalism by large crabs; however, small juveniles do not seem to move in a net direction along the axis of the subestuary as do larger prepubertal and adult crabs (Hines and Ruiz, 1995; Hines et al., 1995; Hines and Wolcott, unpublished data). Diver-deployed tethering and lab experiments indicated that the impacts of agonism is particularly acute for blue crabs in the upper Chesapeake Bay, where cannibalism by adults is the major (>90%) source of mortality of juveniles (20–70 mm cw) (Hines and Ruiz, 1995; Hines, 2007). Juveniles obtain an important partial refuge from cannibalism in shallow water (<50 cm deep), where foraging by adult crabs is infrequent and less effective (Dittel et al.,1995; Hines et al., 1995), effectively restricting use of deeper water by juveniles.

Biotelemetry and diver-deployed experiments in the Rhode River subestuary of the Chesapeake Bay were used to study the details of nonmigratory movements of adult and juvenile (>60 mm cw) blue crabs (reviewed by Hines, 2007). These studies showed that intermolt crabs move at an average speed of about 10 m h^{-1} during the warm season, but speed varied by month from a average high speed of about 15 m h^{-1} in July to a low average of about 5 m h^{-1} in May or late September, with no movement of males from late November to March. Speed also varied by size and life stage, with large males (>140 mm cw) moving faster (15 m h^{-1}) than similar-sized females (8 m h^{-1}) or large juveniles (100–120 mm cw; 5 m h^{-1}). Movement of mature males decreased markedly at premolt stage about three days before ecdysis (Wolcott and Hines, 1990). In summer, adults meander while foraging on patches of infaunal bivalve (*Macoma balthica*) for periods of hours to days, and then suddenly depart the patch, moving rapidly in an oriented direction for 0.5–4 km along the estuary before stopping to meander and forage again (Wolcott and Hines, 1989). Departure from the prey patch is triggered by increasing agonistic interactions among crabs as other crabs are attracted to the feeding site by chemical signals released as foraging crabs crush their prey (Clark et al., 1999a, 1999b, 2000). Predation rates diminish as agonistic threat displays increase (Clark et al., 2000). Blue crab foraging can accelerate prey mortality in clam patches separated by moderate (7–10 m) distances by attracting other crabs, or impede predation by agonism among attracted crabs in nearby patches (<7 m) (Hines et al., 2009).

Caging experiments, benthic coring, and analyses of stomach contents showed that predation by demersal fishes and blue crabs regulate abundance and species composition of infaunal invertebrates in the central Chesapeake Bay (Hines et al., 1990). Predator exclusion cages installed and sampled by divers in late spring after recruitment of infaunal invertebrates but before summer activity of predators showed that infauna occurred at much higher densities within cages. Burrowing bivalves (*Macoma balthica*, *Mya arenaria*) comprised ~60% of stomach contents of blue crabs but not fishes. Diver-deployed and -sampled patches of dyed sediment showed that blue crab foraging and burrowing (bioturbation) reworked sediments to a depth of 10 cm, below which bivalve prey attained a depth refuge from predation.

Conclusion

In the case study of the behavioral ecology of crabs, we addressed the problem of how to determine resource use and movement in systems in which it is exceedingly difficult to make direct observations. Niche analysis of cryptic, often very small spider crabs required long hours of bottom time on scuba to quantify and collect crab population dynamics, depth zonation, habitat use, and diet. The crabs showed complex resource partitioning along multiple niche dimensions, driven by intense predation pressure by an array of fish and sea otters. Ultrasonic telemetry and innovative application of tagging studies as well as diver-deployed experiments revealed blue crab movement and behavior in murky estuarine water. Over three decades, these studies showed mechanisms of dispersal and migration, foraging behavior in response to patchily distributed prey, and habitat selection for molting and to minimize intense cannibalism of adults on juveniles.

CASE STUDY: DYNAMIC BEHAVIOR OF FISHERMEN AND THEIR PREY

What is the predatory behavior of humans, and does it follow predictions from predator–prey theory? Fishermen are opportunistic and often use sophisticated equipment and up-to-date information to respond to changes in distribution and abundance patterns of their quarry in a manner similar to natural predator–prey systems (Carpenter et al., 1994; Johnson and Carpenter, 1994; Post et al., 2002). Although recreational fishers often lack the economic incentives that can motivate commercial fishers to overexploit populations (Post et al., 2002), recreational fishers can produce strong direct and indirect effects in aquatic ecosystems (Magnuson, 1991; Kitchell, 1992; Kitchell and Carpenter, 1993; Post et al., 2002; Coleman et al., 2004; Eggleston et al., 2008). Recreational fishers have caused severe declines in marine fish such as red drum, *Sciaenops ocellatus* (Vaughan and Carmichael, 2000), and intense reductions in local populations of abalone (*Haliotis* sp.) in central California (Haaker et al., 1998) and Caribbean spiny lobster (*P. argus*) in the Florida Keys (Eggleston and Dahlgren, 2001; Eggleston et al., 2003, 2008; Eggleston and Parsons, 2008). To prevent overharvesting and associated ecological impacts by recreational fishers, as well as to successfully predict the outcome of fishery management actions such as catch limits or Marine Protected Areas (MPAs), fishery scientists and managers must understand the dynamic behavior of fishermen and their prey.

Interactions between fishermen, their prey, and management actions can be complex. The functional response, which is the relationship between the consumption rate of a predator and the density of its prey, provides a powerful theoretical framework to predict the outcome of fishery management actions on the dynamic relationship between humans and their prey (Hilborn and Walters, 1992; Carpenter et al., 1994; Johnson and Carpenter, 1994; Post et al., 2002; Eggleston et al., 2003, 2008). In this case study, a functional response framework was applied to sport divers harvesting Caribbean spiny lobster (*P. argus*) in the Florida Keys during a two-day, exclusively recreational fishing season that takes place in late July just prior to the opening of the fishing season for commercial fishers and after a three-month closed period that allows lobsters to spawn (Figure 4). Recreational sport divers exploit the gregarious nature of lobsters by targeting dens with high densities of lobsters and coercing them into hand nets with “tickle sticks” (Eggleston et al., 2003). The research approach in this case study used scuba diver surveys of lobster distribution and abundance patterns before and after the two-day fishing season, coupled with counts from recreational diver efforts at each sampling location, including MPAs where lobster harvest was prohibited. Research divers also quantified habitat damage (e.g., percent broken or overturned sponges and corals, percent anchor damage to corals, etc.; Figure 5) and the number of injured, sublegal lobsters from before and after the two-day fishery (Parsons and Eggleston, 2006). They also conducted “sneaky-diver” surveys aboard dive charter boats whereby diver behaviors were recorded via video and the number of contacts with the reef for a given activity (e.g., searching for lobsters, capturing lobsters, bagging lobsters) was recorded. In this case study, we answer four questions: (1) How do human predators and their prey interact? (2) How do sport divers impact their lobster prey? (3) How do Marine Protected Areas (MPAs) mediate (2)? (4) Can observations of diver behavior be used to reduce diver injury to lobsters and impacts to reefs, and enhance diver safety?

Recreational fishers are generally considered more complex in their motivations and behavior than commercial fishermen or the type of predators traditionally represented in predator–prey models (Carpenter et al., 1994; Johnson and Carpenter, 1994; Post et al., 2002). This case study indicates the opposite; exploitation rates of spiny lobster and fishing effort generally varied linearly with lobster density (type I functional response), such that catchability (i.e., proportion of lobsters extracted by divers per fishing effort), although extremely high (~80% in two days), was constant across lobster density in fished areas. There was no reduction of lobsters in MPAs during this time. The extraction rates of ~80% of legal-sized lobsters are some of the highest ever recorded for any recreational fishery in the world. The management implications of the high extraction rates and simple predatory behavior of divers is that recreational landings can be used as a relatively reliable fishery-dependent index of lobster population size, and if there is a need to reduce the catch of lobsters, such as through catch limits, then there should be a proportionate reduction in lobster landings by sport divers due to their harvesting a constant proportion at a given lobster density (Eggleston et al., 2008).

FIGURE 4. Sport divers with catch of *P. argus* during lobster fishing season. Photo by G. Plaia.

Another unexpected finding was an apparent lobster “spill-in” effect to certain reefs and MPAs from before to after the mini-season (Eggleston and Parsons, 2008; Eggleston et al., 2008). Marine reserves have the potential to enhance fisheries productivity by increasing total spawning potential or by spill-over, the migration of juveniles and adults from reserve to non-reserve areas (Sobel and Dahlgren, 2004 and references therein). Spill-over has been the focus of many studies and has been an important argument in promoting the benefits of marine reserves

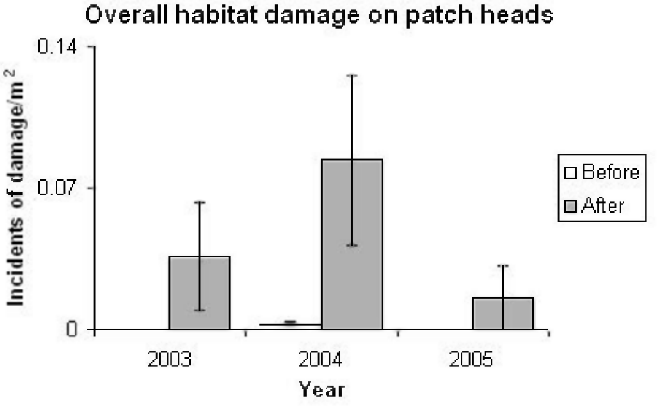

FIGURE 5. Incidents of habitat damage (e.g., broken corals and sponges, obvious anchor damage) per square meter from before and after the two-day mini-season for *P. argus* on patch coral heads in the lower Florida Keys during 2003–2005 (D. Eggleston, unpublished. data).

to gain public support (Sobel and Dahlgren, 2004). Few studies, however, have examined mechanisms for colonization or migrations into marine reserves (i.e., spill-in). This case study highlights how disturbance from an intense sport diver fishery can elevate the abundance of *P. argus* in nearby marine reserves, particularly in reserves containing relatively high densities of undisturbed lobsters, presumably through conspecific attraction where lobsters follow chemical cues to undisturbed sites in marine reserves. The mechanisms underlying this hypothesis are that lobsters disturbed by divers in fished areas would migrate from the shelters where they were disturbed (Herrnkind et al., 1975; Parsons and Eggleston, 2006) and follow queues of lobsters from undisturbed areas back to their shelters at dawn (Herrnkind et al., 1975) or use the attractive odors of conspecific lobsters as a volume-dependent guide effect (Childress and Herrnkind, 1997; Ratchford and Eggleston, 1998; Nevitt et al., 2000), or both. Population redistribution following fishery disturbance has implications for marine reserve design and application. For example, risk-averse fishery management strategies might locate reserves adjacent to intensely fished areas to enhance spill-in of mobile species.

In addition to ~80% removal of legal-sized lobsters in just two days, in situ diver observations revealed that up to 27% of the remaining population of legal and sublegal lobsters may become visibly injured from interaction with sport divers (Parsons and Eggleston, 2005). Lobster injury can result from either an unsuccessful capture attempt or a successful capture and release of a sublegal lobster. These injuries are detrimental to lobsters by reducing their growth (Davis, 1981), causing direct mortality (Parsons and Eggleston, 2005), and increasing exposure to predation by emigration from daytime shelters (Parsons and Eggleston, 2006). Furthermore, the ability to attract other lobsters is eliminated when a lobster becomes injured (Parsons and Eggleston, 2005).

Conclusion

In this case study, we have highlighted how in situ observations helped to refine behavioral ecological theory by testing whether humans display a relatively simple or sophisticated predatory response to varying densities of spiny lobster prey, and the fishery management implications of such a predatory response; improve conservation by demonstrating a novel response of mobile organisms to fishery disturbance and undisturbed habitats via lobster spill-in to MPAs; and, improve the role of diver education in reducing injury to sublegal lobsters and impacts to coral reefs, and improving diver safety.

CASE STUDIES: REPRODUCTION

Diver observations have greatly increased our knowledge of the social and reproductive behavior of fish and invertebrates in their natural habitats, as well as testing ecological theory and informing conservation. Spawning behaviors of fish range from annual spawning aggregations of snapper and grouper at distinct locations along the reef tract in the Bahamas and Caribbean (Colin, 1992; Nemeth et al., 2006) to paired spawning within a male's territory at sunset, as is the case with Caribbean eyed flounder, *Bothus ocellatus* (Konstantinou and Shen, 1995). For fish that form spawning aggregations, understanding the factors influencing the timing of migration to spawning sites, functional spawning migration area (i.e., the area from which fish migrate to an aggregation site), and the similarities and differences in residence time and movement patterns among males and females may provide predictable patterns that can be used in setting spatial or seasonal fishing closures to protect aggregations from overfishing (Nemeth, 2005). In the latter example of fish that spawn within a male's territory, male *B. ocellatus* protect a harem of 2–6 females within their territory, with males and females displaying a courtship ritual that begins one hour before sunset with a male moving beneath a female who is resting on sandy bottom, followed by the pair slowly rising ~15–75 cm above bottom, followed by the release of gametes (Konstantinou and Shen, 1995).

The reproductive success of individuals in paired and grouped spawning has often been highest in the largest and most robust members of a species (Anderson, 1994; Wolcott et al., 2005), however recent studies that have paired diver observations of mating behavior with the ability to genetically sample the involved individuals and their progeny have detected less mating selectivity than originally thought and highly complex sexual competition (Alonzo and Warner, 2000; Naud et al., 2004). For example, diver observations of spawning aggregations of giant cuttlefish, *Sepia apama*, found many more males than females, with fierce competition for females; larger male cuttlefish tended to guard females but females chose both large and small males to mate with (Naud et al., 2004). Sneaker males were small and often colored like females and therefore able to access a guarded female cuttlefish. Females used sperm from paired, unpaired, and sneaker males, as well as from previous matings, to fertilize cuttlefish eggs (Naud et al., 2004).

In terms of evolutionary stable strategies, Alonzo and Warner (2000) developed theoretical predictions of mating strategies in Mediterranean wrasse, *Symphodus ocellatus*, based on simultaneous occurrence of intersexual conflict and intrasexual competition, in this case the conflict between when females spawn their eggs on a substrate in the presence of nesting males and the sneaker males that would then fertilize these eggs. They then tested predictions with in situ diver observations in rocky bottom habitats off the coast of Calvi, Corsica, France (Alonzo and Warner, 2000). The in situ observations were consistent with a dynamic game in which females will not spawn unless in the presence of a male guarding a nest and with no sneaker males present. However, once a given nest has achieved a high reproductive success, females are more willing to spawn in the presence of sneaker males because of a decrease in the chances that a nest will be deserted by a male (Alonzo and Warner, 2000). Thus, a combination of computer simulation modeling and in situ diver observations and experimental manipulations were able to explain counterintuitive mating behavior in *S. ocellatus*, whereby females would deposit eggs in nests in the presence of sneaker males.

Conservation programs often focus on studying extinction risks encountered by small populations and determining minimum population sizes below which they cannot recover. In certain cases, per capita rates of population growth may become negative at low population density, leading to an "Allee effect," or reproductive depensation (Courchamp et al., 1999). An example of how in situ observations tested for Allee effects in a marine invertebrate is the case of declining populations of queen conch, *Strombus gigas*, in the Bahamas. *Strombus gigas* is a large motile gastropod that supports one of the most important marine fisheries in the Caribbean region (Stoner, 1997). The species has been overharvested throughout much of its geographic range, and diverse stock management regulations have been in place in Caribbean nations since the 1980s (Appeldoorn, 1994). Stoner and Ray-Culp (2000) conducted diver observations and surveys of adult density, reproductive behavior, and spawning in natural populations of *S. gigas* at two locations in the Exuma Cays, Bahamas, to test for Allee effects. Mating never occurred when density was <56 conch ha^{-1}, and spawning never occurred at <48 conch ha^{-1}, clearly demonstrating the operation of depensatory mechanisms. Reproductive behavior increased rapidly to asymptotes at densities near 200 conch ha^{-1} (Stoner and Ray-Culp, 2000). Heavily exploited populations of queen conch in the Caribbean have been slow to recover despite fishery closures, and this failure is likely due to spawning stock densities that are reduced to the point at which population growth is no longer possible (Stoner and Ray-Culp, 2000).

Conclusion

In these examples, we have highlight how in situ observation via scuba helped inform conservation and restoration of the reproductive capacity of marine species. For example, observations of fish during seasonal spawning aggregations helped establish spatial boundaries in MPAs or seasonal closures on fishing by quantifying the season of fish spawning, residence time by fish in certain spawning areas, and movement patterns within a given MPA. In situ observations of fish were also valuable in testing mating predictions from evolutionary stable strategies whereby wrasse fish displayed a type of counterintuitive game in which the selectivity of females for males of a certain size varied with the level of current reproductive success in a given nest. In situ observations also indicated that low population recovery of queen conch, despite fishery closures, was due to threshold densities below which conch did not mate.

ADDITIONAL EXAMPLES: SPECIES INVASIONS, RANGE EXTENSIONS, AND NOVEL BEHAVIORS

Range expansion and subsequent population establishment of species can have significant impacts on previously established food webs and predator–prey dynamics (Heatwole and Levins, 1972; Crawley, 1986; Hargeby et al., 1994). Changes in predator–prey dynamics, in turn, often impact population dynamics of both predator and prey species (Moorman et al., 2009). The introduction and colonization of the Indo-Pacific lionfish, *Pterois volitans*, to Atlantic reef communities (Whitfield et al., 2002, 2007) resulted in predation on native fishes and reduced recruitment of those fish species to the reef by an average of 79% (Albins and Hixon, 2008). Similarly, the Humboldt squid, *Dosidicus gigas,* has extended its perennial range in the northeastern Pacific Ocean during a period of ocean-scale warming and concurrent declines in tuna and billfish populations, and may be responsible for the decline of the Pacific hake, *Merluccius productus,* due to predation (Zeidberg and Robison, 2007). Stone crab, *Menippe mercenaria*, have apparently become established on subtidal oyster reefs in Pamlico Sound, North Carolina, at densities equivalent to those in other systems such as the Florida Panhandle, and their predatory impact on oysters can be high (Rindone and Eggleston, 2011). The common traits shared by these examples are the broad impact that relatively novel predators have had on their prey and ecosystems, and the use of in situ observations by divers to first identify these species in new geographic areas, observe their predatory behaviors, and subsequently sample these species for trophic analyses and collect them for laboratory predator–prey experiments.

Localized adaptive behaviors that might never have been imagined were easily documented by diver observations, underwater digital photography, and video. While octopus are well known for their ability to adapt their color and texture to their surroundings, another species that lives on bare sandy bottoms has developed the unique ability to mimic venomous animals as a defense. The mimic octopus, *Thaumoctopus mimicus*, which was recently described by divers for the first time, can mimic poisonous or distasteful animals (Norman et al., 2011). *Thaumoctopus mimicus* has a repertoire of at least five described mimic behaviors, three of which can be identified with local venomous flatfish, lionfish, and sea snakes. Other behaviors noted by divers were those resembling a stinging anemone and jellyfish. This type of mimicry is unique in that more than one behavior is exhibited by an individual octopus and a particular behavior appears to be selected not as a means of blending into the surroundings, but as the most appropriate active response to a specific threat (Norman et al., 2011).

The use of tools was originally regarded as a defining feature of humans and primates, yet tool-use behaviors have been subsequently found in a growing spectrum of mammals and birds (Hansell and Ruxton, 2008). Between 1999 and 2008, Finn et al. (2009) spent more than 500 diver hours (day and night) on subtidal soft-sediment substrates at depths of ~18 m off the coasts of Northern Sulawesi and Bali in Indonesia studying the behavior of more than 20 individuals of the veined octopus, *Amphioctopus marginatus*. They repeatedly observed soft-sediment-dwelling *A. marginatus* carrying around coconut shell halves and assembling them as a shelter when needed. While being carried, the shells offer no protection and placed a requirement on the carrier to use a novel and cumbersome form of locomotion, "stilt-walking" (Finn et al., 2009). While stilt-walking the octopus gains no protective benefits from the shell(s) it is carrying as the head and body are fully exposed to potential predators; the only benefit is the potential future deployment of the shell(s) as a surface shelter or buried encapsulating lair (Finn et al., 2009). Ultimately, the collection and use of objects by animals is likely to form a continuum stretching from insects to primates, with the definition of tools providing a perpetual opportunity for debate. However, the discovery of this octopus tiptoeing across the sea floor with its prized coconut shells suggests that even marine invertebrates engage in behaviors that we once thought the preserve of humans.

CONCLUSIONS

Organisms' behavior is inextricably linked to their fitness and knowledge of these behaviors is therefore paramount in understanding an organism's ecology. Behaviors, their drivers, and subsequent consequences span the spatiotemporal continuum from individual foraging decisions on the order of seconds to annual migrations across ocean basins to multidecadal environmental oscillations. While no single research tool is or will be capable of addressing the entirety of these behavioral scales, it is clear that in situ observations have made, are making, and will continue to make profound contributions to the field of behavioral ecology, and, therefore, should remain a mainstay in ecological research programs. Scuba has been a key to making behavioral observations under water that contributed to understanding the natural history of species, testing hypotheses in situ, and ground truthing technologies such as ultrasonic telemetry and hydroacoustic surveys. Because marine systems are some of the most extensively alterable systems on earth, whether through rapidly changing food webs due to overfishing (Walsh et al., 2006; Jackson, 2008), eutrophication of coastal waters and resulting changes in water quality (Verity et al., 2006; Bricker et al., 2007), or global climate changes such as warming water temperatures and increasing acidification (Dixson et al., 2010; Logan, 2010), behavioral observations in the marine realm are increasing in their importance.

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Kelp Forests in California

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ABSTRACT. Kelp forests, with their complex structure and high diversity and productivity, are the most charismatic of nearshore, subtidal communities in temperate waters. Knowledge of their natural history and ecology, however, was meager until the 1950s when scuba gave investigators the freedom to work under water with relative ease. We highlight some of the knowledge gained using scuba in California kelp forests during the past 60 years. Underwater measurements have revealed that the net primary productivity of giant kelp (*Macrocystis*) and associated seaweeds is among the highest reported for any ecosystem. The producers are a suite of macroalgal canopy guilds that occur in patches and intercept light at various levels in the water column. The patches are dynamic, influenced within forests by biological interactions and among forests by disturbance. Invertebrates partition forest resources in a variety of ways, responding to variation in vegetation, predators, and competition. Grazing sea urchins and abalone have been of great interest relative to the dynamics of kelp forest ecosystems as the former can cause "deforestation" and the latter have severely declined due to overfishing and, more recently, disease. Recent research suggests that sea urchin population dynamics may differ among regions due to differences in disturbance and recruitment. From their beginning, scuba-enhanced studies of kelp forests pursued a variety of ecological questions including understanding human impacts related to degraded water quality, overfishing, and kelp harvesting. Concerns over human impacts have increased with further declines in many fished species as well as changes in ocean climate due to CO_2 emissions, particularly changes in temperature, nutrients, frequency and intensity of ENSO, and pH. The present challenge is to understand the interactive effects of these stressors along with our fundamental understanding of how unperturbed kelp forest ecosystems are structured and function, and use the information to facilitate ecosystem-based management (EBM) of these important and productive coastal marine systems. The hope is that EBM, done in conjunction with the establishment of marine protected areas, will help sustain these remarkable underwater forests.

INTRODUCTION AND HISTORY

> *"The possibility of exploration by diving, and consequently of adding direct vision to direct collecting, ought to make of the eulittoral zone, in the near future, one of the best known parts of the underwater continental shelf."* —Drach, 1958

Giant kelp (*Macrocystis*) forests, dominated by float-bearing plants over 50 m long growing from the bottom and spreading thick canopies across the sea surface, provided food, materials, and no doubt intrigue for humans long before Darwin (1839) published the first insights into their ecology. Darwin's observations and collections were necessarily made from the surface and, like trying to understand the ecology of terrestrial forests by observing tree canopies and trees pulled up from the ground, such study from the waterline could provide only a glimpse of the community. Progress required a suitable air supply and a warm, flexible diving suit to make observation and work under water into a

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FIGURE 1. Conrad Limbaugh (left) and Wheeler J. North (right). Photos from Scripps Institution of Oceanograpy Archives, UC San Diego.

practical pursuit. Primitive surface-supply diving equipment was used by Kitching et al. (1934) in their pioneering studies of kelp beds in the U.K. With the exception of Andrews (1945), however, who used "helmet diving" to collect giant kelp holdfasts for identification and enumeration of their fauna, surface supply was rarely used to study much larger giant kelp forests of the world, likely in part because hoses and lines readily tangle with kelp fronds.

The difficulties of working easily, efficiently, and safely under water were essentially eliminated by the development of scuba by Cousteau and Gagnan in 1943 (Dugan, 1965) and of the neoprene wet suit for divers by Bradner in 1951 (Rainey, 1998). Drach was encouraged by Cousteau to train in the use of the new "scaphandre autonome" with the French Navy and to use the technology for ecological studies (Dugan, 1965). He was the first to publish a paper based on scuba observations in kelp communities, in this case *Laminaria* beds in Europe (Drach, 1949). Drach (1958) later clearly recognized the positive impact this underwater tool would have on understanding the ecology of temperate reefs. Further studies using scuba to observe and describe kelp beds in Europe soon followed (e.g., Forster, 1954; Ernst, 1955; Kain, 1960).

A few marine science graduate students in southern California began using scuba soon after the first Aqua-Lungs were imported from France in 1949. As in France, the availability and use of the equipment was facilitated by collaborations with the navy, in this case the U.S. Navy in San Diego. The beginnings of the use of scuba to study kelp forests were largely due to the curiosity and efforts of Conrad Limbaugh (Figure 1, left), a graduate student at Scripps Institution of Oceanography. He also developed training procedures, offered informal training courses, and began the first institutional marine science diving program at Scripps in 1953 (Dugan, 1965; Price, 2008). Limbaugh's colleagues and students started a local dive store, a consulting firm specializing in underwater surveys, and the Underwater Instructor Certification Course supported by Los Angeles County, the first such program in the USA. Limbaugh's pioneering work led to the rapid spread of scuba as a tool for basic and applied studies as well as recreation—a remarkable legacy.

The use of this new technology in kelp forest ecology was initially concentrated along the southern California mainland, stimulated by concerns over the effects of harvesting giant kelp on sport fishing and of sewage discharges on the health and sustenance of kelp forests. Limbaugh (1955) was the first to investigate the effects of kelp harvesting, providing information on the habitat utilization and feeding habits of numerous kelp forest fishes and the distribution of common invertebrates. This research included comparing fish assemblages in harvested versus unharvested stands, the first field experiment in a kelp forest. Aleem (1956), a research fellow at Scripps in 1955, used scuba to provide the first quantitative description of kelp forest zonation and the standing crop of algae and invertebrates. The studies of Limbaugh and Aleem were followed by those of Limbaugh's colleague Wheeler J. North (Figure 1, right). North's investigations were focused both on kelp harvesting and sewage discharge effects, and done primarily from the perspective of the effects on *Macrocystis* itself (North, 1964; North and Hubbs, 1968). These early studies provided much of the basic descriptive and life history information about kelp forests, their associated organisms, and the phenomena that affect their abundance and distribution (summarized in North, 1971a) that continues to serve as a foundation and stimulus for new research.

Perhaps more important than his studies, North established long-term research projects with the University of California Institute of Marine Resources in La Jolla, and later at the W. M. Keck Laboratory of Environmental Health Engineering at the California Institute of Technology. These long-term studies provided research funding support and research opportunities for numerous collaborators, many of whom went on to establish their own kelp forest research programs, thereby rapidly building this field of marine ecology.

A search of "giant kelp forest ecology" on Google Scholar yields nearly 11,000 results, an indication of the success of these pioneer kelp forest ecologists and the daunting, perhaps futile task of producing a comprehensive review of the topic. Fortunately there have been a number of reviews of kelp forest ecology (Dayton, 1985a; Foster and Schiel, 1985; Schiel and Foster, 1986) since North (1971a). The most recent reviews are by Graham et al. (2007, 2008).

In this paper, rather than write another comprehensive review, we decided to write a brief synopsis of a few selected topics on the ecology of giant kelp forests that focus on our specific areas of expertise and interest, with each author taking the lead in the following themes: Introduction and History (MF), Patterns and Controls of Primary Production (DR), Disturbance and Patch Dynamics (PD), Resource Partitioning (JP), Kelp Forests, Sea Urchins, and Abalone (LRB), and Scuba-Based Management (MC and DM). We hope that this paper provides the reader with up-to-date and interesting perspectives on a few aspects of kelp forest ecology that have been shaped by the use of scuba.

PATTERNS AND CONTROLS OF PRIMARY PRODUCTION IN KELP FOREST ECOSYSTEMS

Net primary production (NPP) is the rate at which autotrophs transform carbon dioxide into organic matter per unit area of the Earth's surface. It is perhaps the most defining attribute of an ecosystem because it influences virtually all ecological processes. When evaluated in this context giant kelp (*Macrocystis pyrifera*) forests have few rivals as their NPP ranks among the highest reported for any ecosystem in the world (Mann, 2000; Reed and Brzezinski, 2009). Had it not been for scuba, this important attribute of kelp forests may have gone undetected.

Numerous methods have been used to estimate the standing biomass of giant kelp, and virtually all of them have involved the use of scuba (Table 1). The most direct method entails measuring the mass of all kelp in harvested plots (Wheeler and Druehl, 1986; Van Tussenbroek, 1989). The destructive nature of this method can limit the size and number of spatial replicates and constrains investigations of temporal dynamics as it eliminates the ability to sample the same plots repeatedly over time. These constraints have been reduced by diver estimates of plant or frond density coupled with simultaneous collections of representative plants or fronds that are returned to the laboratory and weighed and/or measured (Towle and Pearse, 1973; Gerard, 1976). North (1957) devised a stipe index for non-destructively estimating standing crop of *Macrocystis* based on the density of fronds >1 m tall (measured by divers) and a mean value for frond mass, which was adopted by McFarland and Prescott (1959). Rassweiler et al. (2008) modified this technique to include diver measurements of frond length (Figure 2).

Many physical and biological factors interact to influence the biomass of giant kelp at any point in time (reviewed in Foster and Schiel, 1985; North, 1994; Graham et al., 2007), making it difficult to compare estimates from different studies. Regardless of the method used, however, it is unequivocally clear that the standing crop of giant kelp is substantially less than that of terrestrial forests despite it having equal or substantially higher NPP (Reed and Brzezinski, 2009). The relatively high production/biomass ratios (~6 to 7) and low levels of litter accumulation (~0.015 dry kg m^{-2}) reported for *Macrocystis* within giant kelp forests (Gerard, 1976; Harrold and Reed, 1985; Reed et al., 2008) reflect high biomass turnover and little carbon storage because kelp detritus is either rapidly consumed or decomposed within the forests (Gerard, 1976; Harrold and Reed, 1985), or exported to adjacent beach and deep water habitats where it serves as an important carbon subsidy (Harrold et al., 1998; Dugan et al., 2003; Spalding et al., 2003).

The methods used to measure net photosynthesis fall into two general categories: physiological measurements and those based on growth. Each approach has its own strengths and weaknesses, which makes comparisons of NPP based on different methods problematic. In general, physiological measures of NPP are more likely than field measurements of growth to account for a greater fraction of the organic carbon fixed by photosynthesis. This likely explains in part the higher values of NPP reported for *Macrocystis* by Towle and Pearse (1973) and Jackson (1977) compared to those derived from measurements of growth (Table 1). Physiological-based measurements of NPP, however, are not without problems, as they often suffer from sampling artifacts (e.g., enclosures that alter gas and nutrient exchange), assumptions that are difficult to validate (e.g., estimating rates of carbon fixation from measurements of oxygen evolution), and poor replication that constrains the scale of spatial and temporal inference. This latter concern is particularly noteworthy given the high spatial heterogeneity and temporal variability that is characteristic of giant kelp forests. Jackson (1987) developed a physiological model that, in theory, could be used to predict *Macrocystis* NPP over a wide range of environmental conditions. Such models, however, have limited value in examining spatial

TABLE 1. Studies of net primary production in giant kelp forests. To facilitate comparisons, values of NPP were converted to kg dry mass m^{-2} y^{-1} using a wet/dry ratio of 10.31 and a carbon/dry ratio of 0.286, which were derived from monthly values at three sites averaged over 96 months (Rassweiler et al., 2008). NPP estimated in units of oxygen were converted to carbon using a photosynthetic quotient of 1 (following Rosenberg et al., 1995).

Method	Location	Duration of study	NPP (dry kg m^{-2} y^{-1})	Reference
Giant kelp (*Macrocystis pyrifera* unless noted otherwise)				
Product of blade standing crop and net carbon assimilation as measured by in situ incorporation of ^{14}C by individual kelp blades during 3 h incubations	Monterey, CA	Multiple days during 1 month	8.68	Towle and Pearse, 1973
Difference between measured dissolved O_2 concentration and the concentration predicted by temperature for mid-day in the middle of Pt. Loma kelp forest at 3–6 m depth	San Diego, CA	1 day	12.12	Jackson, 1977
Simulation results from a model of whole plant growth as a function of environmental parameters that affect the flux of light	33°N (San Diego, CA)	NA	1.88	Jackson, 1987
Standing crop of harvested plots coupled with rates of frond initiation and loss	Falkland Islands	Spring & fall of 1 year	2.80[a]	Van Tussenbroek, 1993
Product of the density of growing fronds and the mean monthly increase in frond mass	Monterey, CA	Monthly for 21 months	2.23	Gerard, 1976
Changes in standing crop based on allometric measurements of fronds and plants in fixed plots combined with independent estimates of biomass loss from tagged plants and fronds	Santa Barbara, CA	Monthly for 54 months; data collection is ongoing	2.46[b]	Rassweiler et al., 2008; Reed et al., 2008
Product of Leaf Area Index (LAI) from *Macrocystis integrifolia* harvested from Grappler kelp forest, and net photosynthetic rates measured in the laboratory	British Columbia	Bimonthly for 12 months	4.33	Wheeler and Druehl, 1983
Giant kelp forest ecosystem				
Dissolved O_2 concentrations in diurnal water samples collected in a kelp forest at discrete depths	Paradise Cove, CA	2 days	6.39[c]	McFarland and Prescott, 1959
Allometric measurements of changes in standing crop combined with independent estimates of biomass loss for giant kelp (O_2 evolution in enclosed chambers for intact assemblages of understory algae; C^{13} incorporation for phytoplankton)	Santa Barbara, CA	Monthly for 17 months	2.73[d]	Miller et al., 2011

[a] Average of spring and fall.

[b] Average of two sites (Mohawk and Arroyo Quemado).

[c] Average of two days.

[d] Average of three 12-month periods during 17 month study.

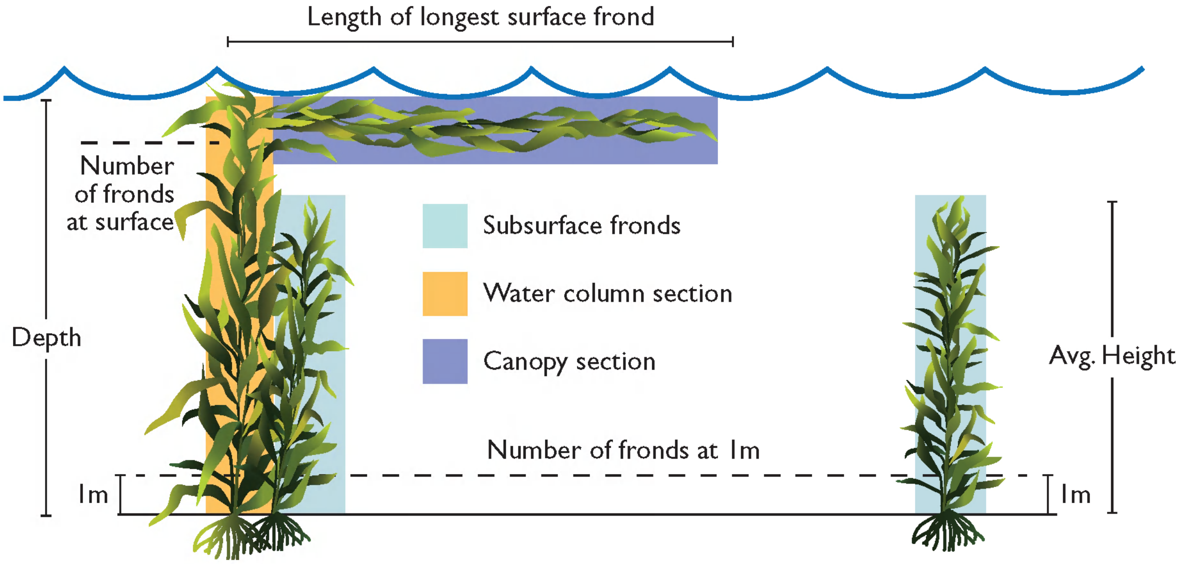

FIGURE 2. Measurements taken to estimate the mass of giant kelp fronds in the water column and surface canopy both for kelp plants that reach the surface and for subsurface kelp plants. See Rassweiler et al. (2008) for details.

and temporal variability in NPP due to the lack of time series data for many of the input variables.

The most useful studies for examining spatial and temporal patterns of NPP by *Macrocystis* and the environmental drivers that control them are those by Gerard (1976) and Reed et al. (2008), which were relatively long term (21 and 54 months, respectively). Both studies used field measurements of growth to estimate NPP and reported remarkably similar values (2.23 and 2.46 dry kg m^{-2} y^{-1}, respectively) despite working in different locations and years (Table 1). These values underestimate NPP because they do not account for production lost as dissolved exudates, which can account for one-third of the production by *Macrocystis* on an annual basis (Miller et al., 2011). One of the most striking (though not surprising) observations reported by Gerard (1976) and Reed et al. (2008) was the strong correlation between NPP and standing biomass.

The first estimate of NPP for the entire kelp forest community was made by McFarland and Prescott (1959), who measured dissolved oxygen concentrations in diurnal water samples collected throughout the water column in the kelp forest at Paradise Cove in Santa Monica Bay. The short-term nature of this study coupled with uncertainties about currents during the measurement period cast doubt on the accuracy of these estimates (Jackson, 1987). The most comprehensive study of NPP by the entire kelp forest community was done by Miller et al. (2011), who simultaneously examined NPP by understory macroalgae (by measuring O_2 evolution from intact assemblages enclosed in benthic chambers), phytoplankton (using ^{13}C-bicarbonate tracer incubations), and giant kelp (using the methods of Rassweiler et al., 2008) in areas with and without giant kelp. They found that the combined NPP by understory macroalgae and phytoplankton can be as high as that of giant kelp and serves to dampen interannual variability in kelp forest NPP caused by the loss of *Macrocystis* from wave disturbance. In the low-light environment beneath the surface canopy of giant kelp neither the architecture of the macroalgal understory nor the diversity of species within it appear to be important in determining the productivity of the forest understory (Miller et al., 2012). By virtue of its greater biomass, the productivity of the foliose component of the understory assemblage was three times higher than that of the turf component despite having a growth rate that was three times slower (Miller et al., 2009).

DISTURBANCE AND PATCH DYNAMICS

All ecological communities are exposed to many types of perturbation varying in intensity and scales; the most common for kelp communities include prolonged periods of nutrient stress, storms, and grazing, usually by sea urchins. The greatest disruption to giant kelp forest communities typically occurs during El Niño, when large waves associated with severe winter storms combine with warm, nutrient-depressed surface waters caused by a deepening of the thermocline (Dayton and Tegner, 1989). The impacts of this combined set of conditions can be profound because they result in selective reduction of giant kelp in relation to understory species (Tegner et al., 1997). This is because the greater drag on *Macrocystis* makes it more prone to removal from large waves than smaller, lower-lying understory species (Dayton and Tegner, 1984). In addition, because the vast majority of *Macrocystis*'s biomass resides near the sea surface, it is much more vulnerable to the nutrient-depleted surface waters associated with El Niño conditions compared to understory species.

The physiological stresses associated with El Niño are greater at the low-latitude limits of *Macrocystis*'s range, where nutrient limitation occurs more routinely. It is generally understood that the nutrient limitations associated with warm water have more severe effects than temperature (Dayton et al., 1999: fig. 1). For example, during the 1997–1998 El Niño nearly all giant kelp disappeared from the southern and central portions of its range in North America (i.e., Baja California, Mexico, and southern California), whereas only minor losses were observed in the northern portion of its range off central California (Edwards and Estes, 2006). Moreover, recovery from the El Niño generally took longer in the south, but varied substantially within regions due to a variety of factors including proximity to upwelling areas, competition with other algae, grazing, and propagule availability. Similar latitudinal patterns were observed in the Southern Hemisphere, where the northern limit of three species of brown algae shifted south toward higher latitudes following the El Niño event of 1982–1983 (Peters and Breeman, 1993). Such stresses may make kelps more susceptible to disease, and low-latitude kelps in northern New Zealand have succumbed to a disease that may have resulted from physiological stress (Cole and Babcock, 1996; Cole and Syms, 1999).

Scuba diving observations, collections, and experiments have been central to understanding sea urchin–giant kelp interactions. Disturbance from sea urchin grazing occurs unpredictably in space and time and varies with the species of urchin, their abundance, and their nutritional condition. It leads to the creation of bare patches that range in size from several square meters to several square kilometers, which in some cases led to the complete loss of local populations of giant kelp and associated algae in southern California (Leighton et al., 1966; North and Pearse, 1970; Ebeling et al., 1985; Harrold and Reed, 1985; see the "Kelp Forests, Sea Urchins and Abalone" section in this paper). The deforestation of giant kelp forests from sea urchin grazing was ubiquitous in southern Chile in the early 1970s, patchy in other areas, and nonexistent in parts of Tierro del Fuego and Isla de los Estados in southern Argentina (Dayton, 1985b).

It is difficult to generalize patchiness in kelp communities because the taxonomic patterns differ across regions. Nevertheless, underwater surveys have shown kelp communities are characterized by distinct canopy guilds, including floating canopies at or near the surface (*Macrocystis pyrifera, Nereocystis luetkeana*), stipitate canopies in which the fronds are supported off the substrata by stipes (*Pterygophora californica, Eisenia arborea, Laminaria* spp.), prostrate canopies in which the fronds move back and forth across the bottom (*Laminaria farlowii, Dictyoneurum*), and various associations of foliose, turf, and crustose algae (Figure 3).

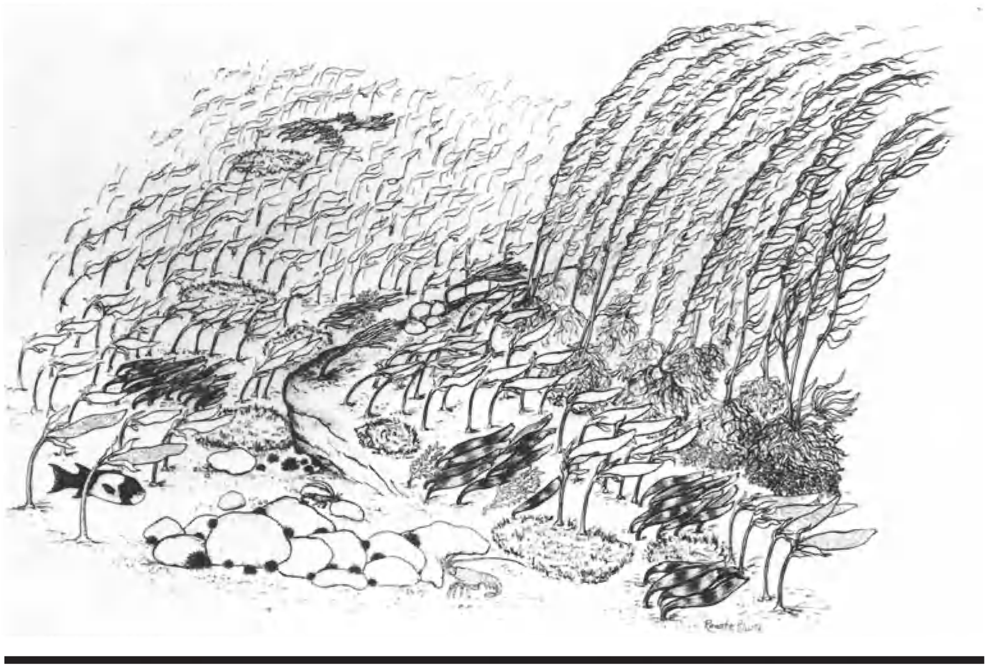

FIGURE 3. Sketch of a portion of the Pt. Loma kelp forest showing patches of algae with characteristic canopy guilds, including the floating canopy of giant kelp, *Macrocystis pyrifera*, the stipitate canopy of the understory kelps *Pterygophora californica* and *Eisenia arborea*, the prostrate canopy of the kelp *Laminaria farlowii* and the fucoid *Cystoseira osmundacea*, and patches of turf and nongeniculate (crustose) coralline algae. From Dayton et al. (1984).

Discrete monospecific patches of these different guilds can be very persistent and resist invasion for more than 10 years (Dayton et al., 1984). The dynamics of the patches relates to the postdisturbance succession. In this case, succession relates to the recruitment processes that tend to be inhibitory or neutral; usually the succession pathways follow relative dominance relationships that can be very site specific.

Dominance patterns in giant kelp forests vary across environmental gradients, especially gradients in depth, available nutrients in the surface waters, and wave exposure (Dayton et al., 1984). However, the general processes are remarkably similar almost everywhere, such that questions have been asked and necessarily answered by diving observations and experiments. For example, dominance patterns and canopy interactions similar to those for California kelp communities have been reported for other types of kelp communities in Alaska (Dayton, 1975a), Washington State (Dayton, 1975b), Nova Scotia (Johnson and Mann, 1986), the northeast and northwest Atlantic (Kain, 1975; Witman, 1987), and Australia (Kennelly, 1989). The species defining the patches differ, but the biological and physical processes that maintain them tend to be general. Taller perennial canopy guilds tend to be dominant competitors for light (Reed and Foster, 1984; Santelices and Ojeda, 1984) but are much more susceptible to nutrient and wave stress (Jackson, 1977; Dayton and Tegner, 1984). Dominance hierarchies in the competition for light appear to be reversed in areas with low surface nutrients or with persistent wave stress (Dayton et al., 1984). During strong El Niño events, surface canopies lack sufficient nutrients to exert dominance; the cooler waters below the thermocline have more nutrients, thereby selecting for interactions among the understory species. In situations in which the surface waters are nutrient depleted, internal waves and other physical processes often result in nutrient infusion along the bottom in kelp habitats (Zimmerman and Kremer, 1984; Fram et al., 2008). More highly wave-stressed habitats tend to be characterized by mixing and replete nutrients, but the wave stress tends to remove species with surface canopies such that with increasing wave stress, lower-level canopy guilds become dominant (Dayton, 1975a; Cowen et al., 1982; Schiel et al., 1995).

The different morphological adaptations of the canopy guilds appear to have been selected for different environmental situations in which exploitation of light is enhanced by higher canopies and superior stress tolerance of lower canopies. The adaptations of kelp forest algae appear to represent four distinct tactics: (1) ephemeral species with opportunistic life histories such as *Desmarestia ligulata* and filamentous algae in the order Ectocarpales; (2) surface canopy kelps such as *Macrocystis* and *Nereocystis* adapted to exploitative competition for light; (3) lower-level canopies such as stipitate kelps and foliose red algae adapted to lower light and/or physical stress from wave surge; and (4) algae such as corallines or those with chemical defenses that are adapted to resist grazing (Vadas, 1977). Within any particular site the relative patch dynamics are determined by biological relationships such as grazing resistance or competition, but the broad differences in patch dynamics among regions are determined by physical factors (Edwards, 2004).

RESOURCE PARTITIONING

Resource partitioning among similar, often closely related species is well known in the rocky intertidal where there are steep physical gradients related to wave exposure and tidal immersion (Stephenson and Stephenson, 1972). Different species of barnacles, for example, are found at different tidal heights and have different growth and reproductive modes reflecting differences in exposure to air, competition, and predation (Connell, 1961; Hines, 1978). Moreover, the multitude of similar, closely related species found in the intertidal (e.g., snails, limpets, nudibranchs, isopods) are seen on close observation to be in specific microhabitats or exhibit different trophic or reproductive traits (Ricketts et al., 1985; Foster et al., 1988; see the “Disturbance and Patch Dynamics” section above). On the other hand, the subtidal habitat of kelp forests, always submerged and flushed with seawater, might be expected to be more homogeneous, and while the high diversity in kelp forests has long been known (Darwin, 1839), that diversity might not be expected to partition into different uses of available resources. Such an expectation is quickly dispelled when kelp forests are entered using scuba diving. Subtidal zonation patterns reflecting different levels of surge and light are evident as one descends into deeper water (Limbaugh, 1955; Aleem, 1956; McLean, 1962; Pequegnat, 1964; North, 1971b; Foster and Schiel, 1985). Close observation reveals that similar species utilize different resources even within the same zones, illustrating as well as anywhere in the world the competitive exclusion principle and resultant resource partitioning (Hardin, 1960; Rosenzweig, 1991; McLoughlin et al., 2010). Here we present an example of resource partitioning among species of morphologically similar trochid gastropods that has been dissected out of the kelp forest in the Hopkins Marine Life Refuge (HMLR, now a portion of Lovers Point State Marine Reserve) in Monterey Bay off Pacific Grove, California. This kelp forest has been the site of ongoing research and teaching since 1971 (Pearse and Lowry, 1974; Pearse et al., this volume).

Lowry et al. (1974) first documented habitat differentiation by six species of trochid snails—two of *Chlorostoma* and one of *Promartynia* (all formerly in the genus *Tegula*, commonly called turban snails), and three of *Calliostoma* (commonly called top snails)—on four contrasting species of kelp forest algae. They simply removed all the snails from different portions of the algae and found that while the top snails occurred mainly on the seasonal reproductive fronds of *Cystoseira osmundacea*, turban snails were found mainly on fronds of *Macrocystis pyrifera*. Moreover, the species were arranged along the length of the floating fronds, with some species being higher from the sea bottom than others, and the smaller individuals of all species being either near the sea bottom or on the two species of understory algae that were sampled. This preliminary study was followed-up in more detail by Riedman et al. (1981), who quantified the species of turban snails on both *M. pyrifera* and the sea bottom in both March and August. Most of the turban snails were on the sea bottom in March after the winter storms had thinned the canopy and knocked many snails off the kelp. However, in August *Chlorostoma brunnea* and *Promartynia pulligo* were mainly in the canopy of the well-developed kelp forest. Moreover, the species were concentrated in different portions of the kelp forest, with *P. pulligo* mainly in the outer, seaward side of the kelp forest and *C. brunnea* in the shoreward side extending into the lower intertidal, where it overlapped with the intertidal congener *Chlorostoma funebralis* (Figure 4). *Chlorostoma montereyi* was found mainly near or on the bottom in the middle of the kelp forest.

In a beautiful series of observational monitoring and field experiments, Watanabe (1983, 1984a, 1984b) dissected out some of the factors responsible for this habitat partitioning among the turban snails. Larval recruitment appeared to be of major importance because adults showed little lateral movement and juveniles were found on the bottom in the same areas as the adults: *C. brunnea* recruits in the low intertidal/shallow subtidal on alga-covered rocks, *P. pulligo* recruits in the outer portion of the kelp forest on shell rubble, and *C. montereyi* recruits in between. On the other hand, little evidence was found for interspecific competition for either food or space, with little difference seen between interspecific and intraspecific competition on growth and reproduction. Predation on adult snails, however, appeared to reflect the habitat partitioning, with benthic predators (e.g., sea stars, demersal fishes) driving poorly defended, light-bodied individuals of *P. pulligo* up onto the kelp and keeping heavy-shelled individuals of *C. brunnea* in shallow water where surge and dense algal cover makes them more difficult to detect. *Chlorostoma montereyi*, with the most active escape response from predatory sea stars and a deep shell within which to retreat if caught, did the best on or near the bottom. By offering actively foraging individuals of the predatory sea star *Pisaster giganteus* (in situ on the kelp forest floor) choices of narcotized versus nonnarcotized individuals of *P. pulligo*, Harrold (1982) further demonstrated the effectiveness of the escape responses (running, twisting, tumbling) in these snails. On the other hand, it remained unclear what limits *P. pulligo* from occurring in shallow water.

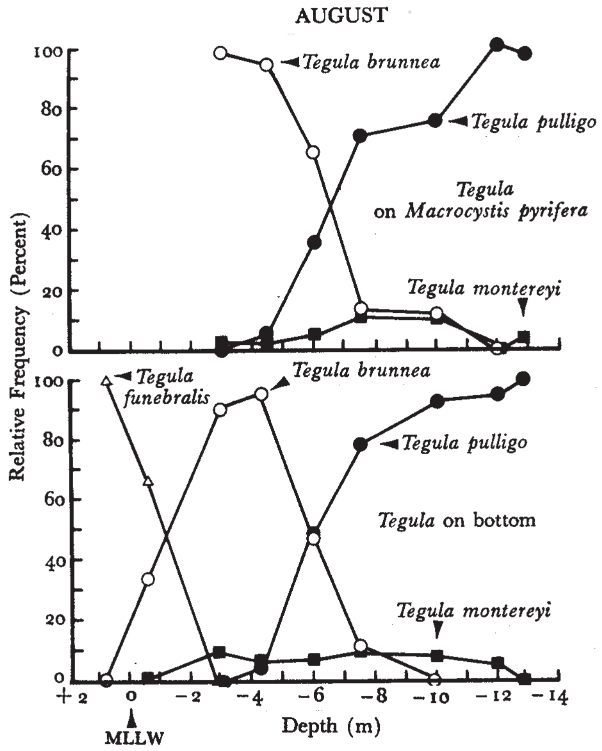

FIGURE 4. Distribution of 3 species of *Chlorostoma* and *Promartynia pulligo* (both genera were within the genus *Tegula*) on fronds of *Macrocystis pyrifera* and on the bottom within the kelp forest of the Hopkins Marine Life Refuge from the upper intertidal to the seaward edge of the forest. At each station about 200 snails were collected from the bottom, and all snails collected at stations between depths 3 and 12 m were collected from single large kelp plants. From Riedman et al. (1981).

Harrold (1982) did the same experiments with *Calliostoma ligatum*, the top snail Lowry et al. (1974) found to occur mainly near or on the bottom. These snails display an especially lively escape response when they detect sea stars nearby, and upon contact in the field were seen to vigorously twist or even jump and tumble away. Moreover, they cover their shells with mucus, making it difficult for the sea star to grasp them, and at least in laboratory aquaria were seen to bite at the tube feet of pursuing sea stars.

A second species of *Calliostoma*, *C. canaliculata*, was found by Lowry et al. (1974) to be mainly on the seasonal reproductive fronds of *Cystoseira osmundacea* in the summer, shifting to *Macrocystis pyrifera* in the fall after the reproductive fronds of *C. osmundacea* disintegrate. But it and the other species of snails also occur on the bottom, especially in the winter when the kelp is much reduced, where they all encounter sea star predators. Bryan et al. (1997) reported that not only does *C. canaliculata* have an escape response to sea stars, but if captured clamps down to the substrate and produces a noxious mucus that repels the sea star. The active compound, a cationic neurotoxin, has been isolated and characterized by Wolters et al. (2005). Studies by Schmitt (1982, 1987) on other species of closely related trochid snails in southern California kelp forests have revealed similar differences in responses to predators, with species that flee predators or are distasteful being found in different areas.

Clearly, different species of kelp forest snails differ in their responses to predators in relation to where they mostly occur in kelp forests, and their responses appear to reflect natural selection in their main habitats. However, whether their antipredator responses as well as the differential recruitment patterns seen in turban snails in the HMLR led to or are a consequence of resource partitioning remains unresolved.

Physiological differences among these closely related snails also could reflect resource partitioning. Response to temperature, as evidenced by heat shock proteins (Tomanek and Somero, 1999, 2002) and heart rate (Stenseng et al., 2005), for example, has been demonstrated to differ between the intertidal *Chlorostoma funebralis* and *C. brunnea* and *C. montereyi* in the adjacent kelp forest (Figure 4). However, little or no difference was found between the two species of kelp forest snails, even though they differ in their depth distributions.

The example of resource partitioning in trochid snails can be repeated with other groups of related species. For example, Hines (1982) thoroughly documented resource partitioning among five species of spider crabs in the HMLR. These species varied in size, distribution, food, and mechanisms to avoid predation so that there was a multidimensional niche separation among them, and similar utilization of one resource was generally complemented by dissimilar utilization of another resource. This work has not been repeated elsewhere, nor has it been taken to greater depths to understand the mechanisms involved. However, Hultgren and Stachowicz (2008, 2009, 2010) have compared variation in color and extent of decoration as camouflage from predators in these and related crabs in northern California, extending Hines's work on that aspect of their biology.

Another suite of species that are conspicuous members of kelp forests in the HMLR are corals and corallimorpharians, and these vary in their distributions and life histories. The corals *Balanophyllia elegans, Paracyathus stearnsii*, and *Astrangia lajollaensis* generally occur on the tops, on the middle portions, and near the bases of vertical surfaces of rocks, respectively, while the corallimorpharian *Corynactis californica* occurs mainly on the tops and upper portions. Chadwick (1991) showed that this distributional pattern seen while diving reflects an interspecific dominance hierarchy demonstrated in the lab with *C. californica* and influences the abundance and population structure of *B. elegans* by reducing reproductive output, increasing larval mortality, and altering recruitment patterns. Moreover, *C. californica* kills all three species of corals (Chadwick, 1987), in particular *A. lajollaensis*, which, like *C. californica*, grows by cloning, with clones of both species able to cover large areas (Fadlallah, 1982; Chadwick and Adams, 1991). Both *A. lajollaensis* and *C. californica* broadcast spawn eggs that produce pelagic larvae (Fadlallah, 1982; Holts and Beauchamp, 1993) whereas the other two coral species are solitary but differ in life span and mode of reproduction. *Balanophyllia elegans* is relatively short lived, broods embryos, and produces demersal, crawling larvae (Fadlallah and Pearse, 1982a; Fadlallah, 1983), while *P. stearnsii* is long lived, broadcasts eggs, and produces pelagic larvae (Fadlallah and Pearse, 1982b). These differences in reproductive modes not only affect patterns of recruitment (high in *B. elegans*, low in *P. stearnsii*), but also influence the genetic structure of the populations over their range on the west coast (Beauchamp and Powers, 1996; Hellberg, 1996).

These three examples illustrate quite different forms of resource partitioning among similar taxa within a kelp forest. With the trochid snails and spider crabs, the issue appears to be mainly predators and dealing with them in different portions of the kelp forest with different defensive tactics, while with the corals and corallimorpharians direct interspecific competition is more important and is dealt with both spatially and temporally. Although these interactions are general, and can be looked at in all habitats, terrestrial or marine, they differ in specifics depending on the particular taxa involved. Testing and understanding the mechanisms of resource partitioning in kelp forests has been enabled by the use of scuba, allowing for both the evaluation of the robustness of ecological theory and the teasing apart of how similar species live together in this important coastal ecosystem.

KELP FORESTS, SEA URCHINS, AND ABALONE

Sea urchin grazing is well known to impact algal communities (Lawrence, 1975; Harrold and Pearse, 1987), knowledge gained primarily through observations, quantitative sampling, and experiments done with scuba. In some regions, two alternate stable states have been reported: lush kelp forests with high species diversity, and deforested areas, which have been described as depauperate barrens dominated by sea urchins and crustose coralline algae (Leighton et al., 1966; Steneck et al., 2002). While this description highlights the extremes, many locations fall along a continuum (Graham, 2004). In California, kelp forests exist that exhibit a range of community compositions, with large-scale deforestation being characteristic of less than 10% of forests described (Foster and Schiel, 1988). The composition of individual forests varies, in part due to changes in sea urchin feeding behavior from passive capture of drift algae to active grazing in "fronts" that remove giant kelp, subcanopy, and turf algae alike (Dean et al., 1984). Severe storms appear to be important triggers for this behavioral switch as they decrease the availability of drift algae (Ebeling et al., 1985; Harrold and Reed, 1985).

While human fishing has dramatically reduced large predators in giant kelp forests in southern California (Dayton et al., 1998), there are conflicting views concerning the importance of fishing in determining the state (forested or barren) of rocky reef communities in this region (Jackson et al., 2001; Foster and Schiel, 2010). In addition to fishing, disease and physical and chemical factors such as temperature, nutrients, sedimentation, and large waves are also known to control algae and the herbivores that graze on them (Pearse et al., 1970; Cowen et al., 1982; Dayton et al., 1999; Behrens and Lafferty, 2004). It is becoming increasingly clear that all such factors acting alone or in combination contribute to kelp deforestation and the formation of sea urchin barrens.

As Polis and Strong (1996) proposed for terrestrial systems, the complex food webs of California kelp forests may buffer the community from trophic cascades that result in deforestation. Byrnes et al. (2006) argue based on kelp forest monitoring data from southern California that kelp abundance is related to predator diversity, not predator density. Strong trophic cascades, however, have been described in Alaska where food webs are simpler (Estes and Palmisano, 1974). Elsewhere in the world, local environmental factors such as wave action and sedimentation appear to impact kelp forest trophic cascades (Shears et al., 2008).

There is little evidence for kelp deforestation in northern California (from San Francisco north to the Oregon border). Canopy-producing kelps in the region are predominantly bull kelp, *Nereocystis luetkeana*, one of the fastest growing and most productive annual kelps in the world. This region has relatively high nutrients, and intense wave action that can cause sea urchin mortality (Ebeling et al., 1985) and impede feeding (Lissner, 1983) for much of the year (Foster and Schiel, 1985). Drift algal abundance is highly seasonal with a peak in the fall when the first winter storms rip out summer's growth, providing a brief pulse of drift algae (Rogers-Bennett, 1994). In addition, sea urchin recruitment in the area appears to be lower and more sporadic than in southern California (Ebert et al., 1994), suggesting sea urchin recruitment may not be as successful in the north.

To examine the potential effects of fishing red sea urchins on kelp deforestation in northern California, one study compared kelps and subtidal algae inside and outside two areas closed to sea urchin fishing for 20 years (Figure 5). There was no evidence for deforestation inside the closures despite more than double the density of red sea urchins compared to fished areas outside. Aerial surveys from multiple years showed interannual variability in surface canopy cover, but no differences in surface canopies inside and outside the sea urchin closures. Furthermore, subtidal surveys inside and outside the closed areas showed no differences in canopy, subcanopy, turf, or crustose coralline algae cover (Rogers-Bennett et al., 2011). This study suggests that areas where sea urchin fishing is prohibited will not become overpopulated with sea urchins and deforested at these spatial scales within a twenty-year time period. Behrens and Lafferty (2004) found that rocky reefs inside one reserve in southern California were more likely to support kelp compared to fished sites, and the difference was attributed to fishing for sea urchin predators such as lobster (Lafferty, 2004). This differs from northern California where the reserve protected sea urchins from the sea urchin fishery.

Sea urchins directly and indirectly modulate shelter and food resources within kelp forests and can be regionally important ecosystem engineers (Rogers-Bennett, personal observation). Through their role as dominant grazers, sea urchins act to structure surrounding assemblages of algae and sessile invertebrates. Urchin grazing of giant kelp holdfasts can weaken structural integrity and lead to increased mortality during storms, while even slight damage to stipes can result in substantial losses of biomass even during relatively calm conditions (Tegner et al., 1995; Duggins et al., 2001). Sea urchins can also modify rocky substrates by forming home scars, which they maintain free of algae and invertebrates (Rogers-Bennett, 1994).

The canopies of spines of individual and groups of sea urchin species provide important biogenic structures in kelp communities in many parts of the world (Tegner and Dayton, 1977; Kojima, 1981; Mayfield and Branch, 2000; Townsend and Bologna, 2007). In California, red sea urchins provide refuge for both juvenile

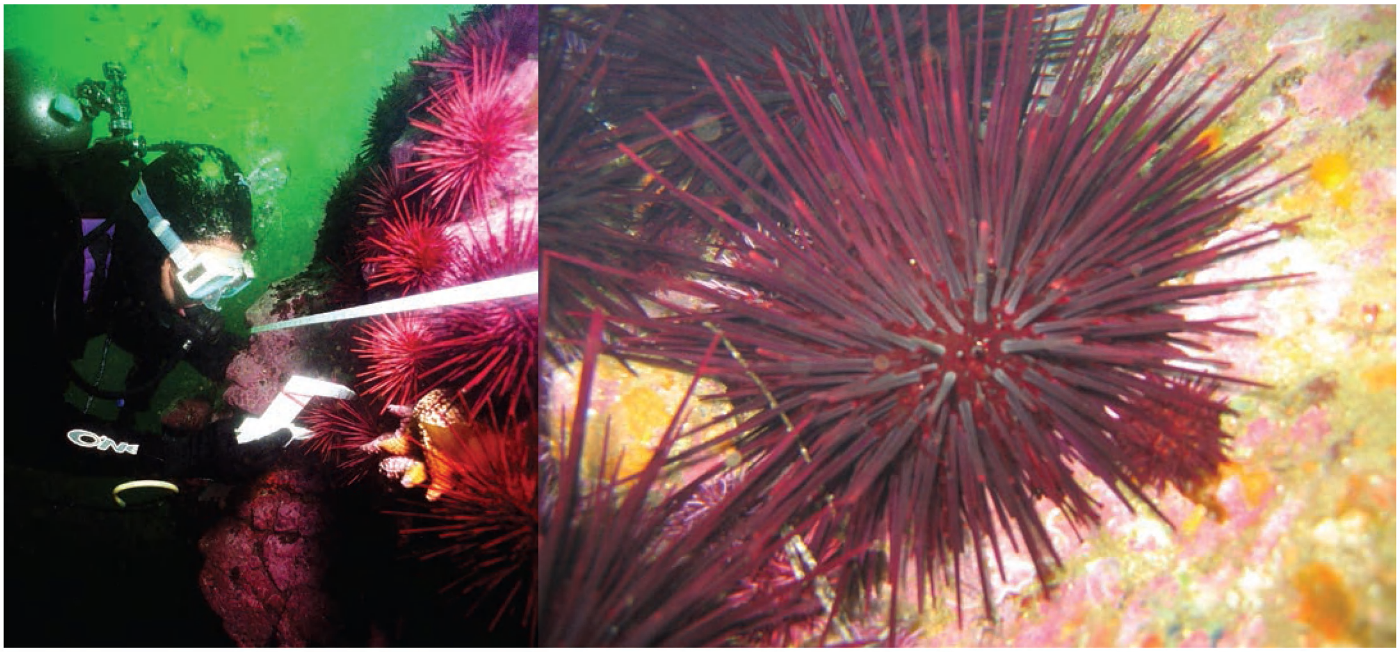

FIGURE 5. Divers surveying red sea urchins along a subtidal transect in northern California (left; photo by S. Fitzgerald) and red sea urchin spine canopy with juvenile sea urchins beneath (right; photo by L. Rogers-Bennett).

conspecifics (Figure 5; Tegner and Dayton, 1977; Rogers-Bennett et al.,1995) and a suite of other organisms such as juvenile fishes, crabs, and snails (Rogers-Bennett and Pearse, 2001). Juvenile abalone have been shown to utilize sea urchin spine canopies in California (Rogers-Bennett and Pearse, 2001), Canada (Tomascik and Holmes, 2003) and South Africa (Mayfield and Branch, 2000). Animals that take shelter under the spine canopy garner protection from wave action and predators, but do not appear to benefit from additional food (Nishizaki and Ackerman, 2004). In the laboratory, the number of juvenile sea urchins moving toward spine canopy shelter increased with increasing water flow and predators (Nishizaki and Ackerman, 2001). Similar behavior observed in the presence of predators was attributed to the release of a chemical cue by adults that triggered juveniles to seek shelter. Adults did not respond to the cue presumably because they have a size refuge from predation (Nishizaki and Ackerman, 2005).

Much like that by sea urchins, grazing by abalone alters the structure of kelp forest communities by maintaining patches dominated by crustose coralline algae (Douros, 1985; Miner et al., 2007). The formation of such patches provides chemical cues critical for successful settlement and metamorphosis of their larvae (Morse et al., 1979). This in turn maintains coralline algal patches over time. Sedimentation (Onitsuka et al., 2008) and conditions that lead to overgrowth by fleshy algae hinder settlement of abalone larvae, ultimately leading to the demise of coralline patches. In one long-term study of intertidal black abalone, *Haliotis cracherodii,* in California, sites with few black abalone had recruitment failure following population devastation from a virulent disease, which led to a dramatically altered community structure (Miner et al., 2007). Sites without abalone had less crustose coralline algae and more fleshy algae and sessile invertebrates such as tube worms, sponges, and tunicates, which further hinder abalone recruitment (Miner et al., 2007). With this negative feedback further preventing abalone recovery, these changes in community structure may be long term.

As described above, interactions among kelp, sea urchins, and abalone can have profound effects on the structure and dynamics of giant and bull kelp forest communities. Moreover, there is a growing awareness of the role oceanographic processes play in driving kelp dynamics (Dayton and Tegner, 1984; Tegner and Dayton, 1987; see “Patterns and Controls of Primary Production in Kelp Forest Ecosystems” and “Disturbance and Patch Dynamics” sections in this paper), sea urchin recruitment (Watanabe and Harrold, 1991; Ebert et al., 1994), and abalone growth (Haaker et al., 1998) and reproduction (Vilchis et al., 2005; Rogers-Bennett et al., 2010). All of these species are (or have been) fished for recreational and commercial use in California. Overfishing can have widespread detrimental impacts on biodiversity (Coleman and Williams, 2002). Consequently, a management approach for kelp forests based on the ecosystem rather than on individual component species will likely be most successful in conserving the diversity and ecological function of these prominent and important coastal ecosystems and their services. The establishment of a network of marine protected areas in California is one tool managers can use to implement ecosystem-based management (see “Scuba-Based Management” section in this paper).

Ocean warming has the potential to have major impacts on kelp forest communities in California (Schiel et al., 2004). Extensive work has shown that low nutrients associated with warm water conditions lead to reductions in the extent of giant kelp canopies (Tegner and Dayton, 1987; Edwards, 2004). Warm water is also associated with increases in sea urchin recruitment, perhaps due to increases in planktonic food for larvae or higher larval settlement enhanced by reductions in offshore advective currents (Ebert et al., 1994). When prolonged, such conditions lead to greater competition for food among adult sea urchins, reducing gonad development and subsequent larval production. When food is in short supply, sea urchins may switch from passively feeding on drift algae to more destructive, active grazing, which in turn further reduces the availability of their food resources. Not surprisingly, commercial landings of the red sea urchins in southern California are negatively associated with El Niño (Foster and Schiel, 2010) as the warm, nutrient-poor water coupled with large waves leads to drastic reductions in kelp and subsequent decreases in sea urchin gonad production, thereby reducing the quality of fishery gonad product.

During periods of warm ocean conditions, abalone have decreased growth (Haaker et al., 1998), decreased reproduction (Vilchis et al., 2005), and enhanced mortality due to starvation or disease events (Rogers-Bennett et al., 2010). Warm water along with bacterial infection is needed to trigger the expression of the lethal disease Withering Syndrome (Moore et al., 2000). One species of abalone protected in California, the flat abalone, *H. walallensis*, has shifted its range north into Oregon, perhaps as a consequence of ocean warming, making it vulnerable to a small commercial fishery (Rogers-Bennett, 2007). At the same time, warm water events may enhance the recruitment of abalone predators such as sheephead (Cowen, 1985) and spiny lobsters in southern California, further evidence of the need for an ecosystem perspective.

The collective evidence to date suggests that fishing, ocean warming, andnutrient reduction may act synergistically to negatively impact giant kelp forest communities (Harley and Rogers-Bennett, 2004; Ling et al., 2009). As ocean warming increases, sustainable management of species within kelp forest communities will be critical and complex. A greater understanding of the direct and interactive effects of physical and biological processes that drive population dynamics of key species in California’s kelp forests will be needed to successfully implement ecosystem management and sustain kelp forest communities; this understanding will demand the observational and experimental research on kelp forest systems enabled by scuba.

SCUBA-BASED MANAGEMENT

When Aqua-Lungs arrived in California, they were almost immediately used to investigate concerns raised by the public, fishers, and resource managers about human impacts on kelp forest ecosystems. These concerns reflected the great diversity of resources and services that kelp forests provide society, their economic and recreational values, and the growing intensity of uses. Most recently, ecosystem-based approaches to management have fueled appreciation for a more holistic understanding of these forests and assessment of the cumulative impacts of humans. The many contributions of science to fundamental advances in conservation and management of kelp forests in California and elsewhere would simply not have happened without scuba.

In its present form, ecosystem-based management (EBM) represents a movement away from single species and toward comprehensive consideration of the structural and functional attributes of ecosystems, how these attributes contribute to ecosystem resiliency and the production and sustainable use of resources, and how ecosystems respond to both environmental perturbations (e.g., climate variation) and human interventions (e.g., fishing and pollution). Ecosystem-based management employs and evaluates new approaches and tools to best manage human impacts. In this section, we provide brief examples to illustrate the contribution of scuba-based research in kelp forest ecosystems to various aspects of EBM.

Scuba-based research has been essential as it provides quantitative descriptions of kelp forest ecosystems that are the basis of numeric and conceptual models of these ecosystems (e.g., Foster and Schiel, 1985; Graham et al., 2008; Byrnes et al., 2011). Particularly important is understanding the relationships between the abiotic and biotic components. One example of this approach is the design of mitigation for human-caused losses of forests. When the discharge of cooling waters from a power plant in southern California led to kelp forest losses, it was decided to mitigate that impact by creating a comparable forest and its associated recreational and commercial fisheries on a man-made reef placed nearby (Ambrose, 1994). To determine the most appropriate physical structure for the reef, wide-ranging regional surveys (Ambrose and Swarbrick, 1989) and experimental modules that varied reef size and substrate type, size, and complexity were conducted by divers to quantify how the structure of the kelp forest community responded to variation in these reef features (Reed et al., 2006). Based on the responses (California Coastal Commission, 2008), a large man-made rocky reef was constructed that, as revealed by continuing surveys, appears to support a kelp forest with the biotic attributes of natural forests in the region (Reed et al., 2012). In this example, surveys to determine species–habitat relationships were used to inform a mitigation program, but these relationships are also useful for identifying "essential fish habitat," habitat like kelp forests that, if protected, helps ensure sustainable populations of temperate reef fishes and invertebrates.

Some species have particularly influential functions in ecosystems, and identifying these species and their functions and understanding the consequences of their loss are critical requirements for EBM. Canopy-forming kelps are a clear example; changes in their abundance affect, directly or indirectly, the species composition, abundance, and diversity of other algae, invertebrates, and fishes associated with kelp forests (e.g., Reed and Foster, 1984; Graham, 2004). Their influence is also manifested at the highest trophic levels (e.g., fishes, birds, marine mammals, human use) by extending habitat structure and fueling phenomenally productive detritus- and grazer-based trophic pathways (e.g., Duggins et al., 1989; Salomon et al., 2008) that support the production of valuable fished species such as abalone, sea urchins, and, indirectly, spiny lobster. As habitat structure, kelps and other algae provide refuge from predation for adult and young fishes (reviews by Carr and Syms, 2006; Steele and Anderson, 2006), and habitat for predatory fishes to hide in, allowing a greater occupation of the water column of the reef. Early studies (e.g., North and Hubbs, 1968) used scuba to experimentally evaluate the effects of harvesting giant kelp canopies (for chemicals and food) on adult fish and giant kelp populations, and the results were used to inform harvest management. Recent studies are producing recommendations for harvest practices that would minimize impact on the canopy function of nursery for young fishes (M. W. Beck, The Nature Conservancy, personal communication).

Ecosystem-based management of kelp forest systems is also concerned with understanding and predicting how they respond to climate variation, information that can be used to adjust management scenarios to accommodate that variation. Studies using scuba have characterized the response of kelp forests to climatic variation and how these responses vary geographically and over time for both shorter- (e.g., El Niño/La Niña) as well as longer-term (e.g., Pacific Decadal Oscillations [PDO]) changes in oceanographic conditions. For example, long-term monitoring of recruitment dynamics of kelp forest fishes using visual surveys or larval collectors (e.g., light traps, SMURFs [Standard Monitoring Units for the Recruitment of Temperate Reef Fishes]), has been coupled with oceanographic observations and indices (e.g., upwelling indices) to identify conditions that drive temporal and spatial variation in the replenishment of fish populations (e.g., Findlay and Allen, 2002; Carr and Syms, 2006; Caselle et al., 2010a, 2010b). Such knowledge is critical to predictions of year-class strength of fisheries and longer-term changes in the productivity of fishery stocks. Large-scale, long-term surveys of kelp forests have characterized the marked response of kelp forest ecosystems to episodic storm events, including those associated with El Niño and La Niña events (Dayton and Tegner, 1984; Ebeling et al., 1985; Dayton et al., 1992, 1999; Reed et al., 2000), and how the scales of response and recovery vary geographically (Edwards, 2004). Such surveys have also identified how fish assemblages in kelp forests change in response to longer-term oscillations in oceanographic conditions such as the PDO (Holbrook et al., 1997). By explaining variation in population abundance and productivity of entire kelp forest ecosystems, fisheries managers can modify fishing mortality accordingly. These studies also provide insight into how kelp forests and associated fisheries production may respond to impending changes in ocean climate (Carr et al., 2011), as do studies that have capitalized on artificially altered environmental conditions such as warm water discharged into kelp forests by coastal power plants (Schiel et al., 2004).

Key to the success of EBM and the sustainable use of kelp forest resources is the development of management strategies that facilitate ecosystem integrity, productivity, and resilience. One strategy of growing attraction is networks of marine protected areas (MPAs), including marine reserves, designed to protect structural and functional attributes of whole ecosystems. In addition to their conservation potential, ecosystems inside MPA networks provide reference conditions which, when compared with carefully selected, similar ecosystems subjected to human uses (Hamilton et al., 2010), can better identify the ecosystem-wide consequences of those activities. For example, coupled with oceanographic observations, monitoring MPA networks with scuba can distinguish responses of ecosystems to fishing from responses to climatic variation (Carr et al., 2011), a problem that has vexed fisheries management from its inception. One common goal of MPA networks is to preserve biodiversity within and among ecosystems, and knowledge of the geographic variation of kelp forest community structure is critical to ensure that the distribution of MPAs encompasses that variation. Large-scale surveys of kelp forest ecosystems with scuba were used to inform the design of MPA networks developed along the coast of California. These surveys were critical to identifying geographic patterns of ecosystem structure and were used to define "bioregions" with distinct community composition (California MLPA, 2009). Marine protected area networks were then designed to ensure protection of replicate areas of key habitat in each "bioregion," thereby ensuring protection of the diversity of community or ecosystem types across the network.

Scuba studies along the California coast (Figure 6) have played a critical role in informing the size and spacing of MPAs, and fisheries management in general by facilitating observational and telemetric studies of fish movement. Scuba greatly enhances the deployment and maintenance of telemetry equipment, and the collection, return, and supplemental observation of tagged fishes. The data allow scientists to determine the home range sizes of important fish species targeted by fishing, which are used as a guideline to determine the minimum size of individual MPAs. Likewise, quantitative relationships between species diversity and habitat area generated from surveys with scuba are used to determine the MPA size necessary to include substantial portions of the biodiversity present in a given region (California MLPA, 2009).

Functioning MPA networks require population connectivity through larval dispersal of the species they protect, so spacing MPAs at distances within the range of larval dispersal enhances replenishment between adjacent MPAs and to habitats between MPAs to help replenish fished populations. Collection of recently settled fish larvae with hand nets (e.g., BINCKE [Benthic Ichthyo-fauna Net for Coral/Kelp Environments] nets; Anderson and Carr, 1998) and larval collectors (e.g., SMURFs; Ammann, 2004) facilitates estimates of larval durations derived from counting daily increment formation in otoliths (ear bones of fishes). These larval duration estimates have been used in conjunction with ocean circulation models to estimate dispersal distances to inform the spacing of MPAs in a network.

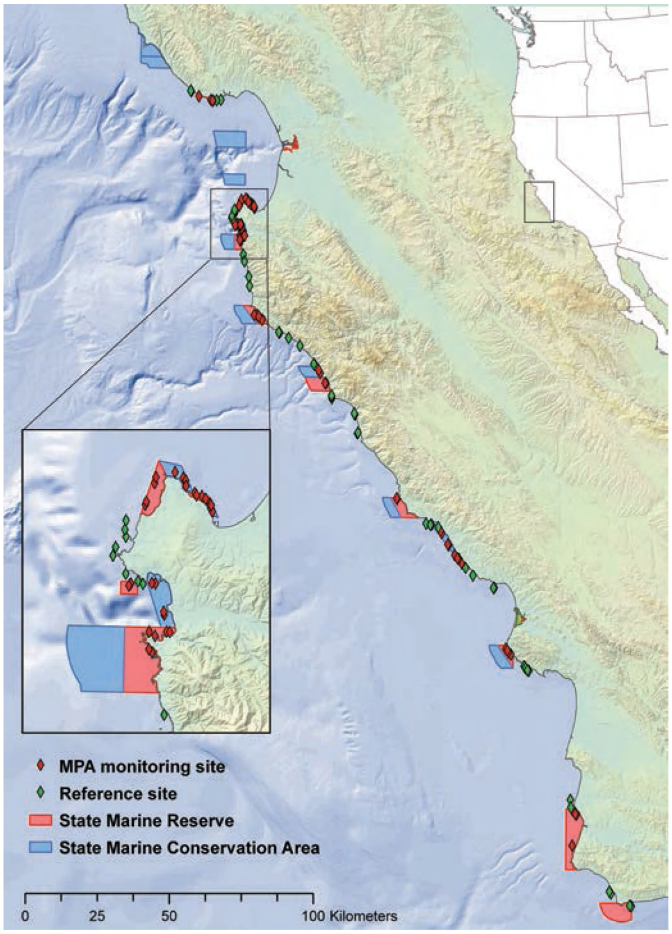

FIGURE 6. Map of marine protected areas (MPAs) on the coast of central California between Monterey Bay and Point Conception. Monitoring sites surveyed to evaluate responses of kelp forest–associated species are indicated inside (red diamonds) and outside (green diamonds) of individual MPAs.

Diving surveys play a critical role in monitoring MPAs and evaluating how effective they are in protecting kelp forest ecosystems (Figure 6), and have been used to identify population and ecosystem responses to MPAs in California (e.g., Hamilton et al., 2010) and elsewhere (e.g., Ling et al., 2009). However, it is all too often lost on management agencies and policy makers that these MPA monitoring programs produce information of far wider-ranging application. Comparison of changes in abundance of species inside and outside MPAs has allowed the discovery of important species interactions, functional roles of species, and species' responses to fishing effects (Babcock et al., 1999; Shears and Babcock, 2002, 2003; Barrett et al., 2009). As such, monitoring studies for MPA evaluation simultaneously provide the information necessary to identify the ecosystem-wide effects of fishing, a fundamental objective of EBM as mentioned above. Moreover, recent studies have demonstrated how scuba surveys can produce more precise and comprehensive descriptions of fish assemblages than fishery-based sampling methods alone (hook and line, traps, etc.), thereby better identifying the local changes in fish assemblages in response to fishing (Starr et al., 2010). Scuba surveys in and out of MPAs can also produce better estimates of the trends in fishery stocks associated with kelp forests than can be gleaned from fishery-dependent data alone, which are often confounded by serial depletion (i.e., by serially sampling populations in previously unfished locations, no evidence of overharvesting is detected; Schroeter et al., 2001). The insights gained from such an approach have been clearly shown by Ling et al. (2009), who unraveled complex relationships between ocean warming, sea urchin dispersal and abundance, kelp forest dynamics, abalone abundance, and lobster fishing. This ecosystem-based study led to the recognition of the important function of large lobsters in Tasmanian kelp forest ecosystems altered by climate change.

CONCLUSIONS

The use of scuba as a research tool in the USA has its holdfast in the giant kelp forests of California. The above discussions cover only a few of the past and present uses of scuba but clearly show it has been and will continue to be an indispensable tool for scientists, conservationists, and resource managers. In addition to scuba and the accessory research tools and techniques for use with it, there have been significant advances in and deployment of satellite and in situ systems that can record a variety of relevant oceanographic phenomena (and often require scuba diving for placement and maintenance). The implementation and integration of these ocean-observing systems, MPA networks, and long-term monitoring studies provides unprecedented opportunities (Carr et al., 2010). Never before have such valuable tools been available to explore kelp forest ecosystems. The knowledge gained from their exploration informs conservation efforts, ensuring that humans continue to benefit from these fascinating and valuable ecosystems but do not impair their integrity, biodiversity, productivity, and resilience. Moreover, scuba allows scientists to observe obscure biological phenomena and interactions among species in a formerly inaccessible world, reviving the ability for people to follow their curiosity into understanding both intricate details and a grander perspective on how our world functions as a whole.

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Kelpbeds As Classrooms: Perspectives and Lessons Learned

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ABSTRACT. Field courses using scuba allow university students to experience kelp forests and other shallow, subtidal ecosystems. They are unusually effective for instilling essential scientific values: an appreciation of natural history and an enhanced ability to ask meaningful questions and think holistically. After teaching such courses at six institutions over the past 40 years, we discovered common aspects in how our students developed; how the courses were taught; issues of logistics and safety; and the regulatory obstacles we had to overcome. We highlight the opportunities and the need for getting more students into observing natural history through such field courses, thereby enabling them to better grasp and address the looming crises of the world's ecosystems that support the human population.

INTRODUCTION

Natural history—the description and study of organisms and natural objects, generally using observational approaches—has been the bedrock of science since Aristotle. Although the discipline was largely ignored during the medieval period, it was resurrected during the Renaissance in Europe (Rudwick, 2005; Holmes, 2008), which in turn led to Darwin's biological revolution in the mid-nineteenth century. Subsequent technological and laboratory successes and experimentation in science steadily eroded the prominence of natural history and observational science in much of the twentieth century, even though understanding the natural history of systems has remained the cornerstone of ecological work (Bartholomew, 1986). Now, in the first decade of the twenty-first century, it is clear that an understanding of natural history is essential for understanding and responding to the multiple anthropogenic environmental crises that are appearing all around us (Dayton and Sala, 2001; Sagarin, 2008).

Instilling an appreciation of natural history and the accompanying sense of wonder of the natural world in the next generation of students and teachers is challenging. Science is not simply a collection of facts, but a search for mechanistic understanding of patterns. However, the development of subdisciplines in science has led to a decline in the thrill of observing and learning from natural objects and processes—the essential nature of science that is both tentative and creative (Bickmore et al., 2009). For ecology, these losses and difficulties are associated with a society that has become increasingly urbanized, with individuals spending less time in nature (Pergams and Zaradic, 2008). Unfortunately, in

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many institutions students are no longer trained in the fundamentals of natural history, which underpin a more holistic view of nature, so it is difficult to find people able to mentor subsequent generations of students about the natural world.

Much current teaching of biology is based on theoretical constructs of mathematical theory and model systems. The ability to translate these perspectives to the real world, with its complexity and inherent variability, let alone validate model predictions, requires embedded field experience in order to develop functional cognitive pattern recognition. Experience in the field, or natural settings and environments, effectively juxtaposes academic constructs with the realities of the natural world that we hope to better understand, protect, and, in some cases, restore. Yet from our experience, and those of our colleagues, neglecting field courses is not only an impediment to teaching how ecosystems function, but also imposes severe restrictions on the potential to recruit and excite young scientists. We need to develop the cognitive abilities in students to intuitively visualize patterns in nature, which in turn open new directions to explore. It is through many hours of observing species, community patterns, and their natural settings that our minds can develop the skill to address and understand complex interactions between species and their environments.

Observing nature and creating stories that can be continuously refined and clarified with subsequent observations is the heart of science (Grobstein, 2005). The process is intrinsic in children as they become cognizant of their world, but all too often vanishes as people age. An appreciation of natural history fans the flame of curiosity throughout a person's life, benefiting him or herself but also society in general by providing context for a coherent, rational, and nature-based world view. Indeed, research has shown that there is a positive correlation between experience with nature and support for legislation on environmental issues (Zaradic et al., 2009).

A lifelong appreciation of natural history can be developed and promoted in students through field courses in which they conduct structured and meaningful observations of their world. Among such courses is one simply called Field Quarter, which has been taught for many years at the University of California, Santa Cruz (UCSC; Norris, 2010). Such courses, however, because they are difficult and expensive to conduct and are sometimes viewed as extraneous by other academics, appear to have been increasingly eliminated from college curricula. Despite such barriers, there are strong arguments for supporting natural history at the university level (Dayton, 2003), both in the curriculum and in the enterprises of research.

The authors of the present paper have successfully taught such field-oriented, natural history–based courses in a variety of habitats, including subtidal temperate kelp forests. Accordingly, our paper summarizes our field courses in kelp forest ecology: how they were developed over the past 40 years, their strengths and problems, how they advanced our knowledge of subtidal (kelp forest) ecology, and what they offer to students and education. Most importantly, we explore how scuba has facilitated these advances and the opportunities for and ability of researchers and students to personally experience one of the most productive and species-rich ecosystems on Earth.

A BRIEF HISTORY

In his pioneering work in kelp forest ecology, Wheeler J. North (Foster et al., this volume) employed undergraduates from the California Institute of Technology to assist in his summer research. Although students were not part of a formal course, they were taught to use scuba and conducted directed underwater research in kelp forests, providing North with information that was otherwise nearly unattainable. At the same time, in the 1960s, faculty at Stanford University's Hopkins Marine Station (HMS) developed a very successful one-quarter "Spring Class" that involved directed student research in the rocky intertidal, both providing students with rich field experiences and generating basic information of that marine habitat (Abbott et al., 1968).A diversity of scuba-based field courses eventually radiated along the U.S. west coast and into New England (Table 1). Most of us were inspired by these approaches that engaged students in the field while generating data.

Complementary field courses at UCSC involving scuba are now alternately taught in other locations (e.g., Gulf of California, Moorea, Corsica). Foster likewise alternated his kelp forest ecology class in later years with a similar field course taught in rhodolith beds in the Gulf of California, which is also now taught by Steller and various Moss Landing Marine Laboratories (MLML) faculty (Foster et al., 2007).

Although there are other courses at other institutions that introduce students to the subtidal environment using scuba, especially in tropical settings, this essay describes courses taught in temperate, subtidal environments by the contributing authors. By combining our collective experiences and perspectives gleaned from teaching similar courses at different institutions and with different sets of species, we provide an overview of the value and challenges of such courses for bringing natural history perspectives to students.

GENERAL COURSE STRUCTURE AND APPROACHES

The students in our courses are generally upper-division undergraduates (e.g., University of California Santa Cruz [UCSC], Hopkins Marine Station [HMS], Shoals Marine Laboratory [SML], Friday Harbor Laboratories [FHL], University of Alaska Fairbanks [UAF]) and beginning graduate students (e.g., Moss Landing Marine Laboratories [MLML], UCSC, and UAF). Their backgrounds vary, but many students, and more so in recent times, have had little exposure to organismal biology or doing any kind of science, except for those at MLML. Despite this inexperience, we encourage highly motivated students, even those

TABLE 1. Chronology of the radiation of scuba-based kelp forest courses in the United States.

Course titles	Institution	When offered	Instructors
Special Projects; Biology for Divers; Subtidal Communities; Ecology and Conservation of Kelp Forest Communities	Stanford University, Hopkins Marine Station (HMS)	1971 to present	John Pearse, Charles Baxter, Steve Webster, James Watanabe, David Schiel, Michael Foster
Neritic Ecology; Kelp Forest Ecology	University of California, Santa Cruz (UCSC)	1972 to present	John Pearse, Baldo Marinovic, Giacomo Bernardi, Peter Raimondi, Mark Carr
Advanced Methods in Underwater Research	University of Southern California, Wrigley Marine Science Center on Catalina Island	1970s (no longer taught)	Robert R. Given and Andrew A. Pilmanis
Subtidal Ecology	California State universities, Moss Landing Marine Laboratories (MLML)	1978 to present	Michael Foster, Michael Graham, Diana Steller, Scott Hamilton
Underwater Research	Cornell University/University of New Hampshire, Shoals Marine Laboratory (SML)	Late 1970s to present	Larry Harris, James Coyer, Jon Witman, Phil Levin, Jon Grabowski, Deb Robertson, Elizabeth Siddon
Kelp Forest Ecology; Field Studies in Subtidal Ecology	University of Alaska Fairbanks (UAF)	2000 to present	Brenda Konar
Research Apprenticeship Program; Scientific Diving	University of Washington, Friday Harbor Laboratories (FHL)	2009 to 2010 (*Research Apprenticeship Program*); 2010 to present (*Scientific Diving*)	David Duggins, Kevin Britton-Simmons, Pema Kitaeff

who have little or no background in biology or even in science, to enroll in these courses. Even though they lack the background of some students, most students currently enrolling in our courses are highly motivated, this being almost a requirement because the courses tend to be physically and mentally demanding. Our collective experiences highlight many examples of students with little background in science being among the best students, with some of them changing fields to pursue degrees in biology/science.

Regardless of institutional affiliation and field locations, our courses are similar in that they place an initial emphasis on (1) familiarity with the local flora and fauna, (2) concepts of scientific research in general (observing, recording, generating hypotheses, experimenting, analyzing, and interpreting), (3) fundamental ecology and natural history, and (4) practices for safely conducting research under water. The natural history of the species in the kelp forest was the main objective of Pearse's first few classes; students were assigned different groups of organisms to learn about and document in order to develop a good annotated list of the species in the Hopkins Marine Life Refuge (Pearse and Lowry, 1974). An annotated list was used for many years as a central teaching tool in the UCSC course, and updated web versions are now used by the classes at both UCSC (http://bio.classes.ucsc.edu/biol161/) and HMS (http://seanet.stanford.edu/).

Similarly, the first few years of the course at SML had students conducting replicated underwater transects to gauge spatial and temporal patterns of abundance of species present, and that database has been used in subsequent years. At MLML, a collection of photos of common organisms has been assembled and annotated to help students get to know what they are observing under water. Moreover, a select set of original papers is provided to show students what has been done (e.g., Foster and Schiel, 1985). All of these teaching aids and references are now made available to students at course web sites.

The diving conducted in the summer course now taught by Watanabe at HMS is augmented by lectures covering organismal, population, and community ecology. Concepts of physiology, biomechanics, population regulation, competition, predation, and disturbance are made tangible and relevant by what the students see while diving. Instruction on sampling methods and basic statistics are integrated with data collected for a growing set of time series that document the abundance of sea stars, abalones, and an invasive bryozoan. These data are invaluable for demonstrating the year-to-year variation seen in kelp forests

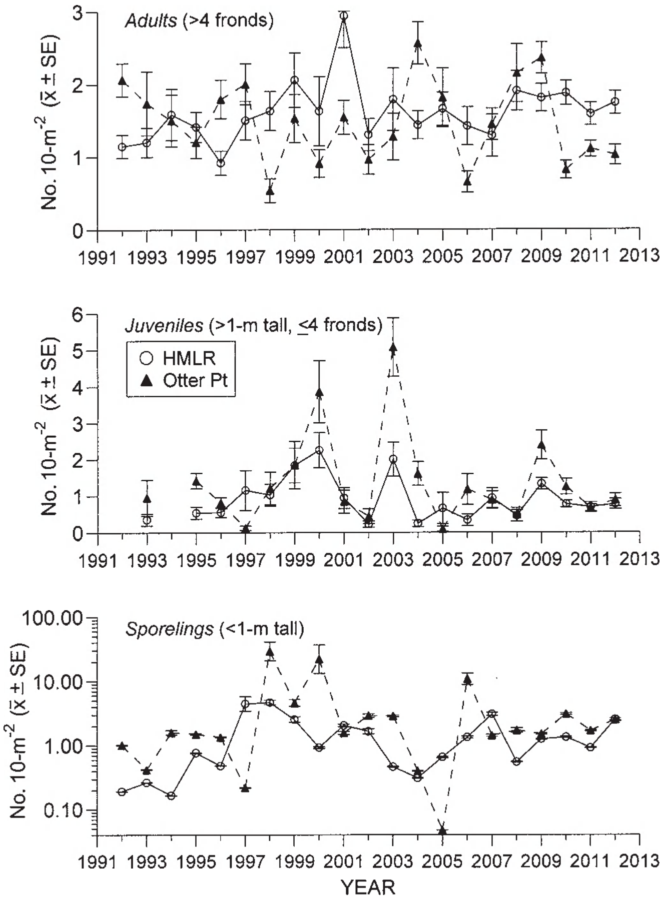

FIGURE 1. Abundance of giant kelp *Macrocystis pyrifera* collected yearly (usually in early July) by J. Watanabe's kelp forest ecology summer course at Hopkins Marine Station. Populations are sampled at two sites in southern Monterey Bay, California: Hopkins Marine Station within a fully protected state marine reserve (36°37′N, 121°54′W), and Otter Point within a state marine conservation area that allows recreational fishing and kelp harvesting (36°38′N, 121°55′W). Data are from either 10 m^2 circular plots or 10×2 m transects placed randomly within each site; values have all been standardized to number (No.) per 10 m^2. Sample sizes range from 20 to >50 for each year. Plants <1 m tall are sporelings, those >1 m tall but with 4 or fewer fronds are juveniles, and all other plants are considered adults (J. Watanabe, unpublished data).

(Figure 1). The course ends with an emphasis on conservation issues, which is particularly appropriate at HMS, the site of one of the oldest marine protected areas in the country.

A major portion of the courses taught at UCSC, MLML, UAF, and FHL is devoted to directed projects involving sampling and experiments that are pursued by individual or small groups of students and culminate in both written and oral reports. Some students from these courses present their reports in talks and posters at local and national scientific meetings. At UCSC, with a quarter-long course, and at MLML and UAF, with semester-long courses, students are responsible for project development: they find and digest original papers relevant for their proposed research, identify questions and goals, and design sampling and analysis protocols. Experiments are encouraged where appropriate and feasible. While the much shorter duration summer course at UAF also has projects and reports, the summer courses at SML and FHL preclude detailed projects. Instead, SML students individually collect preliminary results, which are then integrated into a formal research proposal that forms an essential component of the course. Project proposals are developed after initial exploratory dives, which are critical for getting students to ask questions based on their own field observations combined with guidance from relevant literature. Using exploratory dives, SML students compile a list of 20 questions that are of personal interest. The five best questions are presented before the entire class, with the resulting discussion invariably helping to formulate one of the questions into the student's project proposal. The proposal format allows students to creatively extrapolate project design beyond the course's two-week limitation. Friday Harbor Laboratories has an apprenticeship model for student project activities that groups a small number of undergraduate researchers with an active research project, and relies less on a classic lecture–lab format than on a mentor–apprentice structure based on a specific research question.

Projects as a pedagogical tool give students first-hand exposure to actively engaging in creative science and developing questions through direct observations. This teaches them to develop a hypothesis and then design and carry out manipulations, experiments, data analyses, and further observations to test that hypothesis. It is important, of course, for the students to realize that answers are rarely definitive in science, especially those obtained during courses only 2–15 weeks in duration. In short-term student projects, there is always some concern about data quality, so alert instructors and teaching assistants are essential for helping to provide quality control.

Some student projects from our classes have been published nearly as completed in the class (e.g., Lowry and Pearse, 1973; Towle and Pearse, 1973; Lowry et al., 1974; Aris et al., 1982; Foster et al., 2007); others have led to senior theses at UCSC and published master's theses at MLML and UAF (Reed and Foster, 1984; Singer, 1985; Hoelzer, 1988; Hymanson et al., 1990; Carr, 1991; Konar and Foster, 1992; Konar, 1993; Leonard, 1994; Edwards, 1998; Clark et al., 2004, Brewer and Konar, 2005; Chenelot and Konar, 2007; Hamilton and Konar, 2007; Daly and Konar, 2008, 2010). Some have contributed useful data to other papers (e.g., Hines and Pearse, 1982; Harrold and Pearse, 1987; Pearse and Hines, 1987; Watanabe and Harrold, 1991; Figure 2). At FHL, the 2009 Subtidal Ecology Apprenticeship class generated much of the preliminary data used for a successful NSF proposal on the fate of kelp detritus. Other student projects in our courses have facilitated successful NSF Graduate Research Fellowships. Additionally, the SML course led to production of

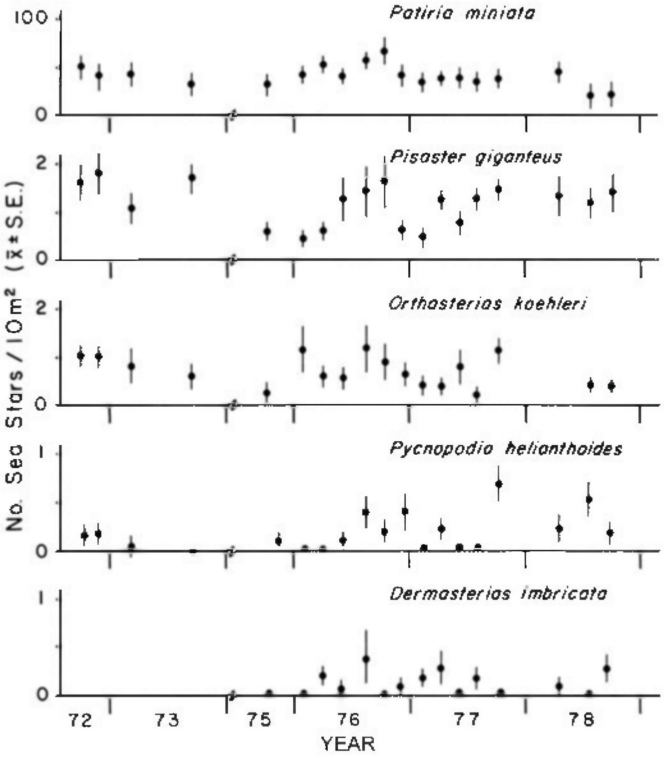

FIGURE 2. Densities of five species of asteroids in the Hopkins Marine Life Refuge, Pacific Grove, California. Densities were determined by counting all individuals within 10–21 circular plots, each 10 m^2, located at random in a 1600 m^2 study area. The data for the fall of 1973, 1975, and 1977 were taken by students who were in the kelp forest ecology class of the University of California, Santa Cruz; much of the other data were taken by students who followed the class with independent study or by assisting the researchers. From Pearse and Hines (1987).

The Underwater Catalog (Coyer et al., 2011), a techniques guide for subtidal research that is now used in many classes.

Regardless of which career path students follow after completing our classes, it is our conviction that they are enriched by experiencing field courses such as those mentioned here on kelp forest ecology, and society in general benefits by having these graduates dispersed throughout academics, business, politics, and indeed all walks of life.

THE DISTINCTIVE NATURE OF KELP FOREST ECOLOGY COURSES

Although similar to many other field courses that include a focused, independent research module, our courses in kelp forest and subtidal ecology feature distinctive aspects with the potential to make them more effective in giving students a full appreciation of natural history and ecological research. To begin with, scuba diving is a challenging and exciting endeavor for students. By having a course using scuba as a tool for conducting research, we have a magnet for recruiting motivated students yearning for something different. This is particularly true in areas such as Alaska, where the diving is taken to an even more challenging level, requiring drysuits and other tools for cold water. To students arriving from noncoastal states, the nearshore subtidal environment is literally another world, but even students raised in view of (and in some cases on and in) the oceans find the subtidal world to be very engaging. To both sets of students, in-depth exploration of life history characteristics and/or different forms of organisms can present a whole new world of discovery, setting the stage for fresh perspectives. To use a contemporary example, the experience is quite similar to the effect of the uniqueness and beauty of Pandora in the movie *Avatar*, which captured the imagination of a large and diverse audience. Discussions in our classes of the magnitude and implications of the differences between marine and terrestrial ecosystems with regards to evolutionary and ecological processes as well as approaches for conservation and management (e.g., Carr et al., 2003; Shurin et al., 2006) reinforce and build upon student impressions from their experiences in the field. For any of us, whether a beginning student or experienced marine researcher, focusing on a small copepod while we are suspended in a visually infinite body of water is a moving and profound experience. Peering at the world through the confines of a facemask while swimming close to the bottom brings a focus not experienced on land, where it is easy to be distracted in many different directions.

There is no substitute for seeing organisms up close and personal in their habitat, rather than in drawings, photos, videos, or movies. Observing organisms in their habitat is three dimensional, whereas the other depictions are two dimensional. In the Monterey area, for example, sea urchins and abalones are tucked away in crevices, holding and munching on pieces of kelp, while broken shells litter the bottom in evidence of sea otter predation on those same urchin and abalone species. Kelp crabs and snails move about and graze on the kelp, and their predators, rock fishes and sea stars, are conspicuous on the bottom. There are also all of those strange, sessile, suspension feeders, some overgrowing others, suggesting severe competition for space. The total picture cannot be perceived by looking at two dimensional representations such as photos or videos. Only by literally being there and experiencing three-dimensional space can the entirety of the interactions be appreciated, which then leads to the creative endeavor of posing questions, hypotheses, experiments, and generalizations. Even statistics become palatable to students when framed with kelp-forest denizens and the opportunity to design a small study that includes collecting their own data.

Moreover, kelp forests and similar nearshore communities are extremely dynamic. Kelps grow rapidly, but then entire beds can be removed almost overnight by storms. Evidence of change and turnover are often conspicuous from one dive to the next. In addition, dramatic changes can also take place over the years, and time-series datasets to which each new cohort of students contributes connect the relatively brief contact each student has with a longer-term temporal component of the kelp forest. For example, at SML the nearshore community has changed from lush kelp forests to sea urchin barrens to meadows of an invasive green alga (*Codium fragile*) then back to lush kelp forests and now (2013) to extensive beds of an invasive red alga (*Heterosiphonia japonica*) within the past 33 years. Invasive species are common in the Gulf of Maine and synergistic interactions between two invasive species, *Codium fragile* and the invasive bryozoan *Membranipora membranacea*, shaped the entire community. In the Monterey Bay area, we have seen the kelp forest recover after being almost stripped from the bottom by storms or sea urchin grazing. In Kachemak Bay, Alaska, canopy-forming kelps have alternated between *Nereocystis luetkeana* and *Eualaria fistulosa* over the last 30+ years for as yet unknown reasons. Also in Kachemak Bay, the small gastropod *Lacuna vincta* can overgraze kelp beds, leaving the same destruction as sea urchins elsewhere. Consequently, kelp forest systems, regardless of the species of kelp or dominant grazer, are excellent for introducing students to the concept of resiliency, thereby broadening their appreciation of ecosystems beyond the more familiar experience of seasonal changes on land and how humans contribute to changes.

Being completely immersed in kelp beds makes students realize that nature is everywhere, all around them, whether under water or on land. It is not just somewhere else, as seen in those spectacular videos with the never-ending string of superbly filmed but sanitized, digitized, razor-edited, or once-in-a-lifetime shots complete with background music. Students can experience the reality themselves in the gritty, cold, murk under water, and realize that nature is all around them as they rekindle their innate childhood curiosity.

Finally and importantly, most underwater experiences are for the most part intensely private, without conversation or interactions with others, and without distractions such as iPods, cell phones, text messaging, or internet access (Carr, 2010). On the other hand, scuba requires frequent attention to the equipment that allows one to survive the experience, underscoring how well-trained and experienced divers can benefit most from these experiences. Nonetheless, the wonder and solitude ignite the process of thinking, of questioning, and of finding potential answers. Only afterward can the students share their experiences with others in the class. And they often do so with excitement, enthusiasm, and considerable reflection.

CHALLENGES

SAFETY

Most of us have been involved with the development of our institutional diving programs, both through our own research programs and by serving on our institutions' Diving Control Boards. Working with our institutions' Diving Safety Officers and Risk Management Departments, our courses have developed diving safety prerequisites over time that now include diver certification, a complete medical examination, certifications in CPR/First Aid/Emergency Oxygen Administration, standardized swim and scuba practical exams, and possession of appropriate equipment. We are fortunate in having active diving safety programs on our respective campuses that can certify the students, at least as Divers-in-Training, before they take our courses, although many students obtain certification from other sources. In some cases, scientific diving certification through the American Academy of Underwater Sciences (AAUS) guidelines is also necessary, although students who successfully complete the "Underwater Research" course at SML receive a letter of reciprocity and AAUS Scientific Diver status (as long as annual requirements are met). At Friday Harbor, students are required to have logged at least 20 open-water dives and, as at many institutions, take a short rescue diving course or refresher diving course during the first week of their "Subtidal Ecology" course. Furthermore, many programs provide mixed gas (enriched air nitrox) and nitrox certification with additional training.

A key element of our teaching is to do whatever is necessary to safely get students under water so they can begin the process of discovery. This means that we closely watch hesitant (but otherwise enthusiastic) divers and many times accompany them on their initial dives. Our primary goals are safety and "get-into-the-water"—goals that are by no means mutually exclusive.

Diving is usually restricted to depths less than 15 m, always done in buddy pairs, and always under supervision of dive-experienced faculty and teaching assistants (who serve as the lead diver and divemaster). Diving occurs from shore (with a standby boat with additional tanks for emergencies), small boats (inflatable or hard shell), or a dive float (anchored floating platforms with a standby boat) (Figure 3). Dive locations are usually in protected areas with easy access and relatively calm conditions. In nearly 40 years of teaching our courses, involving nearly one thousand students and tens of thousands of dives, very few dive incidents have occurred. The rare accidents (e.g., decompression sickness) occurred while diving within the standard no-decompression limits and were successfully treated in nearby recompression chambers. Other minor incidents include the predictable ear (external and middle) and respiratory (upper and lower) infections. The experience the students gain from diving safely with a group of experienced subtidal instructors and teaching assistants no doubt contributes to their development into safe, confident, and independent underwater researchers.

LOGISTICS

Kelp forest ecology courses are not much different from other field courses that demand logistical preparation beyond the lectures and organized laboratory sessions. Students need to have operable and certified diving equipment available, have transportation to diving field sites, and be able to clean and service their gear after diving. We generally have students take the course at the field site (a marine station), or they are transported

FIGURE 3. Students in their "classrooms." Top: Stanford University's *Ecology and Conservation of Kelp Forest Communities* class at Hopkins Marine Station preparing for a surf entry at Monastery Beach, Carmel Bay (left), and returning in small boats from a dive in the kelp classroom behind them (right) (photos by James M. Watanabe). Bottom: Shoals Marine Laboratory's *Underwater Research* class on their tethered dive float off Appledore Island in the Gulf of Maine (photo by Amy E. Broman).

in university vehicles or drive on their own to the field sites. The latter raises the specter of liability, which needs to be addressed institutionally. We expect the students to provide their own equipment in good working condition (usually with annual safety inspections), although tanks, weights, and/or air fills are often provided. Small boats (Boston Whalers, inflatables, skiffs) are used for conveying students and equipment to and from the dive sites, as well as for safety. At most institutions, instruction on small boat safety and operation are part of the course. Most marine laboratories now have dive lockers or equivalent infrastructure that provide students with dressing rooms, after-dive showers, and areas for cleaning gear and logging dives.

Field courses at remote sites such as those offered by UCSC and MLML in Baja California (Figure 4), Moorea, and Corsica, and by UAF at the Kasitsna Bay Laboratory present additional logistical challenges, but these are more than compensated for by the total immersion and lack of distraction for one to several weeks of almost continuous discussion of projects and observations. Not all of these remote-site courses, of course, focus on kelp forest ecology, but rather on a broader context of shallow subtidal ecology. Such courses can introduce the students to very unfamiliar natural environments, opening eyes and minds to new organisms and ecologies for comparison with kelp forests near their home institutions.

REGULATIONS FOR COLLECTING AND FIELD EXPERIMENTS

State and federal regulations governing coastal ocean activities and impacts have increased dramatically over the past 40 years, even for scientific research and education.

FIGURE 4. Moss Landing Marine Laboratory's *Subtidal Ecology* class at a remote dive site on the shore of the Gulf of California, Baja California, Mexico. (Photo by Michael S. Foster.)

Nongovernmental groups have surged in their activity aimed at increasing public awareness and pushing for additional regulations for environmental protection, resulting in remarkable regional improvements of our ocean environment (e.g., Palumbi and Sotka, 2010). Although we welcome strong regulation of human activities in the ocean along our coasts, as well as on land, and recognize the benefits of protecting the environment for present and future generations, regulation can hamper and constrain our ability to carry out scientific studies and collections. In some cases, the regulatory demands are more than a mere nuisance; they seriously discourage or prevent scientific monitoring, collecting, and experimental manipulations to the extent that areas or species are effectively off limits for science. Restrictions on working with vertebrates (fishes) can be particularly constraining. Regulation needs to be given careful consideration in teaching field courses such as kelp forest ecology, where reasonable and prudent collecting and experimental manipulations are needed to adequately educate future scientists as well as keep a finger on the pulse of community changes in local habitats. It would be particularly good if the regulators themselves better understood science by taking our courses.

Another type of regulation with potential negative impacts on the conduct of our field courses pertains to diver safety and associated liability issues. When the courses discussed in this essay were initiated, there were very few regulations; students received diver certification from a commercial dive shop and provided evidence of passing a standard medical exam. As student numbers increased, concerns about liability also increased, inevitably leading to more and more regulations requiring the need for (and expense of) dive programs and diving safety officers to run the programs at a home institution. In some cases, diver certification courses are also offered. Fortunately, the guidelines currently developed by AAUS strike a reasonable balance between the sometimes conflicting demands of academics and risk management (essential training and exams) so that students are not precluded from obtaining first-hand experience of diving and working within kelp forest ecosystems. We believe it is crucial for this balance to continue and that easy access for training scientific divers is imperative to making subtidal scientific discoveries. Our continued involvement as diving researchers and instructors on the Diving Control Boards of our institutional dive programs greatly assists in maintaining diving access for these introductory courses.

It is important to realize that excessive regulation can and has destroyed research programs. For example, scientific diving is so restricted in parts of the European Union that it would be virtually impossible to offer any of our courses, as regulations regarding standby divers, training, diving medical certifications, and required equipment (among other items) combine to make scientific diving as a course prohibitively expensive. It is no surprise, therefore, that although pioneered in Europe (e.g., Kitching, 1941), the amount of shallow subtidal scientific research now conducted in Europe pales in comparison to what is done in the US. While we all recognize the need for diving regulations, we stress that they need to be reasonable, as reflected in the current level of AAUS regulations and program certifications.

FUTURE CHALLENGES AND RECOMMENDATIONS

There are continual challenges to both justify and offer field courses such as ours in kelp forest ecology. At the same time, the need to develop an awareness and appreciation of natural history in the next generation of students is greater than ever. As our human population grows and is matched in the levels of consumption and exploitation of our environmental resources, more and more of the Earth systems that support us will deteriorate, even the vast and seemingly indestructible oceans (Jackson et al., 2001; Worm et al., 2006; Danson, 2011).

The need for more strategic regulation in the use and harvesting of marine resources based on ecosystem-based management (EBM) is becoming increasingly evident (Ruckelshaus et al., 2008; McLeod and Leslie, 2009; Foster et al., this volume). Major components of EBM are marine protected areas (MPAs), which can be monitored to evaluate the effectiveness of regulating human activities. Such monitoring, and the interpretation of the information collected, demands well-trained personnel. Not only will kelp forest ecology courses help provide such people, but the courses themselves can assist with required monitoring within and outside MPAs. Friday Harbor Laboratories and Hopkins Marine Station, for example, are located within MPAs where no fishing or take of marine life is allowed except for scientific research. The MPA at HMS is bounded on both sides by state marine conservation areas that allow recreational fishing and the harvesting of kelp biomass to feed cultured abalones. Students taking kelp forest ecology classes taught at HMS by UCSC and HMS faculty can monitor fish and kelp populations both inside and outside of the state marine reserve to evaluate the impact of recreational fishing and kelp harvesting (see Figure 1), a win–win scenario for the courses and the regulatory agencies. In addition, UAF's "Subtidal Ecology" course collects data that are loaded into the Ocean Biogeographic Information System (OBIS; http://www.iobis.org/) database, which is publically accessible and allows any user to search distribution of marine species from all of the world's oceans.

The oceans increasingly are considered the last places on this planet with the ample resources needed to support our growing human population. These resources are not just seafood, but also minerals, energy, and even potable water. Students in field courses such as the kelp forest ecology courses noted here should become better-informed citizens, regardless of whether they pursue a career in science. Accordingly, they will form a pool of educated citizens to serve not only as scientists working in laboratories around the world, but also as policy makers, business leaders, and voters who become involved in issues related to our interactions with the natural world. With a better appreciation of all that natural history teaches about complex ecosystems (obtained by participation in field courses), they just might find a way to attain a more balanced approach to human ecology and a steady-state, sustainable future.

CONCLUSIONS

Kelp forest and subtidal ecology courses in which students use scuba and are literally immersed in an ecosystem have been offered successfully and continuously for over 40 years. Students emerge with an appreciation of natural history, the mother lode of science as a way of knowing about the world. There is a strong rationale for teaching university-level field courses: students with such a broadened world view are far better equipped with the critical skills they need, now and in the future, to deal with the multiple crises faced by human populations and the ecosystems that support them.

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Rhodoliths and Rhodolith Beds

Michael S. Foster, Gilberto M. Amado Filho, Nicholas A. Kamenos, Rafael Riosmena-Rodríguez, and Diana L. Steller

ABSTRACT. Rhodolith (maërl) beds, communities dominated by free living coralline algae, are a common feature of subtidal environments worldwide. Well preserved as fossils, they have long been recognized as important carbonate producers and paleoenvironmental indicators. Coralline algae produce growth bands with a morphology and chemistry that record environmental variation. Rhodoliths are hard but often fragile, and growth rates are only on the order of mm/yr. The hard, complex structure of living beds provides habitats for numerous associated species not found on otherwise entirely sedimentary bottoms. Beds are degraded locally by dredging and other anthropogenic disturbances, and recovery is slow. They will likely suffer severe impacts worldwide from the increasing acidity of the ocean. Investigations of rhodolith beds with scuba have enabled precise stratified sampling that has shown the importance of individual rhodoliths as hot spots of diversity. Observations, collections, and experiments by divers have revolutionized taxonomic studies by allowing comprehensive, detailed collection and by showing the large effects of the environment on rhodolith morphology. Facilitated by in situ collection and calibrations, corallines are now contributing to paleoclimatic reconstructions over a broad range of temporal and spatial scales. Beds are particularly abundant in the mesophotic zone of the Brazilian shelf where technical diving has revealed new associations and species. This paper reviews selected past and present research on rhodoliths and rhodolith beds that has been greatly facilitated by the use of scuba.

INTRODUCTION

Relative to other abundant nearshore communities like kelp forests and coral reefs, rhodolith or maërl beds have been little investigated by marine ecologists. Even in clear, shallow water, their lack of vertical structure in the water column makes them difficult to distinguish from entirely soft bottoms. Observed and sampled from the bottom with scuba, however, these purple and pink fields are complex communities formed by aggregations of unattached, nongeniculate (lacking uncalcified joints) coralline algae with individual thalli ranging in size on the order of one to tens of cm and in shape from highly branched twigs and fans to spheres. Live individuals may be stacked a few cm deep, often grading below into dead fragments mixed with carbonate and terrigenous sediment (Figure 1). They provide hard habitat for numerous other marine algae that live on their surfaces, and for invertebrates living on and in the rhodoliths and surrounding sediments (see the "Rhodolith Systems: Communities and Conservation" section in this paper).

There are few descriptive or experimental data to characterize the environmental conditions that lead to rhodolith bed formation and persistence. It does appear that beds are generally found on fairly level bottoms where light is sufficient for growth and water motion and bioturbation are sufficient to prevent burial and anoxia from sedimentation and to move the rhodoliths. High water motion, however, can inhibit bed formation by transporting individuals out of otherwise suitable habitat or causing mechanical

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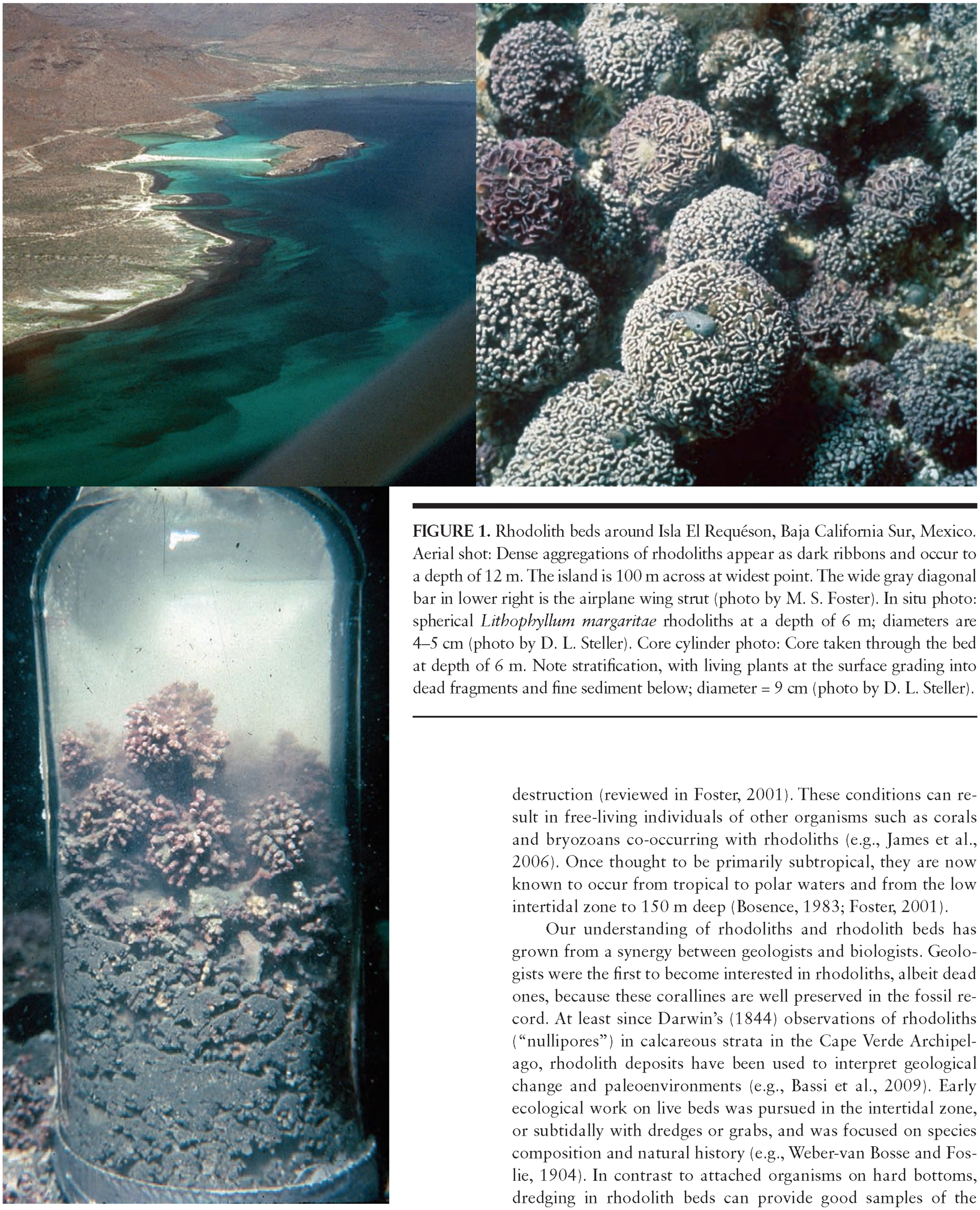

FIGURE 1. Rhodolith beds around Isla El Requéson, Baja California Sur, Mexico. Aerial shot: Dense aggregations of rhodoliths appear as dark ribbons and occur to a depth of 12 m. The island is 100 m across at widest point. The wide gray diagonal bar in lower right is the airplane wing strut (photo by M. S. Foster). In situ photo: spherical *Lithophyllum margaritae* rhodoliths at a depth of 6 m; diameters are 4–5 cm (photo by D. L. Steller). Core cylinder photo: Core taken through the bed at depth of 6 m. Note stratification, with living plants at the surface grading into dead fragments and fine sediment below; diameter = 9 cm (photo by D. L. Steller).

destruction (reviewed in Foster, 2001). These conditions can result in free-living individuals of other organisms such as corals and bryozoans co-occurring with rhodoliths (e.g., James et al., 2006). Once thought to be primarily subtropical, they are now known to occur from tropical to polar waters and from the low intertidal zone to 150 m deep (Bosence, 1983; Foster, 2001).

Our understanding of rhodoliths and rhodolith beds has grown from a synergy between geologists and biologists. Geologists were the first to become interested in rhodoliths, albeit dead ones, because these corallines are well preserved in the fossil record. At least since Darwin's (1844) observations of rhodoliths ("nullipores") in calcareous strata in the Cape Verde Archipelago, rhodolith deposits have been used to interpret geological change and paleoenvironments (e.g., Bassi et al., 2009). Early ecological work on live beds was pursued in the intertidal zone, or subtidally with dredges or grabs, and was focused on species composition and natural history (e.g., Weber-van Bosse and Foslie, 1904). In contrast to attached organisms on hard bottoms, dredging in rhodolith beds can provide good samples of the organisms present. This method is still being used to locate beds and their boundaries (e.g., Foster et al., 1997), especially over large areas where scuba is inefficient and acoustical mapping equipment (e.g., Ehrhold et al., 2006) is not available. Dredging can be effective for species information and mapping, but as in other shallow-water habitats, observation of microhabitat distribution and use, studies of processes, and field experimental manipulations require scuba.

One of the first and the most comprehensive in situ studies on rhodolith systems was by Bosence (1976), a geologist interested in using characteristics of living rhodoliths and rhodolith beds to better interpret fossil deposits. Bosence (1976) carefully mapped rhodolith distribution in a bay in Ireland, and examined the relationships between the environment (especially water motion) and rhodolith species distribution and morphology. He wrote the first review of rhodolith ecology (Bosence, 1983), highlighting the advantages of scuba as a research tool and providing a foundation and stimulus for future studies that now include the full spectrum of ecological topics and approaches, including past and present climate change. Rhodoliths are particularly useful for the latter as they are widely distributed, grow slowly (~mm/yr) and, like temperate trees and hermatypic corals, leave a record of their growth as bands within the thallus (see the "Rhodoliths as Environmental Recorders" section in this paper). Sadly, reduced growth and dissolution caused by future changes in ocean pH and temperature may result in the absence of bands and the decline of rhodolith beds.

A thorough review of rhodoliths and rhodolith bed ecology is beyond the scope of this paper. Instead, each author discusses a current topic in his or her area of interest and expertise: Introduction (MSF), Diving to the Edge of Rhodolith Taxonomy and Evolution (RRR), Rhodolith Communities and Conservation (DLS), Deep Beds in Brazil (GAF), and Rhodoliths as Environmental Recorders (NAK). Investigations of these topics have all been greatly facilitated by the use of scuba. We hope the reader will find the discussions interesting and informative, stimulating further interest in and study and conservation of these tumble weeds of the sea.

DIVING TO THE EDGE OF RHODOLITH SYSTEMATICS AND EVOLUTION

Seaweed distribution and the factors that affect it are key scientific questions; Setchell (1893) clearly understood the importance of temperature limits to the geographic distribution of kelp species and the importance of distribution to systematics. The utility of such information, however, depends on the validity of the species identification and how well collections represent the geographic and depth distributions of species in nature. These problems have been particularly difficult to overcome in coralline red algae (Corallinales, Rhodophyta), and especially with the nongeniculate species that occur as rhodoliths. The characteristics used to classify rhodoliths in the early 1700s could not segregate them from corals or stones (Woelkerling, 1988) and names such as *Lithophyllum* are still in use for both algae and corals (Veron, 1995). After recognizing rhodoliths as calcified, photosynthetic organisms, most investigators thought that species of *Lithophyllum* were characteristic of warm waters and *Lithothamnium* of cold waters (Foslie, 1900). Such relationships were based on sampling and observations from the intertidal zone or on specimens dredged from the shallow subtidal. Distributional knowledge was further compromised by the numerous species that were described based largely on external morphology. For example, investigators like Mikael Foslie described 485 species and varieties (Woelkerling et al., 2005) based primarily on external morphology, at least half of which were rhodolith-forming species.

As a consequence of developments in underwater technology including scuba, other diving methods, and better remote sampling devices, it soon became clear that coralline red algae were abundant, widespread, and often a key component of the ocean floor at depths to nearly 300 m. These developments also dramatically increased extraction of live and dead rhodoliths (maërl) for commercial purposes, an activity that has occurred since the seventeenth century along French and U.K. coasts (Grall and Hall-Spencer, 2003; see the "Rhodolith Systems: Communities and Conservation" section in this paper).

While large rhodolith beds have long been known in the northeast Atlantic, the surge in ocean exploration beginning in the twentieth century revealed the presence of coralline banks in Malaysia (Weber-van Bosse, 1904), the Galapagos (Lemoine, 1930), the eastern Pacific (Dawson 1960a, 1960b), and Brazil, where beds cover hundreds of square km (Kempf, 1970; see the "Deep Beds in Brazil" section in this paper). These explorations were followed by extensive surveys in Brazil (Lavrado, 2006) and around the Hawaiian Islands (Adey et al., 1982). Hundreds of species were described from deeper areas, strongly suggesting that more species would be found as surveys continued. However, these collections were all made by dredging, and the few specimens obtained may not have been representative of local variation. Taxonomic analyses could be biased by describing new species based on a limited number of specimens.

This situation greatly improved in the 1950s when E.Y. Dawson started to use scuba for his research, diving with only mask, fins, tank, regulator, and a very rudimentary buoyancy compensator, with shorts and a shirt for a diving suit (Norris, 2010: figs. 7, 8). Dawson could observe and collect numerous representative specimens under water, including what became *Porolithon castellum* and *Sporolithon pacificum*, the latter a very distinctive species (Dawson, 1960b). The allure of the visual record meant that underwater photography began to be used in the early days of diving. Dawson soon added a camera to his equipment, and his dive partner took one of the first underwater photographs of a coralline alga. Scuba diving quickly became part of the usual collecting approach for many researchers. It was a boon for taxonomists, who need to collect hundreds of individuals for rigorous morphological, anatomical, and now molecular analyses.

As scuba was recognized as an essential tool for marine scientists, scientific diving facilities and training programs, both fixed and portable, were developed around the world. There are a number of excellent examples of the success of such facilities in helping contribute to our knowledge of coralline taxonomy and diversity, including the descriptions of *Tenarea tesselatum* (Littler, 1971) from the tropics and *Ezo eppiyessoense* (Adey et al., 1974) from a temperate region. Scuba investigations continue to discover new and interesting subtidal coralline species, including *Synarthrophyton schielianum* (Woelkerling and Foster, 1989), which has one of the strangest morphologies among the red algae.

In situ ecological studies of rhodolith-forming species began in the 1970s, including the seminal studies of Bosellini and Ginsburg (1971) and Bosence (1976). These studies documented the large effects of the environment, especially variation in water motion, on rhodolith shape and branching characteristics. The results enlightened paleoenvironmental interpretations but also served as a warning to taxonomists that many described rhodolith species might be morphological variants of the same species. For Mediterranean waters, Ballesteros (1988) wrote the first review of rhodolith species using information obtained by diving, and Basso (1998) critically evaluated species boundaries. Taxonomic evaluations based on scuba collections using research stations in the western Pacific were done by Verheij (1993) in Indonesia and Ballesteros and Afonso-Carrillo (1995) in the Indo-Pacific. In the eastern Pacific, the diving study of Steller and Foster (1995) further showed the influence of the environment on rhodolith morphology. This environmentally induced morphological plasticity (Figure 2) obscured the real taxonomic boundaries used for the species until detailed anatomical work was done (Riosmena-Rodríguez et

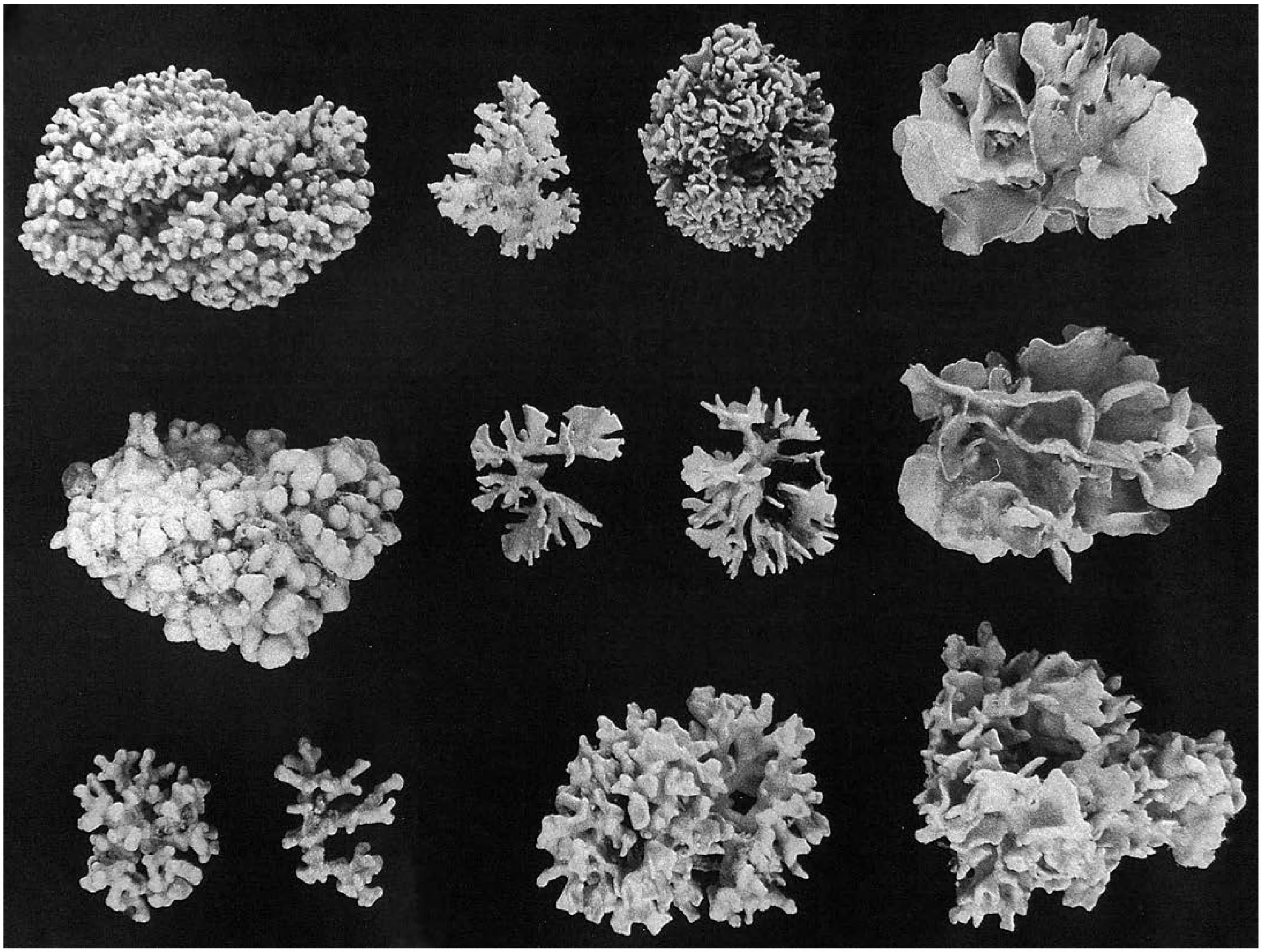

FIGURE 2. Growth-form variation in the rhodolith *Lithophyllum margaritae* from the Gulf of California. The small rhodolith in lower left corner is 1.5 cm wide. From Riosmena-Rodríguez et al., 1999.

al., 1999). Additional genetic information from Schaeffer et al. (2002) has shown that some isolation occurs among populations. New descriptions and studies of rhodolith beds (e.g., Harvey et al., 2005; Konar et al., 2006) and collections and species analyses of the rhodoliths found are helping to refine our understanding of growth forms, species, and species distributions.

Rhodolith beds are distributed worldwide but a thorough bathymetric evaluation has not been produced at the global scale. Harvey and Woelkerling (2007) did an excellent review of the rhodolith-forming species in the coralline algae, concluding that there are 8 genera and 71 species cited in modern studies. Most of the records in this review came from dredging, not scuba collection, again suggesting that more of the latter is needed to clarify the boundaries between species. New technologies for working under water, along with the traditional methods of ocean exploration, provide very exciting opportunities that will contribute to understanding the evolutionary history of rhodolith-forming species via comparisons of subtidal findings with the geological record of well-preserved coralline red algae.

Collections using scuba diving and/or remotely operated underwater vehicles (ROVs) have already provided new records and evolutionary insights based on research occurring around the world (e.g., Brazilian continental shelf, Farias et al., 2010, and Bahia et al., 2011; Galician estuaries, Peña et al., 2011; Gulf of California, Riosmena-Rodríguez et al., 2010). In the future, it might be particularly interesting to examine very old fossil deposits along the coast of the Bahamas where Littler et al. (1985) described the deepest known plant life, a coralline alga. Coralline algae originated in the Cambrian (Woelkerling, 1988) and are one of the oldest clades in red algae. New studies will likely change our current views on rhodolith taxonomy and systematics due to probable discoveries of presently unknown evolutionary clades.

The current challenge with regard to rhodolith systematic biology is to use information from field collections in combination with genetic analyses to better resolve species and answer evolutionary questions. This needs to involve the use of nuclear, chloroplast, and mitochondrial genes to delimit the number of clades among rhodoliths. These genetic approaches, combined with correlations between molecular clock and isotopic ages from carbonate deposits, should allow the construction of a model based on evolution and development (EVO DEVO), as suggested by Aguirre et al. (2010). The origins and development of rhodolith deposits can also be explored using mitochondrial genes to determine the origins of populations and the relative importance to bed persistence of fragmentation versus recruitment from spores. This is the edge of taxonomy and evolution, and scuba will therefore continue to be essential to advances.

RHODOLITH SYSTEMS: COMMUNITIES AND CONSERVATION

Individual rhodoliths, or "nodules," can form intricately branched structures, and large aggregations of nodules form beds, complex biogenic matrices of hard branches that create numerous interstitial spaces. Beds typically form as a living layer on top of an otherwise sedimentary bottom (Figure 1) and harbor a diverse and often unique assemblage of associated species (Cabioch, 1969; Keegan, 1974). In addition to being considered biodiversity hot spots, rhodolith beds are also settlement sites and nursery grounds for important commercial species. Fleshy macroalgae are found on the rhodolith surfaces; invertebrates are found among or bored into rhodolith branches (cryptofauna), moving over and among the rhodoliths, or burrowed into underlying sediments (infauna) (Grall and Glemarec, 1997; Steller et al., 2003). Burrowing fish add further benthic complexity, making these habitats rich sites for ecological exploration.

Rhodolith beds are generally more species rich and support higher population densities than adjacent sedimentary habitats (Birkett et al., 1998; Steller et al., 2003). For example, stratified sampling of subhabitats in a rhodolith bed and a sand flat found richness to be 1.7 times, and total abundance 900 times, greater in a rhodolith bed than in adjacent non-rhodolith habitat (Steller et al., 2003). This has been attributed to the higher number of available niches in rhodoliths relative to sand. Beds support complex food webs of predators, suspension feeders, detritivores, and micrograzers in the eastern Atlantic (Grall et al., 2006).

Early studies using scuba were largely devoted to determining the distribution of rhodoliths and associated species (Keegan, 1974; Bosence, 1979), and such studies encouraged the development of diver-operated sampling devices such as suction dredges to more precisely sample soft-bottom species (Keegan and Konnecker, 1973). This ecological community research continues as new beds are discovered and explored, and many recent studies have shifted their focus to understanding the mechanisms underlying ecological relationships, reflecting the evolution of ecological research as well as changes in research methods. Traditional ship-based benthic sampling with dredges and grabs has been useful in establishing general patterns of distribution and diversity. Combining this type of sampling with scuba allows for (1) efficient visual surveys of large areas, (2) more precise habitat sampling, (3) enhanced detection of rare, seasonal, and fragile associated species and species interactions, and (4) in situ environmental measurements and experimental manipulations. As a result, surveys worldwide now report that the greatest contributors to high richness and abundance are cryptofauna (primarily arthropods, annelids, and cnidarians) that increase as live cover and rhodolith size and branching increases. Such microhabitat associations can be obscured or eliminated in homogenized samples from dredges, grabs, and cores.

Large-scale studies comparing species in rhodolith beds to those in entirely sedimentary habitats have measured species diversity of either the entire community or a dominant group of organisms. In general, higher diversity and abundance of a community (Grall et al., 2006), or of specific invertebrate groups (e.g., polychaetes; Figueiredo et al., 2007), has been correlated with higher density and cover of live rhodoliths and more complex habitat. This pattern is not consistent for all species; infauna such as soft-sediment meiofaunal bivalves can be more diverse on dead (versus live) rhodolith substrate (Jackson et al., 2004).

When rhodoliths grow as distinct, densely branched, spherical individuals (Figure 2) rather than mats of intertwined, jacklike structures, the richness and abundance of species in and on them increases with rhodolith size, branching, and available space (Steller et al., 2003; Hinojosa-Arango and Riosmena-Rodríguez, 2004; Foster et al., 2007). Elucidating such relationships requires using scuba to carefully collect individual specimens, followed by proper fixation and careful dissection. Such studies have shown that 2–6 cm–diameter, highly branched *Lithophyllum margaritae* and 5–9 cm–diameter, knobby, branched *Lithothamnion muellerii* from the Gulf of California can harbor 10–90 cryptofaunal species per rhodolith, with more species in larger individuals. Rhodolith densities can beupwards of 5,000–10,000 m^{-2} (D. Steller, personal observation), resulting in exceptionally high cryptofaunal abundance. The most abundant taxa often include crustaceans, polychaetes, ophiuroids, and mollusks. Collectively, these findings support the notion that large, old individuals act as "old-growth rhodoliths," and are inhabited by species such as stomatopods and burrowing clams not found on and in smaller rhodoliths (Foster et al., 2007).

Diving studies have also revealed rare and new species, and some unique and interesting ecological relationships. Eight species of small (2–10 mm) cryptofaunal chitons were collected from between the branches of *Lithophyllum margaritae* in the Gulf of California, four of which were previously undescribed (Clark, 2000). Reports of complex, fragile nests built by the mollusk *Limaria hians*, a gaping file shell, came from in situ observations (Hall-Spencer et al., 2003). Macroinvertebrates such as the urchin *Toxopneustes roseus* can cover themselves with rhodoliths and also prefer to eat them rather than fleshy algae (James, 2000). The burrowing crustacean *Upogebia deltaura* creates extensive burrows among the rhodoliths that can withstand disturbance (Hall-Spencer and Atkinson, 1999). Such investigations are still few but the use of standardized scuba-enabled subtidal sampling designs and methods (Steller et al., 2007) promises to reveal more new species, as well as ecological and biogeographic insights.

The productivity of rhodolith beds is enhanced by a diverse associated flora that grows on the hard substrata they provide (Jacquotte, 1962; Grall et al., 2006), and some algal species appear to be confined to rhodolith habitat (Leliaert et al., 2009). The associated flora often changes seasonally, as well as with depth. These changes are correlated with variation in rhodolith characteristics such as cover, depth, and the amount of live material. The changes are also correlated with changing oceanographic conditions, such as water motion, which can turn and roll rhodoliths, as well as temperature (Cabioch, 1969; Lieberman et al., 1979; Hily et al., 1992; Birkett et al., 1998; Steller et al., 2003; Amado-Filho et al., 2007; Riul et al., 2009; Peña and Barbara, 2010). In a subtropical Gulf of California bed, Steller et al. (2003) reported up to thirty common macroalgal species in winter, but a maximum of eight species in summer. Year-long sampling at 1½-month intervals has shown similar large seasonal changes in the flora of a European Atlantic bed, as well as relationships between these changes and the depth of the living rhodolith layer and the live/dead rhodolith ratio (Peña and Barbara, 2010).

Qualitative in situ observations in the Gulf of California and elsewhere suggest that the diversity of large fishes in the water column above rhodolith beds is generally low, probably because there is little structure above the bottom. Reports of numerous associated water column fishes (e.g., Aburto-Oropeza and Balart, 2001) are likely an artifact of the beds being in close proximity to reefs that provide macrostructure. Numerous cryptic demersal, benthic, and/or burrowing species such as gobies and blennies are found on, in, and among rhodoliths, and juveniles of species such as cod have been reported to use rhodolith beds as feeding areas (Hall-Spencer et al., 2003). Large, bottom-dwelling or burrowing species can be quite common, including sheephead (*Semicossyphus pulcher*) in California, and tiger snake eels (*Myrichthys maculosus*), bullseye electric (*Diplobatis ommanata*) and other rays, and Cortez garden eels (*Taeniconger digueti*) in the Gulf of California (D. Steller and M. Foster, pers. obs.). The distribution of rhodolith beds appears to be largely constrained by abiotic variables such as water motion and light, but within-bed structure and perhaps even bed persistence may be strongly affected by biological interactions. Bioturbation by invertebrates and fishes moves rhodoliths and resuspends fine sediment, likely facilitating rhodolith growth and bed maintenance (Marrack, 1999).

Rhodolith beds may act as nursery habitat for a variety of species. Bivalves are abundant in rhodolith beds in areas such as Georges Bank (Thouzeau, 1991), the Gulf of California (Steller and Caceras-Martinez, 2009), and the eastern Atlantic (Hily et al., 1992; Hall-Spencer, 1998; Hall-Spencer and Moore, 2000), and rhodolith beds may play a role as nursery habitats for scallops. Scallop–rhodolith bed interactions have been of particular interest because scallops are commercially harvested and their life history is well known. Scallop larvae have been shown to preferentially settle on living (versus dead) rhodoliths (Steller and Caceras-Martinez, 2009). This preference likely contributes to high juvenile scallop densities (Kamenos et al., 2004a)h@ due to greater scallop selection, attachment, and growth (Kamenos et al., 2004b, 2004c). Rhodolith beds may also benefit adult scallops by providing a refuge from predation (Steller et al., 2003; Kamenos et al., 2006). Patterns of water motion responsible for rhodolith maintenance may also influence larval delivery of a number of associated species, a mechanism that remains to be investigated.

While natural disturbances are an essential feature of rhodolith ecosystems, anthropogenic disturbances can be catastrophic. This is readily clear from diving observations made over a once-thriving rhodolith bed that had been crushed by a scallop dredge. Beds have been entirely or partially destroyed by extraction of calcareous sediment, bottom fisheries, and degraded water quality from fish farms (De Grave, 1999; Hall-Spencer and Moore, 2000; Hall-Spencer et al., 2006). Smaller-scale disturbances such as anchoring or mooring in coastal bays also occur, but have received less attention.

In addition to localized destruction, rhodolith beds worldwide will likely be impacted by decreasing ocean pH linked to rising atmospheric CO_2 (Kleypas et al., 2006). Coralline algae, with their very soluble high-Mg calcite, are predicted to be in the first suite of species severely impacted by ocean acidification (Kuffner et al., 2007; Jokiel et al., 2008). Chemical dissolution could make them more susceptible to other physical and biological disturbances and decrease post-disturbance recovery rates. The positive relationship between biodiversity and rhodolith density, nodule size, and branching strongly suggests that factors negatively impacting nodule characteristics would likely lead to negative community-level impacts.

The need for protecting rhodolith beds from dredging, trawling, and other relatively small-scale disturbances has been recognized by conservation directives in the European Union, Australia, New Zealand, and Mexico (review in Riosmena-Rodríguez et al., 2010). On the largest scale, however, little progress has been made toward reducing CO_2 emissions. It remains to be seen how effective local conservation measures will be in the face of global change.

DEEP BEDS IN BRAZIL

The Brazilian coast supports the largest known rhodolith beds in the world, covering extensive areas of the north, northeastern, and southeastern Brazilian continental shelf (Kempf, 1970; Milliman, 1977; Amado-Filho et al., 2007). However, our understanding of the latitudinal distribution and community structure of these beds is still in its infancy. Many rhodolith studies in Brazil, especially the early ones, were focused on the characterization of shelf sediments and prospects for potential commercial exploitation (Milliman and Amaral, 1974; Dias, 2000). Only a few published studies have considered the beds in a biological context that includes consistent information about meso- and small-scale distribution, bed structure, associated organisms, and the species composition of the rhodoliths (e.g., Gherardi, 2004; Riul et al., 2009; Villas-Boas et al., 2009; Amado-Filho et al., 2010).

These latter studies have found a high diversity of organisms associated with rhodolith beds and highlight their ecological relevance. A general evaluation of the marine biota in the Brazilian exclusive economic zone (the marine area extending 320 km offshore) indicated rhodolith beds increase the diversity of epibenthic organisms, with Shannon diversity indices (H’) of 4.0–5.1 found to depths of 250 m in this ecosystem (Lavrado, 2006). These and other data obtained during the 1990s and the early 2000s were, however, based on dredging and the analyses were largely qualitative. Most rhodolith beds in Brazil still remain unexplored or poorly known ecologically. This is largely because the beds occur mostly in mesophotic habitats (~30–120 m depth) that are difficult to adequately access with standard scuba.

As pointed out by Bridge et al. (2010), information on biotic and abiotic aspects of mesophotic habitats remains extremely scarce due to logistical and technological restrictions, particularly when compared with shallow-water habitats. This is true for rhodolith beds in Brazil, but recent advances in mixed-gas diving techniques (Figure 3), complemented by ROV observations and high-resolution, multibeam, bathymetric mapping systems, allow us to begin determining their extent, structure, and dynamics. These tools are now being used to investigate extensive areas of the continental shelf (e.g., Abrolhos Bank), tops of seamounts (Vitoria-Trindade Ridge), and around oceanic islands (e.g., Trindade Island and Fernando de Noronha Island; Figure 4).

One of the most interesting features of these mesophotic habitats, recently investigated using technical diving, are rhodolith beds inhabited by populations of the deep water endemic kelp *Laminaria abyssalis*. This kelp occurs on the continental shelf at latitudes of 19°–23° S and depths of 45–120 m where the bottom is completely covered by rhodoliths (Amado-Filho et al., 2007). Kelp populations are closely associated with the rhodoliths; all *L. abyssalis* holdfasts are attached to one or more rhodoliths. Graham et al. (2007) suggested that such deep water kelp refugia are potential hot spots of tropical marine diversity and productivity. This suggestion has been confirmed in the Brazilian deep water rhodolith–kelp beds, as endemic species of different taxonomic groups have been cited to this area.

The northern limit of Brazilian *L. abyssalis* populations is determined by the southern edge of Abrolhos Bank. The Abrolhos Shelf (16°50′S–19°45′S; Figure 4) is an ~6,000 km^2 enlargement of the eastern Brazilian continental shelf, and encompasses the largest (~325 km^2) and richest reefs in the South Atlantic (Leão and Ginsburg, 1997). These reefs are well known for their unique coral assemblages dominated by Brazilian-endemic, Neogene relics belonging to the genus *Mussismilia*. Investigations combining side scan sonar, ROV images, and scuba diving show that rhodolith beds are the predominant feature from north to south across the Abrolhos Shelf at depths from ~25 m to ~110 m. These beds are composed of at least five non-geniculate coralline species.

The Vitoria-Trindade Ridge (VTR; 20°S–21°S) is a 1,150 km east–west chain of nine seamounts in the South Atlantic that includes two small and highly isolated islands at its eastern end (Figure 4). Previous biological sampling on the VTR was largely restricted to (1) dredging, (2) data from commercial fisheries, and (3) a few scientific diving operations in the shallow waters surrounding Trindade Island. The mesophotic zone on the top of two seamounts (Davis and Jaseur) were surveyed in March 2009 using a combination of ROVs, mixed-gas technical dives, and a single-beam bathymetry system. The seamounts have predominantly flattened tops that result from alternating periods of growth and erosion of carbonate algal deposits over volcanic pedestals during periods of high and low sea level (Almeida, 1965). At present sea level, the flattened summits of the seamounts are all situated in relatively shallow water, with minimum depths ranging from 40 m to 110 m. The seamount tops

FIGURE 3. Technical diving equipment being used to take video images at 60 m on Fernando de Noronha Island shelf, Brazil. Photo by Z. Matheus, courtesy of G. M. Amado Filho.

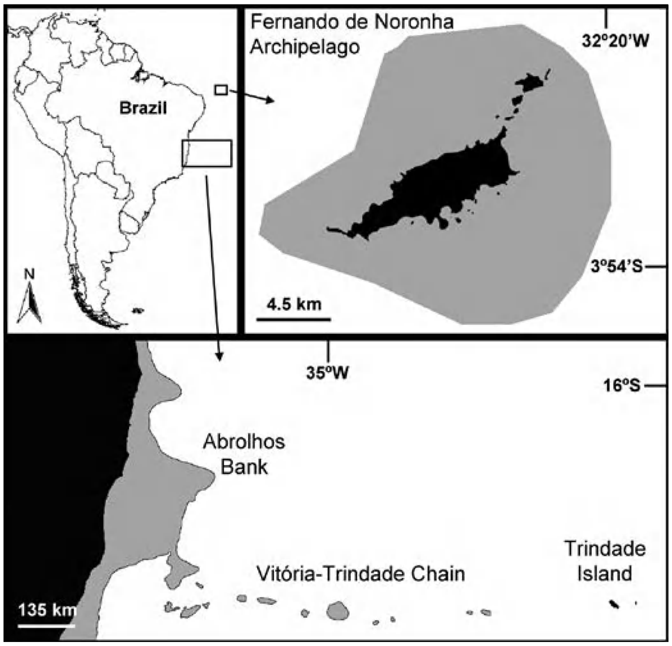

FIGURE 4. Locations of mesophotic rhodolith beds on the Brazilian Shelf.

rise up to 50 m from the bottom, and are dominated by rhodoliths with a high diversity of associated species including seaweeds, sponges, corals, black corals, octocorals, and reef fishes. Rhodolith beds are also the main feature surrounding Fernando de Noronha, a typical tropical island (03°50′S, 32°25′W, about 345 km east of the coast of Brazil; Figure 4) known as the best diving location in Brazil. These beds, found down to 120 m at the edge of the island shelf, were also discovered using technical diving. The ongoing description and study of these unique coralline environments will provide essential information for understanding the ecology, biodiversity, and connectivity of South Atlantic reef communities.

RHODOLITHS AS ENVIRONMENTAL RECORDERS

Coralline algae have several characteristics that make them ideal candidates for recording the environment in which they grow. When these algae grow, they lay down annual and subannual carbonate-derived growth bands composed of high-Mg calcite (Figure 5; Henrich et al., 1996; Kamenos et al., 2008). Groups of subannual primary growth bands resulting from variation in cell size and wall thickness can be grouped into dark

FIGURE 5. Annual banding patterns in a transverse sectioned *Lithothamnion glaciale* branch. Scale = 1 mm. Photo by N. Kamenos.

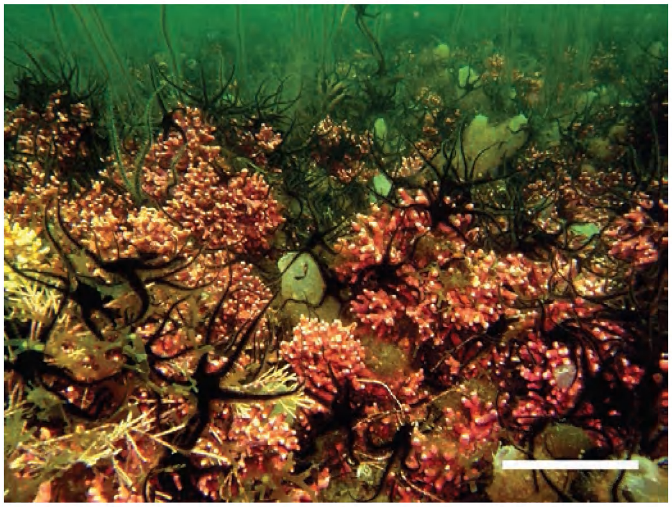

FIGURE 6. A *Lithothamnion glaciale* bed and associated fauna on the west coast of Scotland. Scale = 5 cm. Photo by N. Kamenos.

and light pairs that form higher-order annual banding patterns (Freiwald and Henrich, 1994). While *Lithothamnion glaciale* and *Clathromorphum compactum* show clear annual banding patterns (Halfar et al., 2008; Kamenos et al., 2008), other species such as *Phymatolithon calcareum* show clearer subannual banding patterns (Blake and Maggs, 2003). In some species, growth is not hampered by prolonged periods of low temperature (e.g., *L. glaciale*; Henrich et al., 1996) or darkness (e.g., *L. glaciale*; Freiwald and Henrich, 1994), while in others there is reduced growth in winter (e.g., *C. compactum*; Halfar et al., 2008). As new thalli grow at the surface of the rhodolith bed, older thalli become covered by sediment, die, and form part of the dead deposit. Individual coralline algal thalli can live to at least ~850 years (Frantz et al., 2005) and accumulations of these algal thalli have created maërl deposits spanning the last 20,000 years (Figure 6; Bosence, 1983). Unlike most carbonate-depositing organisms, which have a more restricted distribution, coralline algae occur from polar (Schwarz et al., 2005) to tropical (Littler et al., 1991) shallow seas.

Three key steps are typically used in the development of an environmental recorder (known as a proxy; Kamenos et al., 2009). For coralline algae this involves the following: (1) calibration, which involves understanding the biology of the algae and experimentally determining how growth, for example, responds to environmental stimuli such as temperature (Kamenos et al., 2008); (2) validation of the algae as proxies, which requires appropriate biogeochemical analyses to determine if the observed response of the alga's physical or chemical characteristics to environmental change are a direct response to that change or the record of a tertiary response to a related physiological process (Kamenos et al., 2009); and, (3) application, which establishes that the coralline algae are recording a specific environmental stimulus and can be used to reconstruct and understand environmental changes that occurred before the availability of instrumental records (Kamenos, 2010; Burdett et al., 2011). Unfortunately, many proxies do not undergo this rigorous and important three-step process, rendering their utility questionable.

Scuba has been instrumental in the development of rhodoliths as environmental recorders. Because of their fragile nature, hand collection is the only suitable technique for calibrating the algae in the field or collecting them for calibration in the laboratory. Subsequent to calibration, collection of samples for paleoenvironmental reconstruction involves determination of the most suitable sampling location (e.g., the location likely to provide the longest record) and precise manipulation of sampling apparatus (e.g., corer placement or airlift attachment). These tasks can only be reliably achieved using on-site sampling via scuba. Remote mechanical collection is not suitable due to the absence of specific sampling location information (e.g., what was the orientation of the surface algae on collection?). While suitable remote coring equipment can be used in softer sediments (e.g., vibra corer), the dense nature of rhodolith deposits requires coring techniques capable of penetrating the sediment without causing excessive disturbance. At present, scuba is the ideal tool for conducting such coring activities.

Relationships between environmental parameters and growth have been observed in coralline algae. Significant negative relationships are present between temperature and calcite density in *Lithothamnion glaciale* (Kamenos and Law, 2010), as well as temperature and growth-band width in *Clathromorphum compactum* (Halfar et al., 2011). In both species growth characteristics were correlated to decadal-scale temperature records at collection sites but were characterized by noticeable variability. That variability was attributed to localized control of incident radiation (e.g., algal blooms) and thus it is likely that growth contains a record of both temperature and irradiance (Kamenos and Law, 2010). This was addressed by the development of a growth-environment model that accounts for both temperature and light (as photosynthetically active radiation or PAR; Burdett et al., 2011). By combining a record of summer calcification within individual *Lithothamnion glaciale* growth bands with known temperature records for the area, cloud cover (indicative of PAR) history on the west coast of Scotland was reconstructed that indicated a modest increase in cloud cover trends since 1910 (Burdett et al., 2011).

The chemistry of the calcite deposited by coralline algae within their growth bands also serves as an environmental recorder. Initial observations indicated elemental concentrations within coralline algae varied directly (Chave and Wheeler, 1965) and indirectly (Moberly, 1968) with environmental fluctuations. More recently, Mg concentrations within *Lithothamnion glaciale* have been observed to represent ambient temperature of the seawater in which the algae grew at fortnightly resolutions (Kamenos et al., 2008), as well as sea-surface temperature at seasonal resolution (Halfar et al., 2000). This response allowed *Lithothamion glaciale* to be validated as a paleotemperature recorder (Kamenos et al., 2009), enabling the first biweekly resolution reconstruction of Atlantic marine temperatures since ~1350 (Kamenos, 2010). $\delta^{18}O$ in *Clathromorphum nereostratum* and *Lithothamnion glaciale* represents ambient seawater temperature at seasonal resolutions and has been used to reconstruct northeastern Atlantic sea-surface temperature since 1970 (Halfar et al., 2000, 2008). *Lithothamnion muellerii* and *C. nereostratum* have been shown to record atmospheric ^{14}C concentrations (Frantz et al., 2000, 2005), which are critical for determining long-term growth rates and age in coralline algae as well as dating the exact timing of climatic events recorded by the growth-banding structure or chemistry within the algae. Overall, coralline algae are ideally suited as chemical environmental recorders because (1) they do not suffer diagenetic effects due to the presence of the living membrane covering the carbonate skeleton (Alexandersson, 1974); (2) there is no stress-related geochemical deviation in Mg/Ca–temperature relationships (Kamenos et al., 2008); and, (3) there is no non-equilibrium-associated oxygen isotope fractionation in maërl (Rahimpour-Bonab et al., 1997; Halfar et al., 2007).

Scuba has played a central role in facilitating an understanding of how coralline algae act as environmental recorders through their utility in paleoenvironmental reconstructions. With the need for increasingly resolved spatio-temporal paleoclimate records to better understand recent climate trends, these algae are beginning to receive increased attention as environmental recorders.

CONCLUSIONS

As they have for other shallow subtidal environments, in situ investigations using scuba have improved our understanding of rhodoliths and rhodolith beds far beyond that achievable by dredging and other remote research techniques. Scuba enabled detailed sampling that continues to clarify the taxonomy and evolutionary relationships of rhodoliths and associated species. It has allowed the direct determination of bed distribution and abundance patterns, and field experiments to test hypotheses about the causes of these patterns. Such studies, including those in deep water that use technical diving, continue to provide new insights into bed structure and function. Careful collection and underwater experimentation have also revealed rhodoliths to be exceptional environmental recorders. Beds are, however, very susceptible to disturbance and climate change. Their conservation must be a priority if we are to continue to enjoy, better understand, and learn from these remarkable communities and the plants that dominate them.

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This chapter is dedicated to the memory of Isabella A. Abbott (1919–2010), who contributed enormously to our knowledge of marine algae, championed international scientific collaboration, and always encouraged searches for subtidal seaweeds.

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How Scuba Changed Our Understanding of Nature: Underwater Breakthroughs in Reef Fish Ecology

Mark H. Carr, Daniel P. Malone, Mark A. Hixon, Sally J. Holbrook, and Russell J. Schmitt

ABSTRACT. The development of the self-contained underwater breathing apparatus (scuba) in the mid-twentieth century provided ecologists with unprecedented access to reef fishes and their ecosystems. These studies fostered major advances in our understanding of tropical and temperate reef fishes through comparisons of disparate systems to identify common ecological and evolutionary threads, and through the integration of processes across multiple levels of biological organization. For each of these levels (individuals, populations, communities, and entire ecosystems) we describe the diversity of research approaches enabled by scuba, the insights they generated, and the resulting conceptual contributions to ecology and evolution. Much of the research described here has direct and valuable application to management and policy decisions for fisheries and conservation of reef species and ecosystems.

INTRODUCTION

The use of scuba has had such a profound impact on our understanding of the ecology of reef fishes at all levels of biological organization that it is difficult to imagine what the state of our understanding would be without it. For many decades, fish assemblages associated with shallow reef ecosystems have attracted the attention of ecologists because of their natural beauty, great species diversity, economic and cultural importance for both consumptive (e.g., fisheries) and nonconsumptive (e.g., tourism) uses, and importantly, relative accessibility for conducting ecological experiments and long-term observational studies. The adoption of scuba has allowed researchers to observe how individual and populations of fishes interact with one another and their environment, to conduct complex experiments, and to deploy and maintain in situ sampling devices (e.g., larval collectors, video systems, oceanographic equipment). Scuba is largely responsible for the great advances achieved in the ecology of marine reef fishes. Because scuba has become such a cost effective and ubiquitous research tool, observational and experimental studies can be conducted across a broad range of spatial (up to hundreds of km) and temporal (up to decades) scales. Indeed, the vast majority of publications on the ecology of reef fishes over the past several decades has been either empirical studies that employed scuba or theoretical work that has been informed by scuba-based studies.

Scientific contributions to our understanding of the environmental, evolutionary, and ecological processes that shape the diverse ecological systems of the natural world

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have benefited from two fundamental approaches. The first is the comparative approach that contrasts ecological and evolutionary processes in different environments (e.g., tropical vs. temperate forest and reef systems) to derive fundamental insights into processes (e.g., biotic vs. abiotic determinants of community structure) that underscore the structural (e.g., biodiversity) and functional (e.g., nutrient cycling) attributes of ecosystems. This approach also can involve application of understanding achieved in one ecosystem to a wide range of others. Fish assemblages associated with tropical coral reefs and temperate rocky reefs have been a focus of ecological investigation not only to better understand those particular species and ecosystems, but also to gain insights into broader ecological principles. Indeed, such fundamental ecological concepts as open populations, recruitment limitation, lottery models, and the mechanisms of density dependence and population regulation generated by studies of reef fishes have been applied across marine, freshwater, and terrestrial ecosystems.

The second fundamental approach to ecological understanding entails the investigation and integration of processes acting at multiple levels of biological organization: individuals, populations, communities, and ecosystems. Studies of individual organisms have focused on behavioral and physiological processes that determine growth, survival, reproductive success, and other determinants of individual fitness, as well as on a variety of population-level attributes (e.g., size and age structure). Such studies reveal the mechanisms governing interactions between individuals and their environment, interactions with conspecifics and other species, and the scales of space (e.g., neighborhood size) and time (e.g., stages of ontogeny) over which these interactions occur. Population studies identify the mechanisms that determine population distribution, structure, and dynamics, which influence the persistence of populations and magnitude of interactions with other species in a community. Studies of genetic patterns and diversity reveal past and present patterns and scales of natural selection, gene flow, and population connectivity. Studies that examine the interactions among co-occurring species identify how species interact, the strength of interactions, and the unique functional roles of individual species that all contribute to the structure and functions of ecological communities. Ecosystem-level investigations reveal the collection of interactions among species and their environment that contribute to the integrity, productivity, and dynamics (e.g., resiliency) of ecosystems.

Studies of reef fishes have advanced our understanding of ecology and evolution by their integration across all these levels of organization. For example, factors that influence variation in individual fitness have demographic consequences (size, structure, and dynamics) that in turn affect patterns of species interactions (Johnson et al., 2010). The purpose of this brief overview is to highlight the myriad ways in which scuba has contributed to ecological studies of tropical and temperate reef fishes across the various levels of biological organization and to the field of ecology as a whole.

THE ECOLOGY OF INDIVIDUALS

Ecological studies focused on individual fishes have enlightened our understanding of the behavioral and physiological mechanisms that underlie individual performance and fitness and of the spatial scale at which individuals interact with their environment. In situ observations and experiments have revealed how reef fishes perceive and interact with their environment (e.g., foraging and resource utilization), how they respond to trade-offs between quantity and quality of resources and predation risk, and what the consequences of these responses are for habitat use, growth, and reproductive success (e.g., Holbrook and Schmitt, 1988a, 1988b). Not only has scuba allowed many researchers to spend countless hours over the course of their careers making observations under natural conditions, it has also enabled scientists to experimentally manipulate environmental conditions (both biological and physical) and quantify behavioral responses and their consequences for individual fitness. Examples of some biological factors that have been manipulated include the density, dispersion, distribution, size range, and quality of prey resources; the presence, density, and size distribution of predators and competitors; and combinations of resource and predator characteristics. Manipulations of prey resources have included the deployment of devices that release planktonic prey (Forrester, 1990) and the configuration of portable algal habitats with associated invertebrate prey (Holbrook and Schmitt, 1984). Refuge manipulations include the alteration of algal structure (Levin, 1991, 1993; Carr, 1994a, 1994b; Johnson, 2006), the addition of artificial refuges (Hixon and Beets, 1993), and the elimination of naturally occurring physical features (cracks and crevices). Such experiments have revealed the determinants of foraging behavior and habitat use of consumers and how individuals balance the trade-off between the reward of resource acquisition and the risk of mortality with resulting consequences (i.e., sublethal effects) on various aspects of individual performance including growth and reproduction.

Behavioral studies of the reproductive ecology of reef fishes have leveraged the great diversity of reproductive modes exhibited by reef fishes and their accessibility for observational and experimental studies with scuba. Indeed, coral reef fishes have become one of the most prominent model systems for studies of reproductive ecology, mating systems, and social structures, as evidenced by the expansive literature on these subjects and its impact on evolutionary theory (reviewed by Robertson, 1991; Shapiro, 1991; Warner, 1991; Petersen and Warner, 2002). Observational studies have described the timing (diel and seasonal; Sancho et al., 2000; Gladstone, 2007) of reproduction and the location and movements associated with reproductive behavior (e.g., spawning; Domeier and Colin, 1997), and have linked these behaviors to environmental cues (e.g., moonlight, tides, temperature) and conditions (e.g., ambient light levels, currents) that contribute to the successful release and dispersal of larvae. Orthogonal manipulations of mate and habitat traits have identified the relative contributions of these cues to spawning success.

Observations of the relative effects of mate attributes (i.e., fish size, behavior) and associated habitat attributes (nest size and quality) have revealed the determinants of mate choice (Warner, 1987; Sikkel, 1989). Such studies have also shed light on the relationships between reproductive ecology and social structure, including mating systems (e.g., hermaphroditism; Warner and Hoffman, 1980; Warner, 1984).

Research using scuba has contributed greatly to our knowledge of the movement patterns of reef fishes, the environmental and ecological determinants of these patterns, and their ecological significance in both tropical and temperate reef ecosystems. Scuba has been used widely to describe and quantify movement patterns in three primary applications: direct observation of fish movement, sighting of tagged individuals, and the use of acoustic telemetry equipment. Early studies repeatedly located individually tagged fishes to eventually delimit their home ranges (e.g., Larson, 1980; Hixon, 1981; Holbrook and Schmitt, 1986). Diver resighting of tagged fishes has facilitated mark-recapture studies of fish movement (Starr et al., 2004). Telemetry studies have benefited from scuba by the selective sampling of fishes (e.g., gender, size class) and the deployment and maintenance of arrays of acoustic receivers (Holland et al., 1996; Zeller, 1999; Lowe and Bray, 2006), thereby allowing intrapopulation differences of movement patterns to be ascertained. All of these approaches have been complemented by information on biotic (e.g., distribution and density of conspecifics and other species, distribution and composition of corals and macroalgae) and abiotic (e.g., geologic composition, relief, and current direction and speed) attributes of the reef habitat and used to identify the relative importance of these variables in determining movement patterns and ranges. Most importantly, scuba has enabled experimental manipulations of key biotic and abiotic features to demonstrate their causal and interactive effects on patterns and ranges of fish movement.

POPULATION ECOLOGY

Studies of the population ecology of reef fishes have had a major influence on our understanding of the relationship between environment, life history, and the distribution, structure, and dynamics of populations. Reef fish studies have been a key in the development of the concept of open populations, in which the dispersal of larvae effectively decouples the relationship between production and replenishment of local populations (Caley et al., 1996; Carr and Syms, 2006). This fundamental structure of marine populations was revealed by a plethora of studies that used scuba to quantify the size of reef-associated fish populations and rates of larval recruitment. From this work emerged evidence that the size of a local population can be influenced by recruitment limitation—the limitation in supply of larvae delivered to a population due to the high mortality larvae experience in the pelagic environment—and the vagaries of ocean currents (Doherty, 1981, 1983; Victor, 1983, 1986; reviews by Doherty and Williams, 1988; Mapstone and Fowler, 1988; Sale, 1991; Doherty, 2002). Such observations prompted a great number of empirical studies (both observational and experimental) that examined the relative contributions of larval supply versus processes acting at settlement and early post-settlement (e.g., competition, predation, facilitation) in determining the size and dynamics of local populations (Schmitt et al., 1999; Schmitt and Holbrook, 2000; Osenberg et al., 2002). Because these processes can be density dependent (i.e., rates of growth and survival vary with the density of settlers or adults), these studies contributed to our understanding of mechanisms for the regulation and persistence of populations (Hixon and Webster, 2002). Studies of density dependence further explored the relative and interactive effects of competition and predation through a large number of complex experiments conducted on both coral and temperate rocky reef fishes (e.g., Carr et al., 2002; reviews by Hixon and Jones, 2005). Scuba has been instrumental in enabling researchers to conduct multifactorial manipulations of density of recruits, competitors, predators, and refuge availability to elucidate the interactive effects of these variables on the settlement, growth, and survival of young reef fishes, and their ultimate effects on population replenishment (Holbrook and Schmitt, 2002; Schmitt et al., 2009). Manipulations of fish density and refuge availability have been achieved by the selective removal of individuals on natural reefs and by experimentally creating isolated reef habitat from natural structures (e.g., corals, shells, rubble, rock, kelps; Figure 1a–c) and artificial substrata (e.g., cinder blocks, concrete rubble, tubes; Figure 1d–f). Scuba also has enabled ecologists to understand how the distribution of predators and refuge from predators across landscapes determines the spatial scale of variance in density dependence (Forrester and Steele, 2004; Schmitt and Holbrook, 2007).

Having identified the importance of larval recruitment to the distribution and dynamics of local reef-associated populations, ecologists investigated the role of larval behavior and oceanographic processes in driving variation in larval delivery to and settlement in local populations and in contributing to geographic variation in population dynamics. Scuba has been instrumental in exploring relationships between the spatial and temporal variation in larval recruitment and oceanographic processes in three key ways. First, scuba-based surveys of larval recruitment through time, within and among reefs, coupled with monitoring of local and regional oceanographic processes (e.g., tidal currents, upwelling, El Niño, La Niña) enable ecologists to determine the influence of these processes on geographic and temporal (seasonal, interannual) variation in larval delivery (Schmitt and Holbrook, 2002). Secondly, the efficiency and scale of these studies have increased with the development and deployment of larval collectors (e.g., plankton nets, light traps, Standardized Monitoring Units for Recruitment of Fishes [SMURFs]; Figure 2a–c) using scuba (e.g., Doherty, 1987; Choat et al., 1993; Anderson et al., 2002; Caselle et al., 2010, 2011). Finally, scuba has been necessary in the deployment and maintenance of oceanographic instruments (e.g., swell gauges, current meters,

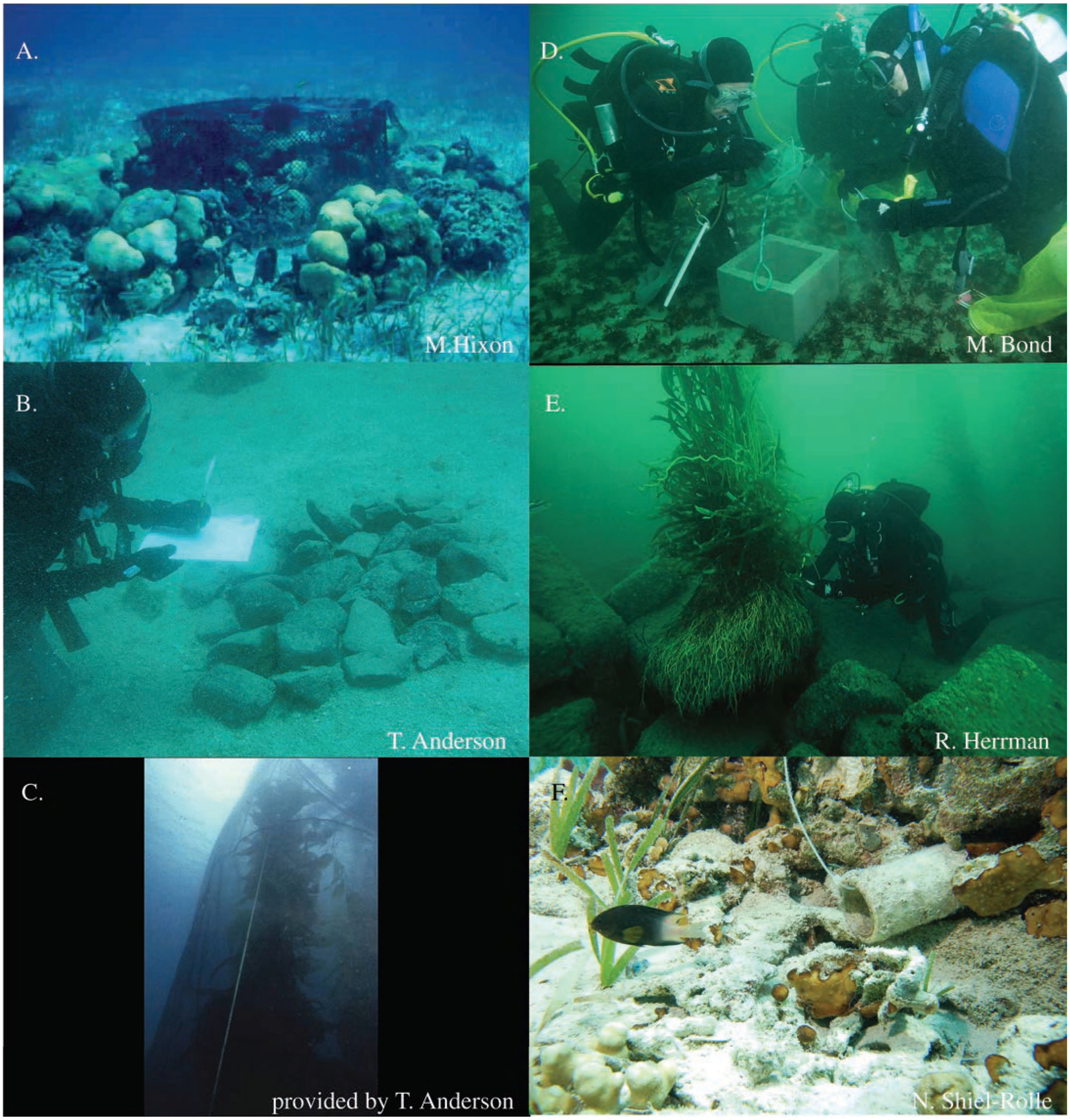

FIGURE 1. Habitat manipulations to create independent isolated experimental treatment levels (e.g., density levels, refuge availability) from natural substrata: (A) corals, (B) rock, (C) kelps; and artificial substrata: (D) cinder blocks, (E) concrete rubble, (F) tubes. (Photo credits given in each image.)

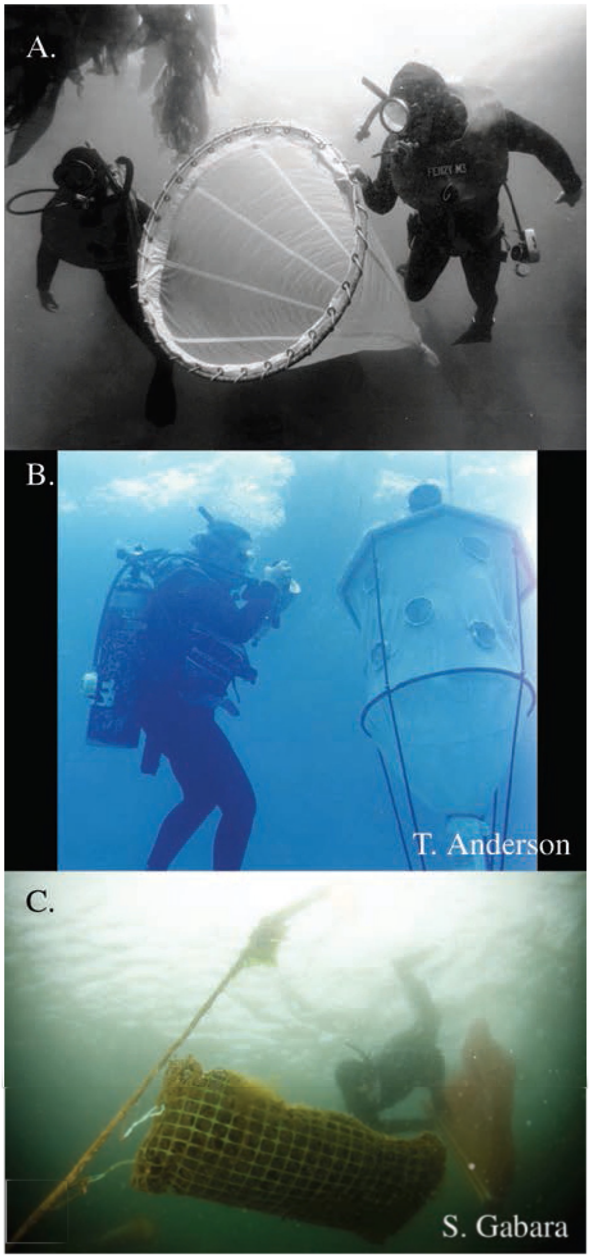

FIGURE 2. Devices for collecting larvae using scuba. (A) Plankton nets, (B) light traps, and (C) SMURFs (see text). (Photo credits: A, reprinted from Hobson and Chess, 1976; B, C, as given in each image.)

thermistors; Figure 3a–c) that resolve oceanographic processes (e.g., swell, currents, upwelling) at the spatial scale of individual reefs. These studies have identified the importance of local and regional variability, including episodic events occurring within (e.g., upwelling and relaxation, internal waves) and between (e.g., El Niño, La Niña) years, in driving seasonal and interannual variation in reef fish recruitment.

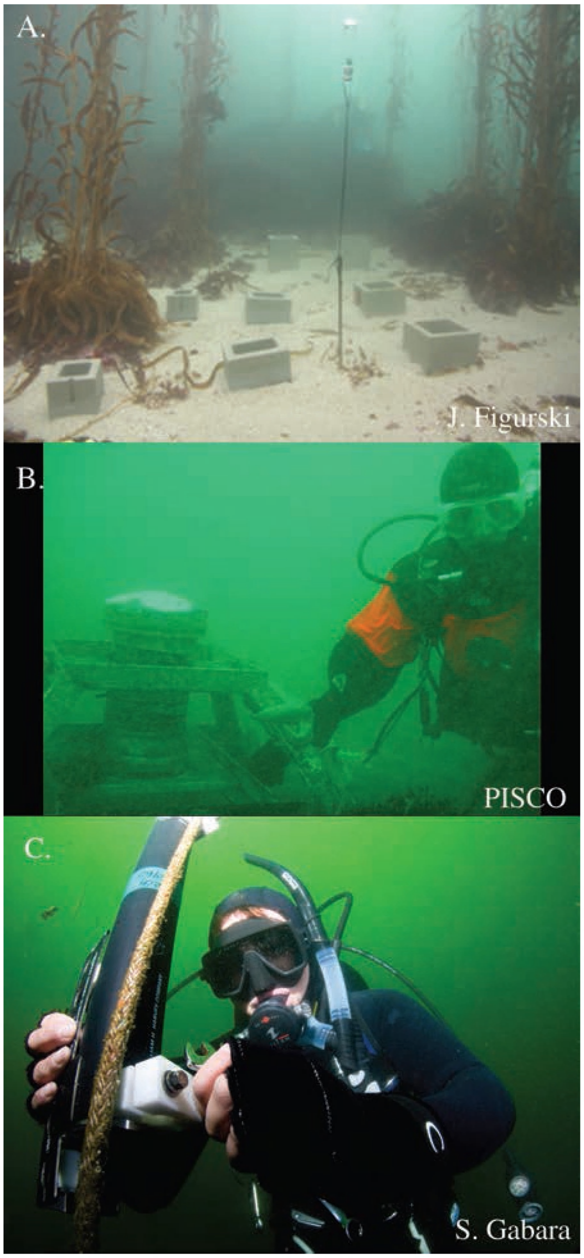

FIGURE 3. Deployment and maintenance of oceanographic instruments using scuba. (A) Swell gauges, (B) current meters, and (C) thermistors. (Photo credits given in each image.)

To determine how larval behavior (e.g., settlement preferences) and variation in habitat types (e.g., different species of corals, algae versus rock) contribute to spatial variation in rates of larval settlement, ecologists using scuba have measured rates of settlement to natural landscapes (reviewed by Leis and McCormick, 2002) and experimental arrays of habitat types (e.g., Almany, 2004). These studies demonstrated how aspects of the

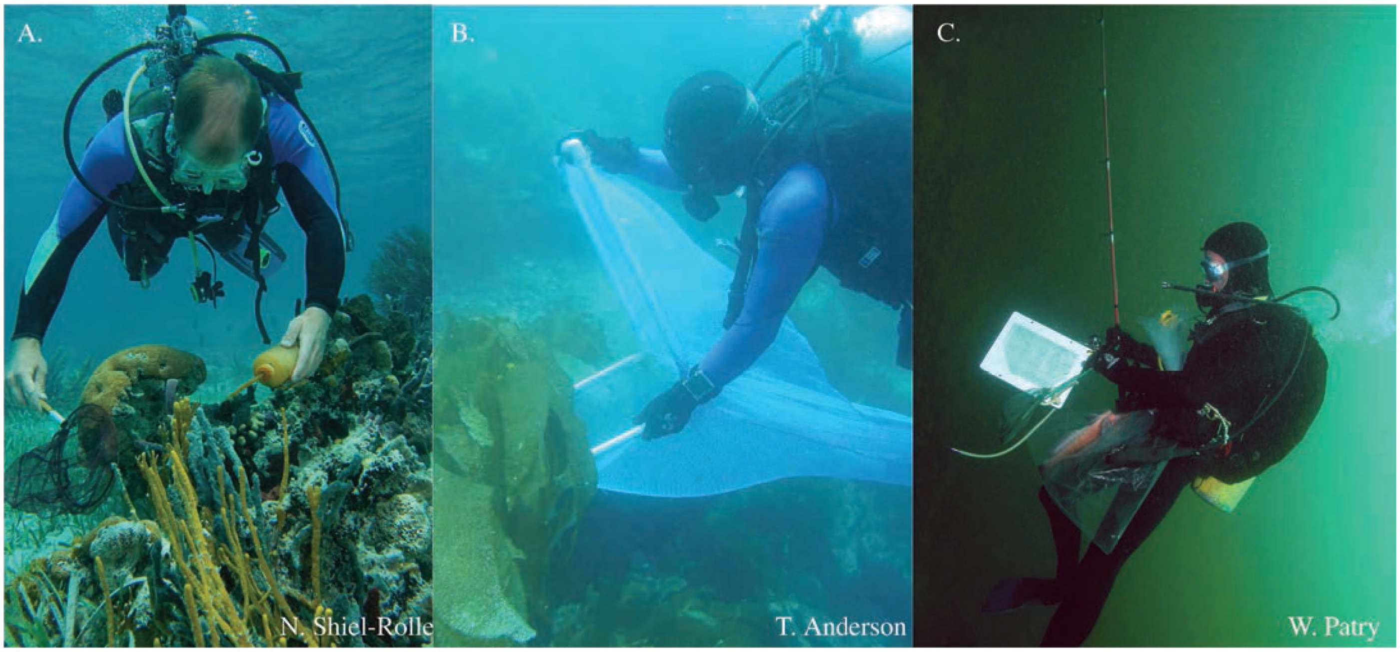

FIGURE 4. Methods for collecting reef fish using scuba. (A) Hand-netting while using anesthesia (clove oil), (B) BINCKE (Benthic Ichthyofauna Net for Coral / Kelp Environments), and (C) hook and line. (Photo credits given in each image.)

local reef habitat could explain variation in settlement rates among reefs and how important certain features of reefs are to the replenishment of reef fish populations.

Fundamental goals of population genetic studies of reef fishes are to identify individual relatedness, mechanisms of selection, the spatial and temporal dynamics of genetic structure, and connectivity of populations via larval dispersal. Scuba has contributed to these studies largely through the ability to target individuals at a very fine scale based on their distribution in space (or habitat), life stage, gender, and size. For example, in situ collection of individuals from particular size or age cohorts has allowed determination of changes in gene frequencies subsequent to settlement as well as identification of intercohort relatedness of social groups (Planes et al., 2002; Johnson and Hixon, 2010). Scuba-based sampling of adults (using anesthesia, underwater nets, or hook and line fishing; Figure 4a–c) allows researchers to efficiently and nondestructively sample and characterize geographic patterns of genetic dissimilarity, which are used to infer the spatial patterns and scale of historic gene flow via larval dispersal (Bernardi et al., 2001; Leray et al., 2010). In situ collection of recently settled juvenile reef fishes can identify patterns and scales of gene flow to estimate dispersal patterns of a single cohort. In combination with oceanographic information (e.g., current patterns, productivity), patterns of genetic similarity can be linked to the oceanographic processes that determine the underlying geographic patterns of larval dispersal (Planes, 2002; Bernardi et al., 2003; Almany et al., 2007; Christie, 2010; Christie et al., 2010). Collection of individuals using scuba has allowed researchers to repeatedly sample cohorts of recently settled reef fishes through time to determine at what stage and under what environmental conditions (habitat type, exposure to predators) gene frequencies change and when and where natural selection or genetic drift establish patterns of local genetic diversity and structure (metapopulations) within larger regional populations. Comparisons of juvenile and adult genotypes (e.g., parentage analysis) from local populations have been used to determine the effect of relatedness on patterns of settlement (Avise and Shapiro, 1986), as well as to identify the origin location of settled larvae and patterns of larval dispersal (Planes, 2002; Almany et al., 2007; Christie et al., 2010).

COMMUNITY ECOLOGY

Ecological studies involving scuba have been particularly important in advancing our understanding of the processes that structure communities of fishes on both coral and rocky reefs and, by extension, communities of organisms in other marine, freshwater, and terrestrial ecosystems. The testing of hypotheses that explain the maintenance of species diversity has been a central focus of community ecology. Reef fish communities have provided highly useful models for such tests and in the process have generated several new and influential hypotheses.

One theory for the maintenance of species diversity that has been examined by reef fish ecologists using scuba is the niche diversification hypothesis—that species specialize in order to partition available resources and thereby facilitate coexistence.

Scuba studies provided observational and experimental evidence for partitioning of habitat and food resources on coral reefs and temperate rocky reefs (reviewed by Ross, 1986; Ebeling and Hixon, 1991). While testing this theory in an assemblage of damselfishes on coral reefs, Sale (1977) generated the lottery hypothesis. This nonequilibrial hypothesis posits that competing species do not partition resources, and that diversity is maintained by the random settlement of species within and among reefs. The lottery model (versus lottery hypothesis) and storage effect posit that changing environmental conditions favoring recruitment of each species relative to others maintains coexistence despite competitive equality (Warner and Chesson, 1985). Recruitment limitation, previously described in relation to population dynamics, has also been cited to explain the coexistence of coral reef fishes by preempting competitive exclusion (Doherty, 1983). Like the other hypotheses for the maintenance of diversity, the recruitment limitation hypothesis was enabled by field studies of coral reef fishes using scuba. These hypotheses have since been tested in a variety of other systems. Studies of reef fishes have also provided evidence of indirect mutualism, whereby a strong interspecific competitor can actually promote the coexistence of the weaker competitor via indirect positive benefits (Schmitt and Holbrook, 2003; Holbrook and Schmitt, 2004).

In addition to testing hypotheses explaining the maintenance of diversity, reef fish ecologists have used scuba to explore the sources of spatial and temporal variation in community structure. For example, scuba-based observational and experimental studies of reef fish assemblages have been used to test island biogeography theory by comparing diversity among patch reefs of varying sizes and isolation (Molles, 1978; Talbot et al., 1978; Bohnsack, 1979). Reef fish ecology has also contributed fundamentally to our understanding of the roles of recruitment, competition, predation, and mutualistic relationships in structuring the composition and relative abundance of species in communities. Research on competition has involved the selective removal of species on natural reefs as well as manipulation of the abundance of species on experimental patch reefs in both coral and temperate rocky reef ecosystems (e.g., Carr et al., 2002). Similarly, the role of predation in structuring communities has been illuminated by the manipulation of predators using isolated patch reefs and predator exclusion cages (Figure 5). The number of these influential studies is too great to cite (see reviews by Hixon, 1991; Hixon and Webster, 2002; Hixon and Jones, 2005; Carr and Syms, 2006; Hixon, 2006; Steele and Anderson, 2006).

In addition to elucidating the consequences of biotic processes, reef fish ecologists have also sought to identify the role that environmental factors (particularly disturbance) play in the structure and dynamics of reef fish assemblages. Studies have capitalized on natural events to study recovery, succession, and evidence for alternative stable states of community organization. Examples include the response of fish assemblages to storm events (e.g., Ebeling et al., 1985) and climatic variation (Stephens et al., 1988; Holbrook et al., 1997). Others include the simulated destruction of coral reefs (Syms and Jones, 2000) and kelp forests (Bodkin, 1988). Studies designed to identify the influence of habitat features on community structure have correlated environmental variables to geographic variation identified from scuba surveys of reef fish communities (Williams, 1991; MacNeil et al., 2009).

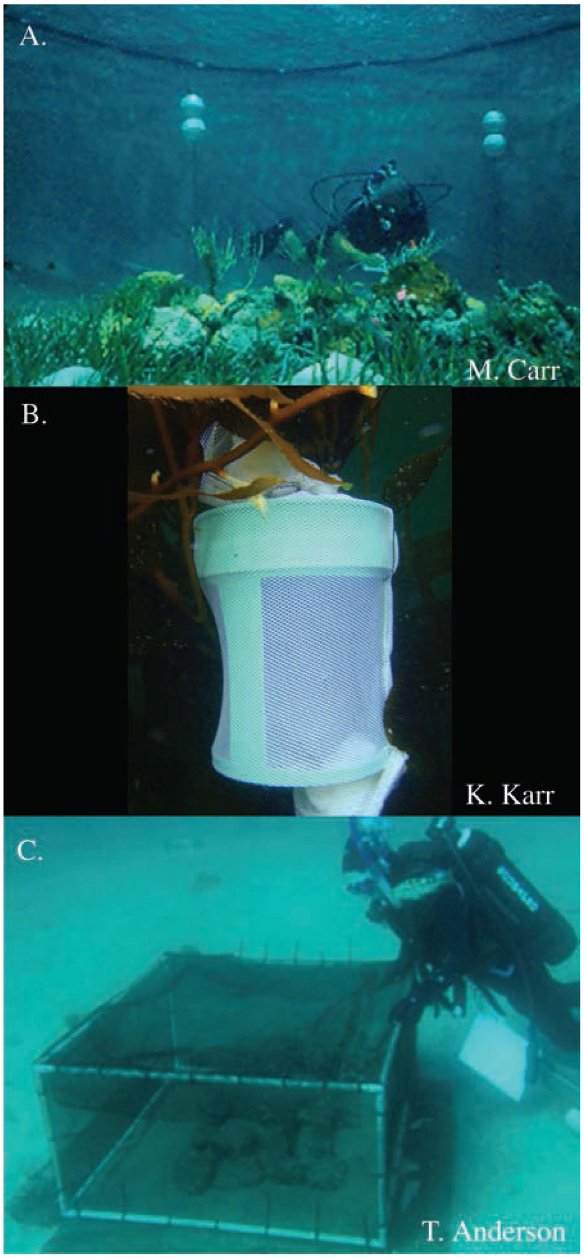

FIGURE 5. Predator exclusion cages used to study the role of predation in structuring communities. (A) Netting surrounding a patch reef to exclude piscivorous reef fish, (B) enclosure placed in the *Macrocystis* canopy to enclose juvenile rockfish (*Sebastes* sp.) and exclude their predators, and (C) exclusion cage surrounding a replicate unit of natural substrate habitat. (Photo credits given in each image.)

ECOSYSTEM ECOLOGY

Traditional ecosystem studies focused on understanding how energy and nutrients flow through food webs and how interactions between biotic and abiotic components of ecosystems determine the pathways and rates of energy and nutrient fluxes. Such studies are largely based on defining trophic interactions, guilds, and pathways by sampling species diets and rates of key ecophysiological processes (production, consumption, and respiration) to parameterize ecosystem models. Scuba studies have been fundamental for dietary studies that define species interactions and guilds (e.g., Hiatt and Strasberg [1960] and Randall [1967], who extol at length the virtue of underwater observation and spear fishing, respectively, for fish diet studies), and for in situ collection of fundamental ecophysiological rates. More recently, ecologists have focused more on the influences of abiotic drivers (oceanographic, geomorphological) on the productivity and structure of fish assemblages and how such variation influences both the functional roles of reef fishes and their effects on reef ecosystem attributes (e.g., productivity, resiliency). For example, several studies have examined or experimentally simulated the impact of hurricanes or bleaching events on coral reef systems and the subsequent responses of reef fish assemblages (Syms and Jones, 2000; Graham et al., 2007). Studies of the influence of fishes on other components of reef ecosystems (invertebrates and algae) have included both direct (e.g., herbivory, predation) and indirect (e.g., bioerosion, trophic cascades) trophic interactions (Williams, 1980). For example, Bray et al. (1981) quantified the increased availability of nitrogen and rate of macroalgal production in cracks and crevices occupied at night by the planktivorous temperate damselfish *Chromis punctipinnis*, thereby demonstrating the role of planktivorous reef fishes in linking pelagic and benthic production in reef ecosystems. Other studies have demonstrated the importance of herbivory in maintaining coral abundance and diversity (Hughes et al., 1987; Choat, 1991; Hay 1991). Similarly, a substantial body of literature based on observational and experimental studies using scuba has documented the effects of reef fishes on the distribution, species composition, and diversity of invertebrate assemblages (reviewed by Jones et al., 1991). More recently, studies have demonstrated cascading effects of fish predation on herbivores and resulting indirect effects on rates of algal production (Davenport and Anderson, 2007; Perez-Matus and Shima, 2010) and other lower trophic levels. How these functional roles of reef fishes contribute to the resiliency of coral and temperate rocky reef ecosystems (e.g., Hughes, 1994; Bellwood et al., 2004), especially in the face of climate change and other perturbations, is a critical research direction (McLeod et al., 2009).

APPLIED ECOLOGY

Much of the research described here has direct and valuable application to management and policy decisions for fisheries and conservation of reef species and ecosystems. Among the benefits gained using scuba to study reef fishes is the greater spatial resolution of population data for stock assessments, including unprecedented opportunity to generate estimates of natural mortality using tagging-and-resighting approaches and of size structure (the relative proportion of small and large individuals) using nondestructive visual census techniques. Data generated by these studies have been used to document population impacts, especially on hermaphroditic species, of selective fishing techniques and the resultant consequences on progeny quantity and quality for the fished populations. Similarly, surveys of larval recruitment produce time series required to identify oceanographic drivers of recruitment variation and predictions of year-class strength. The breadth of species surveyed by divers includes fished and nonfished species and can identify how the fish assemblage as a whole (as well as other species in reef ecosystems) responds to the removal of fished species (Stallings, 2008). Knowledge of the ecosystem-wide effects of fishing is critical for developing strategies that go beyond single-species management and is essential for ecosystem-based fisheries management.

One key tool for ecosystem-based management and conservation is the development of networks of marine protected areas (MPAs), including marine reserves (e.g., Murray et al., 1999; Gaines et al., 2010). These areas provide critical reference sites to compare with fished areas to identify population-level and ecosystem-wide effects of fishing, as well as social, cultural, and nonconsumptive services. Surveys and research conducted with scuba enable nondestructive sampling approaches that can assist in evaluating how effective MPAs are at protecting reef-associated species and ecosystems from the effects of fishing. Monitoring programs inside and outside MPAs designed in conjunction with oceanographic monitoring programs can track ecosystem responses to a changing ocean climate and identify the interactive effects of fishing and climate change on the productivity and resiliency of reef ecosystems (Ling et al., 2009; Carr et al., 2010).

FUTURE DIRECTIONS

One fundamental direction in ecology is the rapidly developing field of spatial ecology. Central to our understanding of patterns and processes at all levels of biological organization is improved understanding of the spatial scales at which ecological processes occur (e.g., interactions between organisms and between organisms and their environment). Similarly, the configuration of habitat in a coastal ocean “landscape” modifies the distribution and strength of ecological processes. Knowledge of the relationships between habitat configuration and these processes is critical to our understanding of how these processes vary spatially and their effects on the structure and dynamics of metapopulations and metacommunities. The current scarcity of studies that have utilized GPS to georeference the location of divers as they collect data, especially in structurally complex habitats (e.g., kelp forests), is a crucial impediment to advancing the spatial ecology of reef ecosystems and linking ecological data with the rapid generation of high resolution seafloor maps. This problem is arguably the greatest hindrance to subtidal ecology relative to recent advances in freshwater and terrestrial ecology.

Another fundamental hindrance is the paucity of coordinated, large-scale, long-term, multidisciplinary (i.e., ecological, physiological, genetic, and oceanographic) monitoring studies for understanding the geographic and long-term scales of variation in dynamics of reef ecosystems. Models for the development of such geographically integrated programs include the U.S. National Science Foundation's Long-Term Ecological Research (LTER) program and the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO). These programs provide not only information fundamental to advancing our understanding of tropical and temperate reef ecosystems, but also information applicable to ecosystem-based management, including how reef ecosystems and their services respond to a changing global climate.

Despite these challenges, it is clear that scuba-based research has contributed critically to many major advances in the ecology of tropical and temperate reef fishes at all levels of biological organization, from genes to ecosystems. Many of these conceptual advances, such as the understanding of ecological processes that maintain biodiversity and their influence on the resiliency of ecosystems, have been so fundamental that they have shed light on the function of ecosystems in general, including those in terrestrial and freshwater settings. Based on the rich history of contributions and the growing number of research programs involving scuba, the advancement of both basic and applied marine and ecological research through scuba is certain to continue at an ever faster pace. The opportunities that scuba provides for scientists to observe reef fishes and their environments firsthand have had profound results that reinforce the importance of training future generations of scientists in the use and applications of scuba, and in doing so safely, through programs like the American Association of Underwater Scientists (AAUS). With continued advances in scuba and associated technology, scientific breakthroughs in these ecologically and economically important marine ecosystems are limited by only our intellectual curiosity and scientific creativity.

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We dedicate this paper to the memory of Conrad "Connie" Limbaugh, whose pioneering efforts studying temperate and tropical reef fishes with scuba led so many of us to follow after him. His great impact on the field of reef fish ecology will be appreciated always and never forgotten.

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Research Facilitated by Scuba

Introduction

Michael A. Lang, Roberta L. Marinelli, Susan J. Roberts, and Phillip R. Taylor

Scuba has played a critical role in marine research. The use of scuba as a research tool has been validated by the quantity and quality of scientific output published in high-impact journals that is cited in this volume. This volume further endorses the strong integration of scientific diving within the overall science domain: "The history of marine research has provided numerous examples of mysteries that would still be unsolved and findings that would have been misinterpreted with confidence if not for direct observation on scuba" (Witman et al., this volume).

The first thirteen papers reported research findings and discoveries around the world in environments such as coral reefs, oceanic blue water, under-ice polar habitats, and temperate kelp forests, providing perspectives on ecological scales and function, physiology, symbiosis and chemistry, biodiversity and behavior, and structured populations. These papers weave scuba through the science, often with a historical and developmental perspective on methods and techniques.

The end product of scientific diving activities is the advancement of science. The following six papers are illustrative of underwater research that was not only greatly facilitated by scuba, but could perhaps not have been accomplished without it. The biology of several marine systems is reported in research involving substantial, often decadal, scuba use. The topics include biological studies on the coral holobiont, ecological roles of major algal groups on reefs, the significance of synchronized sexual reproduction in green algae, and the functional role of small and cryptic metazoans on coral reefs. The research facilitated by scuba and reported in these papers focuses on the scientific results, not necessarily on the research methodologies using scuba to obtain those data and observations, and includes several case studies. Where appropriate, laboratory studies complementary to underwater field observations are referenced.

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Understanding the Coral Holobiont through Science and Scuba

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ABSTRACT. Reef-building corals are a holobiont composed of the coral animal host and its associated eukaryotic and bacterial microbes. Symbiotic dinoflagellates in the genus *Symbiodinium*, which form the basis of the coral–algal symbiosis and provide the coral host with most of its nutrition, are one of the most familiar members of the coral holobiont. Yet reef-building corals also possess diverse communities of bacteria that play important roles in processes such as nutrient cycling and coral immunity. Understanding the complex relationships between the coral, its algal symbionts, and associated microbes is critical because breakdowns in these relationships result in coral bleaching and coral disease outbreaks, both of which are increasing due to global climate change. Here we review recent advances in scuba-based research on the coral holobiont that have expanded our understanding of coral–algal and coral–microbe relationships as well as the role of the coral host in these interactions.

INTRODUCTION

Tropical coral reef ecosystems harbor well known and arguably unrivaled biological diversity that supports the marine world (Knowlton, 2001a, 2001b; Hughes et al., 2003). The macroscopic, or visible, diversity of life on coral reefs, including the array of tropical fish, seaweeds, and invertebrates, is readily apparent to anyone who has snorkeled or scuba dived on reefs. This visible biodiversity tends to capture the most scientific and public interest. Yet there is a greater diversity of microorganisms on reefs that goes unseen (Rohwer et al., 2002; Rosenberg et al., 2007; Dinsdale et al., 2008a, 2008b; Bourne et al., 2009; Ainsworth et al., 2010). This hidden diversity of microbes is arguably more important to the function of coral reef ecosystems because these microorganisms are instrumental in critical ecosystem services like nutrient cycling (Rohwer et al., 2002; Alongi and McKinnon, 2005; Wegley et al., 2007; Thurber et al., 2009).

Reef-building corals are the foundation of coral reef ecosystems. These reef-building coral species are host to an amazing diversity of organisms including representatives from all three domains of life (eukarya, bacteria, archaea) and viruses (Rohwer et al., 2002; Rosenberg et al., 2007; Ainsworth et al., 2010). Eukaryotic organisms associated with the coral host include the well-known, phototrophic, symbiotic dinoflagellates in the genus *Symbiodinium* (Rowan, 1991; Trench, 1993; Baker, 2003; Stat et al., 2006), which translocate fixed carbon to the host (Muscatine, 1973; Muscatine et al.,1981; Falkowski et al., 1984; Edmunds and Davies, 1986) as well as other eukaryotes associated with the coral tissue and skeleton, including endolithic algae, fungi, and sponges (Rohwer et al., 2002; Rosenberg et al., 2007; Bourne et al., 2009). Corals house a high abundance and diversity of bacterial and archaeal groups in their tissue, surface mucus, and skeleton (Rohwer et al., 2002; Wegley et al., 2004; Rosenberg et al., 2007; Bourne et al., 2009).

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These bacteria and archaea can benefit the coral by cycling nutrients (Rohwer et al., 2002; Lesser et al., 2004; Wegley et al., 2004; Beman et al., 2007; Wegley et al., 2007) and producing antimicrobial compounds (Kelman et al., 1998; Ritchie, 2006; Nissimov et al., 2009). However, some of the coral-associated bacteria are also detrimental to the coral, including pathogenic bacteria that cause disease (Kushmaro et al., 1996; Rohwer et al., 2002; Sutherland et al., 2004; Harvell et al., 2007; Rosenberg et al., 2007; Bourne et al., 2009; Ainsworth et al., 2010).

The collection of organisms associated with and including the host coral animal has been called the coral holobiont (Rohwer et al., 2002). The concept of the coral holobiont (Rohwer et al., 2002) originated in part from the need to understand the newly discovered diversity of microorganisms on corals in a more comprehensive or holistic way, (i.e., by viewing the coral as the sum of its parts—the animal host plus all of the associated eukarya, bacteria, and archaea). This expanded view of the coral organism began to emerge as it became apparent that the symbiotic dinoflagellates within corals, which were once thought to be one species, *Symbiodinium microadriaticum* (Taylor, 1971, 1974), actually comprised many diverse lineages (or clades) of *Symbiodinium* (Rowan, 1991; Rowan and Powers, 1991), even within a single coral (Rowan and Knowlton, 1995; Rowan et al., 1997). The diversity of algal symbionts led to the view that the coral and its algal symbionts represent a holosymbiont (Iglesias-Prieto and Trench, 1997). Rohwer et al. (2002) further defined the coral holobiont to include the coral host, its symbiotic algae, and other associated microbes.

The coral holobiont concept not only represents an assemblage of microbes and a host, but also allows us to better understand how the associations among the groups composing the coral holobiont benefit each other, as well as how breakdowns in these associations might impact the coral and the holobiont community (Figure 1). The holobiont perspective helps to solidify a departure from the earlier tendency in the study of coral biology to focus separately on each component—coral, symbiont, and other microbes. The two most familiar symptoms of breakdowns in the associations between the coral host and its associated microorganisms include (1) coral bleaching caused primarily by the breakdown in the coral–algal symbiosis (Brown, 1997; Hoegh-Guldberg, 1999; Douglas, 2003), and (2) coral disease resulting from the breakdowns between the coral and its associated bacteria (Sutherland et al., 2004; Harvell et al., 2007; Rosenberg et al., 2007; Bourne et al., 2009).

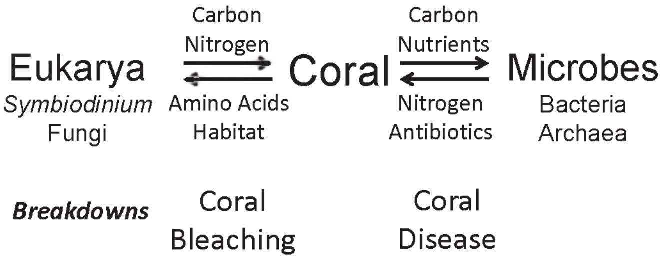

FIGURE 1. Schematic view of the coral holobiont (modified from Rohwer et al., 2002, and Thurber et al., 2009) showing some of the potential benefits and breakdowns between the coral host and its associated eukaryotes, bacteria, and archaea.

The goal of this paper is not to provide a comprehensive review of the literature on the coral holobiont since there are already many excellent and recent reviews on the coral–algal symbiosis (e.g., Baker, 2003; Stat et al., 2006) and coral–microbe interactions (e.g., Sutherland et al., 2004; Rosenberg et al., 2007; Bourne et al., 2009; Ainsworth et al., 2010). Instead, our goal is to highlight recent findings, as well as to characterize the state of knowledge of the coral holobiont, including knowledge gaps that warrant further investigation. Scuba diving research has played a prominent role in all of this work, particularly because it allowed for the experimental manipulation and collection of specimens from the reef environment. We begin by discussing recent advances in our knowledge of the nature of the coral–algal symbiosis, and in particular their ontogeny. We then discuss recent advances in understanding coral–microbe interactions. We conclude by highlighting the role of the coral host as a key member of the coral holobiont.

THE CORAL–ALGAL SYMBIOSIS

All reef-building corals exhibit mutualistic associations with symbiotic dinoflagellates in the genus *Symbiodinium*. These algae were originally identified as *Gymnodinium*-like dinoflagellates by Kawaguti (1944), axenically cultured by McLaughlin and Zahl (1959), and formally described (from the scyphozoan *Cassiopeia* sp.) as *Symbiodinium microadriaticum* by Freudenthal (1962). Despite early cautions to the contrary (e.g., McLaughlin and Zahl, 1966), all symbiotic dinoflagellates were initially classified as members of a single pandemic species adapted to life in a symbiotic state (Taylor, 1971; Taylor, 1974). However, beginning in the mid-1970s evidence drawn independently from a variety of approaches (biochemical, physiological, behavioral, morphological, and genetic) indicated that these dinoflagellates were in fact unusually diverse. Then, in the 1990s, our understanding of diversity in *Symbiodinium* was revolutionized by the application of contemporary PCR-based molecular genetics. The use of scuba allowed scientists to collect a wide variety of symbiotic hosts from a broad range of habitats and environmental conditions. These two factors greatly improved our understanding of how *Symbiodinium* diversity can influence the physiology and ecology of various hosts, particularly corals.

Algal Diversity and Distribution

Rowan and Powers (1991) were the first to PCR-amplify and sequence *Symbiodinium* from reef corals. They recognized three distinct clades of *Symbiodinium* (named A, B, and C) and demonstrated that the genetic distance between these clades was comparable to that between some nonsymbiotic dinoflagellate orders. In the 20 years since these articles appeared, further evidence of the extraordinary diversity of this genus has accumulated, with six additional clades now recognized: D (Carlos et al., 1999), E and F (LaJeunesse, 2001; Pochon et al., 2001), G (Pochon et al., 2001), H (Pochon et al., 2004), and I (Pochon and Gates, 2010). However, of the nine clades of *Symbiodinium* (A–I) that have been documented to date, only six have been identified from corals: A, B, and C (first recorded by Rowan, 1991), D (Baker, 1999; see also Rowan, 1991; Baker, 2003), F (LaJeunesse, 2001), and G (Van Oppen et al., 2005). The majority of these studies depended on the use of scuba to collect specimens (Figure 2), and the ready access to diverse specimens obtained using this technology has played an important role in these discoveries. Previously, *Symbiodinium* researchers tended to be restricted to working on cultures, which are highly selected and thus can limit studies of diversity by favoring symbionts that can be cultured over others (Santos et al., 2001).

Our knowledge of how different *Symbiodinium* are distributed within and among different coral species has progressed rapidly over the last decade. Additional clades have been documented, and the diversity of subcladal *Symbiodinium* types within some

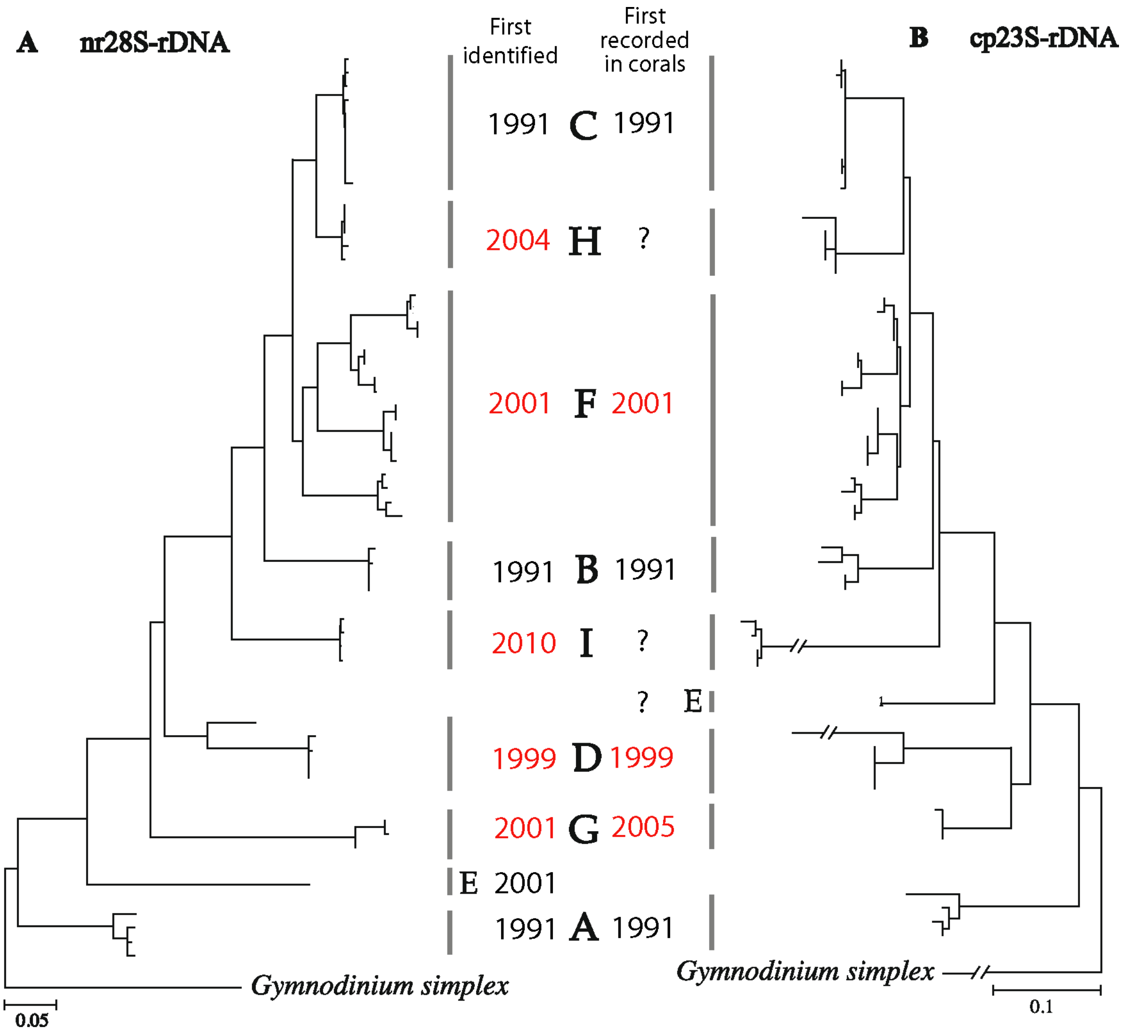

FIGURE 2. Phylogenetic reconstructions of the genus *Symbiodinium* inferred using maximum likelihood analysis of (A) nuclear large subunit ribosomal DNA (nr28S-rDNA) and (B) chloroplast large subunit ribosomal DNA (cp23S-rDNA) (modified from Pochon and Gates, 2010). Next to each of the nine *Symbiodinium* clades (A–I) are the year each clade was first reported (left) and the year each was first recorded in hexacorals or octocorals (right). Discoveries marked in red indicate those that involved scuba to collect field samples. Question marks (?) indicate that *Symbiodinium* in clades E, H, and I have not been detected yet in corals.

clades has been shown to be spectacularly rich (e.g., LaJeunesse, 2002, 2005; Coffroth and Santos, 2005). A long-standing tenet in algal symbiosis holds that different invertebrate host species are specific to particular *Symbiodinium* (Trench, 1989, 1992), and that although a particular symbiont taxon might be found in a variety of diverse hosts, each host species uniquely associates with only one algal type. The use of scuba, combined with the development of PCR-based molecular methods, has allowed researchers to directly test this theory by obtaining snapshots of algal symbiont diversity in corals over time and space. These surveys have shown that while most corals indeed tend to be dominated by particular symbionts (LaJeunesse, 2001, 2002; LaJeunesse et al., 2004a, 2004b; Goulet, 2006; Goulet et al., 2008), many host species show a surprising degree of intraspecific symbiont diversity and exhibit considerable variability over time and space, with ontogenetic and environmental factors often driving observed specificity (Baker, 2003; Baker and Romanski, 2007). The use of scuba has been essential in this research by allowing coral species to be sampled from a variety of different sites, habitats, and depths. Coral species that routinely host multiple symbiont taxa (variously described as "flexible," "generalist," or "polymorphic" coral host species) have been distinguished from other species that have (to date) been found to contain only one particular symbiont type ("specific," "specialist," or "monomorphic" coral species). The reported diversity of symbionts from corals depends to a large degree on the breadth and depth of sampling effort, as well as the taxonomic and numeric resolution of the molecular methods used (Baker and Romanski, 2007). Scuba-based surveys of *Symbiodinium* diversity have therefore been a very active area of research for the last decade.

Rowan and Knowlton (1995) and Rowan et al. (1997) provide early examples of how scuba was employed to reveal these relationships. Their work showed that the dominant Caribbean corals *Montastraea annularis* and *M. faveolata* each contained *Symbiodinium* in three clades (A, B, and C), and that the distribution of clades in these coral species was determined by irradiance, both among colonies at different depths and within individual colonies. Moreover, during bleaching, symbionts in different clades varied in their sensitivity to high-temperature bleaching as a result of differences in their irradiance sensitivity. Together, the two studies convincingly showed that irradiance affects symbiont distribution over a coral landscape. The latter study also showed for the first time the important conclusion that symbiont genotype can directly influence fitness of the coral host.

Symbiodinium distributions also show strong biogeographic patterns. In scleractinian corals, perhaps the most obvious pattern is the contrast between the Atlantic and Indo-Pacific, with corals in the tropical western Atlantic (Caribbean) being codominated by *Symbiodinium* in clades A, B, and C but corals in the Indo-Pacific being dominated by clade C (Baker and Rowan, 1997; LaJeunesse, 2002). In both oceanic provinces, clade D is commonly found in environments characterized by chronic temperature stress (Chen et al., 2003; Baker et al., 2004; Fabricius et al., 2004) or in coral hosts that have recently experienced bleaching (Glynn et al., 2001; Baker et al., 2004; Jones et al., 2008; LaJeunesse et al., 2009a).

More recently, diversity assessments have focused on the identification of symbionts at finer taxonomic scales. LaJeunesse (2001) first formalized these investigations by proposing the Internal Transcribed Spacer 2 region of ribosomal DNA (rDNA) as a suitable marker for investigating subcladal diversity in *Symbiodinium*. This marker has since been extensively used to investigate diversity in samples of natural populations worldwide that were collected using scuba (e.g., LaJeunesse et al., 2010). Additional investigations of fine-scale diversity have used length heteroplasmy in chloroplast large subunit ribosomal DNA (rDNA) to survey symbiont diversity in Caribbean octocorals (Santos et al., 2004) and variation in microsatellite flanking sequences to further assess variation within these types (Santos et al., 2004). Allelic variation in microsatellite loci have been used to screen intraspecific variation in soft corals on the Great Barrier Reef (Howells et al., 2009) and octocorals in the Bahamas and the Florida Keys (Santos et al., 2003; Kirk et al., 2009), and to study reef endemism, stability, and fine-scale host specificity of symbionts in *Montastraea* spp. in the Florida Keys and the Bahamas (Thornhill et al., 2009).

The findings from these studies have revealed that *Symbiodinium* is extraordinary, not just for its taxonomic breadth (nine clades, each of which might ordinarily be considered a genus in its own right), but also for the taxonomic richness within many of these clades, with some (such as clade C) potentially containing dozens of distinct taxa (species), each of which is characterized by additional intraspecific variation. Some debate exists over the functional role of this *Symbiodinium* genetic diversity (Van Oppen and Gates, 2006; Apprill and Gates, 2007), but this has not prevented several new species of *Symbiodinium* from being introduced informally into the literature even though from a genetic standpoint they differ very little (e.g., LaJeunesse et al., 2009b). Drawing generalized conclusions from this sometimes bewildering level of diversity has proved difficult, as evidenced by the fact that no review has yet attempted to reconcile the data from the many dozens of papers published over the last decade. It seems clear that some degree of taxonomic revision is required when one compares diversity within *Symbiodinium* to that found in other groups (Stern et al., 2010), yet there is surprisingly little consensus on how to proceed.

Stability in Coral–Algal Symbiosis through Time

One area where scuba has contributed significantly to our understanding of coral–algal symbiosis is the degree to which the composition of symbiont assemblages in individual coral colonies can change over time. Of particular interest are the role of the environment in controlling potential changes and the importance of human-mediated disturbance, including global climate change, in determining the rate at which change might occur. These ideas were first introduced as the adaptive bleaching hypothesis (Buddemeier and Fautin, 1993). This hypothesis posited that recovery from bleaching provides an opportunity for corals to become populated with different symbionts, and that changes in symbionts might prove beneficial to the coral host (i.e., have adaptive value). These ideas were further refined (Ware et al., 1996) and clarified to include quantitative changes in mixed symbiont assemblages as a result of bleaching (Baker, 2003; Buddemeier et al., 2004; Fautin and Buddemeier, 2004).

Numerous studies have tested this hypothesis and found evidence both in support of it (Baker, 2001; Kinzie et al., 2001; Berkelmans and van Oppen, 2006; Jones et al., 2008) and against it (Goulet and Coffroth, 2003a, 2003b; Rodriguez-Lanetty and Hoegh-Guldberg, 2003; Iglesias-Prieto et al., 2004; LaJeunesse et al., 2004a, 2004b; Kirk et al., 2005; LaJeunesse, 2005; Hannes et al., 2009). Although a consensus has not yet been reached, the combined evidence suggests that changes in symbiont assemblages that occur following bleaching are the result of changes in the relative abundance of preexisting symbionts, not the result of the acquisition of symbionts from external sources during bleaching or initial recovery (Baker, 2004). Although adult corals have been shown to be capable of acquiring symbionts from the environment (Lewis and Coffroth, 2004), these symbionts may be transient (Coffroth et al., 2010) and might not be able to achieve dominance within colonies regardless of environmental conditions or disturbance regime. Consequently, the extent to which bleaching can lead to new symbiotic combinations hypothetically depends largely on which symbionts are already present in the symbiotic assemblage of different coral species. In this context, attempts to identify and quantify background symbionts using real-time PCR are essential in determining whether corals routinely host a variety of symbionts at low abundance, or whether most coral species exclusively host specific symbiont types. An improved understanding of corals' specificity and the molecular, environmental, and ontogenetic factors that drive this specificity will allow us to critically assess the potential for adaptive bleaching in response to changing environmental conditions.

Ontogeny of Coral–Algal Symbiosis

The tremendous dinoflagellate diversity that exists among and often within host species is first established during the early ontogeny of the coral–algal symbiosis. Although in some cnidarian symbioses the symbiont is passed from parent to offspring (vertical or closed symbiont transmission), among the majority of corals, especially corals that free-spawn eggs and sperm, the offspring lack symbionts (aposymbiotic) and must obtain them anew each generation from the surrounding environment (horizontal or open transmission; Stat et al., 2006). Laboratory studies have demonstrated that in corals and other cnidarians initial uptake is relatively nonspecific and a range of different symbiont types can be acquired (Schwarz et al., 1999; Coffroth et al., 2001; Weis et al., 2001; Rodriguez-Lanetty et al., 2004; Poland, 2010). For example, *Montastraea faveolata* and *Acropora palmata* larvae acquired nine of eleven *Symbiodinium* types offered (Table 1) although only a subset of these types are dominant in the adult holobiont. These studies generally demonstrate that although juvenile corals can take up a broad range of potential symbionts early in ontogeny, not all symbionts are ultimately incorporated (or acceptable) to the coral species as adult colonies. These findings are similar to other laboratory studies that show that while newly settled corals and other cnidarians can harbor a diverse range of symbiont types, there is a degree of selectivity within the coral host such that not all types offered are taken up and even fewer are able to establish and sustain the symbiosis (Coffroth et al., 2001; Weis et al., 2001; Rodriguez-Lanetty et al., 2006; Mieog et al., 2009; Voolstra et al., 2009b).

TABLE 1. Different strains of *Symbiodinium* used to infect larvae of *Montastraea faveolata* (6d) and *Acropora palmata* (8d). Strain nomenclature is based on sequence variation in the 23S rDNA gene. Symbols: (-) indicates no infection observed; (+) and (++) indicate intensity of infection observed.

Culture	Strain	*M. fav.*	*A. pal.*
Control	None	-	-
ELI	A198	-	-
KB8	A194	++	++
04-503	A194	++	++
Acp343	B184	-	-
Mf1.05b	B184	++	++
Mf1.05b.01	B184	++	++
Mf10.14b.02	B224	++	++
Mf11.05b.01	B224	++	++
Mf6.07B	F178	+	+
Mf8.3T	F178	++	+
Mf10.08	D206	++	++

While these laboratory studies are informative of the potential symbiont diversity within cnidarian symbioses, in nature the symbiont pool is more diverse. Field studies enabled by scuba of initial host infection have shown that the developing coral acquires a wide assortment of *Symbiodinium* by accepting not only multiple strains from the same clade, but also multiple clades. This diversity is recorded both within and among juveniles (Coffroth et al., 2001; Little et al., 2004; Coffroth et al., 2006; Thornhill et al., 2006; del C. Gómez-Cabrera et al., 2008; Abrego et al., 2009a, 2009b; Mieog et al., 2009; Poland et al., 2013. For example, using scuba to deploy recruits to the reef and then monitor symbiont uptake over time, Poland et al. (2013) found between five and nine symbiont types among newly settled octocoral recruits (*Briareum asbestinum*) at any site or during any year (symbiont richness). Within the individual recruits, however, the majority hosted one or two symbiont types simultaneously. Fewer recruits (0.2% or less) harbored five or six symbionts simultaneously, even when the total number of symbiont types found across all juveniles at a particular site and/or year was higher (i.e., the diversity of available symbionts was higher than *in hospite* diversity within a single juvenile (Poland et al., 2013). This leads to a symbiont complement within and among newly settled recruits that is more diverse than that within the adult holobiont (Coffroth et al., 2001; Little et al., 2004; Coffroth et al., 2006; del C. Gómez-Cabrera et al., 2008; Abrego et al., 2009a, 2009b; Thornhill et al., 2009).

Many studies confirm that the symbiont type initially acquired by a host is often not the symbiont type that predominates in the adult symbiosis. Some host species may acquire the symbiont types found within the adult along with other symbiont types (Coffroth et al., 2001; Weis et al., 2001; del C. Gómez-Cabrera et al., 2008), while in other host species the symbiont type that predominates in the adult symbiosis is not detected initially in symbiont assemblages of the juveniles (Little et al., 2004; Thornhill et al., 2006; Abrego et al., 2009a; Poland, 2010; Poland et al., 2013). For example, in a study utilizing clade-level analysis (del C. Gómez-Cabrera et al., 2008), newly settled recruits (10d) of *Acropora longicyathus* harbored mainly clade A *Symbiodinium* although clade C *Symbiodinium* dominated the adult symbiosis. After 83d, the proportion of *Symbiodinium* clade A decreased, *Symbiodinium* type C increased, and *Symbiodinium* type D was also observed. Similar observations have been reported for other acroporids (*A. tenuis* and *A. millepora*) where juveniles quickly acquired *Symbiodinium* within clade D although adults of these species predominantly harbor *Symbiodinium* types within clade C (Little et al., 2004; Abrego et al., 2009a, 2009b). Contrasting symbiont diversity among juveniles (higher) versus adult (lower) hosts is also seen in other groups such as octocorals, scyphozoans, and tridacnid clams (Coffroth et al., 2001; Belda-Baillie et al., 2002; Thornhill et al., 2009). In each of these studies, the use of scuba enabled the high-resolution sampling of the adult colonies, the detailed placement of new recruits at different sites, and the careful monitoring of symbiont uptake. These studies imply that over time (hours to years) a winnowing process occurs (sensu Nyholm and McFall-Ngai, 2004), so that only one to a few types establish and sustain the long-term symbioses found in the adults (Coffroth et al., 2001; Weis et al., 2001; Belda-Baille et al., 2002; Little et al., 2004). In some species this winnowing process involves large-scale, clade-level changes (e.g., Abrego et al., 2009a, 2009b) whereas among other groups the change is seen at the subcladal level (e.g., Poland, 2010). In some corals, the symbiont assemblage that is typical of an adult host colony does not become established until three to four years into the coral's ontogeny (Abrego et al., 2009b; Poland, 2010). It is not presently resolved at this time if this is the case in the majority of host species.

Future Directions

Scuba has enabled us to routinely sample symbiont diversity within important reef symbioses and to conduct careful in situ experiments to elucidate mechanisms that might be driving this diversity. However, we are still faced with many unanswered questions. Although numerous studies have contributed knowledge of processes involved in the initial infection and winnowing (e.g., Lin et al., 2000; Rodriguez-Lanetty et al., 2004; Wood-Charlson et al., 2006; Dunn and Weis, 2009; Voolstra et al., 2009a), the underlying processes and the ecological significance of initially accepting multiple types and then narrowing the assemblage to a single or a few types remains to be elucidated.

CORAL–MICROBIAL ASSOCIATIONS

Corals possess a high abundance and diversity of associated bacteria and archaea in their tissues, carbon-rich surface mucus layers, and skeletons (Ferrer and Szmant, 1988; Banin et al., 2000; Frias-Lopez et al., 2002; Rosenberg, 2007; Rosenberg et al., 2007; Shnit-Orland and Kushmaro, 2009). The diversity of coral-associated microbes has now been reasonably well documented using a variety of culture-independent gene surveys of microbial diversity (Rohwer et al., 2002; Bourne and Munn, 2005; Wegley et al., 2007; Thurber et al., 2009; Sunagawa et al., 2010). These surveys indicate that it is typical for a single coral to house many of the known divisions of bacteria. We now recognize this diversity, yet the functional roles and influences (positive, negative, or neutral) of the different microbes within these diverse coral–microbial assemblages are still poorly understood.

There are clear examples of microbes negatively impacting the coral host, most notably the pathogenic microbes associated with more than twenty documented coral diseases (Sutherland et al., 2004; Rosenberg et al., 2007; Bourne et al., 2009) and the case of *Vibrio*-induced coral bleaching (Kushmaro et al., 1996; Rosenberg et al., 2007). There are also clear examples of positive impacts of coral-associated microbes (Mouchka et al., 2010), including their roles in nutrient cycling (Rohwer et al., 2002; Lesser et al., 2004; Wegley et al., 2004; Beman et al., 2007; Wegley et al., 2007) and the production of antimicrobial compounds (Kelman et al., 1998; Ritchie, 2006; Nissimov et al., 2009; Mao-Jones et al., 2010; Rypien et al., 2010). In many cases, however, we still do not have a good picture of what natural, versus perturbed, coral–microbial assemblages look like, and it has been difficult to document clear species-specific associations between microbes and their coral host, including symbiotic microbial associations. Despite these knowledge gaps, coral–microbiological research has made great strides over the last 20–30 years. Here we focus on two recent advances in coral–microbial research: (1) increased knowledge of the ontogeny of coral–microbe associations and (2) the use of coral metagenomics to characterize microbial diversity and function. Both promise to transform our understanding of coral–microbial interactions.

The Ontogeny of Coral–Microbe Associations

While our understanding of the nature of the coral–algal symbiosis has improved greatly in recent years, only recently has research focused on the ontogeny of coral–microbial associations.

Pioneering work on this subject comes from two studies (Apprill et al., 2009; Sharp et al., 2010) wherein the authors followed the establishment of the microbial assemblage through the early stages of larval development in multiple broadcast-spawning corals. The first study, by Apprill et al. (2009), examined the ontogeny of microbial associations in the Hawaiian coral *Pocillopora meandrina*, a broadcast-spawning coral that vertically transmits its algal symbionts by seeding its eggs with *Symbiodinium* cells. Apprill et al. (2009) found that unlike vertically transmitted algal symbionts, bacteria are not taken up vertically but instead are acquired horizontally from the environment by the planula larvae after approximately 79 hours in the water column. Interestingly, they discovered that a clade of *Roseobacteria* in the genus *Jannaschia* consistently associated with the coral planula larvae. *Roseobacteria* are known to form associations with both phytoplankton and *Symbiodinium* (Littman et al., 2009b; Littman et al., 2010). This suggests that they might be associated with *Symbiodinium* inside the coral host, and yet if that is the case it is not clear why they would not be transmitted vertically with the *Symbiodinium* in *Pocillopora* eggs.

The second study, by Sharp et al. (2010), examined the ontogeny of microbes associated with seven species of broadcast-spawning corals (both Pacific and Caribbean species) that do not vertically transmit *Symbiodinium* in their eggs. By following the development of bacterial associations from the coral gametes through the swimming planulae to the newly settled polyps by using fluorescence in situ hybridization (FISH) techniques, Sharp et al. (2010) showed that microbes were only prevalent in the corals in the settled polyp stage (i.e., postsettlement), rather than established in the planula larvae as observed by Apprill et al. (2009) in *Pocillopora*. Taken together, these early results indicate that the ontogeny of these microbial associations differ in their timing depending on the coral. Nothing is known yet about microbial transmission in coral species that brood larvae, where vertical transmission of *Symbiodinium* is the most common mode.

Work by Littman also sheds light on how microbial assemblages change during ontogeny. Newly settled corals have a far more diverse microbial assemblage than older recruits, which are characterized by relatively more predictable, lower-variance assemblages (Littman et al., 2009b). This suggests a winnowing process whereby the more diverse microbial assemblage of juveniles is gradually replaced by the more characteristic adult microbial assemblage, much like what is seen with *Symbiodinium*. This ontogenetic pattern coupled with persistent variation in composition among sites (Littman et al., 2009b) provides a large role for environment in determining final composition.

CORAL METAGENOMICS

Next-generation sequencing techniques are providing unprecedented access to and information about the genetic diversity of coral-associated microbes. Culture-independent genetic profiles of coral–microbial assemblages have become a mainstay of coral microbiology and are the primary tool used to examine the diversity, abundance, and associations of microbes on corals. The first genetic surveys relied heavily on Sanger sequencing bacterial 16s rDNA diversity from coral microbe clone libraries. Sequencing 16s rDNA clone libraries from corals revealed the high microbial diversity on corals (Rohwer et al., 2002; Bourne and Munn, 2005; Pantos and Bythell, 2006; Sunagawa et al., 2009), but the depth of sequencing has typically been limited to tens to hundreds of sequences per coral sample because of the high cost. Recent advances in high-throughput sequencing techniques now allow us to profile coral microbial diversity across hundreds of thousands, even millions, of sequences (Sunagawa et al., 2010) using either a target gene approach, like 16s rDNA sequencing (Sunagawa et al., 2009, 2010), or a metagenomic approach where the DNA or RNA content of an entire sample is shotgun sequenced, assembled, and annotated by bacterial group and gene function (Dinsdale et al., 2008a; Vega Thurber et al., 2008, 2009).

Deep-sequencing profiles of microbial 16s rDNA diversity from seven Caribbean corals (Sunagawa et al., 2010) uncovered even greater levels of novel coral-associated microbial diversity than had been seen with traditional Sanger 16s rDNA sequencing efforts. The Sunagawa et al. (2010) study also indicates that each coral species harbors an unprecedented level of endemic microbial diversity, toppling prior estimates of diversity in coral reef ecosystems (Sunagawa et al., 2009, 2010). While there was an overlapping of the microbial lineages from the adjacent water column and those from the sampled coral species, the large number of microbial taxa that were present on each coral species suggests that coral research will continue to contribute newly discovered microbes to science (Sogin et al., 2006; Pedros-Alio, 2007). These findings add an important microbial diversity–based perspective to the significance of conserving coral reefs.

Recent metagenomic approaches applied to corals demonstrate that it is possible to simultaneously profile coral microbes with rDNA sequences and categorize and annotate functional genes (Wegley et al., 2007; Dinsdale et al., 2008a, 2008b; Marhaver et al., 2008; Vega Thurber et al., 2008, 2009). Wegley et al. (2007) first demonstrated that metagenomics could be used to successfully profile the coral microbiome—including the algal, fungal, bacterial, and viral components—as well as to characterize the responses of members of the coral holobiont based on the function of particular gene sequences. The Wegley et al. (2007) study documented the high abundance of viral phages on corals plus an underappreciated role of fungi in nitrogen fixation.

Thurber et al. (2009) extended this coral metagenomic approach and profiled the changes in coral–microbial assemblages on *Porites compressa* associated with four important coral stressors: increased temperature, increased nutrients, increased dissolved organic carbon, and higher acidity (i.e., lower pH). They observed strong shifts in the microbial assemblages between healthy and stressed corals, as well as shifts to genes involved in virulence and stress resistance due to coral stress. Interestingly, their results indicate that *Vibrios* caused strong shifts in the microbiome metabolic profiles during the temperature-stress treatment.

Future Research Directions for Coral–Microbial Interactions

New insights into the ontogeny of coral–microbial interactions and metagenomic approaches are allowing us to characterize the onset and dynamics of coral–microbial assemblages with more depth than ever before. Significant questions remain about the specific roles of particular microbial groups in corals. For instance, what is the role of the microbial assemblage in host fitness? How flexible is the partnership between corals and their microbial assemblage in coping with climate change? How flexible is the partnership between the a coral host's *Symbiodinium* of choice and its algal-associated microbes? If the coral–algal symbiosis is being threatened by chronic stress, are there microbial-antagonistic effects driven by the holobiont or are opportunistic microbes driving the holobiont physiology?

EMERGING ROLE OF THE CORAL HOST

Although great strides have been made that increase our understanding of the importance and roles of *Symbiodinium* and microbial diversity in corals, we know far less concerning the role of the coral host in regulating and maintaining this diversity. This lack of knowledge about the role of the coral host has in some cases led to bias in favor of the importance of algae or microbes in the relationship (Baird et al., 2009). For example, studies of *Symbiodinium* diversity and flexibility have suggested that changes in algal symbiont assemblages will help corals survive environmental change but have tended to downplay how coral specificity might limit this process (Baker, 2001; Baker et al., 2004; Berkelmans and van Oppen, 2006; Jones et al., 2008). Similarly, with coral–microbe interactions, the probiotic hypothesis championed by some coral microbiologists proposes that microbes regulating microbes act as the de facto coral immune system (Ben-Haim et al., 2003; Rosenberg et al., 2007a, 2007b) even though there is clear evidence that coral have innate immune systems as well (Mydlarz et al., 2006, 2010; Miller et al., 2007; Dunn, 2009). Yet new data from coral genomics and transcriptomics are providing novel insights into the genetic mechanisms controlling the relationship between the coral host and its algal symbionts, and into the nature of coral immunity.

The Role of Coral Genomics

Recent advances in coral genomics and transcriptomics are elevating our understanding of the role that the coral host plays in maintaining the stability of the coral holobiont. Gene expression analyses using microarrays have examined the response of the coral host to a variety of environmental stimuli during early ontogeny (Grasso et al., 2008; Reyes-Bermudez et al., 2009; Voolstra et al., 2009a; Polato et al., 2010; Portune et al., 2010) as well as in adult colonies (DeSalvo et al., 2008; Reyes-Bermudez et al., 2009; DeSalvo et al., 2010a, 2010b). Transcriptome profiles of larvae exposed to different choices of *Symbiodinium* strains were correlated with the profiles of unsuccessfully infected larvae, and the profiles of control larvae were correlated with those of successfully infected larvae (Voolstra et al., 2009b), suggesting that successful *Symbiodinium* strains enter the host in a stealth manner rather than triggering a cellular response (Voolstra et al., 2009b). In the case of adult symbioses under slight stress (e.g., thermal), particularly in the coral *Montastraea faveolata*, which harbors multiple strains at once, the transcriptome response seems to be driven mainly by the algal complement (DeSalvo et al., 2010a). In contrast, when the stress is severe the transcriptome profiles indicate clear cellular responses driven by the host coral (DeSalvo et al., 2008).

Recently there has been an explosion of next-generation sequencing that is expanding this initial set of coral and algal transcriptomes, but few are published (Meyer et al., 2009; Meyer and Matz, 2010). With costs dropping and high-throughput capacity increasing exponentially, de novo whole-genome shotgun sequencing is now within reach for coral reef science. Several coral, *Symbiodinium*, and microbial genome projects are expected to come online in the near future. Once host, algal, and microbe genomes are complete, and as transcriptome sequencing becomes more commonplace, our ability to move coral research to a systems biology level will be greatly enhanced and new "-omic" technologies can be brought into the study of the coral holobiont.

Coral Immunity

Recent progress also has been made in understanding the coral immune response in fighting off disease (reviewed by Mydlarz et al., 2006, 2010; Miller et al., 2007; Dunn, 2009) as well as in the coral–algal symbiosis (Weis, 2008; Weis et al., 2008; Weis and Allemand, 2009). Like other invertebrates, corals have innate immune systems capable of self-/non-self-recognition (Hildemann et al., 1975; Neigel and Avise, 1983) and the ability to identify and react to pathogen infection (Mydlarz and Harvell, 2007; Mydlarz et al., 2008, 2009, 2010). Recent genetic surveys demonstrate that corals and their anthozoan relatives possess a relatively full set of the genes and gene pathways involved in innate immunity (Miller et al., 2007; Dunn, 2009; Mydlarz et al., 2010), including the three major innate immune pathways: the Toll-like receptor (TLR) pathway (Miller et al., 2007), the Lectin Complement pathway (Miller et al., 2007; Kvennefors et al., 2010), and the Prophenoloxidase (PPO) pathway (Mydlarz et al., 2008). Corals lack adaptive immunity (i.e., immune specificity and memory), which is restricted to jawed vertebrates.

To date, most of the information that we know about the immune responses of corals (hard and soft) comes from histological and biochemical data focused on specific immune assays from a few coral species (Mydlarz et al., 2010). Histological data suggest that mobile amoebocytes, which move between the coral ectoderm and endoderm in the mesoglea, act like immune cells and aggregate at regions where tissues are damaged (Mydlarz et al., 2008, 2009; Palmer et al., 2008). For example, Mydlarz et al. (2008) documented aggregations of these mobile amoebocytes in the sea fan *Gorgonia ventalina* at the site of infection by pathogenic *Aspergillus sydowii* fungus. Likewise, in the reef coral *Acropora millepora* Palmer et al. (2008) documented amoebocyte aggregations associated with inflammation and melanization in abnormally pigmented coral tissues. Other studies reveal potential for antioxidant activity associated with coral fluorescent proteins (Palmer et al., 2009). Recent work increases the taxonomic range of comparison to 10 coral families and shows links between susceptibility to bleaching and disease and sizes of melanin granules, levels of PPO activity, and fluorescent proteins (Palmer et al., 2010).

At the biochemical or genetic level, characterizations of the coral immune response thus far have focused primarily on the Prophenoloxidase (PPO) pathway using biochemical assays of enzymatic activity. Prophenoloxidase immune response acts via the PPO pathway, which causes pathogens to be targeted, encapsulated in melanin, and ultimately degraded by phagocytosis (Mydlarz et al., 2006, 2008, 2010). Increased PPO activity and melanization has been detected in *Aspergillus*-infected sea fans (Mydlarz and Harvell, 2007; Mydlarz et al., 2008), as well as in the pigment anomalies in the reef coral *A. millepora* (Palmer et al., 2008) and in bleached *Montastraea faveolata* corals (Mydlarz et al., 2009). These data suggest that melanization and degradation by the PPO pathway is an important innate immune response in both soft and hard corals. No one has yet profiled the immune response of an infected coral using gene-expression approaches across the full range of possible immune pathways, and thus it is not yet known what other pathways might be important in coral immunity in general.

Weis and colleagues (Weis, 2008; Weis et al., 2008) have begun to focus on the potential links between the coral innate immune response and the relationship between the coral host and its symbiotic algae. According to the current hypotheses, one key to the maintenance of the coral–algal symbiosis is the ability of symbionts to modify the host's immune response. Algal symbionts are contained in specialized vacuoles in the coral endoderm and are acquired through a process similar to phagocytosis of pathogens. Early data suggest that the acquisition of the symbionts is mediated by pattern recognition receptors (PRR) (Weis et al., 2008), such as lectins (Wood-Charlson et al., 2006; Kvennefors et al., 2010), that are down-regulated during the early ontogeny of the coral–algal symbiosis (Wood-Charlson et al., 2006). Phagocytosis also appears to be arrested during symbiont acquisition (Chen et al., 2005; Schwarz et al., 2008) and reactivated when nonspecific symbiont types enter the host cells (Dunn and Weis, 2009). These preliminary data suggest that there is a strong and important link between the coral immune system and the evolution of the coral–algal symbiosis that warrants further investigation.

FUTURE DIRECTIONS

These recent studies demonstrate that the coral host has a viable innate immune system and can respond to pathogen infection. Genetic data examining the relationship between the coral host and its symbionts also indicate clear links between the innate immune response of the coral and the mechanisms by which algal symbionts become established within their hosts. These early findings are just beginning to elucidate how the coral immune system operates and how symbionts evade or modify the host's immune response during uptake. Many questions remain unanswered. For example, does the innate immune response show specificity according to the type of pathogens (i.e., viral, bacterial, or fungal)? If so, what innate immune pathways are involved? Similarly, if *Symbiodinium* modifies the immune response during uptake, what genes or gene pathways are also modified and how does this impact coral innate immunity? In the future, experimental work combining infection experiments and genetics promises to answer these questions about the nature of coral innate immunity and the role of the coral host in responding to pathogen and symbiont infection.

CONCLUSIONS

Great progress has been made in understanding the nature of the interactions within the coral holobiont since Rohwer et al. (2002) proposed the concept. We now have a much stronger understanding of the coral–algal symbiosis, including knowledge about its ontogeny, specificity, and flexibility. Knowledge about the nature of coral–microbe interactions is growing by leaps and bounds with increasing interest in coral microbiology and the incorporation of new (meta) genomic techniques to address questions about the makeup and dynamics of coral microbial assemblages. Knowledge about the role of the coral host is growing as we gain insights into the nature of coral innate immunity, including how pathogens are detected and how eukaryotic and/or microbial symbionts modify response or elude detection. As we continue to progress, the concept of the coral holobiont will remain important because the greatest strides in the field will be made by understanding how the complex sets of organisms making up the coral holobiont— the coral host and associated eukarya, bacteria, archaea, and viruses—interact and function both synergistically and sometimes antagonistically as a community or ecosystem.

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The Nature of Macroalgae and Their Interactions on Reefs

Mark M. Littler and Diane S. Littler

ABSTRACT. What was known about tropical reef algae prior to the use of scuba came largely from dredging studies or drift collections, which usually resulted in highly mutilated specimens and questionable habitat data. Scuba allows a precise determination of ecological conditions and permits in situ photography, two techniques our group has relied on during the past three decades for quantitative studies and field guide production. A goal of this review is to familiarize the scientific diving community with the kinds and roles of algae on tropical reefs, with the hope that seaweeds will be utilized more fully as tools for addressing important ecological questions.

Because of the rapid degradation of tropical reefs worldwide, it is imperative that the role and diversity of macroalgae be studied in a timely, efficient, and scientifically verifiable manner. It is of paramount importance to characterize the world's coral reef environments and to understand the responses of foundation species. The fleshy macroalgal forms are the food of herbivores, and only become abundant when their production rate exceeds the capacity of herbivores to consume them. On healthy oligotrophic coral reefs, even very low nutrient increases may shift relative dominance from corals (Cnidaria) to macroalgae by both stimulating macroalgal production and inhibiting corals. As a result, frondose macroalgae are generally recognized as harmful to the longevity of coral reefs due to the link between excessive blooms and coastal eutrophication.

Reef plant complexity has evolved along very different evolutionary lines. The range of sizes, shapes, life histories, pigments, and biochemical and physiological pathways is remarkable. The biodiversity of coral reef plant life is unequalled. Macroalgae from four evolutionary lines dominate and, in conjunction with coelenterate corals, are the primary producers and builders of coral reef habitats and carbonate architecture. Previously, marine plants were understudied on coral reefs; however, new scuba-based field guides are alleviating this problem. Their rapid growth and short generation time make them ideal subjects for experimental studies.

INTRODUCTION

While extensive taxonomic and distributional data were derived before diving was common in the collection of algae (Boergesen, 1916; Taylor, 1960), scuba has afforded science the opportunity to greatly expand the understanding of the nature of macroalgal diversity with new species, new distribution data, and the mechanisms by which diversity is produced and maintained in reef systems. This of course is true for all three groups of eukaryotic algae—Rhodophyta (red algae), Chlorophyta (green algae), and Phaeophyceae

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(brown algae)—as well as the larger prokaryotic, colony-forming cyanobacteria/Cyanophyta (blue-green algae). These four groups do not have a common ancestor (i.e., collectively polyphyletic) although chloroplasts—common to all the eukaryotes—appear to have had a single blue-green algal (cyanobacteria) origin. The presence of chloroplasts and subsequent capacity for photosynthesis gives marine macroalgae ecological roles as primary producers that are similar to other marine plants, notably sea grasses. Sea grasses are not seaweeds; rather, they are rooted flower- and seed-bearing "higher" plants (Angiosperms).

The macroalgal thallus (i.e., plant body) consists of filaments, sheets and blades (leaflike laminae), reproductive sori (spore clusters), gas bladders (floatation organs on blades in rockweeds, and between lamina and stipes in kelps), stipes (stemlike structures [may be absent]), and holdfasts (with or without haptera, fingerlike extensions anchored to substrates). The stipe and blade combined are known as the frond.

Macroalgae grow attached to stable substrata in seawater (or brackish water) under light levels sufficient for photosynthesis. Seaweeds are most commonly found in shallow waters on rocky shores; however, the giant-celled green algal group Bryopsidales includes rhizoidal forms adapted to proliferating in sedimentary environments. At the shallowest level are algae that inhabit the high-intertidal spray zone whereas at the deepest level are forms attached to the seabed under as much as 295 m of water (Littler and Littler, 1994; see Littler and Littler, this volume: "Coralline Algae," fig. 13,). The deepest macroalgae are calcified crustose coralline species (Rhodophyta).

HUMAN UTILIZATION OF MACROALGAE

Macroalgae have a variety of uses. They are utilized extensively as food by coastal cultures, particularly in Southeast Asia. Seaweeds are also harvested or cultivated using scuba or hookah for the extraction of alginate, agar, and carrageenan—gelatinous substances collectively known as hydrocolloids or phycocolloids. Colloids have great commercial importance, especially in the production of food additives. The gelling, water-retention, emulsifying, and other physical properties of colloids are critical to the food industry. Agar is used in foods such as candies, canned meats, desserts, bottled drinks, and gelatin molds. Carrageenan is used in the manufacture of salad dressings, condiments, and dietary foods, and as a preservative in canned meat and fish, milk products, and bakery goods. Alginates are utilized for many of the same purposes as carrageenan, but are also used in the production of paper sizings, glues, colorings, gels, explosive stabilizers, fabric prints, hydrosprays, and drill lubricants. Macroalgae have long been used as fertilizers and soil conditioners. Seaweeds are currently being investigated as sources of biodiesel and biomethane. Algal extracts are also widely used in toothpastes, cosmetics, and paints.

In the biomedical and pharmaceutical industries, alginates are used in wound dressings and production of dental molds. In diagnostic microbiological research, agar is the culture substrate of choice for pathogens. Seaweeds are also sources of iodine, an element necessary for human thyroid function. The vast array of natural products that algae produce represents a gold mine of potential medicinal compounds and is presently being investigated using both scuba and submersibles.

ECOLOGICAL SIGNIFICANCE OF MACROALGAE

The concepts of top-down and bottom-up controls have long been used (e.g., Atkinson and Grigg, 1984; Carpenter et al., 1985) to describe mechanisms where either the actions of predators or resource availability regulates the structure of aquatic communities. These opposing concepts can be particularly useful in understanding complex coral reef ecosystems. The Relative Dominance Model (RDM; first proposed by Littler and Littler, 1984) predicts that the competitive outcomes determining the relative abundances of corals, crustose coralline algae, microalgal turfs, and frondose macroalgae on coral reefs are most often controlled by the complex interactions of environmental factors (bottom-up controls such as nutrient levels) and biological factors (top-down controls such as grazing).

The study of top-down control of macroalgae by abundant populations of large mobile herbivores is particularly well developed for coral reefs, beginning over five decades ago with the caging study of Stephenson and Searles (1960). As examples, Sammarco et al. (1974), Ogden and Lobel (1978), Sammarco (1983), Carpenter (1986), Lewis (1986), Morrisson (1988), and numerous other researchers (reviewed by McCook et al., 2001) have demonstrated that lowering herbivory usually results in rapid increases in fleshy algae. However, when coral reefs are exposed to increases in nutrients, fleshy macroalgae (Figure 1) may be favored over the slower-growing but highly desirable corals (Lapointe et al., 1997). On healthy oligotrophic coral reefs, even very low nutrient increases may exceed critical levels and shift relative dominances by stimulating macroalgal biomass production while inhibiting corals (Littler and Littler, 1984). Large biomasses/standing stocks of slow-growing perennial macroalgae (e.g., rockweeds) can, given sufficient time, develop even under low inorganic nutrient concentrations (McCook, 1999). Also, *Sargassum* spp. can coexist with corals in oligotrophic waters by utilizing particulate organic sources of nutrients (Schaffelke, 1999). This information suggests that large macroalgal biomasses do not necessarily require, nor indicate, detrimentally abundant dissolved nutrients.

Fleshy macroalgae can outcompete corals (Birkeland, 1977; Bellwood et al., 2006), many of which are inhibited under elevated nutrient levels (reviewed in Marubini and Davies, 1996). Fast-growing macroalgae are opportunists that benefit from disturbances, which release space resources from established, longer-lived organisms. They can also take over space from living

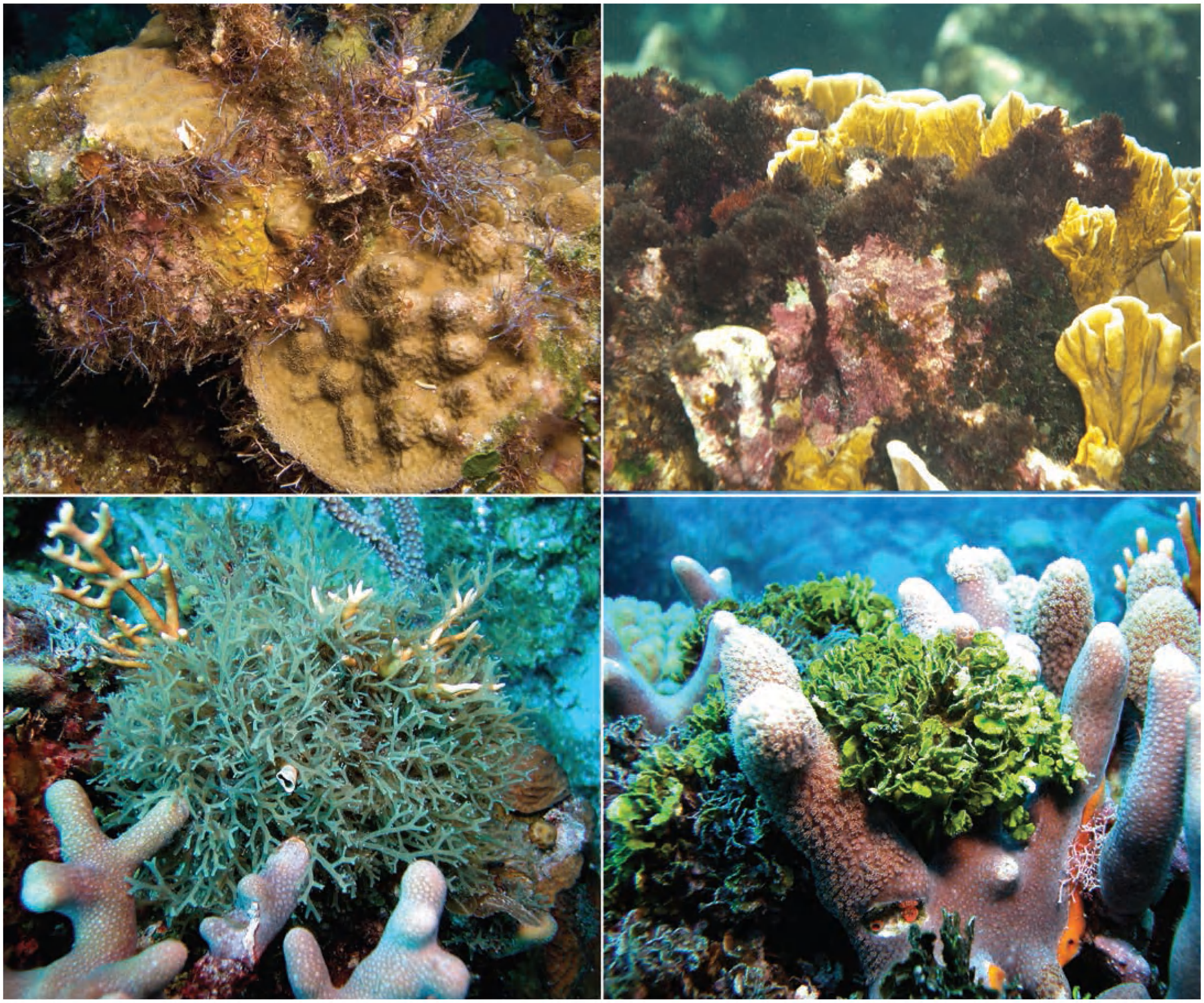

FIGURE 1. Ecological interactions (competition) between coral and algae. Top left: *Coelothrix irregularis*. Top right: *Laurencia obtusa*. Bottom left: *Dictyota cervicornis*. Bottom right: *Halimeda opuntia*. (Photos by D. Littler.)

corals (Birkeland, 1977) when provided with sufficient nutrients. As a result, frondose macroalgae (those that form carpets of horizontal thalli) are generally recognized as harmful to coral reefs due to the link between excessive blooms of these algae and coastal eutrophication (Anderson, 1995). The competitive dominance of fast-growing macroalgae is inferred from their overshadowing canopy heights as well as from inverse correlations in abundances between algae and other benthic producers (Lewis, 1986), particularly under elevated nutrient concentrations (e.g., Littler et al., 1993; Lapointe et al., 1997). Macroalgae, such as *Halimeda* spp. (Figure 2), also can gain competitive advantage by serving as carriers of coral diseases (Nugues et al., 2004). The fleshy macroalgal form group has proven to be particularly attractive to herbivores (see Hay, 1981; Littler et al., 1983a, 1983b) and only becomes abundant where grazing is lowered or swamped by excessive algal growth (chemically defended forms such as cyanobacteria [Figure 3; Paul et al., 2007] are exceptions). Overcompensation with high levels of herbivory may explain some of the reported cases (e.g., Smith et al., 2001) of specific corals surviving high-nutrient coral reef environments.

FIGURE 2. *Halimeda opuntia* overgrowing coral. (Photo by D. Littler.)

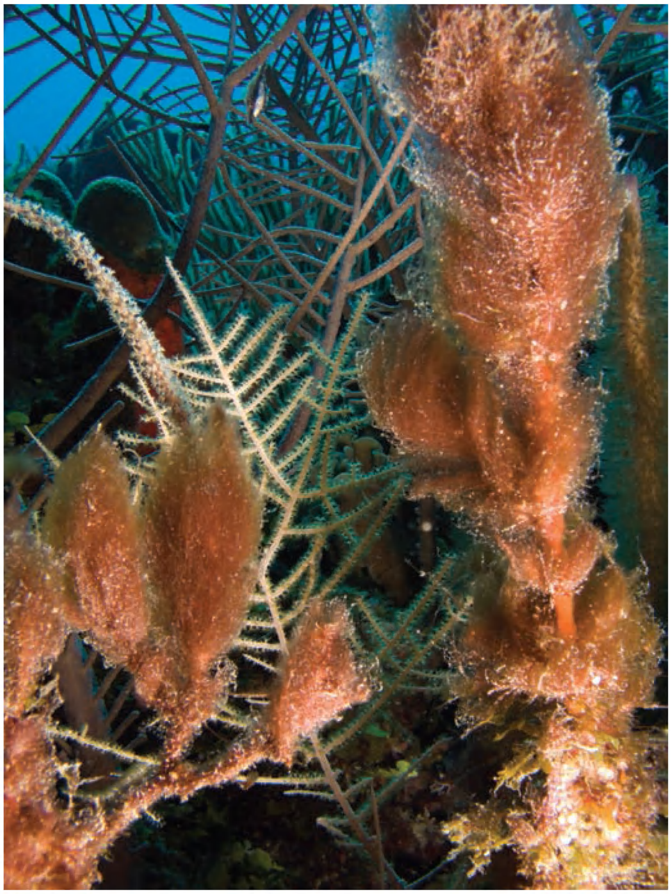

FIGURE 3. *Lyngbya polychroa*, a chemically defended blue-green alga. (Photo by D. Littler.)

MAJOR MACROALGAL GROUPS

What was known about tropical reef algae prior to the use of scuba came largely from shipboard dredging studies or drift collections. These often produced highly mutilated specimens and lacked habitat data since the scope of the dredge cable varied greatly. Scuba allows a precise determination of ecological conditions and permits in situ photography, two techniques our group has relied on during the past three decades for quantitative studies and field guide production. A goal of our three reviews in this volume is to familiarize the scientific diving community with the kinds and roles of algae on tropical reefs, with the hope that seaweeds will be utilized more fully as tools for addressing important ecological questions. The critical role that seaweeds play in reef ecosystems overlaps other fields of marine sciences, such as fisheries resources, marine chemistry, ecology, geology, and coral reef conservation.

RHODOPHYTA (RED ALGAE)

Rhodophyta generally have large quantities of the red pigment phycoerythrin in their photosynthetic cells. This red pigment in combination with various other pigments is responsible for the vast array of colors ranging from translucent pale pink, lavender, purple, maroon, and burgundy to iridescent blue (Figure 4). The pigment phycoerythrin is water soluble; therefore, red algae immersed in hot water will stain the liquid red or pink and the thalli will eventually turn green. Other red-algal cellular characteristics include eukaryotic cells lacking motile gametes (without flagella and centrioles), floridean starch as the food reserve, and (if present) chloroplasts containing unstacked thylakoids without an external endoplasmic reticulum. Pit connections and pit plugs are unique and distinctive features of red algae that form during the process of cytokinesis following mitosis. Most red algae are also multicellular, macroscopic, and reproduce sexually. They display alternation of life-history phases including a gametophyte phase and two sporophyte phases.

The red algae are almost exclusively marine and are the largest and most diversified group of tropical reef plants, with population estimates of up to 10,000 species. The diversity of their forms is astonishing, ranging from small filamentous turfs to some of the larger and most beautifully delicate organisms on coral reefs (Figure 4). Calcareous red algae can dominate some reefs and often surpass corals in reef-building importance (e.g., *Porolithon (Hydrolithon) craspedium*; Figure 5). Most often, corals (Cnidaria) supply the bulk building blocks whereas coralline algae do much of the cementing together of debris. The crustose coralline algae (forms that deposit a type of calcium carbonate [calcite] that is harder and denser than the aragonite of corals) also build the algal ridge (see Littler and Littler, this volume: "Coralline Algae," fig. 9) on many reef systems. By absorbing wave energy, the raised algal ridge not only protects land masses that would otherwise erode, but also shelters the more delicate corals and other reef organisms.

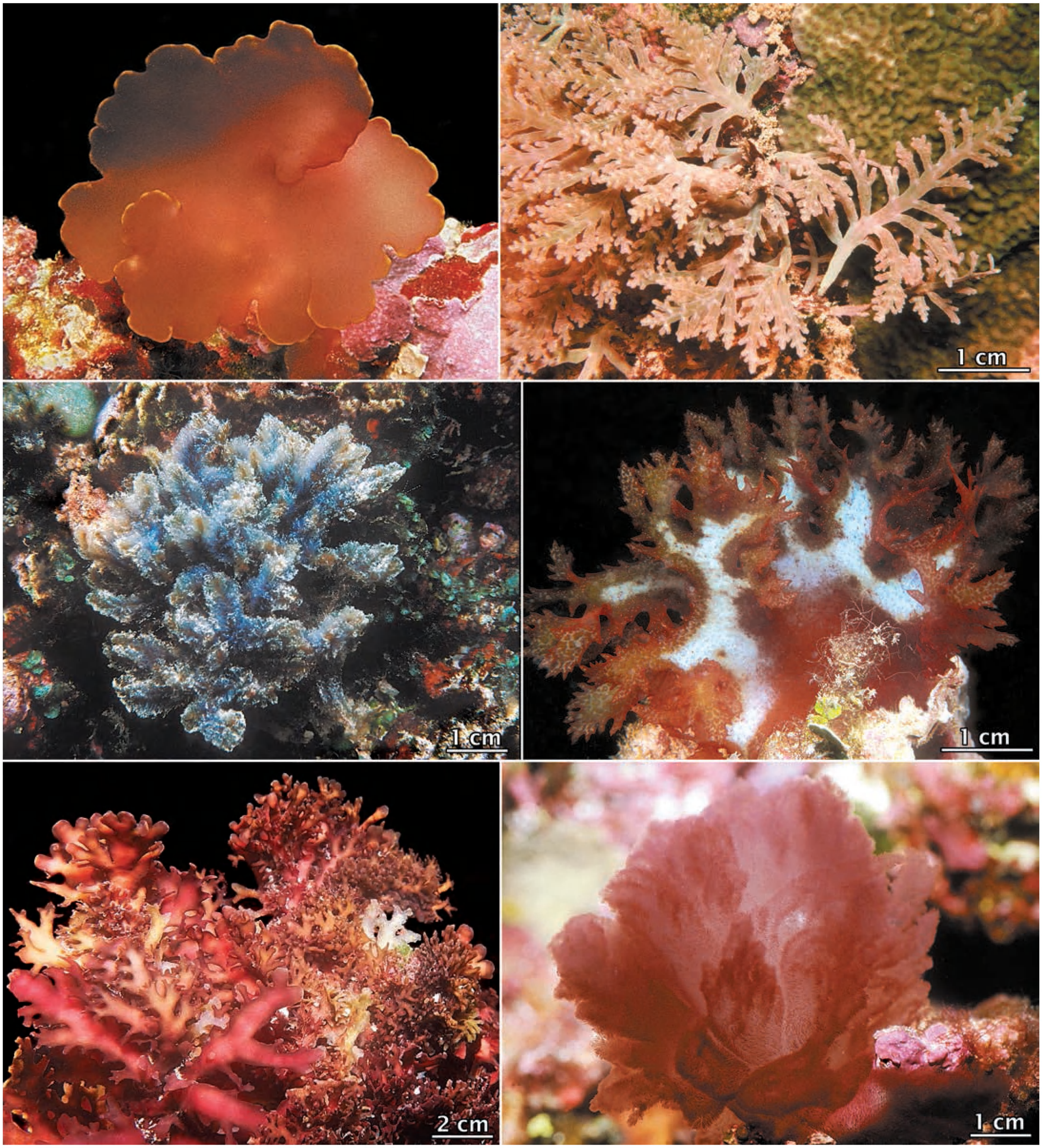

FIGURE 4. Different forms and colors of red algae. Top left: *Halymenia* sp. Top right: *Osmudea pinnatifida*. Middle left: *Dasya iridescens*. Middle right: *Halymenia maculata*. Bottom left: *Carpopeltis maillardii*. Bottom right: *Dudresnaya hawaiiensis*. (Photos by D. Littler.)

FIGURE 5. The reef-building calcareous macrophyte *Porolithon* (*Hydrolithon*) *craspedium*. (Photo by D. Littler.)

Phaeophyceae (Brown Algae)

Phaeophyceae contain large quantities of the brown pigment fucoxanthin. They have cellulose walls; alginic acid and fucoidin are also important components. Brown algae are unique among macroalgae in their developing into multicellular forms with differentiated tissues, and they reproduce by means of motile flagellated spores. Most brown algae have a life history that consists of an alternation between morphologically similar haploid and diploid plants. *Scytosiphon lomentaria* alternates between four distinct morphological generations, which is considered to be a bet-hedging survival strategy (Littler and Littler, 1983).

The Phaeophyceae comprise about 2,000 species and are almost exclusively marine algae. Tropical brown algae include microscopic filament, sheet, coarsely branched, and crust forms (Figure 6). Nearly all brown algae have fine (microscopic) hairs emanating from their surfaces that may serve to increase surface area for nutrient uptake. Kelps attain their greatest abundance, size, and diversity in cold temperate to polar waters. They occur from the intertidal (Fucales) to 115 m depth (*Sargassum hystrix*; Littler and Littler, 1994) on reefs.

Brown algae are also well represented in coral reef ecosystems, particularly in back-reef areas. For example, *Sargassum* and *Turbinaria* (Figure 7) can form small-scale forests up to several meters high that provide biomass, habitat, and shelter for numerous fishes and invertebrates.

Chlorophyta (Green Algae)

Chlorophyta generally have predominantly green chlorophyll pigments. The green algae also contain subordinate carotenoid and xanthophyll pigments and are the ancestral relatives of vascular plants (grasses, trees, sea grasses, etc.), which also contain these same basic pigments. Green seaweeds range from microscopic threadlike filaments to thin sheets; can be spongy, gelatinous, papery, leathery, or brittle in texture; and reach up to 1.5 m in length (Figure 8). The green algae store their energy reserves as starch. All produce flagellated spores and gametes, giving them the advantage of motility (Hoek et al., 1995).

Green algae are always present on tropical coral reefs and lagoon floors, often intermixed among sea grass shoots. Chlorophyta are usually the siphonaceous (giant-celled) forms of Bryopsidales, such as *Halimeda, Avrainvillea, Udotea,* and *Caulerpa*, that employ a unique cytoplasmic streaming/blade abandonment mechanism to eliminate epiphytes (Littler and Littler, 1999). Most Bryopsidales have a rhizophytic, rooted growth form and readily take up pore-water nutrients by cytoplasmic streaming (Williams, 1984). The deepest-occurring fleshy upright alga (*Rhipiliopsis profunda*) is a member of this group and was found by submersible attached to bedrock at a depth of 210 m (Littler and Littler, 1994). Many of these same very deep living species were later found by scuba divers in shallower shaded locations. Some genera of filamentous or sheetlike green algae are extremely tolerant of stressful conditions and can be indicators of freshwater seeps, recently disturbed areas (as early colonizers of newly exposed substrates), habitats of low herbivory (high herbivory eliminates palatable greens), and especially areas with an overabundance of nutrients (e.g., bird roosting islands, polluted areas).

Calcified green algae are major contributors to the production of marine sediments. Some genera, such as *Udotea* and *Penicillus*, produce enormous amounts of fine silt and other sediments due to continual sloughing of thalli and the subsequent disintegration. In many tropical locales, the sparkling white sand beaches are mostly bleached and eroded calcium carbonate (aragonite) skeletons of *Halimeda*. *Halimeda* “hash” (i.e., the coarse oatmeal-like accumulations of *Halimeda* segments, Figure 9) has been used in power plants and other fossil fuel industries as a smokestack scrubber/neutralizer to precipitate sulfurous acid and other precursors to acid rain.

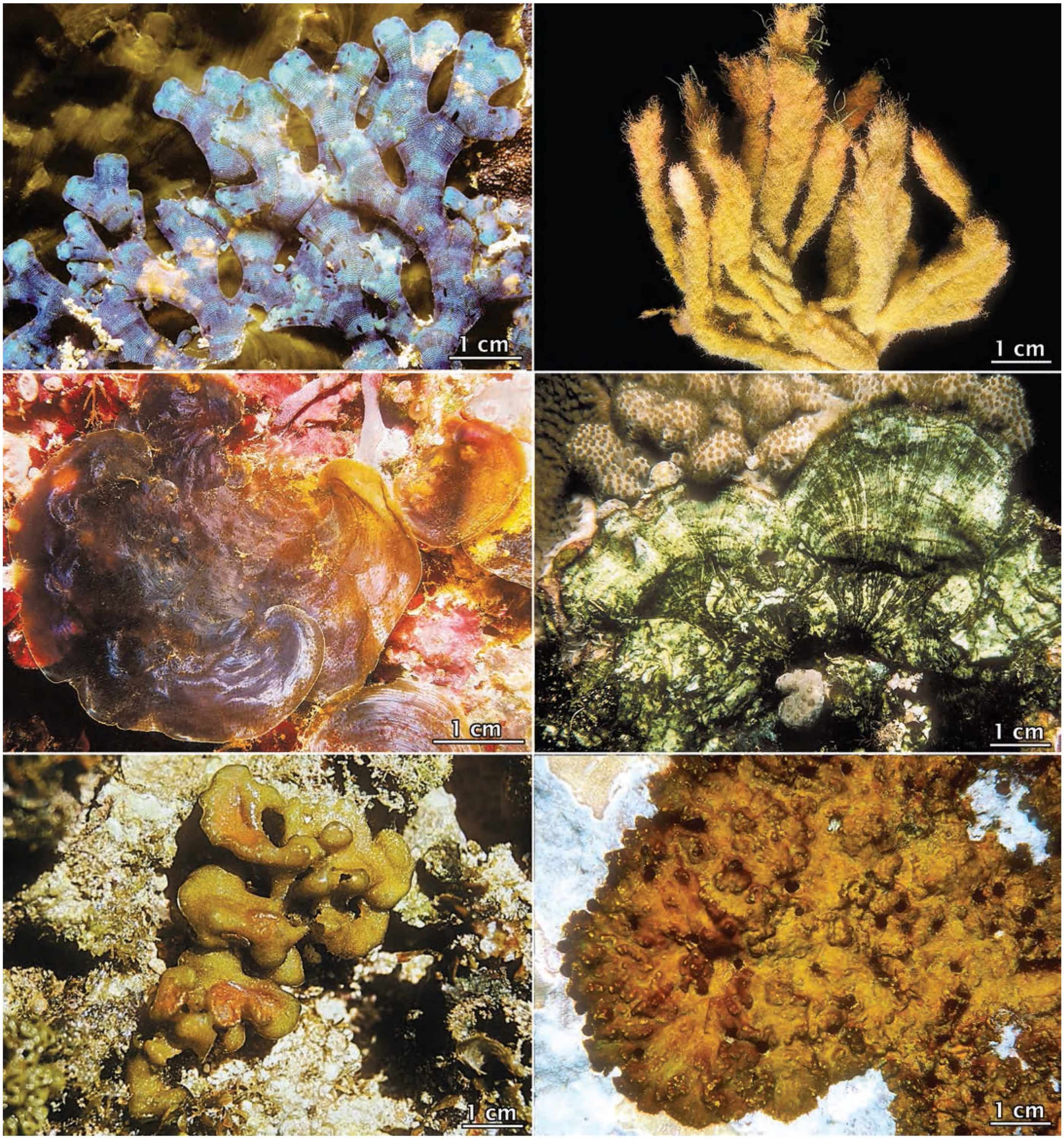

FIGURE 6. Different forms and colors of brown algae. Top left: *Dictyota humifusa*. Top right: *Asteronema breviarticulatus*. Middle left: *Distromium flabellatum*. Middle right: *Cutleria* sp. Bottom left: *Iyengaria stellata*. Bottom right: *Ralfsia extensum*. (Photos by D. Littler.)

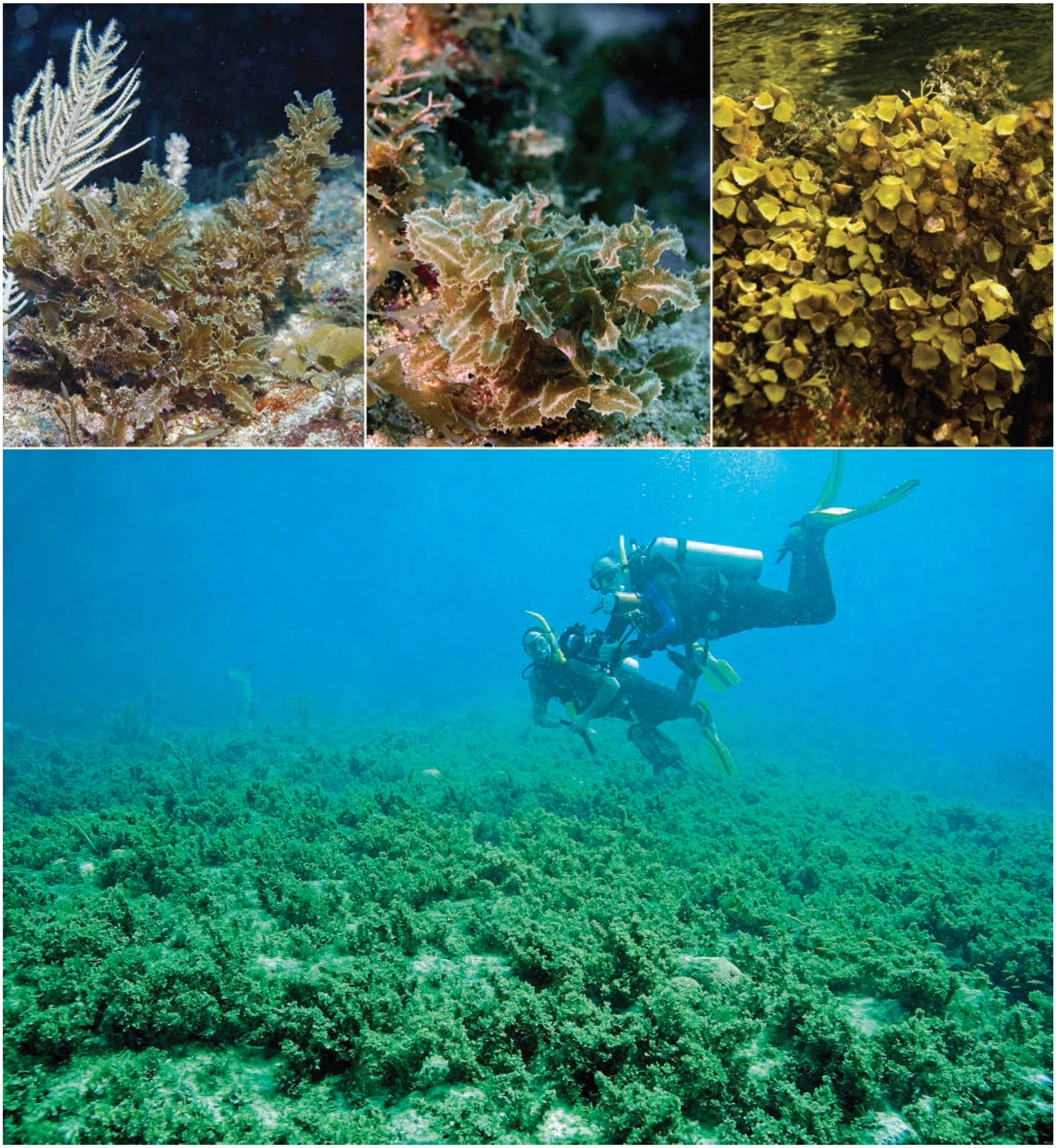

FIGURE 7. Top left and middle: *Sargassum hystrix*. Top right: *Turbinaria turbinata*. Bottom: *Sargassum polyceratium* forming vast, dense beds on the windward side of Bonaire. (Photos by D. Littler.)

FIGURE 8. An array of different green algal forms. Top left: *Codium intertextum*. Top right: *Halimeda copiosa*. Middle left: *Ventricaria ventricosa*. Bottom left: *Udotea cyathiformis*. Bottom right: *Caulerpa sertularioides* f. *farlowii*. (Photos by D. Littler.)

FIGURE 9. *Halimeda* “hash” (i.e., dead calcareous segments). (Photo by D. Littler.)

Cyanobacteria (Blue-Green Algae)

This ancient, highly controversial, and difficult group is prokaryotic, and not a member of the true plants. Cyanobacteria’s simple, mostly filamentous, colonial thalli lack sophisticated characters, making their taxonomy highly technical. Saltwater species at scuba depths have seldom been collected and their important roles are only recently being appreciated. Cyanobacteria were the first group to evolve aerobic photosynthesis, the process that generates food for most of the biological world. On tropical reefs, cyanobacteria form masses of microscopic organisms that are strung together into large filamentous clumps or colonies (Figure 10), and they have specific colors, shapes, or growth forms that are distinctive. However, these are lost in preserved specimens, and before scuba went unappreciated by earlier museum/herbarium–bound taxonomists. Most commonly, the color of blue-green algae is some peculiar shade of pink to purple to black—a combination of red from the pigment phycoerythrin, blue from phycocyanin, and green from chlorophyll.

FIGURE 10. An array of different blue-green algal forms. Top left: *Rivularia nitida*. Bottom left: *Schizothrix minuta*. Right: unidentified. (Photos by D. Littler.)

Some filamentous colonies show the ability to differentiate into several specialized cell types: vegetative cells (the normal, photosynthetic cells that are formed under favorable growing conditions); akinetes (the stress-resistant, long-lived spores that form when environmental conditions become harsh); and thick-walled heterocysts, which contain the enzyme nitrogenase for nitrogen fixation (Herrero and Flores, 2008). Many cyanobacteria also produce motile reproductive filaments called hormogonia that glide free from the parent colony and disperse to form new colonies.

High standing biomass of cyanobacteria is usually considered detrimental to the health of both coral reef systems and people. They produce chemical compounds that can be toxic to fish, plankton, and invertebrates. For example, one type of swimmer's itch, a skin irritation that beach-goers commonly experience, can be caused by blooms of the blue-green alga *Lyngbya majuscula* (Figure 11). Black band disease of corals (Figure 12),found throughout all tropical oceans, is caused by blue-green algae and associated microorganisms (Ruetzler et al., 1983). Certain cyanobacteria produce neurotoxins, hepatotoxins, cytotoxins, and endotoxins that can be dangerous to animals and humans (Paul et al., 2007).

FIGURE 11. *Lyngbya majustula*, the cyanobacteria (blue-green alga) that causes one type of swimmer's itch. (Photo by D. Littler.)

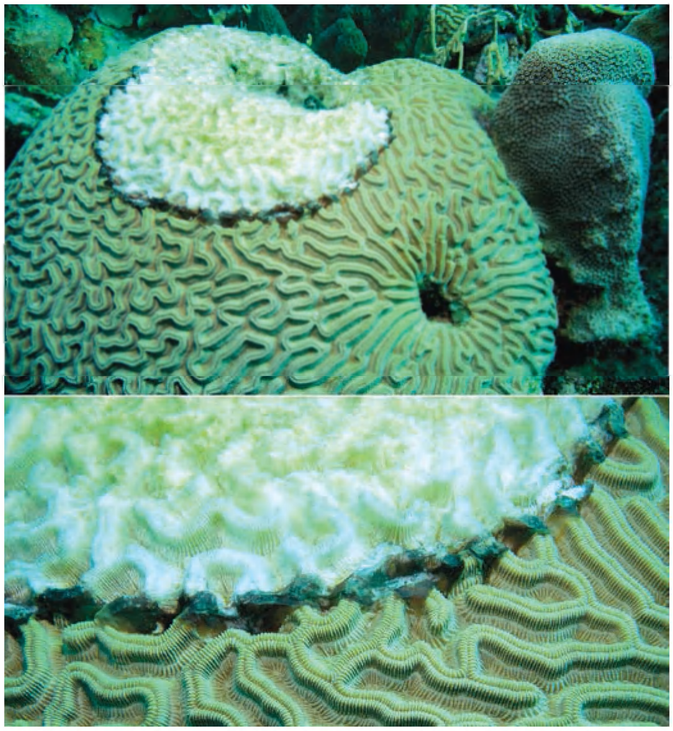

FIGURE 12. Black band disease, *Phormidium corallyticum,* attacking a brain coral. (Photos by D. Littler.)

The nitrogen-fixing capacity of some blue-green algae is extremely important. Heterocyst-forming species bind nitrogen gas into ammonia (NH_3), nitrite (NO_{2-}), or nitrate (NO_{3-}) that can be absorbed by all plants. This role is crucial for tropical reef systems and especially nutrient-depauperate atoll reefs, which are extremely low in fixed nitrogen. Some of these cyanobacteria contribute significantly to global ecology and the oxygen cycle. For example, the marine cyanobacterium *Prochlorococcus* (0.5–0.8 µm diameter) accounts for >50% of the total photosynthetic production of the open ocean and 20% of the planet's atmospheric oxygen (Partensky et al., 1999). Cyanobacteria are the only group of organisms that are able to reduce nitrogen and carbon in aerobic conditions, a feature that may be responsible for their evolutionary and ecological success in certain coral reef habitats.

Blue-green algae are abundant worldwide and ubiquitous on coral reefs, where they often occur under extreme environmental conditions. The universally present black band in the splash zones that make rocks or boat ramps slippery is a layer of microscopic blue-green algae. Such blue-greens can withstand exposure to severe drying, extreme salinity, rain, bright sun, and high heat and still flourish. Cyanobacteria are among the oldest known life forms on Earth. Stromatolites containing fossilized oxygen-producing cyanobacteria date to 1.5 billion years ago (Zhang and Golubic, 1987).

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The Nature of Crustose Coralline Algae and Their Interactions on Reefs

Mark M. Littler and Diane S. Littler

ABSTRACT. What was known about crustose coralline algae (CCA) prior to the use of scuba came mostly from dredging collections. This method usually resulted in damaged specimens and questionable habitat data. Scuba has allowed a more accurate determination of ecological conditions and facilitated in situ photography, two techniques our group has relied on during the past three decades for quantitative ecological studies and field guide production. A goal of this review is to familiarize the scientific diving community with the kinds and roles of CCA on tropical reefs, with the hope that the diving community will more fully appreciate the role of this important group of organisms that is so critical to healthy reef structure and function.

Crustose (nongeniculate) coralline algae occur worldwide from polar to tropical regions, reaching their highest diversity in tropical reef environments. Coralline algae occupy the entire depth range inhabited by photosynthetic organisms, from upper-intertidal regions to depths as great as 295 m. The great abundances of corallines in the poorly known deep-sea realm underscore their widespread contributions to productivity, the marine food web, sedimentology, and reef biogenesis in clear tropical seas. The diversity of CCA forms is astonishing, ranging from small filamentous strands to some of the larger and most beautiful head-forming organisms on coral reefs. The predominant members of this functional indicator group tend to be slow-growing, competitively subordinate taxa that are abundant in most reef systems. As an indicator group they are functionally resilient and able to expedite the recovery and restoration of coral reef systems relatively quickly since some thin forms of crustose coralline algae accelerate colonization and chemically attract and facilitate the survival of coral larvae; the other two fleshy algal functional indicator groups (i.e., turfs and macroalgae) tend to overgrow and inhibit coral settlement, survival, and recovery. Because most crustose coralline algae continually slough off upper surface layers, they play a key cleaning role and physically prevent the settlement and colonization of many fleshy fouling organisms on coral reefs.

INTRODUCTION

Prior to scuba, studies by dredging provided most of the sparse knowledge of crustose coralline algae (CCA), which focused primarily on taxonomy and distributional records. Scuba has enabled studies on ecology, physiology, interactions, etc., that were impossible before its development (Figure 1). Since crustose coralline algae are often overlooked or ignored due to their complex taxonomy and life histories, it is now paramount to understand their fundamental structure and development so that we can utilize

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FIGURE 1. The research team surveying an extensive rhodolith bed at 30 m. (Photo by D. E. Hurlbert.)

this important functional group to answer many questions about marine biology and ecology.

Coralline algae (also "corallines") are red algae (Rhodophyta) characterized by a thallus that is stony because of calcareous deposits contained within and between the cell walls. The extensive crystalline calcium carbonate (calcite) deposits provide a geological history of reefs and an excellent fossil record. These algae are typically pink or other shades of red, but some species can be variations of purple, blue, gray-green, or brown.

Corallines rank among the major reef builders in coral reef systems. Coralline algae are exclusively marine plants and occur throughout all of the world's oceans, attached to substrates by cellular adhesion or root-like holdfasts. Many corallines are epiphytic (on other plants) or epizoic (on animals), and some are even endophytic parasites within other corallines. Despite their ubiquity, all aspects (e.g., taxonomy, biology, ecology) of the coralline algae remain poorly understood, and corallines are often overlooked or intentionally ignored by coral reef scientists.

When they were discovered in 1707 (Sloane), corallines were thought to be animals. In 1837, Philippi recognized that coralline algae were plants and proposed the two generic names *Lithophyllum* (for flat forms) and *Lithothamnium* (for erect, branched forms). However, in an overlooked earlier treatment Bory de Saint-Vincent (1832) had recognized *Tenarea undulosa* as a crustose calcareous alga, making it the oldest species name originally applied to the group in a botanical context. Coralline algae were included in the order Cryptonemiales as the family Corallinaceae until 1986 (Silva and Johansen), when they were elevated to the order Corallinales.

LIFE HISTORIES

Corallines reproduce by sori, which are specialized, volcano-shaped, domed conceptacles containing haploid tetraspores, diploid bispores, or either male or female gametes. Gametes fuse to form the parasitic diploid carposporophyte stage within the female conceptacles, and the resultant carpospores germinate into diploid tetrasporophytes. Haploid tetraspores germinate to produce the male and female gametophytes. Some crustose coralline populations are unusual in that uninucleate bispores (diploid) are commonly the sole means of reproduction. The plant body (thallus) is composed of strands of pit-connected cells (filaments) that may fuse laterally or form secondary pit connections. Pit connections and pit plugs are translocational structures characteristic of red algae (Rhodophyta). These reproductive and vegetative structures provide the critical anatomical characters used in coralline algal taxonomy, but also create major obstacles for researchers, since complicated decalcification techniques and microtome sectioning of infrequently present cryptic features are required.

Articulated (geniculate) corallines are upright or pendulous branched, bushy plants (Figure 2), with shallower and warmer

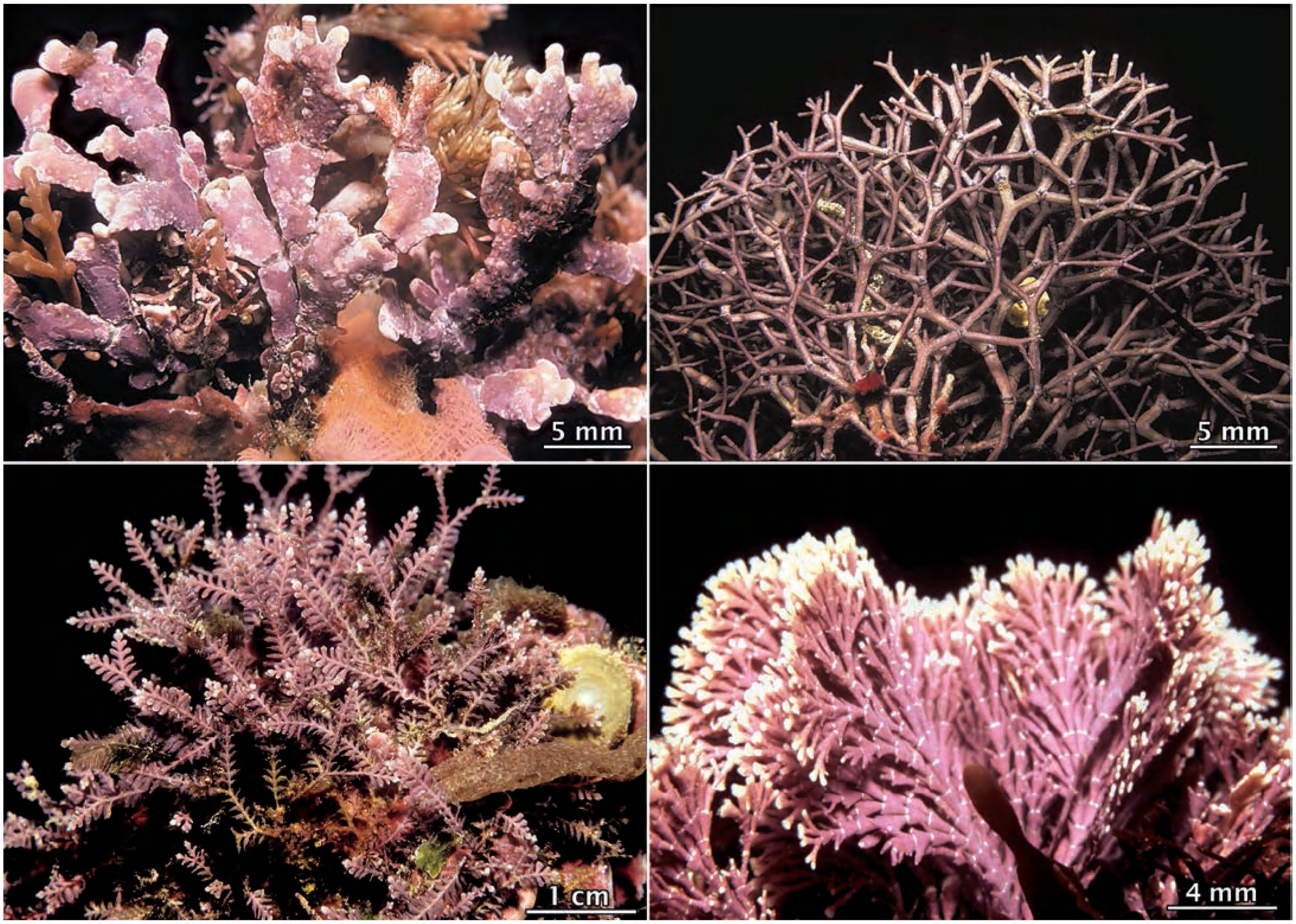

FIGURE 2. Spectrum of articulated (jointed, geniculate) coralline algal forms. Top left: *Amphiroa foliacea*. Top right: *Jania rubens*. Middle left: *Cheilosporum acutilobum*. Middle right: *Amphiroa beauvoisii*. Bottom left: *Corallina berteroi*. Bottom right: *Amphiroa ephedraea*. (Photos by D. Littler.)

distributions than nongeniculate species. The multiple clumped thalli are flexible due to noncalcified zones (genicula, joints) separating longer calcified segments (intergenicula). Many articulated and upright crustose corallines can also form extensive two-dimensional adherent crusts, allowing them to spread laterally, and thereby providing those species with multiple bet-hedging ecological survival strategies (called heterotrichy; Figure 3) (Littler and Kauker, 1984). The upright portions receive relatively more light and nutrients, and are faster growing with increased fertility; horizontal crusts are more resistant to physical forces such as grazing, wave shearing, and sand scouring, and allow the plants to regenerate and invade horizontal primary space.

Crustose (nongeniculate) corallines range in thickness from a few micrometers to many centimeters (Figures 4–7). The thinner forms are faster-growing early colonizers and occur on all hard substrates and other marine organisms. Crustose corallines span a spectrum of morphotypes from thin, sheetlike crusts to thick, slow-growing massive pavements (Figure 4) and from shelf forms (Figure 5) to upright branched (Figure 6) and columnar coral-like heads and nodules (Figure 7) that contribute to both cementation and bulk. On oceanic reefs, the highest part of the reef is often a massive intertidal algal ridge of crustose corallines in the reef's breaker zone (Dawson, 1961). Thalli of thicker forms often consist of three recognizable layers: an attached lower hypothallus, a middle perithallus, and an upper epithallus. Trichocytes (hair cells, megacells) occur as horizontal plates within the epithallus layer in some genera such as *Porolithon*. The protected meristematic (growing) region is usually located as a layer beneath the uppermost intercalary perithallus cells, a feature which is unusual in the Rhodophyta, whose

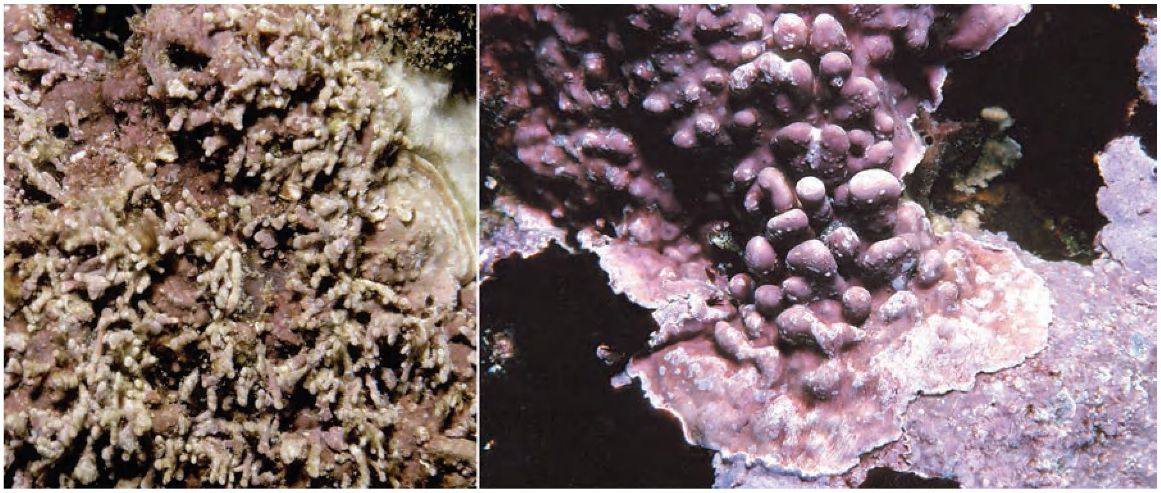

FIGURE 3. Heterotrichy: multiple bet-hedging ecological survival strategies. Left: Jointed corallines with the upright portions receive relatively more light and nutrients and are faster growing, whereas horizontal crusts are more resistant to physical forces and invade horizontal space. Right: Knob-forming coralline with two-dimensional leading crust invading and overgrowing neighboring species. (Photos by D. Littler.)

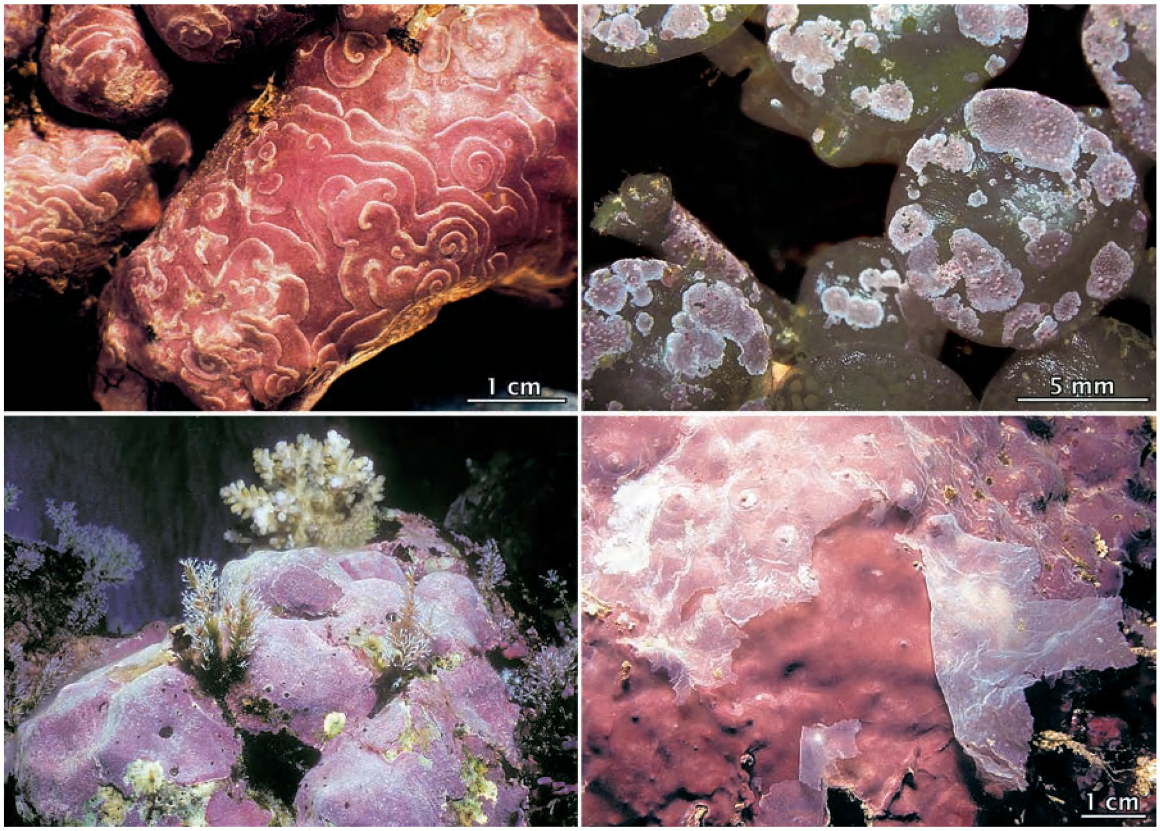

FIGURE 4. Spectrum of simple two-dimensional forms of nongeniculate (crustose) corallines. Top left: *Titanoderma tessellatum*. Top right: *Titanderma pustulatum*. Bottom left: *Porolithon onkodes*. Bottom right: *Neogoniolithon fosliei* showing synchronous sloughing. (Photos by D. Littler.)

FIGURE 5. Spectrum of shelf-forming crustose corallines. Top left: *Mesophyllum funafutiense*. Top right: *Mesophyllum mesomorphum*. Bottom left: *Mesophyllum* cf. *lichenoides*. Bottom right: *Mesophyllum* sp. Note abundant examples of conceptacles in bottom left image. (Photos by D. Littler.)

members (except for Delesseriaceae) typically show strictly apical cell growth. Because of the upright branched head formers (Figures 6, 7), some specialists prefer the term nongeniculate over crustose; however, all have extensive crustose bases and whether branched or simple they are still elaborations of crusts.

RHODOLITHS

In the absence of hard substrates, many nongeniculate species can propagate as free-living rhodolith nodules colonizing sedimentary seafloors (Figure 8). Some of the attached crustose corallines break free and then continue spherical growth as they are tumbled by wave action and bioturbation to ultimately cover vast areas as free-living rhodoliths (also called nodules, rhodolites, maërl, red algal balls, algaliths). Rhodolith beds have been found throughout all of the world's oceans. Globally, rhodoliths fill an important niche in marine ecosystems, serving as transitional habitats between rocky substrates and barren sedimentary areas (Littler and Littler, 2008). Under favorable preservation conditions, rhodoliths can be the predominant contributors of carbonate sediments, often forming rudstone or floatstone depositional beds consisting of large fragments of rhodoliths contained in grainy matrices. Although they can be rolled by infrequent tropical storms, stationary rhodoliths nevertheless provide a three-dimensional microhabitat by intercellular translocation onto the lower shaded layers that continue to expand. A wide variety of species attach to rhodoliths, including other algae, corals, and commercial species such as clams, oysters, and scallops. Rhodoliths are a common feature of modern and ancient carbonate shelves worldwide. Fossil rhodoliths commonly are used to derive paleoecological and paleoclimatic information, and rhodolith communities contribute significantly to the global calcium carbonate budget.

Quantitative submersible studies in conjunction with scuba-based research (Littler et al., 1985, 1986, 1991; Littler and Littler, 1994) on deep-water rhodolith development, distribution, abundance, and primary productivity, at sites of both active formation and breakdown, provided the following detailed case study. The 1.27 km^2 upper platform (67 to 91 m deep) of a ~1,000 m high Bahamian seamount (San Salvador Seamount) averaged 95.8% cover of rhodoliths, contributing an impressive 391 tons of organic

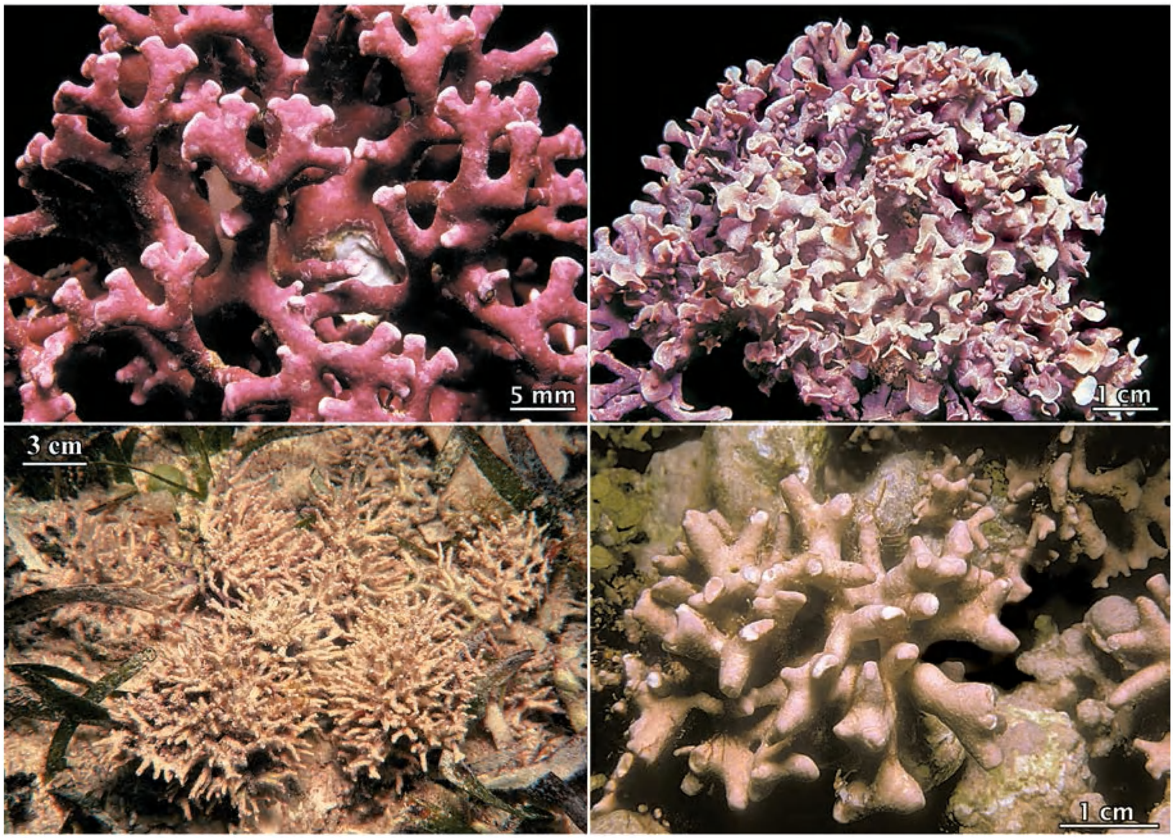

FIGURE 6. Spectrum of head-forming crustose corallines with upright branched excrescences. Top left: *Lithophyllum bamleri*. Top right: *Mastophora pacifica*. Bottom left: *Neogoniolithon spectabile*. Bottom right: *Lithophyllum pygmaeum*. (Photos by D. Littler.)

carbon per year to deep-sea productivity. The predominant crustose coralline alga was acclimated to extremely low light ranges, with an extremely narrow photosynthesis versus irradiance (PI) curve of net primary productivity (0.005 to slightly beyond 0.24 µmol per meter square per second of photosynthetically active radiation). Horizontal platform areas contained accumulations up to five rhodoliths deep (about 45 cm thick), with their visible planer (two-dimensional) crustose algal cover (68.5%) being composed of 41% *Lithophyllum* sp., 14.9% mixed crustose corallines, and 12.6% *Peyssonnelia* sp. The platform rhodoliths also contained an average 25% cover of the foraminiferan *Gypsina* sp.; by contrast, *Gypsina* cover was minimal on the slope rhodoliths. Rhodoliths that had spilled down from the relatively flat platform tended to be concentrated in fan-shaped deposits that were more prevalent near the tops of the slopes. Cover of living crustose algae on the deeper slope rhodoliths averaged only 22.8% and was made up of 14.8% unidentified crustose corallines, 6% *Lithophyllum* sp., and 2% *Peyssonnelia* sp.

Throughout platform depths from 67 to 91 m, rhodoliths were fairly uniform in composition and abundance. They ranged from 4 to 15 cm in diameter, with an average diameter of about 9 cm, and were roughly spherical with smooth living surfaces. The rugose rhodoliths spilling down the steep slopes of the seamount to depths below 200 m were characteristically smaller (about 5 cm average diameter), much rougher, and pitted by boring organisms. Cross-sections through the centers of upper platform nodules showed relatively thin (1–3 cm thick), well-preserved, outer envelopes overlying dead laminated crustose layers. These layers surrounded much thicker cores of biotically altered carbonates (comprised mostly of corallines, foraminiferans, and corals) that had been extensively reworked by boring sponges, boring algae, polychaetes, and pelecypods. Radiocarbon dating indicated that the outermost unaltered envelopes beneath actively growing platform crusts averaged 429 years old (range = 112 to 880 ybp), while the innermost unaltered layers showed an average age of 731 ybp (range = 200 to 1,100 ybp).

GEOLOGY AND EVOLUTION

Crustose coralline algae appeared in the early Cretaceous and have been important components of shallow marine communities

FIGURE 7. Spectrum of crustose coralline that form knoblike branched excrescences. Top left: *Mesophyllum erubescens*. Top right: *Lithothamnion proliferum*. Bottom left: *Hydrolithon reinboldii*. Bottom right: *Lithophyllum congestum*. (Photos by D. Littler.)

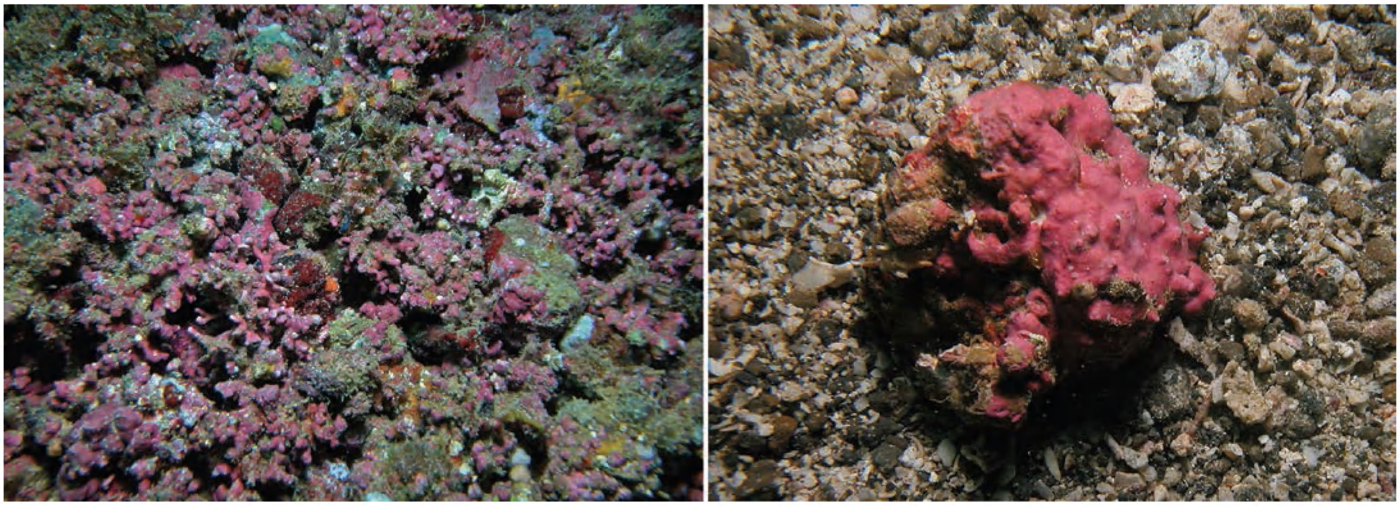

FIGURE 8. Examples of coralline algal rhodoliths. (Photos by D. Littler.)

throughout the Cenozoic, mostly showing long-term increases in species richness during much of their history. There are currently over 1,600 described species of crustose coralline algae (Woelkerling, 1988) and ~649 fossil species (Aguirre et al., 2000). Interestingly, Miocene coastal carbonate habitats are characterized by a worldwide bloom of coralline red algal deposits (termed rhodalgal facies). These extensively developed facies (i.e., characteristic sedimentary deposits) temporarily replaced corals throughout the tropics and subtropics as dominant carbonate producers (e.g., Esteban, 1996). By calibrating modern carbonate assemblages to local oceanographic conditions in the Gulf of California, Halfar et al. (2004) demonstrated that the predominance of rhodalgal facies occurred under mesotrophic to slightly eutrophic conditions. In the Mediterranean region, early to middle Miocene carbonates contain more rhodalgal components than coral reef deposits (Esteban, 1996). In addition to being widespread globally, fossil coralline algae also exhibited their greatest species richness during the early and middle Cenozoic (early Miocene peak of 245 species; Aguirre et al., 2000), with a collapse to a late Pleistocene low of 43 species. In reviewing 37 representative late-Pliocene studies, Halfar and Mutti (2005) concluded that although rhodalgal facies were clearly the dominant components at specific study sites, they often were not emphasized as extensively as the much better known coral assemblages. A number of the above studies focused mainly on coral reef components although rigorous reanalyses of the facies studied actually indicated a relatively low percentage of corals and a predominance of rhodoliths. Esteban (1996) noted a similar bias in a review of Miocene Mediterranean coral reefs and rhodalgal facies. Such discrepancies can be attributed mostly to poor knowledge of coralline red algae and rhodolith facies in conjunction with the tendency for researchers to apply classic coral reef depositional models, even in settings where corals were sparse.

Throughout the world's oceans during the late-early to early-late Miocene, while many phototrophs declined globally, coralline red algae radiated and diversified greatly. In fact, corallines have shown a long-term overall increase in species richness throughout most of their history. Despite this, coralline species diversification was not sustained after the Miocene (Aguirre et al., 2000) and coralline algae suffered a series of extinction events, each of which eliminated at least 20% of the species. In fact, during the two largest extinction events of the late Cretaceous and late Miocene–Pliocene, about 66% of all coralline species were lost. Each extinction event was followed by substantial episodes of rapid radiation and speciation, particularly in the early Paleocene and Pleistocene.

The conspicuous Miocene shift from coral- to rhodolith-dominated carbonate communities has been attributed to global climate changes. Halfar and Mutti (2005) argued that the prevalence of rhodolith facies, which developed under broader nutrient and temperature ranges than did the coral reef facies, was initially triggered by a global enhancement of nutrient resources. In the middle Miocene, nutrient availability was apparently augmented by increased upwelling- and erosion-related nutrient inputs into coastal ecosystems. These nutrient increases together with declining temperatures following the early to middle Miocene climatic optimum led to further expansion of rhodalgal facies. Hence, a global phase shift in dominance occurred in nearshore shallow-water carbonate producers from corals to coralline species that were tolerant of the higher nutrient levels (in accordance with the Relative Dominance Model [RDM]; Littler et al., 2006). Geological deposits of coralline algae contain organic carbon compounds such as cellulose (due to photosynthesis), as well as massive calcareous compounds due to calcification (precipitation of inorganic $CaCO_3$). The resultant carbon stores may be among the most important in the biosphere as neutralizers of global oceanic acidification and as reservoirs of excess greenhouse CO_2.

A striking geological pattern is an inverse relationship in the species richness of two of the families of Corallinales. From the Cretaceous to Pleistocene, Corallinaceae (both warm- and cold-water species) increased, while the tropical Sporolithaceae declined. This climatic link for Sporolithaceae and Corallinaceae was supported by both direct and inverse correlations, respectively, between species diversity and documented Cretaceous to Cenozoic paleotemperatures. Coralline diversification since the Cretaceous (Steneck, 1983, 1985) may have been driven by simultaneous coevolutionary increases in herbivores (mainly limpets, echinoids, and grazing fishes) that physically scrape and remove fleshy algal competitors, though that remains to be more firmly established.

DISTRIBUTIONAL PATTERNS AND FUNCTIONAL SIGNIFICANCE

Crustose (nongeniculate) coralline algae occur worldwide from polar to tropical regions, reaching their highest diversity in tropical reef environments. Three subgroups of Corallinales show characteristic distributions (Aguirre et al., 2000): (1) Sporolithoideae, low latitude/mainly deep waters; (2) Melobesioideae, high latitude/shallow waters to low latitude/deep waters; and (3) Lithophylloideae/Mastophoroideae, mid to low latitude/shallow waters.

The abundant occurrence of crustose corallines (and corals) in Indo-Pacific reefs was initially recognized by Darwin (1842); however, their important role as reef builders was first emphasized by Agassiz (1888). Most often, corals (Cnidaria) supply the bulk building blocks whereas coralline algae do much of the cementing together of debris. Barrier, fringing, and atoll reefs are complex ecosystems that depend on calcareous coralline algae for the development and maintenance of wave-resistant outer fronts (Figure 9). The crustose coralline algae, which deposit a type of calcium carbonate (calcite limestone) that is harder and denser than the aragonite of corals, build this raised algal ridge (Dawson, 1961). The intertidal–outer algal ridge habitat, to which crustose corallines (mainly species of *Porolithon*) are crucial for constructing the framework, characterizes surf-pounded

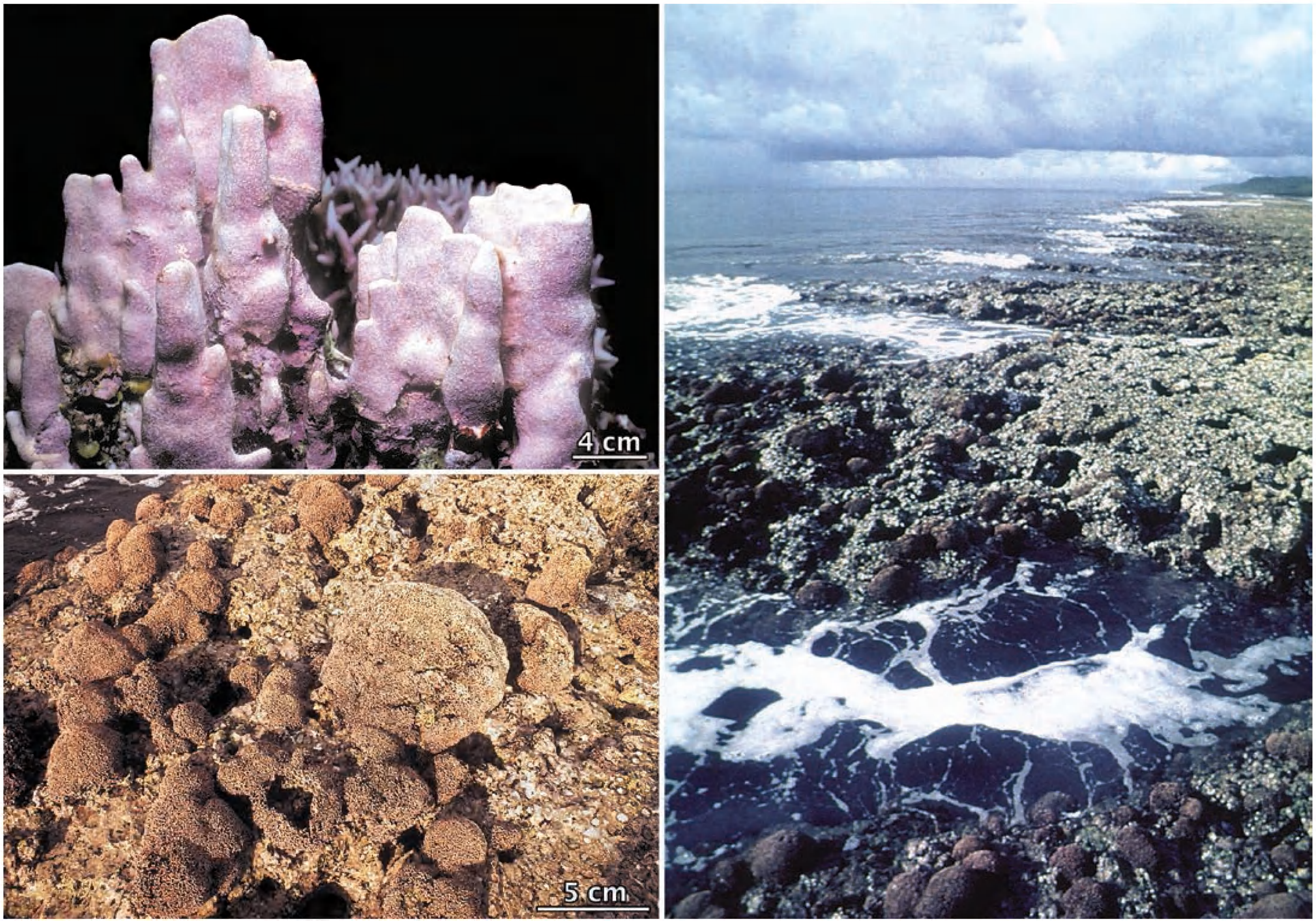

FIGURE 9. Right: A well-developed algal ridge from windward Guam. Top left: close-up of the pink crustose *Porolithon craspedium*. Bottom left: close-up of the head-forming *Lithophyllum kotschyanum*. (Photos by D. Littler.)

windward coral reefs of tropical Indo-Pacific and, to a lesser extent, Atlantic regions. The Pacific algal ridge builder *Porolithon onkodes* fixes a remarkable 3.2 mg of organic carbon per square meter per hour and 1.9 mg calcium per square meter per hour during an average-daylight day (Littler, 1973). By extending above the waterline, the algal ridge absorbs tremendous wave energy, not only protecting coastal shorelines that would otherwise erode, but also sheltering the more delicate corals and other reef organisms. Algal ridges develop intertidally and, therefore, require intense and persistent wave action to form, so are best developed on windward areas where there are consistent trade wind conditions.

Some of the coralline algae that develop into shelf-like crusts (Figure 5), upright branches (Figure 6), or thick knobby crusts (Figure 7) provide microhabitats for countless vulnerable invertebrates that would otherwise suffer increased mortality due to fish predation. Coralline algae also constitute a food source in the energy webs of coral reefs. Sea urchins, parrotfishes, surgeonfishes, limpets, and chitons all readily feed on coralline algae, which are usually not destroyed due to sunken, intercalary meristems that replenish the upper, damaged areas. Crustose corallines accelerate colonization by chemically attracting and facilitating the survival of coral larvae (Harrington et al., 2004), as well as the larvae of certain grazing invertebrates. This is beneficial for the corallines because the herbivores then remove epiphytes that might preempt available light or otherwise smother the crusts. Because of their stony texture, indigestible acid-neutralizing $CaCO_3$, and covered intercalary meristematic layer, corallines are uniquely resistant to considerable levels of grazing. As examples, the most common Indo-Pacific crustose coralline, *Porolithon onkodes*, often forms an intimate relationship with the chiton *Cryptoplax larvaeformis* (Littler and Littler, 1999), as does the Atlantic coralline *H. pachydermum* and the chiton *Choneplax lata* (Littler et al., 1995). The chitons live in

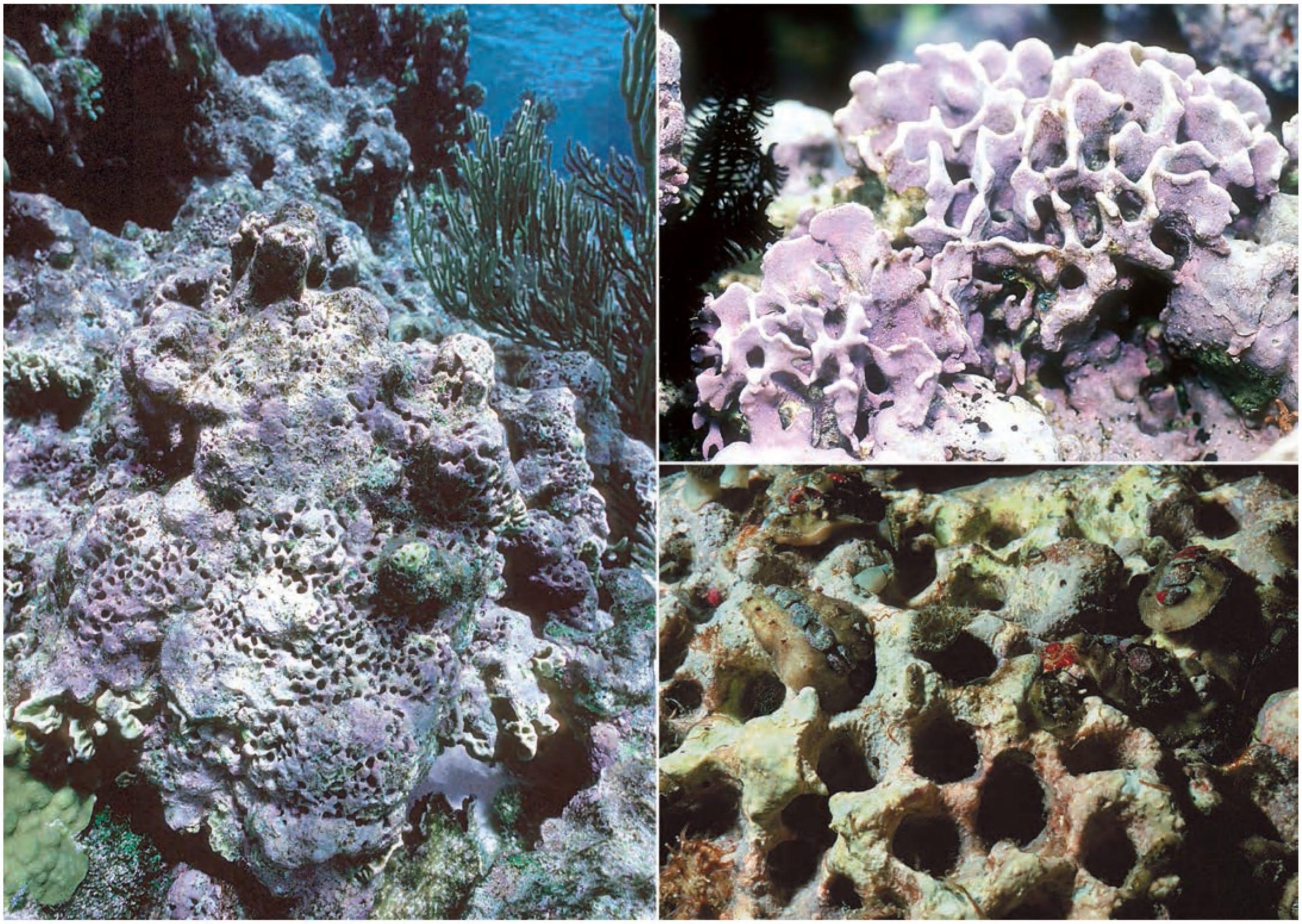

FIGURE 10. Castle forms of the crustose corallines created by their association with herbivorous chitons. Left and top right: *Hydrolithon pachydermum*/*Choneplax lata* (Pacific). Bottom right: *H. onkodes*/*Cryptoplax larvaeformus* (Atlantic). (Photos by D. Littler.)

burrows that are overgrown by *Porolithon* and graze nocturnally on the surfaces of the corallines (Figure 10). The pattern of grazing causes rapid meristematic differentiation and redirection in which the coralline produces an abundance of vertical, blade-like lamellae, resulting in a spectacular growth form resembling castles. This type of relationship is unique in the marine environment, whereby the predator actually increases the biomass, surface area, and reproductive capacity (i.e., fitness) of its principal prey (Littler et al., 1995).

PATHOGENS

Instances of coralline algal pathogens were unknown until 1993, when Coralline Lethal Orange Disease (CLOD) was first discovered using scuba (Littler and Littler, 1995) on Aitutaki Atoll, Cook Islands (Figure 11). The occurrence of CLOD at 25 Great Astrolabe, Fiji, sites increased from 0% in 1992 to 100% in 1993, indicating that the pathogen was in an early stage of virulence and dispersal. The bright orange bacterial pathogen grows as fan-shaped or circular bands at a mean linear rate of 1.5 mm per day, totally consuming host corallines that are in its path. All species of articulated and crustose species tested to date are easily infected by CLOD, and it has now become circumtropical throughout all coral reef habitats. In recent years, a white CLOD-like pathogen has become even more abundant worldwide; this is in addition to the recently recorded dispersion of a virulent black fungal pathogen (Figure 12) of coralline algae first found in American Samoa (Littler and Littler, 1998) and an unknown species of target-shaped coralline pathogen (Figure 13) first reported from the Great Astrolabe Reef (Littler et al., 2007). Without scuba, none of the above pathogens would have been discovered.

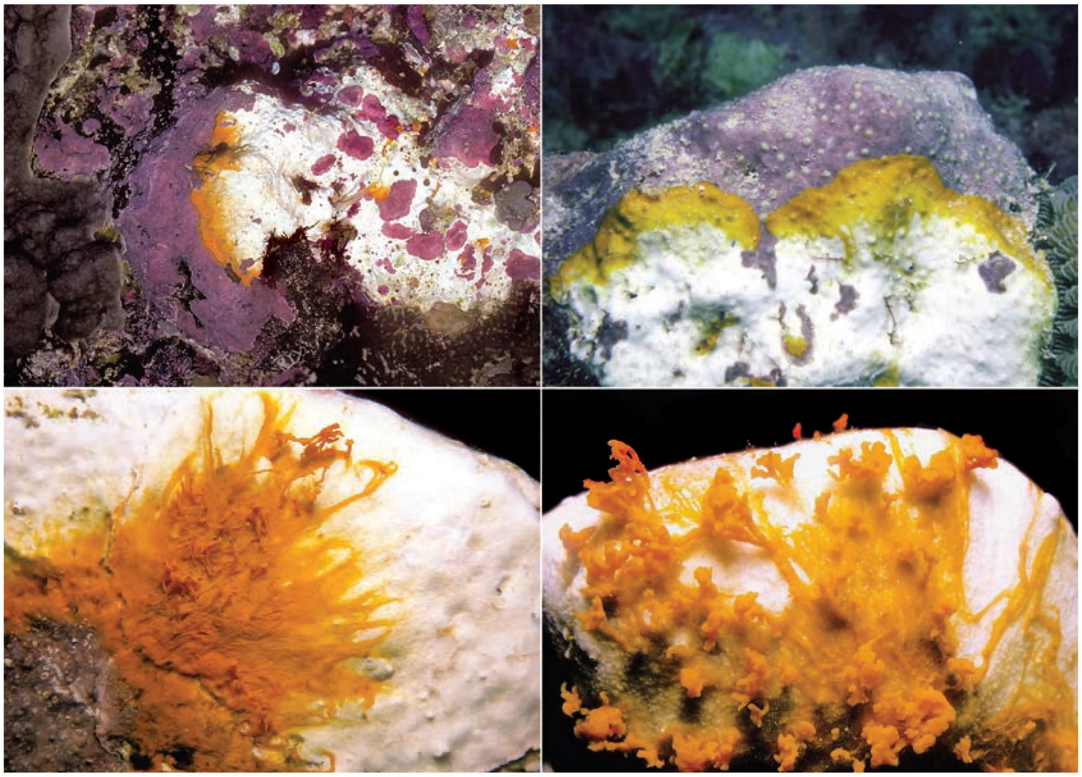

FIGURE 11. In situ images of the worldwide CLOD pathogen. (Photos by D. Littler.)

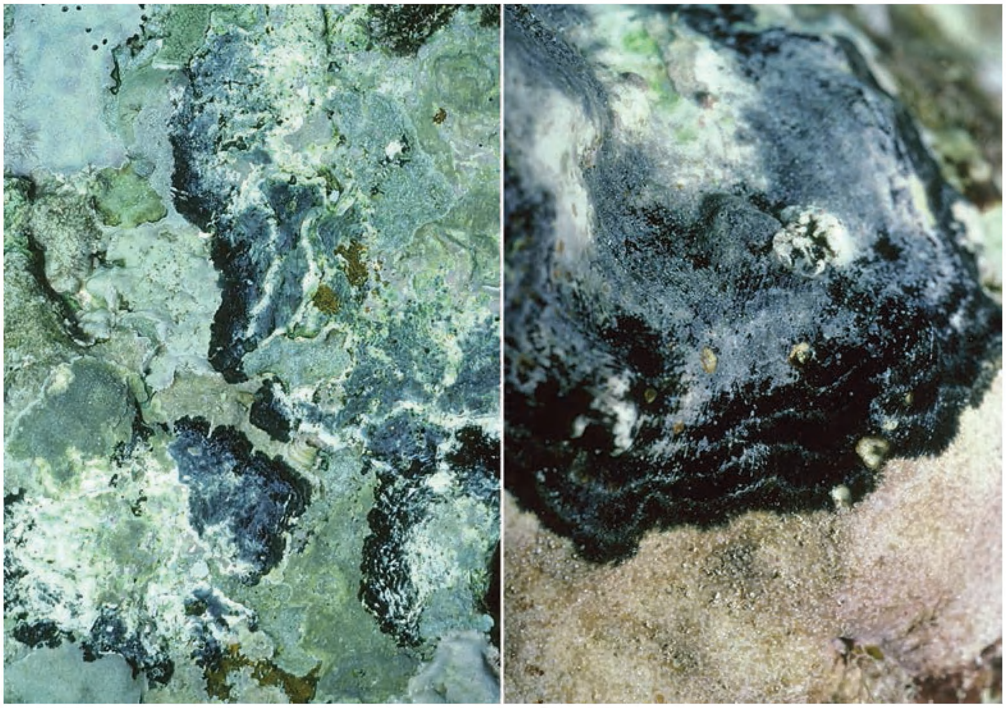

FIGURE 12. In situ images of black fungus disease in the Pacific. (Photos by D. Littler.)

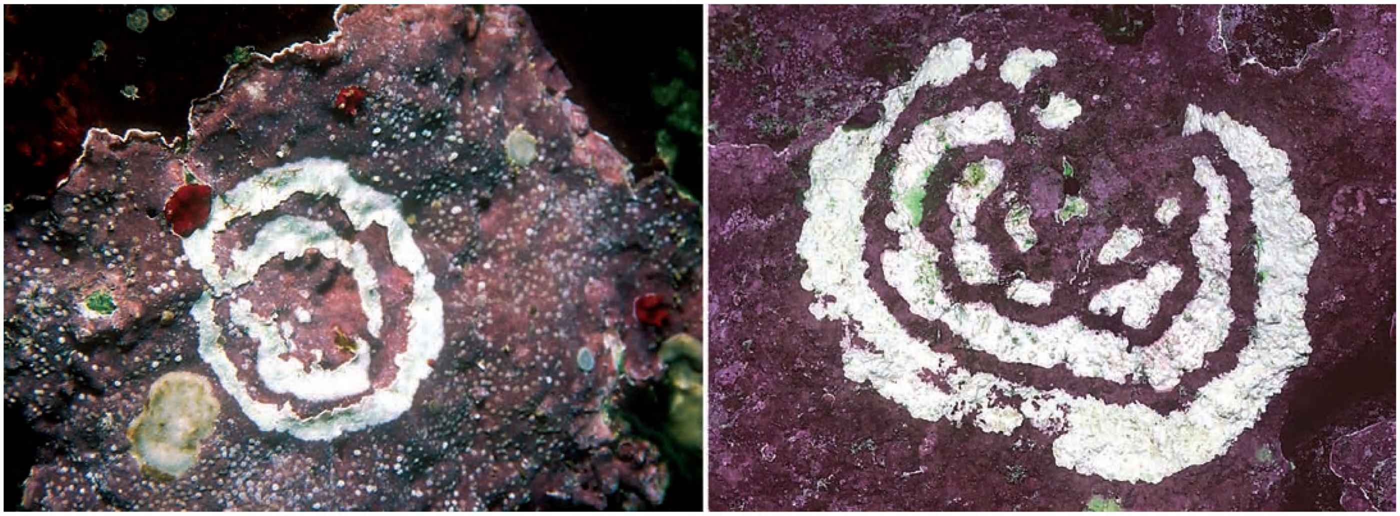

FIGURE 13. In situ images of target pathogen in the Pacific. (Photos by D. Littler.)

IMPORTANCE AND ROLE

The findings reviewed here are based mainly on extensive scuba research. Crustose (nongeniculate) coralline algae occur worldwide from polar to tropical regions, reaching their highest diversity in tropical reef environments. Coralline algae occupy the entire depth range inhabited by photosynthetic organisms, from upper-intertidal regions to depths as great as 295 m (Figure 14; Littler and Littler, 1994). The great abundances of corallines in the poorly known deep-sea realm underscore their widespread contributions to productivity, the marine food web, sedimentology, and reef biogenesis in clear tropical seas. The diversity of coralline algal forms is astonishing, ranging from small filamentous strands to some of the larger and most beautiful head-forming organisms on coral reefs (Figures 4–7). The predominant members of this functional indicator group (Littler and Littler, 2007) tend to be slow-growing, competitively subordinate taxa that are abundant in most reef systems. As an indicator group they are functionally resilient and able to expedite the recovery and restoration of a particular coral reef system relatively quickly since some thin forms of crustose coralline algae accelerate colonization and chemically attract and facilitate the survival of coral larvae (Harrington et al., 2004); the other two fleshy algal functional indicator groups (i.e., turfs and macroalgae) tend to overgrow and inhibit coral settlement, survival, and recovery. Because most crustose coralline algae continually slough off upper surface layers (bottom left, Figure 4), they play a key cleaning role and physically prevent the settlement and colonization of many fleshy fouling organisms on coral reefs (Littler and Littler, 1997).

Crustose corallines, because of their slow growth, tolerate a wide range of nutrient levels and generally are conspicuous, but not as predominant as corals, under low concentrations of nutrients and high levels of herbivory (Littler and Littler, 2007). Accordingly, they do well in the presence of both low and elevated nutrients (i.e., most are not inhibited by nutrient stress and many are maintained competitor free by surface cell-layer shedding [Johnson and Mann, 1986], even at lower levels of grazing [Littler and Littler, 1997]). Therefore, crustose coralline algae do not require elevated nutrients as might be inferred (Littler and Littler, 2007); instead, the degree to which they rise to dominance is largely controlled indirectly by the factors influencing the abundances of other functional groups, primarily the corals and fleshy macroalgae. The key point is that crustose corallines dominate mainly by default (i.e., under conditions of minimal competition) where corals are inhibited (e.g., by elevated nutrients or by strong wave action) and where fleshy algae are removed by intense herbivory. The wave-pounded intertidal algal ridges are built predominantly by *Porolithon (Hydrolithon) onkodes, P. gardineri*, *P. craspedium*, and *Lithophyllum kotschyanum* in the Indo-Pacific and by *P. pachydermum* and *L. congestum* in the Atlantic; all are coralline species that appear uniquely tolerant of aerial exposure. The transition from frondose- to turf- to coralline-algal communities has been reported (Steneck, 1989) to closely correlate with increasing herbivory gradients on coral reefs.

In addition to their protective reef-building nature, coralline algae provide a number of other goods and services. Since the eighteenth century, unattached corallines (maërl) have been harvested as acid-soil pH conditioners. In Britain and France, hundreds of thousands of tons of *Phymatolithon calcareum* and *Lithothamnion corallioides* continue to be dredged annually. Enormous maërl beds several km^2 in area, mainly composed of species belonging to the genera *Lithothamnion* and *Lithophyllum*, are present off the coast of Brazil and have begun to be

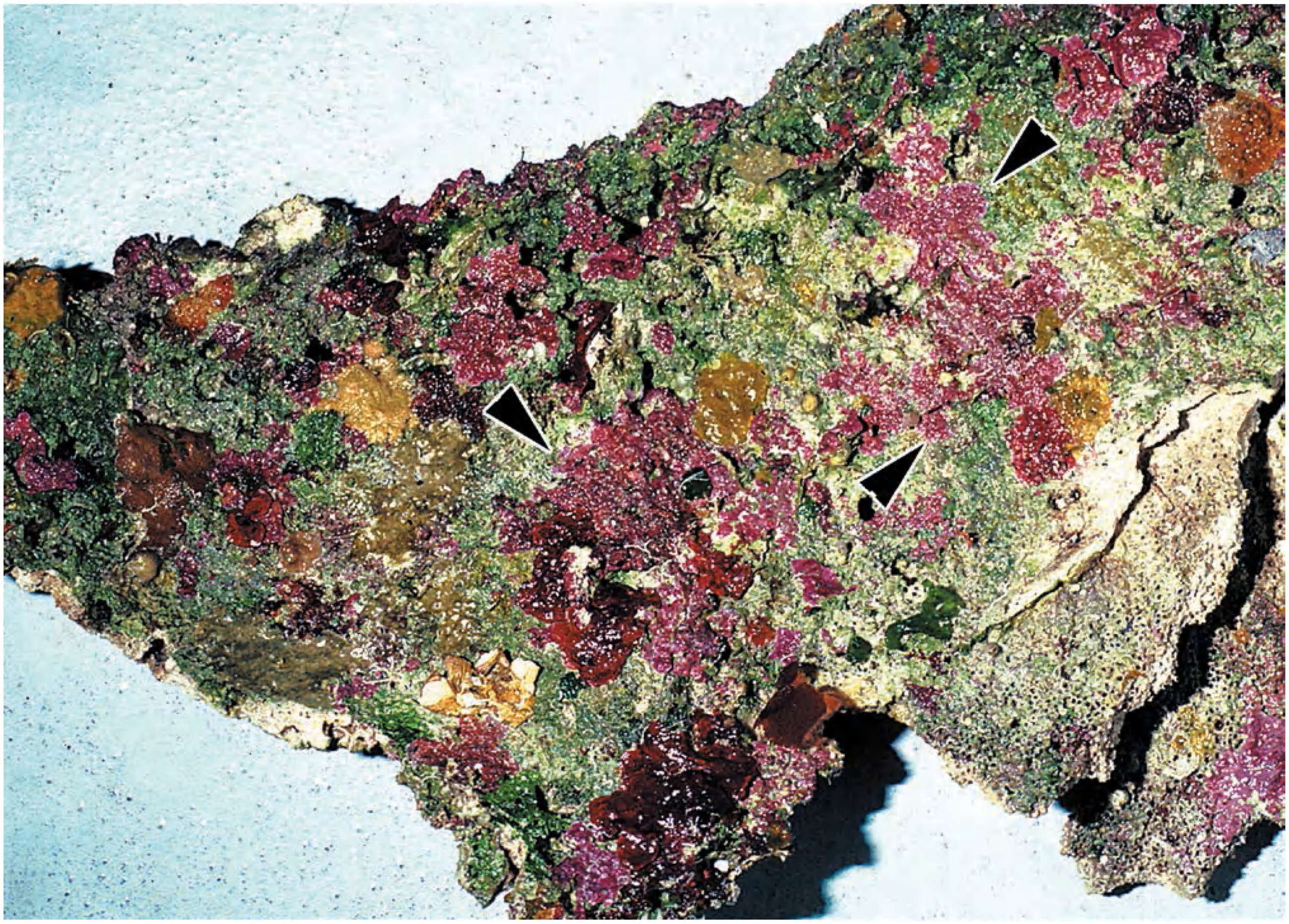

FIGURE 14. Rock taken by submersible from >200 m depth off San Salvador Seamount, Bahamas, showing the deepest plant life (a crustose coralline alga) on Earth. (Photo by D. Littler.)

commercially harvested. Maërl is also used as a mineral food additive for cows, hogs, and other livestock, as well as in the filtration and neutralization of acidic drinking water. Corallines are used in modern medical science in the preparation of dental bone implants (Shors, 1999). The cellular carbonate skeleton provides an ideal matrix for the adherence and regeneration of bone and tooth structures. Coralline algal fossils have proven to be extremely beneficial in deriving paleoecological and paleoclimatic information, and also have been employed as stratigraphic markers of particular significance in petroleum geology. As a spectacularly colorful component of live rock for the flourishing marine aquarium trade, coralline algae are highly desired for their architectural and attractive aesthetic qualities. However, the most important contribution of coralline algae worldwide may well prove to be in ameliorating the greenhouse CO_2 buildup associated with global climate change. It is the balance between calcification and respiration—which produces carbon dioxide—and the consumption of CO_2 by photosynthesis that will determine whether corallines act as a "sink" (absorbing CO_2) or as a source of CO_2. Experiments that studied how various calcifying systems take up and give off carbon dioxide have shown that the rise in CO_2 produced by calcification is mitigated by its removal through increased photosynthesis (Ohde, 1999; Iglesias-Rodriguez et al., 2008), with a net effect that is unlikely to either greatly contribute to or significantly reduce the rise in atmospheric CO_2. However, rising levels of CO_2 and concomitant acidification of seawater inhibit all reef builders, including coralline algae (Kleypas et al., 1999). By binding vast accumulations of $CaCO_3$ during calcification and photosynthesis, corallines may play a role in slowing future acidification of marine habitats such as coral reefs.

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The Nature of Turf and Boring Algae and Their Interactions on Reefs

Mark M. Littler and Diane S. Littler

ABSTRACT. A major goal of this short review is to familiarize the scientific diving community with the importance, seasonality, and high diversity of juvenile and microalgal turf assemblages and rock-boring cyanobacteria on coral reefs to stimulate further interest in research on these groups. Boring endolith activity not only negatively inflicts damage to living carbonate coral reef hosts, but also positively benefits primary productivity and provides the nutritional base for excavating grazers in otherwise dead substrates. Algal turfs, like all subtidal assemblages on reefs, are best studied by scuba techniques, which have greatly facilitated observation, collection, photographic sampling, and manipulative studies. Prior to scuba, studies in the shallow intertidal and by dredging dominated, which focused by necessity primarily on taxonomy and distributional records. Scuba has enabled studies on ecology, physiology, interactions, etc., that were impossible before its development.

TURF ALGAE INTERACTIONS

Turf algae are multispecies assemblages of diminutive, mostly filamentous algae that attain a vertical height of only 1 mm to 2 cm (Figure 1). Turf algae often exist as assemblages (algal turfs), are ubiquitous in reef systems and are composed of the small, juvenile stages of macroalgae (e.g., *Gelidium* spp., *Gelidiella* spp., *Digenia simplex*) along with faster-growing filamentous species (usually red algae such as *Polysiphonia* spp., *Herposiphonia* spp., and *Ceramium* spp.; blue-green algae (cyanobacteria); diatoms; brown algae; green algae; and coralline algae) and detritus and sediments. The assemblages of juvenile and microalgal species have a high diversity, exceeding 100 species in some western Atlantic turfs, although 30–50 species co-occurring is more common (Steneck, 1988). Within the turf assemblage, there is often a high turnover of individual turf algal species seasonally, and only a few taxa are able to persist or remain abundant throughout the year. However, the assemblages, when viewed as a functional indicator group, remain relatively stable year round. They are often able to recover rapidly after being partially removed by physical disturbance.

Algal turfs characteristically trap ambient sediments and smother corals and other competitors for space by gradual encroachment. These algal forms become predominant under minimal inhibitory top-down (e.g., herbivory) and stimulatory bottom-up (e.g., nutrient supply) controls (Littler et al., 2006). Algal turfs have been shown to form extensive horizontal mats under reduced nutrient-loading rates (Fong et al., 1987) or infrequent nutrient inputs (Fujita et al., 1988). Domination of horizontal reef space by turf algae suggests desirably low nutrient levels but an inadequate herbivory component required for healthy coral-dominated reefs. Their relatively small size and rapid regeneration from basal remnants (perennation) result in only moderate losses to herbivory at low grazing pressures.

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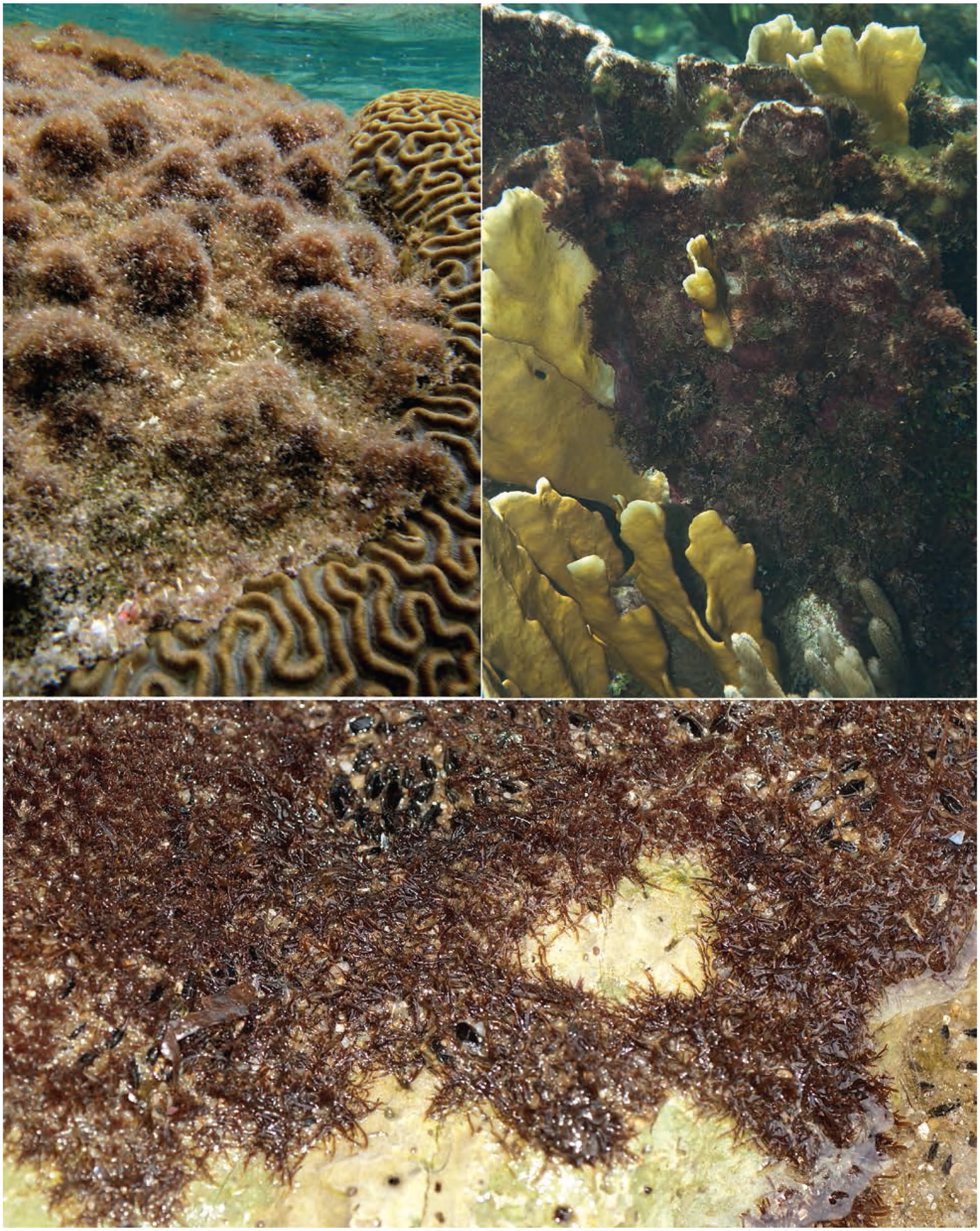

FIGURE 1. Naturally occurring algal turf communities. Top left: *Polysiphonia* sp. Top right: *Laurencia obtusa*. Bottom: *Gelidium pusillum*. (Photos by D. Littler.)

Turf algal assemblages are very much affected by the behavior of territorial damselfish that chase off any larger herbivores that may come into their areas. Because of their preferential grazing and protection, damselfish cultivate more diverse alga turfs with higher biomass within their territories.

Turf algae have opportunistic ("weedy") life-history characteristics, including high surface area to volume ratios and the ability to maintain substantial nutrient uptake and growth rates under low-nutrient conditions (Rosenberg and Ramus, 1984). Turfs also contain populations of nitrogen-fixing cyanobacteria (Adey, 1998) that can enrich the other low-growing members within the dense turf assemblage in oligotrophic waters. Turf algae have been utilized effectively as a functional group in the burgeoning saltwater aquarium trade, where they are grown in brightly lit, circulating flumes (i.e., patented scrubbers; Adey et al., 2011) to remove excessive nutrient pollutants.

BORING CYANOBACTERIA INTERACTIONS

Boring cyanobacteria are filamentous, prokaryotic, mostly photosynthetic organisms that chemically bore into calcareous rock and limestone. Penetrating or boring algae play important roles in the bioerosion of coral reefs; these filamentous microorganisms result in the breakdown of carbonate structure both directly and indirectly (reviewed by Tribollet, 2008). The most common are blue-green algae (Cyanophyta, cyanobacteria) that attack calcareous substrates differentially; the aragonite skeletons of corals are most easily penetrated and the denser calcite deposits of coralline algae are most resistant. However, the mechanism of carbonate dissolution remains largely unknown and actually contradicts geochemical models that predict the precipitation of carbonates by photosynthetically induced pH increases. As a consequence of variable processes such as selective settling, competition, persistence, and subsequent grazing of euendolithic (true endoliths) cyanobacteria, coastal rocks are biodegraded differentially, resulting in grotesque, sharp-edged features called karsts (Figure 2). These processes act as feedback mechanisms by producing diverse microbial habitats with patchy water-retention pockets, which further enhance bioerosion and endolithic community diversity.

Boring endoliths colonize all carbonate substrates on coral reefs and are distributed throughout the world's tropical seas. Intertidal carbonate coasts are most intensively bioeroded (Figure 3). However, although endolithic activity inflicts damage to living hosts, it also can provide positive overall benefits to reefs, including important primary productivity yields in otherwise

FIGURE 2. Irregular and sharp karsts formed from habitats colonized by boring cyanobacteria and their deeply rasping predators. Inset: rasping organisms such as chitons and other mollusks. (Photos by D. Littler.)

FIGURE 3. Extreme undercut formed by boring intertidal blue-green algae grazed by deep-rasping chitons. (Photo by D. Littler.)

dead substrates. Endoliths attract excavating grazers, and this contributes to massive biodestruction processes and sediment formation. In other words, the bioerosional effect of boring cyanobacteria themselves is secondary; their primary significance is in providing the nutritional base for excavating grazers.

Boring cyanobacteria have been important in the destruction of carbonate throughout geological time. They occur from the upper intertidal to abyssal depths (Golubic et al., 1984), but in general show a decrease with depth. Marine limestone can be infested by more than half a million endolithic filaments per square centimeter. The oldest recorded endolithic blue-green—and the earliest known occurrence of bioerosion—was found in 1.5 billion-year-old stromatolite rocks in China (Zhang and Golubic, 1987).

The diversity of boring microflora is thought to be large, comprising not only undiscovered blue-green algae, but also other algae (chlorophytes, rhodophytes) and fungi. Although their taxonomy has been studied for decades, new species are still being discovered, especially with the advent of molecular techniques (Gutner-Hoch and Fine, 2011). However, the taxonomy and diversity of boring blue-green algae remain relatively unknown and there is still much to be learned regarding this important group.

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The Ecological Significance of Sexual Reproduction by Tropical Green Algae

Kenneth E. Clifton

ABSTRACT. The ability of scuba-equipped scientists to directly observe marine organisms in their natural environments has dramatically improved our understanding of marine ecological processes. Despite advances on numerous fronts, however, the basic ecology of many important groups, including the tropical green algae, remains relatively unstudied. This paper examines how aspects of sexual reproduction by these algae relate to their population dynamics and includes discussions of gamete formation, spatial dispersion of males and females, herbivory on fertile algae, the nature and timing of gamete release, fertilization success, and zygote dispersal. Further investigations into any of these topics promise to shed useful light on an ecologically important group of tropical seaweeds.

INTRODUCTION

The field of subtidal marine ecology owes much of its success to the technology of scuba. With the advent of open-circuit air delivery, scientists were no longer forced to rely on samples dredged from the depths or washed up on the shore to infer ecological processes. Organisms could be observed firsthand in their natural setting, and followed through time at a variety of depths and locations. As a result, we have learned a great deal about how marine life forms live and die beneath the waves, but there is still much to be learned.

Perhaps nowhere is this more apparent than in the study of tropical green algae. Five genera of siphonous green algae in the order Byropsidales (*Caulerpa* in the family Caulerpaceae and *Halimeda, Penicillus, Rhipocephalus,* and *Udotea* in the family Udoteacae) are particularly notable for their size, their abundance, and the range of habitats they occupy on or near coral reefs (Bold and Wynne, 1985; Littler and Littler, 1994, 2007; Hay, 1997). Prior to direct observations enabled by the application of scuba, very little was known about the ecological role of these algae.

We now know that these seaweeds are extremely important members of shallow-water, tropical marine communities. As primary producers, these algae help sustain many reef-associated herbivores (e.g., Morrison, 1988; Niam, 1988; Littler and Littler, 1994; Stachowicz and Hay, 1996; Williams and Walker, 1999; Munoz and Motta, 2000). As relatively large, structurally complex benthic flora, tropical green algae provide shelter for numerous invertebrates (e.g., Stoner, 1985; Hendler and Littman, 1986; Hay et al., 1990) while competing directly with others for space (e.g., Carpenter, 1986; Hughes et al., 1987; Littler et al., 1989; Tanner, 1995; Ceccherelli et al., 2000; Beach et al., 2003; Márquez and Diaz, 2005). Correlations between increasing green algal abundance and declining coral cover and reef biodiversity further emphasize the ecological significance of these seaweeds within coral reef communities (e.g., Porter and Meier, 1992; Hallock et

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al., 1993; Hughes, 1994a, 1994b; Ogden and Ogden, 1994; Sebens, 1994; Morand and Briand, 1996; Shulman and Robertson, 1996; Szmant, 2002; Smith et al., 2006; Nelson, 2009). Tropical green seaweeds also produce complex defensive compounds that alter the foraging of herbivorous fishes and invertebrates (e.g., Paul and Fenical, 1986; Paul, 1987; Paul and Van Alstyne, 1988; Hay and Fenical, 1992; Stachowicz and Hay, 1996) and potentially have useful biomedical properties (e.g., Fischel et al., 1995; Isassi and Alvarez-Hernandez, 1995). Even after death, the heavily calcified thalli of the Udoteacae contribute to sand production, reef building, and other important geological processes (e.g., Wefer, 1980; Drew, 1983; Flügel, 1988; Marshall and Davies, 1988; Freile et al., 1995; Braga et al., 1996; Freile and Hillis, 1997; Martin et al., 1997).

Despite the obvious relevance of tropical green seaweeds to reef-associated ecosystems, their basic biology remains rather poorly understood, particularly aspects of their reproductive life history. As with many algae, variable, often subtle modes of reproduction obscure many of the most basic aspects of their life history (Bold and Wynne, 1985; Brawley and Johnson, 1992; Lobban and Harrison, 1994); there is a paucity of careful field studies that focus on the algae themselves (Walters et al., 2002; Vroom et al., 2003; van Tussenbroek and van Dijk, 2007). Indeed, the life cycles of some of the most abundant and important groups (e.g., *Halimeda*) have yet to be followed completely in either the lab or the field (see Meinesz, 1980). Put simply, more studies are needed that examine how tropical green seaweeds live and die. This paper seeks to promote further investigations of this cycle by highlighting the potential ecological significance of different aspects of sexual reproduction by tropical green macroalgae.

As with many algae, Bryopisdales reproduce both asexually and sexually. Early studies of vegetative reproduction via rhizoid extension (Hillis-Colinvaux, 1973; Walters and Smith, 1994) and, more recently, thallus fragmentation (Smith and Walters, 1999; Walters et al., 2002) support a general premise that asexual processes contribute significantly to the dynamics of green seaweed populations on and around coral reefs (e.g., Friedmann and Roth, 1977; Hillis-Colinvaux, 1980; Meinesz, 1980). At the same time, observations of seasonal pulses of highly synchronous sexual activity by green algae on Caribbean reefs (Clifton, 1997, 2008; Clifton and Clifton, 1999; van Tussenbroek et al., 2005) imply a previously underappreciated role for sexual reproduction in terms of population regulation and ecological influence. Because sexually reproducing algae die immediately following gamete release, annual peaks of reproduction by tropical green seaweeds have immediate effects on algal demography as density and cover percentage decline precipitously, often in a matter of weeks (Clifton and Clifton, 1999). While the synchronous nature of gamete release presumably boosts fertilization success during episodes of sex, how these bouts of reproduction contribute to subsequent algal recruitment and repopulation of reefs is currently unknown. The remainder of this paper examines how different aspects of sexual reproduction by green algae may contribute to their ecological significance.

GAMETE FORMATION AND SEXUAL IDENTITY

Although easily detected by a trained observer, fertility and sexual reproduction in tropical Bryopsidales is a transient, often overlooked phenomenon. It begins when, overnight, a fraction of the population (tens to thousands of thalli) changes color and/or develops external gametangia. These macroscopic features are clear and reliable indicators of an impending sexual event (Clifton and Clifton, 1999). What induces this pulse of fertility remains unknown (environmental factors such as tides, moon phase, water movement, temperature, and day length are known to organize bouts of synchronous sexual reproduction in other marine organisms; see reviews by Harrison and Wallace, 1990; Brawley and Johnson, 1992; Levinton, 1995). Within 24 or 48 hours (depending on species) the entire algal protoplasm converts to gametic products that migrate into newly developed gametangia. For all species but those in the monoecious genus *Caulerpa,* the gender of a fertile thallus (based on gametangia color and morphology; see Figure 1) becomes apparent during this time (Clifton and Clifton, 1999), facilitating measures of local sex ratios and nearest-neighbor distances prior to gamete release. For species of *Caulerpa*, macro- and microgametes concentrate in different parts of the thallus and can be identified based on color (green = microgametes, brown = macrogametes; Figure 2). These general patterns of fertility have now been verified for over 30 species in 6 genera (Clifton and Clifton, 1999; KEC, personal observation).

The spatial dispersion of fertile male or female thalli presumably plays an important role in fertilization success. Proximity to other reproductive individuals coupled with the synchrony of release generally influences gamete concentration in broadcast-spawning organisms, and gamete concentration influences the likelihood that gametes of opposite sex will encounter one another following release (Lotterhos and Levitan, 2010). The spatial dispersion of males and females may be especially important for dioeceous, sand-dwelling species that occur in a broad range of densities (from isolated individuals to large “meadows” with densities of hundreds of individuals/m^2; e.g., *Halimeda incrassata, H. monile, H. simulans, Penicillus* spp., *Rhypocephalus phoenix*, and *Udotea* spp.). For these species, small, same-sex clusters of two or three individuals (within 5 cm of one another; KEC, unpublished data) are commonly encountered. It remains to be known whether these represent genetically identical thalli derived from vegetative reproduction (ramets), in which case the synchronous release of gametes would boost gamete concentrations and reduce the likelihood of gamete limitation (sensu Levitan, 1993), or whether they are genetically distinct thalli (genets) derived from sexual reproduction and recruitment into the population, in which case synchronous reproduction would increase gamete competition for fertilization. Gender-specific dispersion is, at first glance, less relevant for monoeceous species such as *Caulerpa.* However, differential patterns of sexual allocation to micro- and macrogamete production coupled with the overall spatial distribution of reproductive thalli could still play an

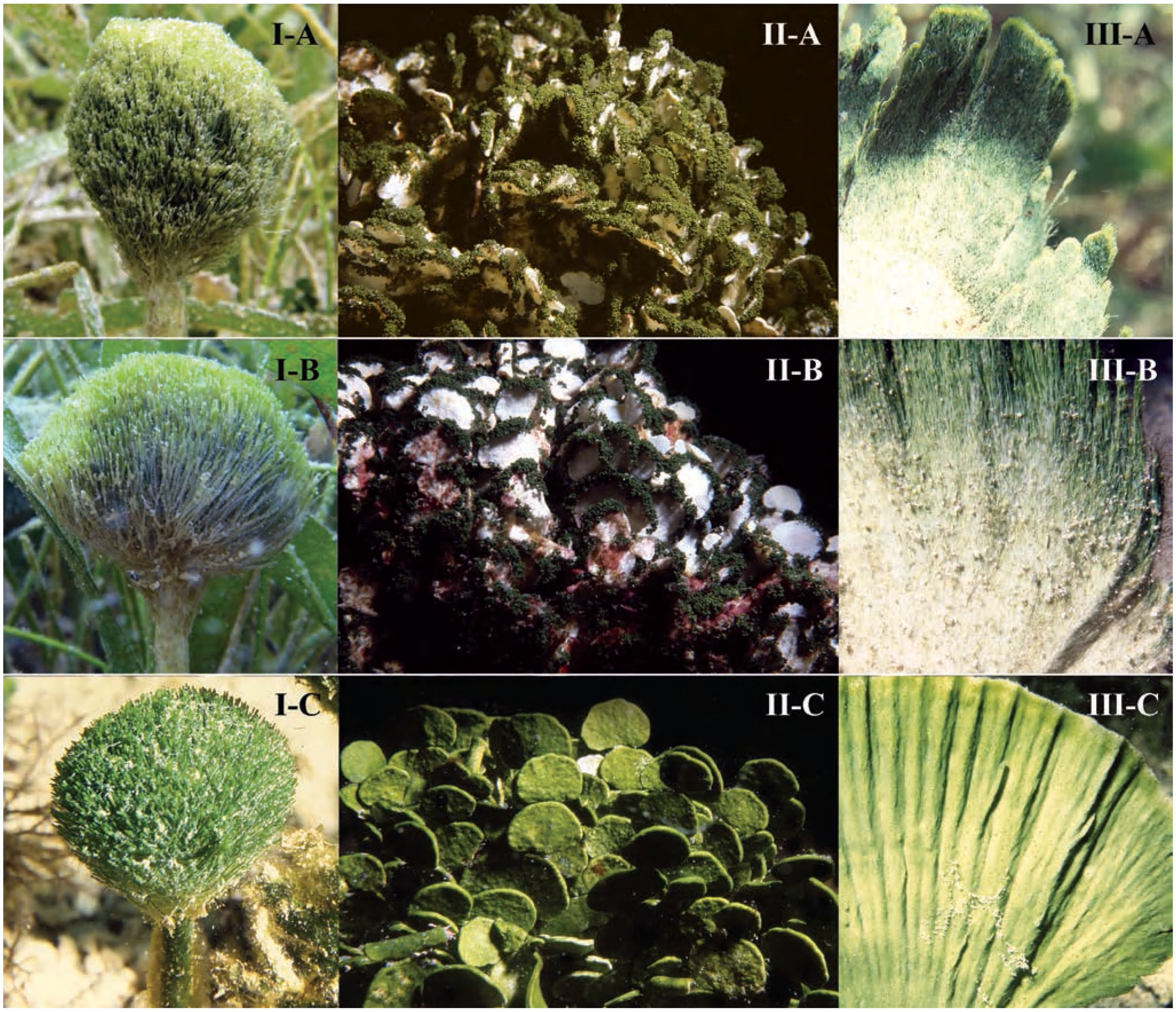

FIGURE 1. Examples of fertility—evident by the presence of gametangia and color change, as well as gender identity—in dioeceous species of siphonous green seaweeds. Species by column: (I) *Penicillus capitatus* (note the white stipe and lighter color of the capitulum in fertile seaweeds); (II) *Halimeda tuna* (external gametangia and white blades denote fertile condition); (III) *Udotea caribea* (note white blade and newly developed gametangia along terminal blade edge). Gender by row: (A) fertile males (lighter green color for all species and rounded tip morphology of gametangia for *U. caribea*); (B) fertile females (darker green/bluish color for all species and spiked tip morphology of gametangia for *U. caribea*); (C) nonfertile thalli for all three species. Photos by Kenneth Clifton.

important ecological role in determining the likelihood of successful zygote formation.

SEXUAL REPRODUCTION AND HERBIVORY

A diverse array of crustaceans, echinoderms, mollusks, and fishes consume siphonous green algae as part of their regular diet. These seaweeds counter with an evolved combination of chemical and physical defenses that deter rates of feeding by different herbivores to varying degrees (e.g., see Hay and Fenical, 1992; Williams and Walker, 1999; Paul et al., 2001; Molis et al., 2008; and references therein). To date, studies of herbivory on Bryopsidales have focused almost exclusively on the consumption on nonreproductive thalli.

The potential for chemical and physical defenses to herbivory to be altered by a shift from vegetative to reproductive

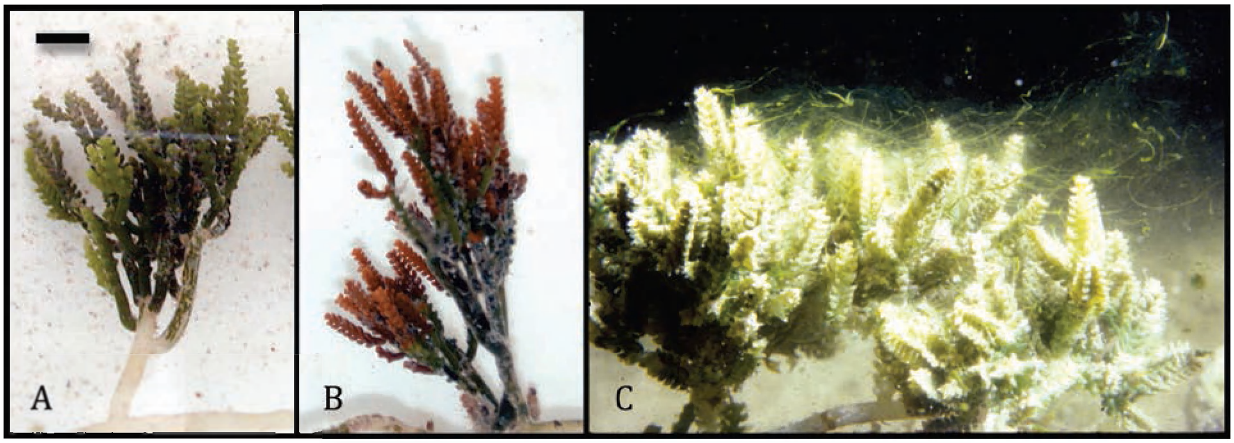

FIGURE 2. Progression of fertility in the monoeceous green alga *Caulerpa cupressoides*. (A) Cellular contents migrate from rhizoids into unspecialized gametangia at terminal ends of blades approximately 48 hours prior to gamete release. (B) Roughly 24 hours later, segregation of macrogametes (brown, terminal areas of blade) and microgametes (greener, basal sections) occurs, leading to a two-colored appearance. (C) The discharge of both micro- and macrogametes occurs from separate small tubular orifices that develop 1–3 hours prior to gamete release. Scale bar = 1 cm (all three images). Photos by Kenneth Clifton.

state seems high. Uncalcified gametangia, the structures that house gametes prior to their release, develop during the initial stages of fertility. Thus, they are potentially exposed to herbivores that would normally be deterred by the presence of $CaCO_3$ for one or more night/day cycles, depending on the species of algae. The chemical defenses of these seaweeds may be similarly altered, as the conversion of the entire thallus from vegetative protoplasm to gametes occurs during a similar time span. While the phenomenon has not been investigated sufficiently, observations of heavy infestations of the sacoglossan sea slug *Elysia tuca* on fertile specimens of sand-dwelling *Halimeda incrassata* and *H. monile* (hundreds of slugs on a single reproductive thallus versus a normal load of one or fewer slugs on a nonreproductive thallus; KEC, pers. obs.) indicate that some species of herbivores respond directly to the expression of sexual reproduction by green algae. Severe herbivory on the gametangia of fertile specimens of *Udotea*, *Penicillus*, and *Rhypocephalus* have also been observed (Figure 3). If a shift to fertility does attract a disproportionate level of herbivory, it may represent an additional cost of reproduction to the seaweed; the phenomenon certainly merits further study.

GAMETE CHARACTERISTICS

The flagellated, anisogamous gametes produced by siphonous green algae are known from a variety of studies (e.g., Goldstein and Morrall, 1970; Meinesz, 1972, 1980; Kajimura, 1977; Hillis-Colinvaux, 1980; Enomoto and Ohba, 1987; Clifton and Clifton, 1999). The size of biflagellated male microgametes is relatively consistent across taxa, whereas female macrogametes occur in two forms, depending on species. *Halimeda*, *Caulerpa*, and one species of *Udotea* (*flabellum*) produce biflagellated, phototactic macrogametes that morphologically resemble microgametes but are 2–34 times larger (Clifton and Clifton, 1999) and possess an obvious eye-spot. Relative gamete size may play an important role in fertilization dynamics in terms of both gamete encounter rates (Levitan, 2006) and gamete behavior. Although negatively buoyant, biflagellated macrogametes can swim relatively long (1–5 m) distances toward light (Clifton, 1997) prior to fertilization. As in other green algae (e.g., Togashi et al., 1998), zygotes of these species show negative phototaxis immediately after fertilization (KEC, unpublished). In contrast, *Penicillus*, *Rhipocephalus*, and three species of *Udotea* (*abbottiorum*, *caribaea*, and *cyathiformes*) produce large (100 µm diameter) stephanokont gametes (Figure 4) with flagella arrayed along a membranous, sheetlike tail (Clifton and Clifton, 1999). To date, these large, macroscopically visible gametes (Figure 5) have not been well studied (Meinesz, 1980; Littler and Littler, 1990); however, observations of freshly released material indicate that these gametes are relatively immotile. Under calm conditions they quickly sink, tail up, to the bottom, where flagellar motion drives water past the gamete. This may increase encounter rates with microgametes. Upon fusion, the membranous tail quickly (30–90 s) stops moving and is absorbed into the zygote. Both negative phototaxis and negative buoyancy presumably limit the distance a zygote disperses, however the extent of this limitation and the degree to which it influences local population dynamics following zygote development and recruitment awaits further study.

Given that siphonous green algae convert their entire protoplasm into gametes, and in keeping with a simple model of quantity versus quality, the number of gametes produced by an alga

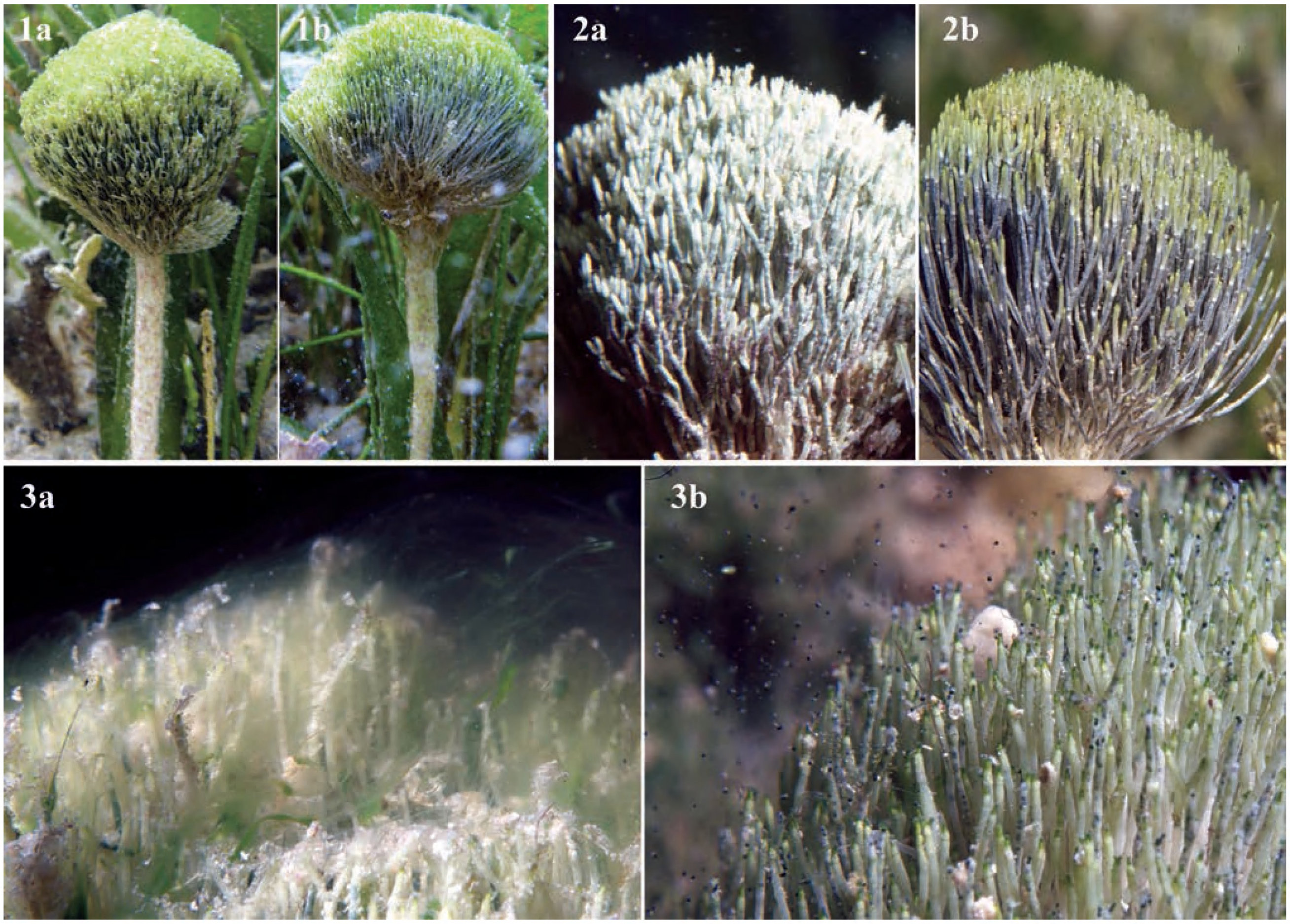

FIGURE 3. Details of protoplasm migration, gametangia development, and gamete release for male and female *Penicillus lamourouxii*. (1) Fertile male (a) and female (b) thalli showing diagnostic white stipe caused by protoplasmic migration. The darker, blue/green coloration of the female and the lighter green color of the capitulum are both reliable indicators of fertility and gender. (2) Closer view of the top section of a fertile male (a) and female (b) 12 hours prior to gamete release. Note the light green, uncalcified extension of siphonous tubes and clearly evident sexually dimorphic colorations. (3) Gamete release from male (a) and female (b) seaweeds. Individual macrogametes can be seen wafting away from the female. Photos by Kenneth Clifton.

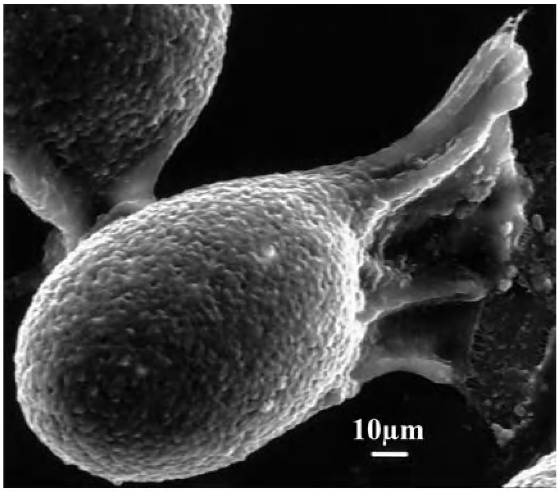

FIGURE 4. Scanning electron microscope image of stephanokont macrogamete from *Rhipocephalus phoenix*. Flagellae that line the edge of the membranous tail are not visible, probably due to loss during sample preparation. Photo by Kenneth Clifton.

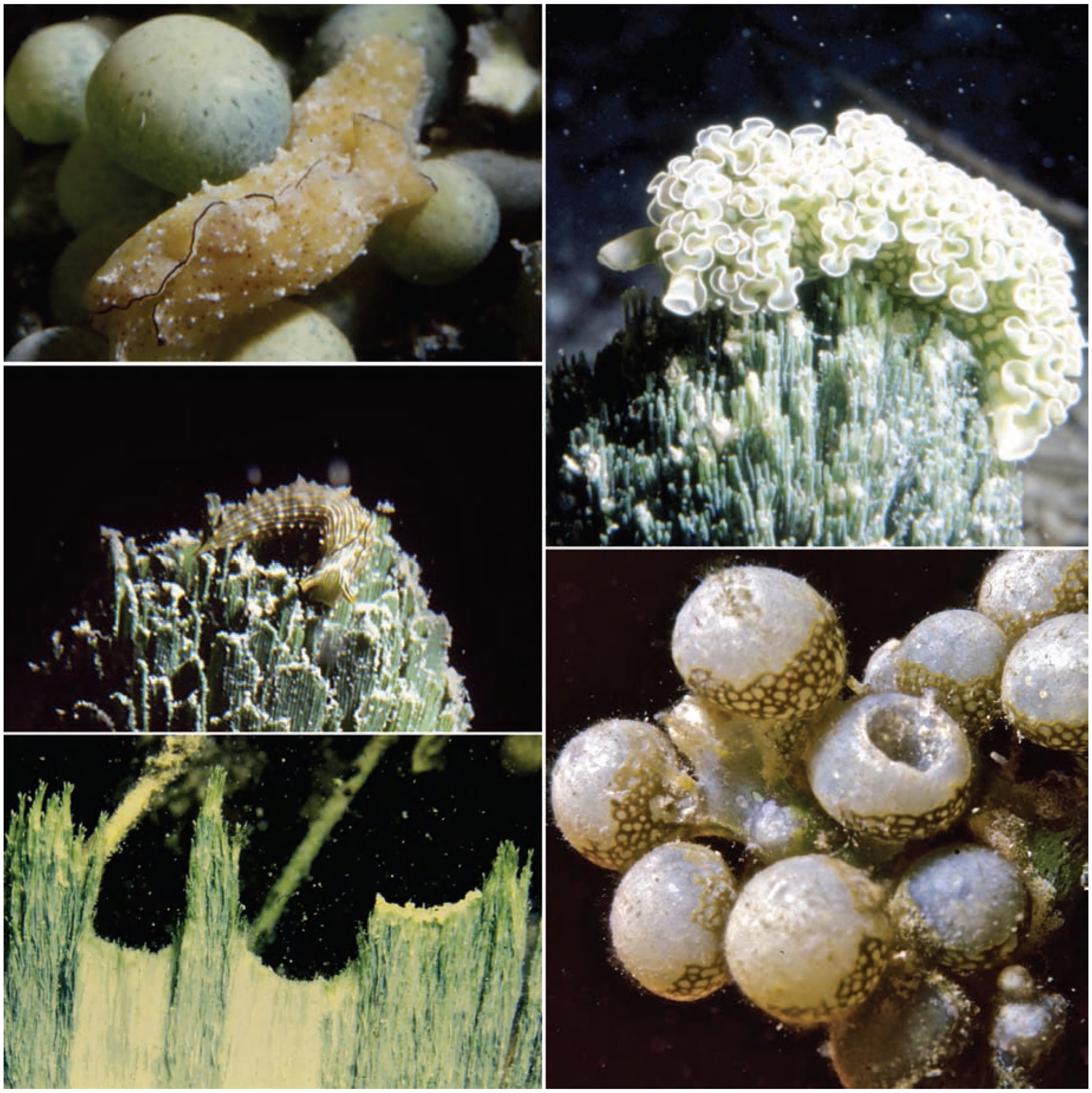

FIGURE 5. Examples of herbivores known to consume siphonous green algae and herbivory on fertile seaweeds. Clockwise from top left: the saccoglossan sea slug *Elysia subornata* on nonfertile *Caulerpa racemosa*; *E. crispata* on nonfertile *Penicillus lamourouxii*; a close up view of fertile *C. racemosa* showing unspecialized gametangia along blade bases and an apparent bite wound (source unknown) to one blade; parrotfish bite wounds to gametangia of female *Udotea caribaea*; and *E. subornata* on nonfertile *Rhipocephalus phoenix*. Photos by Kenneth Clifton.

should be related to gamete size. Preliminary investigations support this contention. Samples of total gamete release by a single thallus into known volumes of seawater reveal that, as expected, larger seaweeds release a greater number of gametes, and further that females produce fewer gametes than males for a given thallus size (Figure 6). There appears to be no relationship between gamete size and thallus size.

THE TIMING OF GAMETE RELEASE

The reproductive synchrony of siphonous green algae can be evaluated on several temporal scales. On the diel scale, in all species studied to date, both micro- and macrogametes are released directly into the water column during a single, brief (typically 5–15 min), highly synchronous pulse of early morning

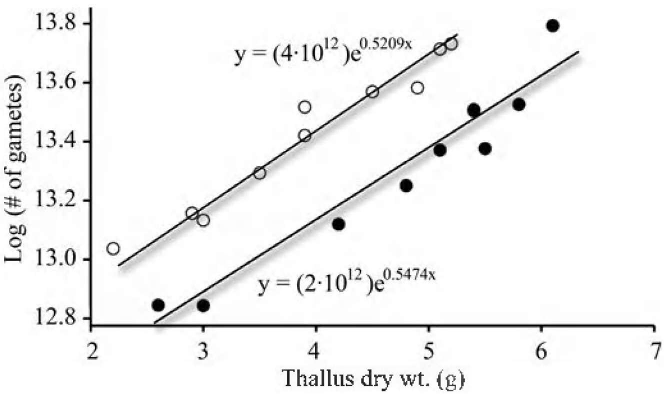

FIGURE 6. Number of gametes released versus thallus size for 10 male (microgametes, open circles) and 10 female (macrogametes, filled circles) *Udotea flabellum*. The effect of sex on the relationship between gamete number and thallus size was significant (ANCOVA; $p = 0.035$).

reproduction (Clifton, 1997). The alga dies immediately following gamete release (holocarpy). The timing of release appears to be organized around changing light levels associated with the onset of daylight, though water temperature also plays a role (Clifton, 1997). The duration of gamete release varies between species, with larger, epilithic species tending to release their gametes more rapidly (Clifton and Clifton, 1999). With many thalli reproducing synchronously, dense gamete clouds may extend down-current for tens of meters, though these generally dissipate within 5–10 minutes even under the calmest conditions. The precise timing of release relative to sunrise remains consistent for a given species across seasons and years. Up to nine species from five genera have been observed to release gametes on the same morning; however, each species has a specific, narrow time of release (Clifton and Clifton, 1999). Some species show overlapping times of gamete release, though more closely related species (Hillis et al., 1998; Vroom et al., 1998; Kooistra et al., 1999) reproduce at different times (Clifton, 1997). This may reduce hybridization if gamete viability is short lived relative to the time between release by different species.

Green algae may show a broad seasonal peak of sexual reproduction that shifts with latitude (Clifton, 2008), but unlike many broadcast-reproducing invertebrates they exhibit no obvious lunar or tidal cycling (Clifton, 1997). During seasonal peaks of reproductive activity, populations of green algae undergo iterative bouts of sexual reproduction with varying degrees of intensity. Only a subset of a given population releases gametes on a particular morning (generally about 5%, though major bouts of sexual reproduction involving more than 45% of the population can occur). Episodes of sexual reproduction typically occur on numerous reefs within a given geographic region on the same morning, including on reefs several kilometers apart.

During the seasonal peak of activity, bouts of sex occur on roughly two-thirds of mornings; this frequency varies somewhat interannually (e.g., bouts of gamete release occurred on 42%, 80%, and 68% of days during the seasonal reproductive peaks in 1995, 1996, and 1997, respectively). When sexual reproduction is observed on a given morning, several species are often involved. On a single Panamanian patch reef in 1996, 16 species of green algae collectively underwent 233 bouts of gamete release between March and July, with 97 additional events occurring between March and mid-May the following year. A recent comparison of algal sexual reproduction in St. Croix and Panama indicates that similar levels of activity occur throughout the Caribbean (Clifton, 2008).

Given the holocarpic life history of these seaweeds, iterative bouts of sexual reproduction have a rapid and dramatic impact on adult algal distribution and abundance (Clifton and Clifton, 1999). Algal cover can drop dramatically, freeing up space for future colonization, perhaps by the same species, or more likely by other members of the benthic community. Our understanding of the nature of algal population dynamics and their effect on the overall organization and function of coral reefs remains in its infancy. Similarly, little is known of how the postreproductive disintegration and dissolution of these calcified seaweeds contributes to rates of $CaCO_3$ input into reef sediments.

ZYGOTE FORMATION AND DISPERSAL

Very little is currently known about the early life history of siphonous green seaweeds. Although mature algae are easily maintained in aquaria (e.g., Hillis-Colinvaux, 1980; Drew and Abel, 1988; Ohba et al., 1992), zygote development in the laboratory has been described for only *Caulerpa serrulata* (Price, 1992) and *Halimeda tuna* (Meinesz, 1972). After five months the latter produced an alga quite different from the parents, and the complete life cycle of the genus remains unresolved. Meinesz (1980) reported adult-like algae from the zygotes of *Flabellia petiolata* (formerly *Udotea*) after seven months, and Friedmann and Roth (1977) describe an "*espera*" (non-adult-like) state of *Penicillus capitatus* that arose after months of culturing. It is unclear whether these nonadult morphs represent a natural stage of development or simply an artifact of in vivo conditions.

These laboratory observations should encourage further study of zygote development, particularly under natural conditions. Such data are fundamental to an understanding of how algal recruitment and rates of growth from zygote to adult thallus influence population dynamics. The relatively slow rates of development reported from the lab coupled with field observations of delayed recovery of populations following peaks of sexual activity suggest that algal recruitment occurs several months after fertilization, with a possible cryptic stage of life history occurring before the production of an adult form. Perhaps this allows green algae to persist through unfavorable seasonal periods of temperature, salinity, or light in a manner analogous to terrestrial seed banks (Hoffmann and Santelices, 1991). Seasonality in Panama (Cubit et al., 1989), where most of the longer-term data on temporal patterns of green algal sexual reproduction have been obtained, is known to be ecologically significant for herbivorous reef fishes and their algal foods (e.g., Robertson, 1990; Clifton, 1995).

CONCLUSION

Numerous studies have implied a significant ecological role for siphonous green algae within tropical marine communities. To date, however, the basic biology of these algae remains poorly understood. The presence of complex life-history strategies and remarkable interspecific variation in the manner in which different algae reproduce are partly to blame for this dearth of information, yet this very same complexity and variation offer marine ecologists unparalleled opportunities to explore the ways in which factors such as timing and location of reproduction, patterns of gamete size and behavior, and fertilization success and zygote development ultimately influence where and how abundantly these algae occur. Investigations of the origins and consequences of algal reproduction remain a critical step toward improved understanding of the biological mechanisms that underlie their ecological significance.

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Fine-Scale Interspecific Interactions on Coral Reefs: Functional Roles of Small and Cryptic Metazoans

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ABSTRACT. Direct underwater observations and experiments aided by scuba technology have greatly advanced the science of coral reef ecology. Coral community species interactions of small (macrofauna) and cryptic metazoans can exercise pivotal roles in the vitality, protection, and perpetuation of reef-building corals. Advances in the understanding of mechanisms underlying coral–metazoan symbiotic and facilitative interactions are examined in six invertebrate phyla (Porifera, Cnidaria, Acoelomorpha, Annelida, Mollusca, and Arthropoda) and in fishes, the latter with emphasis on cryptic coral reef fishes in the eastern Pacific. Crustacean associates of zooxanthellate corals, especially those inhabiting corals with branching morphologies, are notably diverse and can exhibit complex behaviors that greatly benefit their hosts. Several recently proposed positive effects of coral associates are reviewed, including evidence for increased colony stabilization, asexual fragmentation, interbranch circulation, cleansing of coral surfaces, mineral nutrient regeneration, reduction in the settlement of fouling organisms, and the removal of algal overgrowth. In several instances, the shared positive effects resulting from symbiotic interactions suggest that formerly regarded relationships of commensalism and parasitism are best viewed as mutualisms. The presence of a diverse and abundant cryptic fauna in coral communities suggests important roles in predation, selective recruitment effects, scavenging, and nutrient regeneration processes.

INTRODUCTION

Fine-scale studies of interspecific interactions on coral reefs have demonstrated important roles of small and often inconspicuous invertebrate and fish metazoans. Notable advances have been made recently in our understanding of various trophic relationships in this often-neglected area. This paper offers a brief overview of biotic interactions of selected coral reef metazoans with emphasis on trophic relationships involving small, generally unseen or cryptic fauna. Coral symbioses (beyond the well-known microscopic, symbiotic zooxanthellae), reef scavengers, and cryptic fish carnivores are the chief areas addressed because of my personal involvement with research on these topics. Consequently, other groups of organisms such as herbivores, suspension feeders, deposit feeders, and parasites, while of paramount importance to the trophodynamics of reef ecosystems, are considered here only peripherally. This treatment considers mainly field-based observations via scuba diving, a principal method for observation, collection, and experimentation; however,

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relevant laboratory studies are referenced where they shed light on particular processes and relationships.

Coral–metazoan symbioses were generally considered to be interesting and novel when first reported, but with little if any ecological importance. Field studies conducted during the past few decades, however, have revealed several pivotal roles of coral–metazoan associations that can affect the survivorship of both symbionts and hosts and even influence coral community structure, reef growth, and recovery from disturbances.

Several excellent reviews are available on the animal associates of living corals (e.g., Garth, 1964; Patton, 1974, 1976, 1994; Bruce, 1976, 1998; Castro, 1976, 1988), however many new symbiotic relationships and functions have been described over the past two decades. This is due in large measure to a renewed interest in biodiversity and the development of new methodologies. To illustrate the breadth and depth of coral–metazoan interactions, examples are selected from documented studies in six invertebrate phyla (Porifera, Cnidaria, Acoelomorpha, Annelida, Mollusca, and Arthropoda) as well as fishes. Due to the great variety of coral–crustacean symbioses, relationships among the Cnidaria and Arthropoda are highlighted.

In addition to the many invertebrates associated with living corals, an abundant and diverse community of sessile and vagile metazoans is known to take refuge in dead coral crypts, including suspension feeders, necrophagous or scavenging species, carnivorous predators, and grazers (e.g., Jackson and Winston, 1982; Choi and Ginsburg, 1983; Gischler and Ginsburg, 1996; Wunsch et al., 2000). In most studies there has been a bias toward describing sessile taxa due in large measure to their ease of collection and quantification. Here I consider predominantly ecological interactions of motile cryptic fauna. Assemblages of cryptic scavengers from the eastern Pacific are compared with those reported from Lizard Island, Great Barrier Reef, Australia. Finally, the diets of cryptic reef fishes from 20 families in Colombia and Panama are considered. The data collectively indicate the prevalence of predation in cryptic coral reef habitats.

TERMINOLOGY AND PERSPECTIVE

Emphasis in this essay is on the macrofauna (i.e., small invertebrates and fishes in the size range of 1–40 mm body length). This group also includes mesograzers and mesoherbivores, herbivorous taxa that are not microscopic but not easily seen when undisturbed (Hay et al., 1987; Carpenter, 1997). Occasionally reference is made to some taxa (e.g., ostracods, mysids, and isopods) that belong to the microfauna, with body length <1 mm. Moreover, some species examined exceed the size limits of the macrofauna (e.g., cryptic sponges, bryozoans, and tunicates in large cavities that can attain maximum body length in excess of 10–20 cm). Also, small postsettlement and juvenile stages of species that shelter in reefs are only temporary members of the macrofauna, attaining larger size as they grow, mature, and leave the confines of reef frameworks.

Most members of the macrofauna occupy cryptic habitats and remain hidden in reef structures that range from intra- to interskeletal cavities, borings, and interparticle spaces. The complexity of cryptic habitats in terms of physical conditions and biotic composition is highlighted in Ginsburg (1983) and Kobluk (1988). While many coelobites (i.e., cryptofauna or cryptic biota) remain permanently hidden (e.g., various intraskeletal and benthic species), large numbers also are transient and emerge from reefs daily (reef plankton), seasonally, or during development as they mature (e.g., mollusks, crustaceans, and fishes).

Some cautionary remarks are necessary regarding the classification of feeding modes. Clear distinctions between predators, scavengers, and parasites are often difficult to determine. Many consumer species are opportunists, assuming the role of predators or scavengers depending on the availability, variety, and condition of prey. For example, some omnivorous polychaete worms will pursue, attack, and consume preferred live prey when abundant, but will also resort to feeding on moribund and dead animals if their usual prey is in short supply. These feeding modes can also change depending on the developmental stage of the consumer. Other groups of metazoans exhibit feeding behaviors that may be considered to belong to two or more different feeding modes. For example, mesopredators that live in intimate association with coral colonies (e.g., flatworms, prosobranch and nudibranch gastropods, copepods, barnacles, crabs, shrimps, and gobies) typically consume small amounts of tissue and/or secretory products, causing only partial mortality, and therefore they may also be classified as parasites (Castro, 1988; Glynn, 1988). They also may be considered omnivores or even deposit feeders if they feed primarily on mucus or other byproducts of their coral hosts. Additionally, scavengers and detritivores that feed on dead and decaying plant and animal remains differ primarily in the relative size and state of degradation (microbial decay) of the organic matter ingested, which can vary widely depending on the size of the consumers.

Much debate surrounds the definition of symbiosis. Some researchers restrict the term to mutualisms (i.e., mutually beneficial relationships resulting from intimate heterospecific associations). Others have applied more restrictive criteria (e.g., requiring the demonstration of some degree of metabolic dependency [see Castro, 1988] or dismissing relationships in which a host responds to an organism's presence by forming a kind of physical barrier [Pantos and Bythell, 2010]). In this essay Anton de Bary's (1879) broad definition of symbiosis is employed, slightly modified as follows: an intimate and prolonged association between two or more organisms in which at least one partner obtains some benefit from the relationship. This definition avoids the categorization of relationships and preconceptions about outcomes (Saffo, 1993).

Not all cryptic metazoans are engaged in symbiotic interactions, but they may still benefit from the presence of associated species. Positive or facilitative interactions involve encounters that are beneficial to at least one of the participants and harmful to neither (Bruno et al., 2003). Facilitation is best regarded as all encompassing; it can bring about positive effects under many guises. Various types of symbioses can have positive effects, and even predation and parasitism can result in indirect positive effects. For example, several metazoan symbionts of corals that were formerly regarded as harmful or neutral to their hosts are now known to provide various benefits (e.g., defense against predators, tissue irrigation, protection from fouling organisms, and nutrient enrichment). Many of the coral–metazoan associations considered below that are beneficial to at least one member can best be considered under the rubric of facilitation. The challenge is to rigorously quantify such positive interactions so that they can be related to individual fitness, species population dynamics, and community-scale composition and diversity.

REEF MACROFAUNA: CASE STUDIES AND INTERACTIONS

PORIFERA

Coral–sponge interactions are often perceived to be detrimental to corals because of the destructive effects of bioerosion as well as the competitive dominance and overgrowth of corals by sponges. At least two mutually beneficial interactions have been reported, however. These were observed by Goreau and Hartman (1966), who showed that the demosponge *Mycale laevis*, which is often present on the undersurfaces of plating *Montastraea annularis* corals, may provide a benefit to the partnership. Sponge and coral growth are in balance, with neither overgrowing the other. The peripheral skeletal folds of the coral grow around the oscules of the expanding sponge. Potential competitors of sponges (i.e., fouling organisms) and boring organisms capable of penetrating coral skeletons are absent from those parts of the colony overgrown by the sponge. Additionally, the coral may benefit nutritionally from an enhanced feeding efficiency caused by the sponge's effluent currents. The sponge in turn occupies increasing substrate space as the coral grows.

Even excavating sponges, despite their bioerosive effects, may not have a negative influence in all situations. Highsmith (1982) noted several studies in which boring sponges were shown to promote asexual fragmentation in corals. The carbonate skeletons of most coral species are susceptible to erosion by clionaid sponges; both branching and massive coral colonies have been shown to shed live fragments that contribute to lateral reef expansion. This has been reported in the Caribbean for *Acropora* spp. and *Porites furcata* (branching taxa) and *Montastraea annularis* (a massive taxon), and in the eastern Pacific for *Pocillopora damicornis* (branching) and *Pavona clavus* (massive). The shedding, survival, and dispersal of fragments following disturbance events can aid in the rapid recovery of coral cover.

Several sponge species contribute to the stabilization of reef framework structures (Wulff and Buss, 1979; Rützler, 2004; Wulff, 2006). Both epibenthic and cryptic sponges temporarily stabilize coral rubble as they attach to and bind loose coral fragments. Field experiments have demonstrated that sponge fragments can consolidate coral rubble quickly, within a 10-month period (Wulff, 1984). Small corals that had originated from asexual fragmentation (or sexual recruitment) were dependent on sponge binding. Sponge-mediated substrate stabilization provides an opportunity for the successful settlement and survival of corals, bryozoans, vermetid mollusks, and serpulid worms. Another result of the sponge-mediated stabilization was an increase in topographic relief, which was twice that of experimental rubble piles without sponges. Encrusting coralline algae contributed importantly in later stages of the consolidation cycle.

Some quantitative measures of the contribution of cryptic sponge filter feeders to ecosystem-scale trophodynamics have been reported for a fringing Red Sea reef by Richter et al. (2001). By means of endoscopic exploration, these researchers determined that the surface area of reef cavities greatly exceeded that of reef surfaces by factors of 2.5–7.4 m^2. Sponge cover predominated in cavities, amounting to 60% of all coelobites, and exceeded surface filter feeder biomass by twofold. This study concluded that the consumption and mineralization of allochthonous organic matter by cryptic sponges is a principal source of nutrients that support endosymbiotic algal and coral growth. The magnitude of this cycling could help explain how high coral reef productivity occurs in often nutrient-deficient waters.

CNIDARIA

Cnidarians offer numerous resources to reef organisms, and this is reflected in the great variety of taxa associated with zooxanthellate corals, from bacteria and fungi (Rohwer et al., 2002; Knowlton and Rohwer, 2003) to invertebrates and fishes (e.g., Patton, 1976; Castro, 1988; Cole et al., 2008; Glynn and Enochs, 2011). Reef-building or zooxanthellate corals (i.e., those harboring endosymbiotic photobionts [*Symbiodinium*]) provide shelter and protection (cnidocytes) from predators, and trophic resources (mucus, tissues, lipids, zooxanthellae) for their metazoan residents.

Perhaps the most celebrated corals offering shelter and trophic resources to diverse metazoan symbionts are several species in the scleractinian families Acroporidae and Pocilloporidae. Their tissues, secretory products, and endosymbiotic algae provide a rich source of nutrition for numerous crustacean associates, many of which are obligate symbionts of specific coral host taxa. No fewer than four trophic pathways were identified by Rinkevich et al. (1991) for a pocilloporid species (*Stylophora pistillata*) in the Red Sea (Figure 1). At the base of this food web are the microbial community and particulate organic detritus plus minute plankton organisms embedded in the coral host's mucus. This organic matrix is consumed by obligate *Trapezia* crabs and other coral symbionts, as well as various facultative and free-living grazing metazoans. Metabolic byproducts (nutrients) of the coral host are utilized by zooxanthellae, which in turn supply corals with photosynthates. Although early investigators surmised that crustacean symbionts fed primarily on coral mucus,

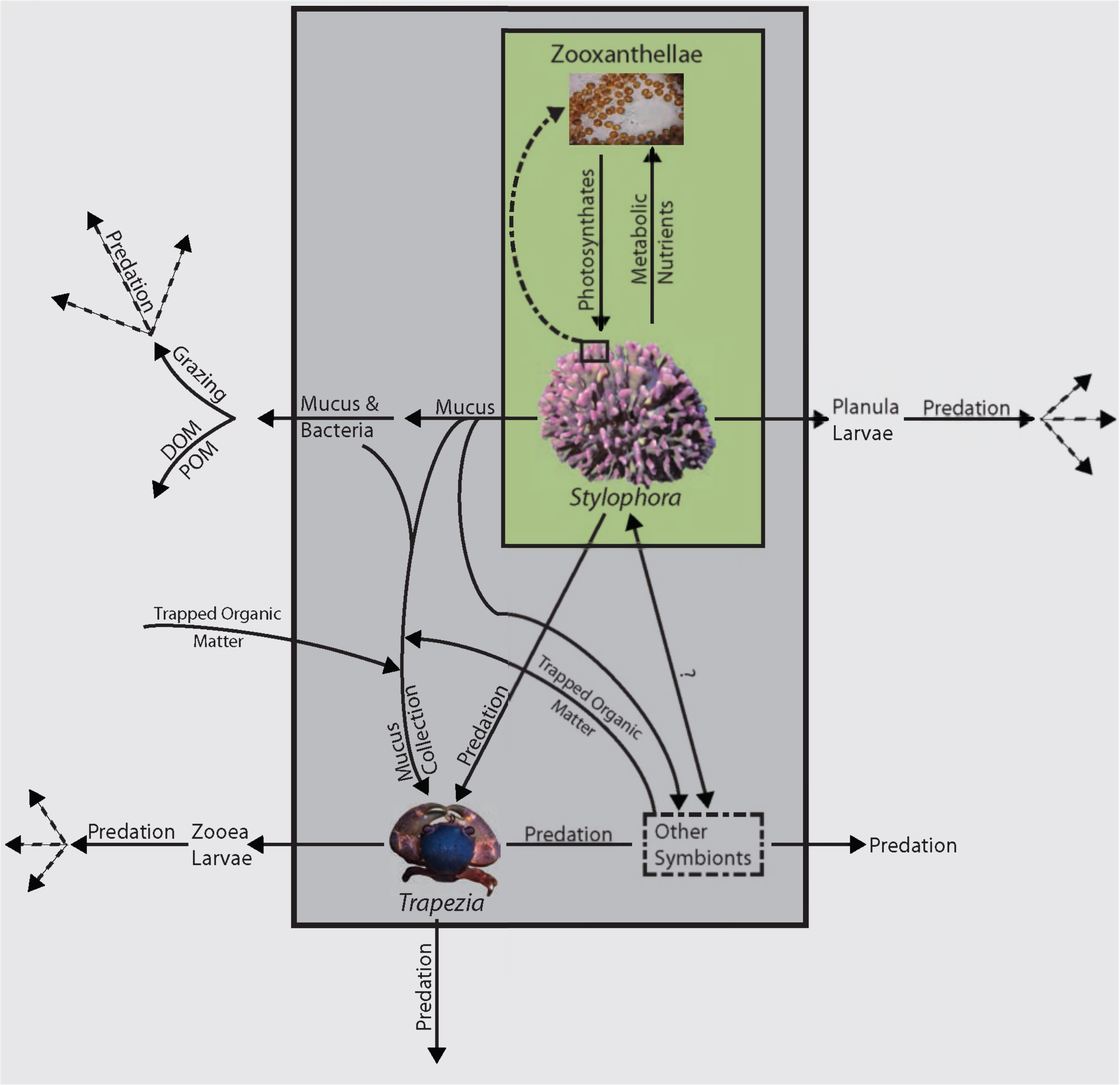

FIGURE 1. Multiple trophic pathways in a coral/microbial/zooxanthella/crab symbiosis (modified from Rinkevich et al., 1991).

Rinkevich et al. (1991) demonstrated conclusively—by employing C-14 isotopic labeling—that *Trapezia* grazes directly on coral host tissues. An additional trophic pathway involves predation of crustacean and other symbiont associates by free-living invertebrates and fishes. Finally, the larvae released by host corals and metazoan symbionts into the water column are consumed by planktivores.

Not only are zooxanthellate corals essential for building reef frameworks, but they also provide a limestone substrate that is actively eroded and occupied by numerous excavating taxa such as fungi, microfilamentous algae, sponges, annelid worms, bivalve mollusks, crustaceans, and fishes (Hutchings, 1986; Glynn, 1996; Perry and Hepburn, 2008; Tribollet and Golubic, 2011). Early studies have described the symbiotic relationship between endolithic bivalve mollusks and fungiid corals, and how embedded mytilid bivalves engulf various items (e.g., phytoplankton, mucus, and extruded zooxanthellae) from the coral host's coelenteron (Goreau et al., 1970). In a classic study, Goreau and Yonge (1968) described the unique relationship between a free-living dendrophyliid coral (*Heteropsammia*) and a sipunculid worm (*Aspidosiphon*). The coral host provides a refuge for the sipunculid, which pulls the coral along the muddy-sandy bottom. This enhanced mobility increases the feeding efficiency of the coral, which sweeps its tentacles across the mud surface. The sipunculid in turn probes subsurface sediments while feeding—neither partner in competition with the other.

A diverse suite of nonexcavating organisms also finds refuge in available cavities. This community of hidden organisms, including those that occupy interskeletal spaces, is referred to as the opportunistic cryptobiota or nestling fauna. Several researchers maintain that the cryptobiota may exceed in diversity and biomass the visible surface biota (Ginsburg, 1983; Reaka-Kudla, 1997; Richter et al., 2001).

ACOELOMORPHA

Another complex symbiotic association, involving corals, epizoic acoel worms, and algal symbionts, is being actively investigated in the northern Red Sea (Barneah et al., 2007). *Waminoa brickneri*, possibly one of a multispecies complex, has been found on the surface tissues of 13 zooxanthellate scleractinian coral species at Eilat. The acoel worms generally demonstrate a low infestation rate (<5%); however, notably high abundances have been observed on some coral hosts. Both *Waminoa* and the coral hosts contain endosymbiotic dinoflagellates. *Symbiodinium* sp. and ?*Amphidinium* sp. were present in the worm, as was *Symbiodinium* sp. in the corals. Molecular genetic evidence and histological examination indicated that the two genera of dinoflagellates in the acoel worm are unique and therefore not present in the coral host. The symbionts are independently and vertically transmitted by the worm via oocytes during gametogenesis. This is the first evidence of maternal transmission of dinoflagellates in a triploblastic organism. These worms probably consume coral mucus and may have a negative impact on their host coral's photophysiology when present in large numbers.

ANNELIDA

To date, the amphinomid polychaete *Hermodice carunculata* is the only annelid species known to prey consistently on coral tissues (Fauchald and Jumars, 1979). This worm is widely distributed on western Atlantic reefs, where it typically preys on branching corals within the genera *Acropora* and *Porites*. Its preference for these corals is of increasing concern due to population declines of acroporids following hurricane disturbances (Knowlton et al., 1990) and disease outbreaks (Williams and Miller, 2005). In the eastern Mediterranean Sea, *H. carunculata* preys on *Oculina patagonica* and in the process inadvertently infects its prey with *Vibrio shiloi*, a causative agent of coral bleaching (Sussman et al., 2003). It is not presently known if *H. carunculata* can infect acroporid prey in the tropical western Atlantic.

Pherecardia striata, an eastern Pacific amphinomid, is an aggressive reef predator/scavenger and vigorously attacks wounded or moribund *Acanthaster planci* sea stars (Glynn, 1982). *Acanthaster* that are wounded by harlequin shrimp (see below) or fish predators attract the worms, which enter the sea star's body cavity and consume soft organs such as hepatic caeca and gonads. *Pherecardia* are cryptic and patchily distributed within pocilloporid reef frameworks; where present, they can attain median population densities of 90–380 individuals m^{-2} (Glynn, 1984).

A sessile polychaete worm that constructs and occupies calcareous tubes embedded in massive corals has been shown to promote polyp survival following damage from corallivores and bleaching. The polychaete in question has been tentatively identified as *Spirobranchus giganteus*, a member of a possibly 10–12 species complex (Fiege and ten Hove, 1999). Many but not all individuals were observed to defend their coral hosts (*Porites* spp.) on the central Great Barrier Reef by thrusting their hook-adorned operculum at the tube feet and arms of attacking *Acanthaster*. This reaction interrupted the sea star's feeding response, resulting in localized polyp survivorship. Surviving polyps contributed to the regeneration of large, old colonies that experienced tissue mortality on surfaces lacking defending worm symbionts (DeVantier et al., 1986).

Ben-Tzvi et al. (2006) have suggested that *Spirobranchus giganteus* worms living embedded in corals may also benefit their hosts during bleaching events. They found that coral tissues immediately surrounding the serpulids showed no damage and quickly recovered after bleaching events. This led these researchers to hypothesize that sessile tube worms positively influence their immediate surroundings by causing (1) improved water circulation, (2) more efficient dispersal of waste products, and (3) increased availability of nutrients. Additional evidence that nutrients from spionid polychaete worms may be involved in coral tissue regeneration was offered by Wielgus and Levy (2006) in a study at Eilat in the northern Red Sea. Via the application of an active fluorescence technique over infested and noninfested coral colony surfaces, these researchers observed marked differences in holobiont primary production. Photosynthetic activity and coral tissue proliferation were greatest at worm-infested sites, leading to the conclusion that spionid waste products contribute to localized eutrophication. Also, the experimental coral, *Astreopora myriophthalma*, showed knobby growth aberrations at the sites of infestation. They concluded that this was due to an increased nitrogen/carbon ratio near the worms that resulted in greater tissue proliferation compared with calcification.

MOLLUSCA

Most studies examining the effects of mollusks on zooxanthellate corals highlight their negative influences. Noteworthy are the several species of gastropods that graze on coral tissues (Robertson, 1970; Hadfield, 1976; Schuhmacher, 1992; Rotjan and Lewis, 2008) and bivalves that bore into coral skeletons (Kleemann, 1980; Valentich-Scott and Tongkerd, 2008). Obligate gastropod corallivores—for example *Drupella* spp. in the western Pacific and Indian Oceans, *Jenneria pustulata* in the eastern Pacific, and *Coralliophila* spp. in the Caribbean—have caused significant mortality on some reefs. Additionally, *Phestilla lugubris* (=*sibogae*), an aeolid nudibranch, lives its entire life and feeds extensively on *Porites compressa* colonies in Hawaii caused significant mortality on some reefs. Additionally, *Phestilla lugubris* (=*sibogae*), an aeolid nudibranch, lives its entire life and feeds extensively on *Porites compressa* colonies in Hawaii (Hadfield, 1976). It is highly secretive, which helps it to avoid potentially intense fish predation. Remarkably, Haramaty (1991) presented indirect evidence that *P. lugubris* may utilize the photosynthetic products of endosymbiotic zooxanthellae that are ingested (and remain viable) along with coral tissues.

Like the corallivorous polychaete noted above (*Hermodice carunculata)*, *Coralliophila abbreviata* was observed to concentrate on remnant corals (*Acropora* spp.) that survived a severe hurricane disturbance (Knowlton et al., 1981, 1990). Field experiments in the Florida Keys have demonstrated that *C. abbreviata* can transmit a coral disease (tentatively termed "rapid tissue loss") to acroporid corals (Williams and Miller, 2005). Thus, acroporid corals that have experienced recent population declines due to stress and disturbance events may be subject to additional mortality from increased predation and disease outbreaks.

Epizoic vermetid gastropods have been shown generally to reduce coral growth and survival (Colgan, 1985; Shima et al., 2010). *Porites lobata* colonies at Moorea, French Polynesia, suffered both reduced growth (up to 82%) and survival (up to 52%) from the smothering effect of the mucus feeding net of *Dendropoma maxima*. This vermetid also has a marked effect on the morphology of massive and branching corals, transforming both growth forms to flat-surfaced colonies (Zvuloni et al., 2008). *Trapezia* crab symbionts, however, have been observed to mitigate the negative effects of vermetids on coral growth (Figure 2; Stier et al., 2010). This is accomplished by *Trapezia*'s consumption of vermetid mucus, as well as by its both inadvertent and directed dislodging of mucus.

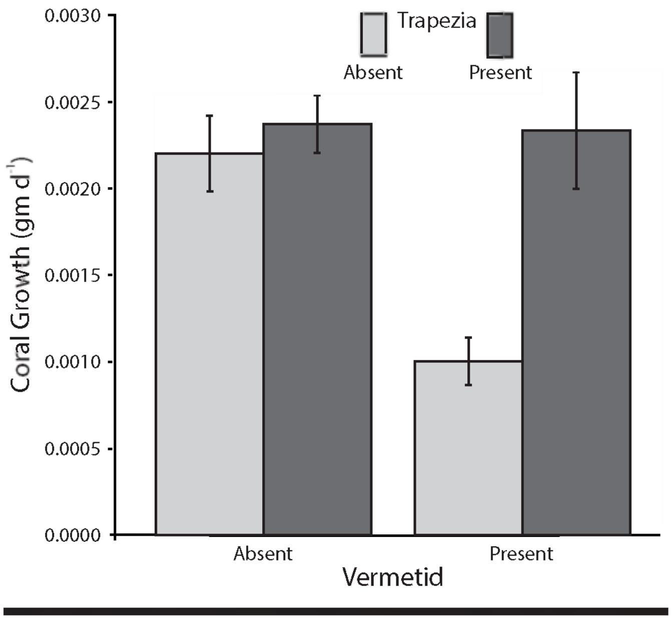

FIGURE 2. Mean (±1 SE) effects of *Dendropoma maximum*, a vermetid gastropod, and *Trapezia serenei* on the growth of *Pocillopora* cf. *verrucosa*. In the presence of vermetids, *Trapezia* can prevent the negative influence of the gastropod's mucus feeding net on its coral host's growth (modified from Stier et al., 2010).

Positive effects of bivalve mollusks on corals range from increased asexual reproduction to coral host defense and nutrient enrichment. Bivalve borers promote skeletal breakage and disintegration, which can enhance the asexual propagation of corals and also provide microhabitats for cryptic metazoans. Similar to *Spirobranchus giganteus*, the polychaete worm noted earlier, the scallop *Pedum spondyloideum* was observed to defend *Porites* spp. colonies on the Great Barrier Reef (DeVantier and Endean, 1988). This scallop lives embedded in the skeletons of *Porites* spp. and often prevents *Acanthaster* from feeding on nearby polyps by repeatedly expelling jets of water. Surviving polyps may then reproduce asexually and assist in colony recovery. Mokady et al. (1998) have questioned the parasitic role of boring bivalves in association with coral hosts. From field and laboratory studies in the northern Red Sea, they found that ammonium nitrogen recycled by *Lithophaga simplex* supplied a significant amount of this nutrient to zooxanthella symbionts in a massive coral (*Astreopora*). They concluded that this tripartite symbiosis may be best regarded as a mutualism.

ARTHROPODA

Crustaceans are the principal invertebrates present on living corals, with numerous species of copepods, barnacles, shrimps, and crabs represented. In terms of species richness and abundance, copepod associates of reef-building corals are noteworthy (Humes, 1985; Stock, 1988). Also, sessile pyrgomatine barnacles are common on eight major scleractinian and hydrocoral higher taxa (updated from Ross and Newman, 1973; Glynn and Enochs, 2011). At least 48 species of pontoniine shrimps in 16 genera are obligate symbionts in several coral genera, especially in branching species of *Acropora* and pocilloporid species of *Pocillopora*, *Stylophora*, and *Seriatopora* (Bruce, 1998). These same branching coral taxa are also known to host numerous species of obligate trapeziid crab symbionts (Patton, 1966, 1974, 1976; Castro, 1988; Castro et al., 2004).

Copepods that belong to the species-rich Xarifiidae inhabit the gastrovascular cavity of corals and have been assumed to be obligate endoparasites. Up to nine copepod species have been found on individual colonies of *Acropora*, and a single colony of *Pocillopora* was found to host 668 individuals belonging to a single copepod species (Humes, 1994). A recent study by Cheng and Dai (2010) presented evidence suggesting that *Xarifia fissilis* associated with *Pocillopora damicornis* consumes zooxanthellae from its coral host. Furthermore, their study indicated that ingested algal cells remained photosynthetically active, and in an experimental starvation treatment copepod hosts supplied with light suffered significantly lower mortality than copepods maintained in the dark. This result suggests that photosynthetically active algae in the gut may provide photosynthate to the copepod, at least over the short term. If zooxanthellae are still viable when voided, it is possible they could disperse to other corals, serve as an innoculum source for planular larvae, or assist in the repopulation of zooxanthellae in bleached corals.

With respect to feeding interactions, barnacles interact in various ways with their coral hosts. While most are suspension feeders, a few barnacles consume coral tissues directly (Ross and Newman, 1995, 2000). For example, *Pyrgoma monticulariae* stimulates coral tissue growth into its aperture to facilitate feeding (Ross and Newman, 1969). Species of *Lithotrya* bore into dead coral skeletons and extend their cirri into the surrounding water when feeding. They probably play a more important role in bioerosion than in any nutritional exchange. Several researchers, however, have hypothesized a mutualistic relationship between barnacles and their scleractinian and hydrocoral hosts. From a study utilizing stable carbon isotopes, Achituv et al. (1997) found that several species of coral-inhabiting barnacles assimilate carbon from their coral hosts via coral tissues (presumably abraded) and zooxanthellae. Barnacle symbionts can also have a positive effect on coral holobionts. The phosphorus and nitrogen excreted by barnacles can be absorbed by endosymbiotic zooxanthellae (Cook et al., 1991; Achituv and Mizrahi, 1996). Finally, a provocative experiment testing the effects of filter-feeding pyrgomatine barnacles on their hydrocoral host suggested an antifouling role (Pasternak et al., 2001). *Millepora* hydrocorals without their barnacle symbionts (experimentally stripped) were subject to higher rates of fouling by algae and fungi compared to corals with their usual complement of barnacles. These results suggest that the filtering capacity of barnacles can offer corals protection from fouling by water-borne organisms.

Some hermit crabs—members of the crustacean order Anomura—are also known to live symbiotically with corals. Species of *Paguritta* live in polychaete tubes present on corals (Schuhmacher, 1977) or in self-constructed boreholes in living coral (Lewinsohn, 1978). Juveniles of *Paguritta harmsi* were reported to live within the tissue-containing corallites of the massive coral *Astreopora* (Patton and Robertson, 1980). Since the corallites of the host coral lack columellae, the hermit crab is able to extend its soft abdomen into the corallite for protection. The crab's right cheliped is flat and covered with spines, thus serving as an operculum when the crab is disturbed and withdraws within the corallite. It was hypothesized that small hermit crab recruits likely remain in the corallites while the coral grows, keeping pace with the growth and thus producing an elongated pit. *Paguritta* spp. possess feathered antennae and depend entirely on a filtering mode of feeding. Species recognition is often difficult; at least six species are known in this genus (McLaughlin and Lemaitre, 1993).

Gall crabs, members of the order Brachyura, are also sedentary obligate crustacean symbionts of reef-building corals. These crabs were long thought to be suspension feeders until Kropp (1986) found that they feed on coral mucus and tissues. Evidence from a chlorophyll spectral analysis indicates that excreta from a gall crab species of *Cryptochirus* fertilizes the immediate surroundings and thus enhances endosymbiotic zooxanthella production (Simon-Blecher et al., 1996).

A rich fauna of mobile trapeziid crabs and pontoniine shrimps occur as obligate associates on pocilloporid and acroporid corals. Branching coral hosts typically provide quality shelter and trophic resources for these crustacean taxa. Early studies suggested that crustaceans were the sole beneficiaries of this partnership, feeding on coral mucus plus entrapped particulate organic matter. Accordingly, these crab and shrimp crustaceans were classified as ectoparasites (Knudsen, 1967) or commensals (Patton, 1974). More recent studies have demonstrated that *Trapezia* spp. crabs actually consume coral tissues directly (Rinkevich et al., 1991) as well as "fat bodies" or lipid globules produced by the coral hosts (Stimpson, 1990). The crabs harvest this food source by inserting their pereopods into polyps. Movements of the pereopods stimulate fat body production, which occurs only when crab symbionts are present.

There are now several lines of evidence showing that mobile crustaceans provide various levels of facilitation to their hosts. Demonstrated positive effects include protection from corallivores (e.g., Glynn, 1983a; Pratchett, 2001); improved water flow within interbranch spaces and the removal of foreign organisms and contaminants (Glynn, 1983b); and reduced sediment deposition and increased coral growth and survivorship (Stewart et al., 2006). Crab and shrimp agonistic behaviors also help regulate the abundances of potential competitors by preventing the overexploitation of host resources. It is likely that strong and persistent selective forces have resulted in the evolution of aggressive behaviors that both reduce competition and limit mortality by corallivores.

In the remainder of this section, a few noteworthy obligate crab and shrimp interaction effects are considered first, followed by selected examples of free-living species that can directly or indirectly affect coral survival. Trapeziid crabs typically form heterosexual pairs and aggressively defend their coral hosts from conspecific individuals (Preston, 1973; Patton, 1974). This aggressive behavior is also directed toward other species that could potentially compete for resources or harm the coral host. *Trapezia* crabs and *Alpheus* shrimp, however, coexist in stable populations on *Pocillopora* corals, with both the crabs and shrimp defending their coral hosts against intruders of both species.

Movement between colonies, usually at night, commonly occurs in *Trapezia* crabs (Castro, 1978). At such times, the migrating crabs are vulnerable to fish invertivores and quickly associate with a coral host. Vannini (1985) observed that a *Trapezia* crab attempting to enter a coral colony must perform cheliped rubbing and body contact with a conspecific resident crab before being accepted (Figure 3A). These appeasement behaviors usually allow an alien crab to successfully establish residency in the colony. *Alpheus* shrimp must also perform similar behaviors with crabs (i.e., cheliped rubbing and body contact to gain access to a defended colony; Figure 3B). While other behaviors occur between resident and intruding (alien) shrimp, cheliped

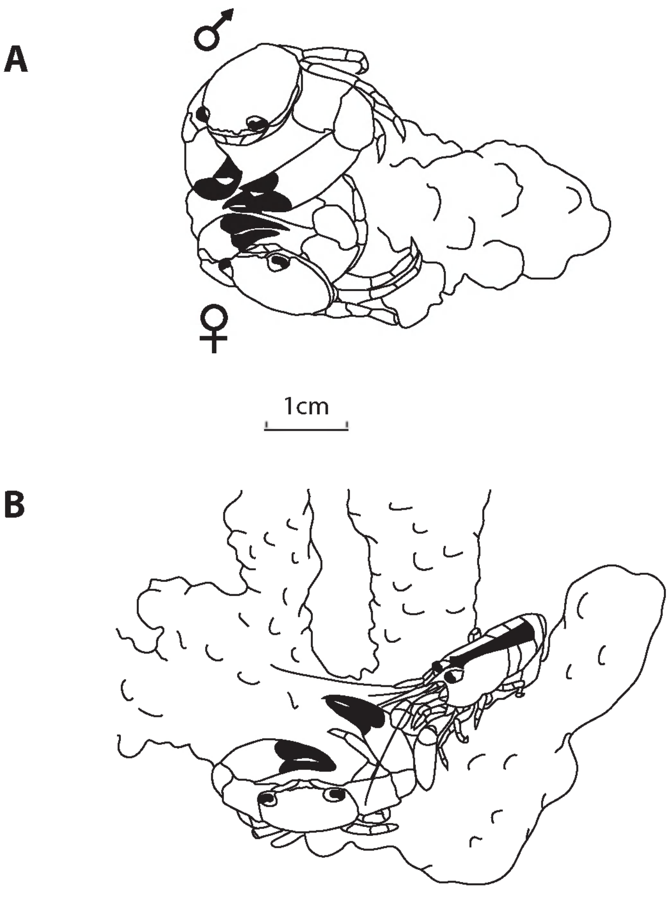

FIGURE 3. Crustacean appeasement interactions preceding acceptance of a nonresident associate into a *Pocillopora* sp. colony. (A) Intruder female *Trapezia ferruginea* rubbing her right cheliped against left cheliped of resident male crab. (B) Intruder *Alpheus lottini* shrimp rubbing both chelipeds against resident *T. ferruginea* (modified from Vannini, 1985).

rubbing and body contact are performed almost exclusively between shrimps and crabs and seldom between alpheid shrimps themselves. Vannini (1985) speculated that shrimp, the weaker of the two combatants, needed to adopt the "language" of the stronger crab aggressor. Since crabs tolerate shrimp more than their own conspecifics, Vannini further suggested that snapping shrimp could be exploited by resident crabs as a clarion warning of approaching intruders and predators (see below).

Behavioral interactions among obligate crab, shrimp, and gobiid fish symbionts of *Pocillopora damicornis* colonies have been shown to facilitate the coexistence and stability of symbiont assemblages (Lassig, 1977). Resident crab–fish interactions were generally nonagonistic. Gobies made contact with crabs in various positions and performed shivering movements (rapid flexion of the entire body and median fins, particularly the caudal fin) similar to those employed in courtship behavior (Figure 4A–C). However, nest sites on coral branches were vigorously defended by *Paragobiodon* spp. during the breeding season. There are two species of gobiid fishes present in *Pocillopora; Paragobiodon lacunicola* mostly occurs near the base of corals, where it overlaps spatially with *Alpheus* more than with the other goby species, *P. echinocephalus*. The appeasement signal system—shivering and antennal contact—exists between the shrimp and *P. lacunicola*, but not between the shrimp and *P. echinocephalus* (Figure 4D–E).

The first reported observations of trapeziid crabs defending their coral hosts from predator attack were by Pearson and Endean (1969) and Weber and Woodhead (1970). These researchers noted how the obligate crab associates of pocilloporid corals could repel attacking sea stars (*Acanthaster planci*) on southern Pacific reefs. Although I refer to the single taxon *A. planci*, four distinct species of *Acanthaster*, each with well-defined geographic distributions, are now recognized (Vogler et al., 2008). It is possible that these species have different feeding preferences and elicit different defensive responses. However, observations in the eastern Pacific have demonstrated a repertoire of relatively consistent crustacean defensive behaviors when compared with coral guards from other Indo-Pacific regions.

Five defensive activities of *Trapezia ferruginea* on eastern Pacific reefs in Panama have also been observed in Guam, American Samoa, and Oman (Glynn, 1976, 1980, 1983a, 1987). An approaching *Acanthaster* typically elicits a startle or meral display in which an alerted crab will move to the coral's peripheral branches and flex its chelipeds widely (Figure 5A). If *Acanthaster* attempts to mount the colony, *Trapezia* may then begin to push the sea star away, executing several thrusts per minute (Figure 5B). If the pushing response is unsuccessful, the defensive behaviors often escalate to the following three patterns: (1) up–down jerking, (2) pinching and clipping of spines and tube feet, and (3) resisting retreat of *Acanthaster* (Figure 5C–E). In the last response, a defending crab will grip a pair of spines near the arm tip and temporarily prevent the sea star from fleeing. When the crab is maximally stretched it will suddenly release its grip, causing the sea star to lurch forward and then quickly retreat from the guarded coral.

If attacking sea stars are approaching corals from an upcurrent direction, chemical cues or danger signals (kairomones) move down-current and alert the crustacean guards, which quickly move to peripheral branches where they assume defensive postures. The first agonistic responses toward attacking *Acanthaster* are pronounced snapping by *Alpheus* and meral displays by *Trapezia*, both of which are directed toward the predator from the coral's peripheral branches (Figure 6). Glynn (1980) demonstrated experimentally that some unknown factor diffuses from the sea star and arouses the crustaceans. It is possible that the high concentrations of saponins in *Acanthaster*, which function as surfactant repellents to predators, alert the crustacean guards, but experimental testing of this hypothesis is necessary (Birkeland and Lucas, 1990).

The most common agonistic response of *Alpheus lottini* was a loud snapping sound that culminated in a directed shock wave.

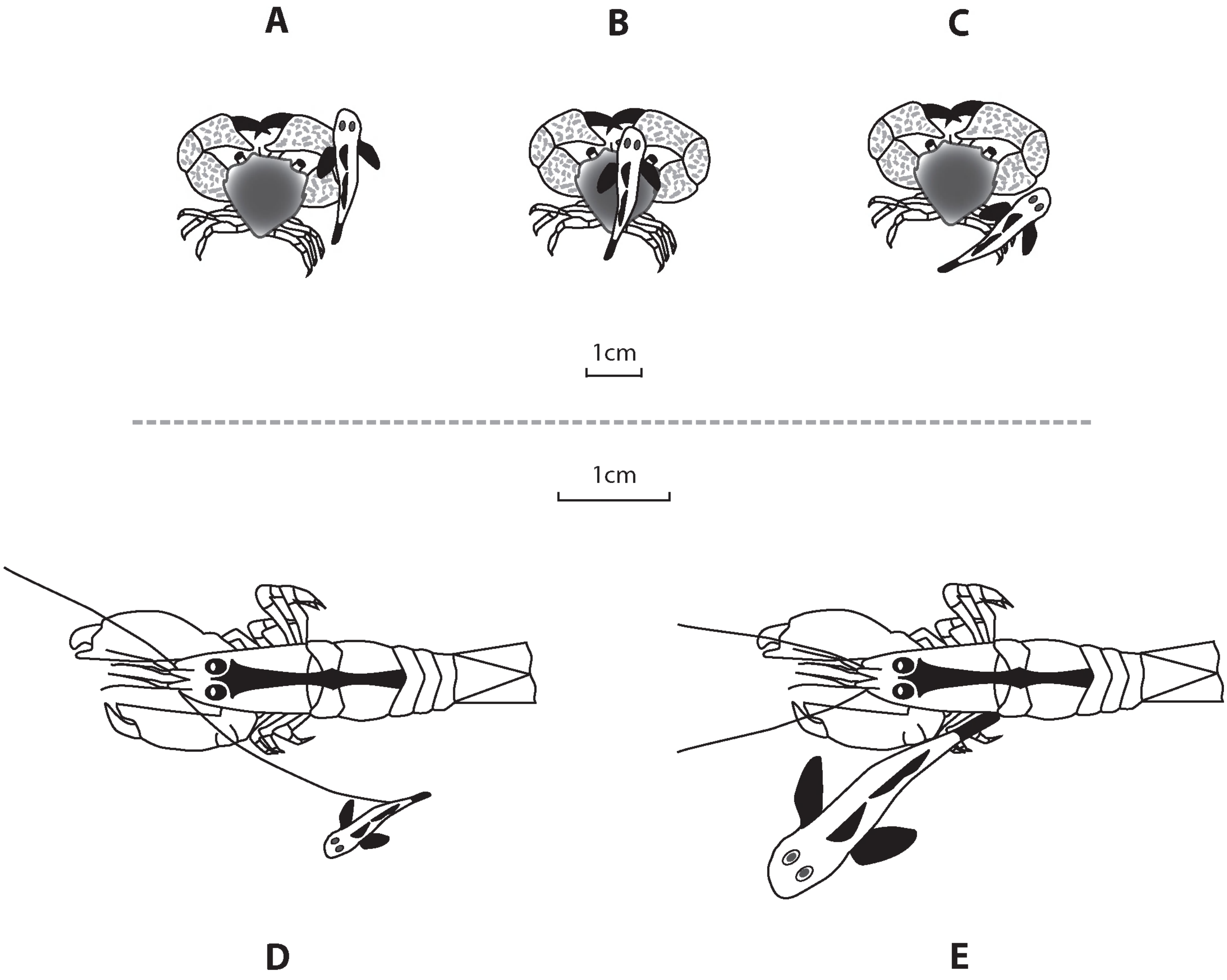

FIGURE 4. Behavioral interactions among crab (*Trapezia cymodoce*), shrimp (*Alpheus lottini*), and gobiid fish (*Paragobiodon echinocephalus*) associates of the coral *Pocillopora damicornis*. (A–C) Various contact positions assumed by crab and fish (modified from Lassig, 1977). (D) Antennal and (E) body contact between shrimp and fish.

This snapping increased in frequency as an *Acanthaster* attack escalated from approaching a coral to contact and finally mounting. The most extreme response involved the shrimp in rapid succession pinching spines and tube feet, grasping the terminal arm spines of *Acanthaster*, and snapping at the sea star while it was in contact with the coral (Figure 5F).

Field observations in Panama indicated that the defensive responses of crustacean guards were overwhelmingly directed toward *Acanthaster* and not at other corallivores such as sea urchins, hermit crabs, snails, and fishes (Glynn, 1983a). This specific, high level of defense against *Acanthaster* corresponds with the level of harm this corallivore could cause to the coral host (i.e., death of the entire colony). *Culcita* spp., sea star corallivores in the Indo-Pacific, commonly feed on small acroporid and pocilloporid branching corals. In Hawaii, only about 50% of small *Pocillopora* colonies harbored crustacean guards (*Trapezia* and *Alpheus*) compared with 100% of large colonies (Glynn and Krupp, 1986). When present in small colonies, the crustacean guards would engage in defensive behaviors when attacked by *Culcita*, but these were generally weak responses that seldom curtailed a sea star attack. Thus, unguarded juvenile corals were particularly vulnerable to predation by *Culcita*.

Scuba-supported field and laboratory studies conducted throughout the Indo-Pacific region have demonstrated that

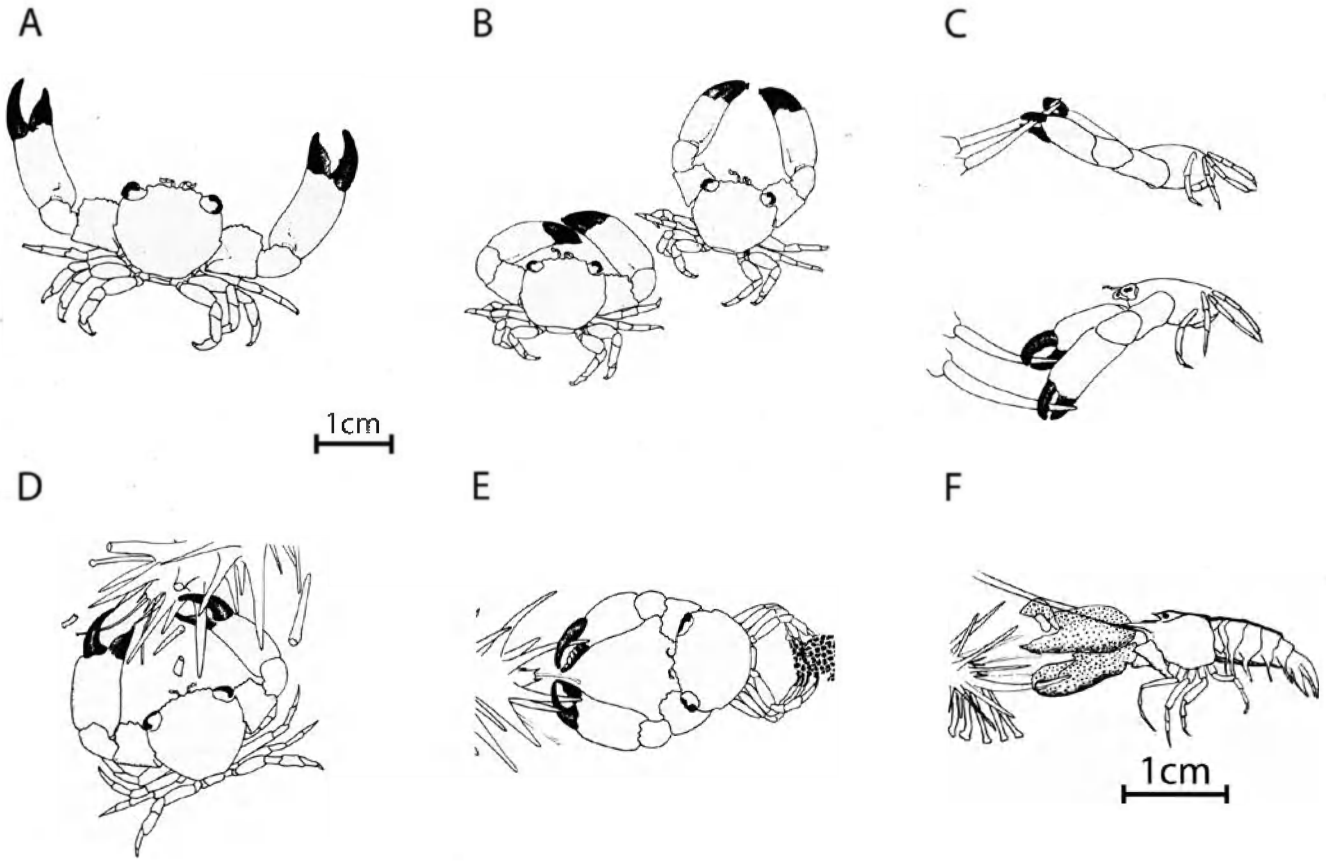

FIGURE 5. Commonly observed defensive responses of crab and shrimp guards toward *Acanthaster* threatening to mount and feed on their coral host. *Trapezia ferruginea*: (A) startle display, (B) pushing sea star, (C) grasping spines with up–down jerking, (D) clipping spines and tube feet, (E) resisting sea star's retreat. *Alpheus lottini*: (F) snapping in contact and pinching sea star's arm tip (from Glynn, 1983a).

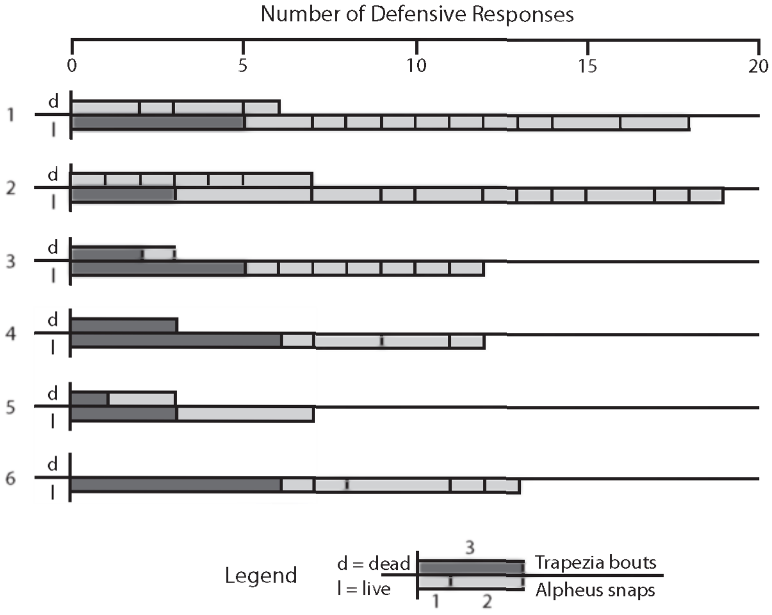

FIGURE 6. Defensive responses of *Trapezia* and *Alpheus* toward simulated attacks of dead (boiled) and live *Acanthaster*. The frequency of *Alpheus* snaps per bout is indicated by the length of each open horizontal bar; the total frequency of *Trapezia* bouts is indicated by the length of each occluded bar (see legend; from Glynn, 1980).

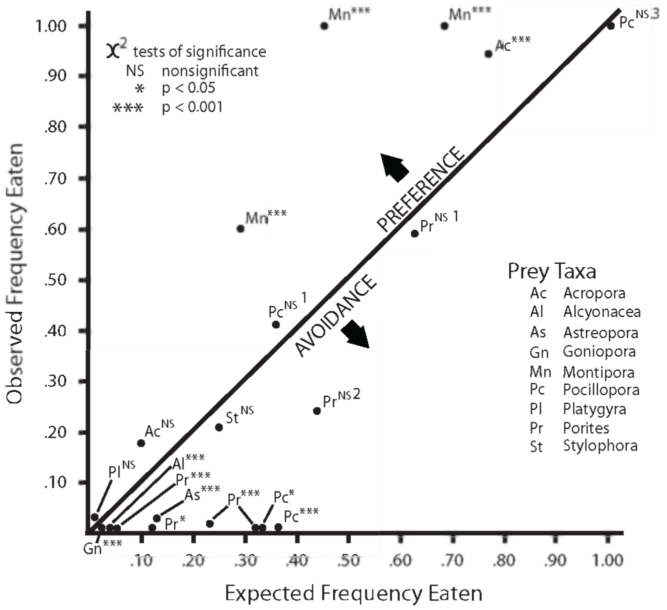

FIGURE 7. Field-sampled coral prey preferred and avoided by *Acanthaster* in the Gulf of Oman. Chi-square significance values are noted beside prey genera eaten and compared to their relative abundances (from Glynn, 1987).

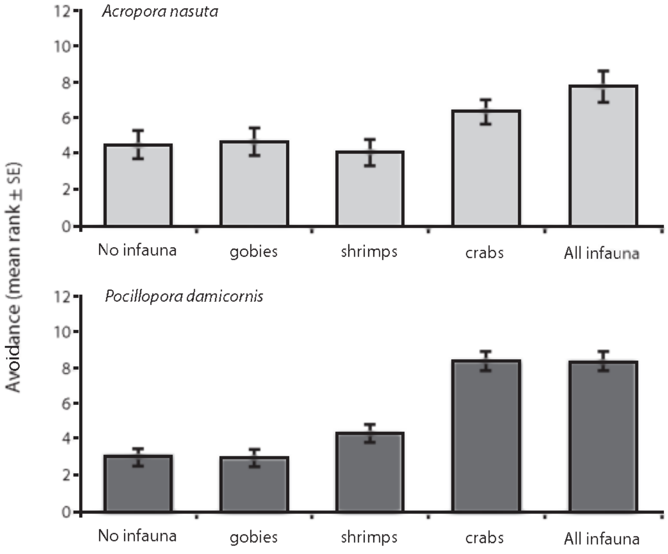

FIGURE 8. Avoidance interactions of *Acanthaster* experimentally presented with different metazoan symbiont assemblages apportioned between two potential coral species prey (modified from Pratchett, 2001). *Acropora nasuta*: crabs (*Tetralia*), shrimps (*Coralliocaris*, *Periclimenes*), and gobies (*Gobiodon*). *Pocillopora damicornis*: crabs (*Trapezia*), shrimps (*Alpheus*), and gobies (*Paragobiodon*).

metazoan symbionts significantly affect the feeding preferences of *Acanthaster*. Field observations in the Gulf of Oman revealed distinct feeding preferences and avoidances of several coral genera (Figure 7). Coral genera in the family Acroporidae (*Acropora*, *Montipora*) were significantly preferred over several genera in other families (e.g., *Astreopora*, *Goniopora*, *Porites*, and *Pocillopora*). There was a close relationship between branching coral taxa and (1) the colonies avoided, (2) the species and numbers of crustacean guards per colony, and (3) the intensity of colony defense. For example, pocilloporid colonies hosting large and aggressive *Trapezia cymodoce* and *Trapezia tigrina* crab guards were seldom attacked by *Acanthaster*, but acroporid colonies with small and less aggressive *Tetralia cavimana* guards were frequently eaten by the sea star. *Montipora* spp. without crustacean guards were preferentially fed upon by *Acanthaster*.

In order to quantify the efficacy of defense by symbiotic crabs, shrimps, gobies, and the entire symbiont assemblage, Pratchett (2001) related coral avoidance interactions of *Acanthaster* to combinations of symbiotic taxa in controlled feeding trials. Two coral species were tested: *Acropora nasuta* with *Tetralia* and *Coralliocaris* guards, and *Pocillopora damicornis* with *Trapezia* and *Alpheus* guards. Crab guards elicited the strongest *Acanthaster* avoidance interactions but were not significantly different from the avoidance of all symbionts present in the two coral species tested (Figure 8). The most pronounced avoidance response was to *P. damicornis* with the aggressive crab guard *Trapezia cymodoce*. The small and weak acroporid crab guard *Tetralia fulva* also performed defensive behaviors, but these were less effective compared with *Trapezia*. *Acanthaster* avoided *Pocillopora* colonies with the *Alpheus* guard alone, but not *Acropora* colonies with *Coralliocaris* shrimp symbionts. Goby symbionts alone in both corals were not effective in thwarting *Acanthaster* attacks.

The effects of *Acanthaster* predation on coral community structure is complex and depends on several factors, such as population size of attacking sea stars, absolute and relative abundances of preferred and nonpreferred coral prey, colony morphology, coral availability, past experience in prey choice, and symbiont defenses. In-depth reviews on this subject are offered by Moran (1986) and Birkeland and Lucas (1990). Observed effects have involved changes in species richness, diversity (both increases and decreases), coral cover (slight to near-total elimination), colony sizes, age distributions, and spatial patterns. Two examples of the last have involved symbiont-defended corals in Panama and Guam. Symbiont-defended corals in Panama were observed to form a protective barrier around preferred, nondefended corals (Glynn, 1985). In this situation, *Acanthaster* was prevented from crossing the barrier and thus denied access to a coral (*Gardineroseris planulata*) ranking high in preference. In Guam, Colgan (1987) observed a halo of uneaten corals surrounding a colony defended by crustacean guards.

In addition to defending corals from corallivores, trapeziid crabs promote the growth and survival of their host corals by increasing interbranch circulation and removing organisms and contaminants from coral surfaces (Glynn, 1983b). A recent study at Moorea quantified the positive effects of crab symbionts in clearing sediments from branching pocilloporid and acroporid corals (Stewart et al., 2006). In a 24-day field experiment, corals without *Tetralia* (*Acropora hyacinthus*) or *Trapezia* (*Pocillopora verrucosa*) experienced ~50% and ~80% mortality, respectively. The crab symbionts were experimentally removed from test colonies. Crabs were observed to predominantly remove sediments of large particle size (0.5–4.0 mm), which were the most damaging to coral tissues. They responded quickly to increased sediment loads by removing sediments with their rear pereopods and chelae. The corals that survived without crabs showed significantly lower colony growth, increased tissue bleaching, and higher sediment loading.

Facultative majid crabs living cryptically with branching *Porites* on a Caribbean reef have been shown experimentally to benefit their coral host indirectly (Coen, 1988). In treatments where *Mithrax* had access to coral colonies (i.e., crab enclosures and natural controls), foliose algae were significantly reduced compared to crab exclosure treatments (Figure 9) after about one month. The feeding activities of the herbivorous crabs were found to prevent algae from overgrowing and killing the corals. This study and others suggest that mesograzers, such as amphipods, isopods, and polychaete worms, may exercise strong control over algal abundance and community structure in some reef habitats (Brawley, 1992; Carpenter, 1997).

Field observations on a coral reef in the Gulf of Chiriquí, Panama, have revealed an abundance of the painted shrimp, *Hymenocera picta* (Glynn, 1977, 1982). This shrimp lives cryptically in reef framework cavities and among the branches of both live scleractinians and hydrocorals (Figure 10), but is visible when attacking and feeding on adult *Acanthaster* and other sea stars. Population abundances, which were determined in part by sea star baiting, reached maximum density estimates of 54–118 shrimp ha^{-1}. These shrimp attack asteroid echinoderms only, cutting through the body wall and amputating arm tips with their sharp chelae; exposed internal organs such as gonads and hepatic caeca are then consumed (Wickler, 1973). While feeding on *Acanthaster*, the shrimp (often a pair) are carried on the sea star's aboral surface for up to several days as it moves about. *Pherecardia striata*, a cryptic polychaete worm, was often observed entering the wounded sea star's coelom, where it also fed on soft tissues. From *Acanthaster* immigration and mortality rates, Glynn (1982) concluded that the shrimp and polychaete worm could control the population size of adult *Acanthaster* on the eastern Pacific study reef. Fiedler (2002) found that the postlarvae of *Hymenocera* begin eating sea stars only five days after metamorphosis. Therefore it is possible that postsettlement and juvenile *Acanthaster* are consumed in cryptic reef habitats before they mature and emerge onto exposed reef surfaces.

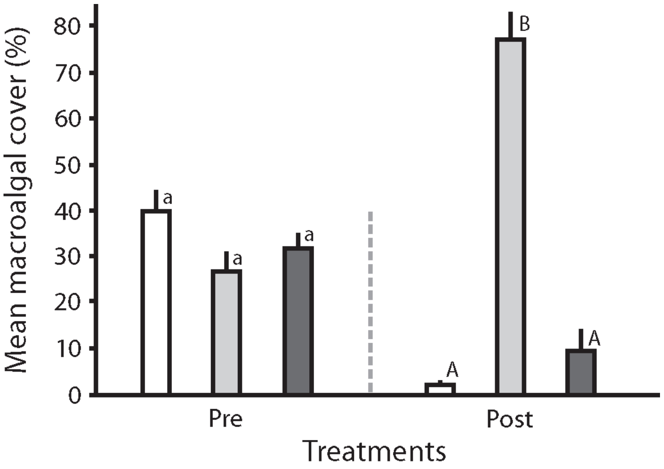

FIGURE 9. Mean (±1 SE) cover of algae on *Porites porites* colonies in relation to the presence of *Mithrax sculptus*, a facultative majid crab associate. Pre- and posttreatment effects: clear bars indicate crab enclosures; light gray bars indicate crab exclosures; dark gray bars indicate natural controls. The same letter is shared among treatments not significantly different ($p > 0.05$).

FIGURE 10. Harlequin shrimp, *Hymenocera picta*, perched on a branch of the hydrocoral *Millepora intricata*, at Uva Island, Gulf of Chiriquí, Panama, 20 m depth. A second member of the pair is only partly visible. Photo courtesy of B. Harris.

Early observations with scuba prompted the pioneer marine ethologist Eibl-Eibesfeldt (1955) to propose that cleaner shrimps could benefit reef fishes by removing parasites. Whether or not cleaner shrimp can effectively remove ectoparasites from coral reef fishes has been vigorously debated (Spotte, 1998). Although this type of interaction is not considered here, convincing evidence that cleaner shrimp do remove crustacean (copepod, isopod) and monogenean flatworm parasites is presented in Bunkley-Williams and Williams (1998) and Becker and Grutter (2004). These new findings, aided by controlled laboratory procedures, support a mutualistic relationship between some shrimps and fishes.

It is apparent that trapeziid crab symbionts have received considerable attention from researchers, due mainly to their relatively large size, complex behaviors, and extraordinary capacity to defend their coral hosts against predators. The ecological roles of smaller taxa (e.g., copepods and smaller shrimps) are still largely unknown with regard to host effects (e.g., tissue consumption or protection from micropredators). Similarly, the potential importance of crustacean symbionts vis-à-vis predation on settling metazoan larvae, recruits, and residents, as well as transmission of zooxanthellae and coral diseases, are also research areas in need of further study. These are all vital ecological functions that can determine the persistence or demise of particular coral populations.

Chordata

Relatively few fishes form close or obligate relationships with living corals. To illustrate fish–coral symbioses, examples are briefly noted from three families, namely Gobeidae (gobies), Cirrhitidae (hawkfishes), and Pomacentridae (damselfishes). These examples range from obligate to facultative associations with branching corals where shelter and food are assumed to be the chief resources sought. For additional information on the range of fish corallivore diets, see Cole et al. (2008). Since the majority of the 128 coral reef fishes (in 11 families) they list are relatively large and conspicuous, they fall outside the scope of this paper.

Several species in four gobiid genera are closely associated with live corals (Munday et al., 1997; Herler, 2007). Among obligate goby symbionts, *Gobiodon* spp. inhabit acroporid corals and *Paragobiodon* spp. reside in pocilloporid corals. Both coral families exhibit branching colony morphologies. Gut content analysis on the Great Barrier Reef has established that three species of *Gobiodon* consume the tissues of their acroporid hosts (Brooker et al., 2010). In addition, relatively large amounts of algae are consumed, which may benefit the host by preventing algal overgrowth and the fish symbionts by maintaining open living spaces.

Even though gobies alone are not effective in repelling *Acanthaster* (Pratchett, 2001), Lassig (1981) found that *Gobiodon quinquestrigatus* could effectively reduce predation by butterflyfishes. In field experiments with *Acropora* colonies with and without *Gobiodon*, Lassig found that the number of bites and time spent at colonies by feeding *Chaetodon* were significantly reduced when the goby was present. *Gobiodon* spp. produce an epidermal secretion that is ichthyotoxic and likely plays an important role in reducing the grazing of butterflyfishes. Due to the mobility of butterflyfishes feeding around a colony and likely rapid dilution of the toxic agent, the efficacy of such a deterrent might be questioned. An ichthyotoxin would be effective, however, if accurate delivery were possible. Lassig speculated that *Gobiodon* could be attracted to areas threatened by butterflyfishes and may abrade their epidermis against the coral in order to release the repellant at targeted feeding sites. This hypothesized defensive behavior is in need of further study.

Donaldson (1990) lists two species of hawkfishes that are obligate coral dwellers, and eight species that occupy either coral or other noncoral microhabitats. *Paracirrhites arcatus* is a facultative associate of *Pocillopora meandrina* in Hawaii, where it finds shelter among this coral's branches and uses the coral as a foraging base (DeMartini, 1996). In Panama, *Cirrhitichthys oxycephalus* is a facultative associate of pocilloporid corals. It typically perches on coral branches, from which it locates and presumably preys on symbiotic and pelagic crustaceans as well as small fishes (Dominici-Arosemena and Wolff, 2006; Robertson and Allen, 2008).

Cole et al. (2008) listed eight species of pomacentrid corallivores; two of these feed exclusively on zooxanthellate corals. Some species of zooplanktivorous damselfishes (*Dascyllus*) seek refuge from piscivores in branching corals. The experimental removal of *Dascyllus* from *Stylophora* in the Red Sea resulted in significantly lowered coral growth compared to colonies hosting fish (Liberman et al., 1995). Similar results were obtained by Holbrook et al. (2008) for *Dascyllus* that shelter in *Pocillopora* colonies at Moorea; sheltering damselfish enhanced coral growth by about 50% and up to nearly 100% when large groups of fish were present. Elevated coral growth was dependent on nutrients (ammonium) excreted by the fish. The magnitude of this effect was positively related to the biomass of fish resident on each coral. Another factor that could indirectly affect coral growth is the presence of predatory hawkfish, which can co-occur with and prey on *Dascyllus* in *Pocillopora* colonies. Hawkfish predation would result in a reduction of the number and biomass of *Dascyllus*, thus resulting in reduced coral growth. A final beneficial effect of note is the sleep-swimming behavior of pomacentrids (*Dascyllus, Chromis*) that are closely associated with pocilloporid and acroporid corals (Goldshmid et al., 2004). These fishes enhance water replenishment, and hence oxygen availability, in the inner branch zones of corals at night (Goldshmid et al., 2004). This sleeping behavior, which involves high-frequency fin motion even when the fish are at rest, is unique; non-coral-associated pomacentrids are motionless during their quiescent period.

When a disturbance disrupts a symbiosis, the proximate cause of the breakdown is not always obvious. In a few cases, however, the reason(s) for the disappearance of coral symbionts has been revealed. For example, during coral bleaching on Panamanian reefs, obligate crustacean symbionts starved and died due to the loss of their coral host and nutritional resources (Glynn et al., 1985). Coral bleaching in Australia has resulted in marked declines of damselfishes that inhabit *Pocillopora* corals. It has been shown experimentally that the predation rate of coral-dwelling damselfishes increased in degraded host colonies (Coker et al., 2009). Predation was highest on bleached and algal-covered corals. In bleached corals, this was likely a result of increased prey visibility against a bleached coral background; in algal-covered corals, it was possibly a result of changes in the behavior of prey fishes that would increase their susceptibility to predation, such as increased movement in search of live corals.

The contribution of small cryptic fishes to reef assemblages and processes is largely unknown (Ackerman and Bellwood, 2000). Although cryptic reef habitats are often noted to be important as refuges for postsettlement and juvenile life history stages of invertebrates and fishes, the presence of diverse cryptic predators is usually not acknowledged. A study focused on the trophic roles of a cryptobenthic fish community on the Great Barrier Reef revealed an abundant carnivore presence (Depczynski and Bellwood, 2003). Five of 16 of the most abundant species examined, representing 40.5% of all individuals, were carnivores. Detritivores made up a large portion of this cryptic assemblage as well (see below). In two eastern Pacific studies conducted on reefs in Colombia (Mora and Zapata, 2000) and Panama (Glynn, 2006), 37 fish species in 20 families were found inhabiting experimentally constructed dead coral rubble structures (Table 1). Thirty-three (~89%) of these cryptic species belong to carnivore or other consumer guilds (planktivores, parasites). The most common dietary items were crustaceans and fishes. The fishes sampled in Colombia recruited to cryptic substrates during a maximum time of just two months. This short period indicates the rapidity with which cryptic predators can invade and become established in newly formed shelters. Thus, cryptic fish predators are likely early colonizers in disturbed reef communities and effective in modulating recruitment dynamics (e.g., species composition and abundances). The presence of particular macropredators could limit the recruitment of species that would positively or negatively affect coral growth.

MESOSCAVENGERS

The first quantitative study of small scavengers on a coral reef, carried out at Lizard Island on the Great Barrier Reef, revealed high abundances of crustacean and mollusk species (Keable, 1995). Traps baited with dead fish were deployed overnight for 18 hours in three reef zones and surrounding sedimentary substrata. From 410 baited traps, 108 crustacean, mollusk, and polychaete species were collected, yielding a total of 112,690 individuals. Amphipod, isopod, and ostracod crustaceans were the most abundant taxa, with maximum capture numbers per trap reaching hundreds to thousands of individuals. The overall mean capture rate was 275 individuals per trap. The dominance of crustacean scavengers was evident in traps sampled in leeward reef slope and reef flat habitats (Figure 11).

Scavenger trap baiting on Panamanian coral reefs in the eastern Pacific revealed a diverse scavenger guild, but with lower abundances than those reported at Lizard Island. Since the trapping methodology in Panama was similar to that employed in Australia—small entrance aperture, fish baits, and overnight, 18-hour deployment—a region-wide comparison is justified (Figure 12). Of the 55 traps set on a Panamanian coral reef, a total of 1,219 individuals were captured, with a mean capture rate of 22 individuals per trap. In addition to the shrimp and crab crustaceans, gastropods, and polychaete scavengers that were likewise captured in Australia, a few other invertebrate taxa were present in Panama, including holothurians, hermit crabs, and one individual each of a polyclad flatworm, bivalve mollusk, and muraenid eel (Figure 13). One small moray eel (*Gymnothorax panamensis*) also was observed to enter a trap and consume part of the bait. At both Australian and Panamanian study reefs, cirolanid isopods were in high abundance and often numerically dominant. Ostracod abundances and diversity were higher in Australia than in Panama. In traps with scavengers, commonly one-half to all of the ~8 cm^3–baits were consumed during the 18-hour period. The rapidity of this consumption suggests a critical role of cryptic reef scavengers in nutrient regeneration processes, and possibly a paucity of food resources.

In the Depczynski and Bellwood (2003) study noted above, detritivores were also well represented, especially small gobiid fishes. Ten of 16 species and 39.3% of individuals examined were assigned to the detritivore guild. Like cryptic invertebrate scavengers, cryptic fishes may also contribute importantly to the recycling of primary production through detrital pathways.

CONCLUSIONS

This overview has shown that several coral–metazoan interactions that were formerly regarded as neutral or harmful to corals are in many instances beneficial. With greater awareness of the critical roles played by small, cryptic reef metazoans, new insights and research directions have emerged.

Sponges offer several key ecosystem services, including water column filtering, nutrient regeneration, binding and stabilization of reef substrates, and facilitation of coral community regeneration and recovery processes. Since sponges represent a vital component of coral communities, their abundances and diversity should be protected. Polychaete worm and gastropod mollusk corallivores can serve as vectors and promote the spread of coral diseases. It is also possible that copepod parasites of corals may assist in the transmission of distinct *Symbiodinium* types among potential coral hosts. This may increase the survival of certain coral species during bleaching stress events. Crustaceans have been highly successful in establishing a variety of facultative and obligate symbiotic associations with live corals. Of note are copepods, barnacles, shrimps, hermit crabs, gall crabs, and trapeziid crabs. In measures of species richness, abundances, and variety of interactions, crustaceans exceed all other metazoans.

Diverse epizoic taxa and endolithic borers (e.g., sponges, polychaete annelids, bivalve mollusks, gall crabs, and barnacles) enhance nitrogen sources for use by coral holobionts. This can lead to localized eutrophication, increased primary production, and elevated coral growth. The activities of epizoic symbionts in thinning boundary layers and creating microturbulence can have several beneficial effects on massive and branching coral hosts. This function has been observed in suspension-feeding sponges,

TABLE 1. Juvenile and adult fishes occupying cryptic habitats on eastern Pacific coral reefs. Habitats: G, 0.5 m aggregate of dead pocilloporid rubble secured in netting and resting on bottom; M&Z, 0.4 m aggregate of dead pocilloporid rubble secured with line and positioned 0.2 m above sand bottom. Trophic roles: CAR, carnivore; PLK, planktivore; PAR, parasite; OMN, omnivore; CLN cleaner; HRB, herbivore.

Family	Species	Trophic role	Diet[a]	Habitat[b]
Muraenidae	*Anarchias galapagensis*[c]	CAR	Crustacea[d], worms, gastropods/bivalves	G
	Gymnothorax panamensis	CAR	Crustacea, bony fishes	G
	Gymnothorax undulata	CAR	Crustacea, cephalopods, bony fishes	G
	Gymnothorax dovii[e]	CAR	Crustacea, cephalopods, bony fishes	G
	Muraena lentiginosa	CAR	Crustacea, bony fishes	G
Carapidae	*Carapus mourlani*	CAR/PLK	Benthic/planktonic crustacea[f]	G
	Encheliophis vermicularis[e]	PLK/PAR	Plankton, echinoderms	G
Bythitidae	*Ogilbia* sp.[c]	CAR	Crustacea, bony fishes	G
	Grammonus sp.[c]	CAR	Crustacea, bony fishes	G
Antennariidae	*Antennarius sanguineus*	CAR	Crustacea, bony fishes	G, M&Z
	Antennarius coccineus	CAR	Crustacea, bony fishes	G, M&Z
	Antennatus strigatus	CAR	Crustacea, bony fishes	G, M&Z
Scorpaenidae	*Scorpaena mystes*	CAR	Crustacea, cephalopods, bony fishes	G
	Scorpaenodes xyris[e]	CAR	Crustacea, cephalopods, bony fishes	G, M&Z
	Scorpaenid sp.[c]	CAR	Crustacea, cephalopods, bony fishes	G
Serranidae	*Serranus psittacinus*[e]	CAR	Crustacea, cephalopods, bony fishes	G, M&Z
	Paranthias colonus	CAR/PLK	Pelagic crustacea, zooplankton, bony fishes	M&Z
	Alphestes immaculatus	CAR	Crustacea, bony fishes	M&Z
	Cephalopholis panamensis	CAR	Crustacea, cephalopods, bony fishes	M&Z
Grammistidae	*Pseudogramma thaumasium*	CAR	Crustacea, bony fishes	G
Apogonidae	*Apogon dovii*[e]	PLK	Zooplankton, pelagic fish eggs/larvae	G, M&Z
Labrisomidae	*Starksia fulva*[c]	CAR	Crustacea, worms	G
Gobiidae	*Gobulus hancocki*[c]	CAR	Benthic worms, crustacea, gastropods/bivalves	G
Tetraodontidae	*Canthigaster punctatissima*[e]	OMN	Benthic microalgae, sessile invertebrates	G, M&Z
Gerreidae	*Eucinostomus gracilis*[e]	CAR	Benthic worms, crustacea, gastropods/bivalves	M&Z
Blenniidae	*Plagiotremus azaleus*[e]	CAR/PAR	Crustacea, bony fishes	M&Z
Lutjanidae	*Lutjanus guttatus*	CAR	Crustacea, bony fishes	M&Z
	Lutjanus viridis	CAR	Crustacea, cephalopods, bony fishes	M&Z
Pomacanthidae	*Pomacanthus zonipectus*	CLN/OMN	Microalgae, sessile invertebrates	M&Z
Pomacentridae	*Stegastes flavilatus*	OMN	Microalgae, crustacea, sessile worms/crustacea	M&Z
	Chromis atrilobata	PLK	Zooplankton, pelagic fish eggs	M&Z
Cirrhitidae	*Cirrhitichthys oxycephalus*	CAR/PLK	Benthic/pelagic crustacea, bony fishes	M&Z
Labridae	*Halichoeres dispilus*[c]	CAR/PLK	Crustacea, worms, gastropods/bivalves	M&Z
	Halichoeres nicholsi	CAR/PLK	Crustacea, worms, gastropods/bivalves, echinoderms	M&Z
	Thalassoma lucasanum	CAR/PLK	Crustacea, worms, gastropods/bivalves, echinoderms	M&Z
Acanthuridae	*Acanthurus xanthopterus*	HRB	Microalgae, detritus, soft corals/hydroids	M&Z
Balistidae	*Sufflamen verres*	CAR	Crustacea, worms, gastropods/bivalves, echinoderms	M&Z

[a] After Robertson and Allen (2008) unless otherwise noted. The majority of the dietary items listed are probably mostly for adult fishes. Even though some juvenile carnivores emigrated to reef surface locations as they matured (e.g., serranids, lutjanids, and labrids), their membership in the feeding guilds noted probably remained the same.

[b] G, Glynn (2006); M&Z, Mora and Zapata (2000).

[c] Diet and trophic assignment inferred from family-level feeding habits.

[d] Crustacea noted under carnivore trophic guild are primarily benthic, and those under the planktivore guild are present in the water column.

[e] Diet and trophic assignment inferred from genus-level feeding habits.

[f] Glynn et al. (2008).

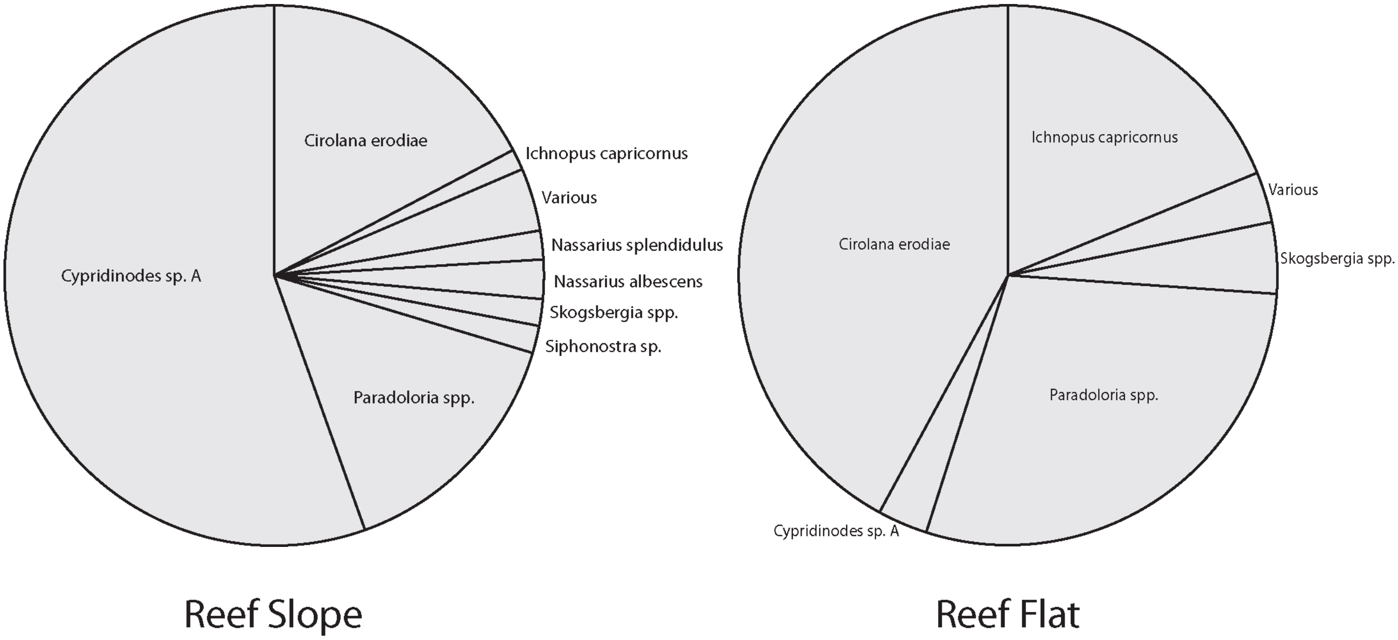

FIGURE 11. Small invertebrate taxa and relative abundances captured in baited scavenger traps, Lizard Island, Australia (1989–1990). Right: Leeward reef flat; Left: Leeward reef slope (modified from Keable, 1995).

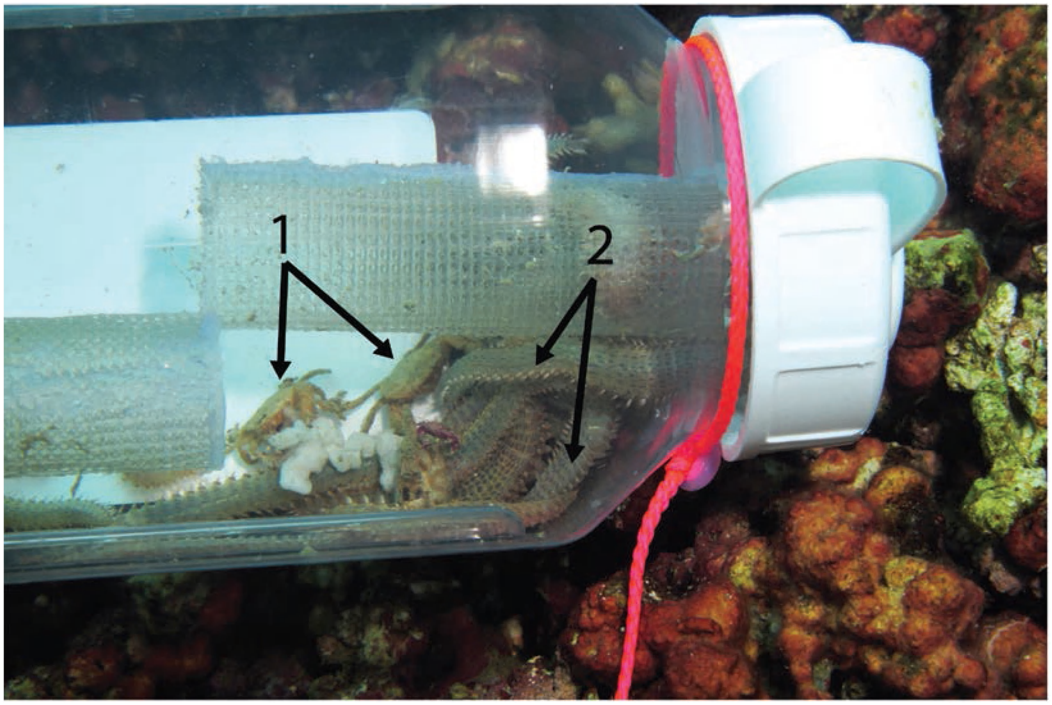

FIGURE 12. Invertebrate scavengers inside a trap being retrieved after overnight exposure on the Uva Island coral reef, Gulf of Chiriquí, Panama, 3 m depth. Arrows 1 and 2 respectively denote captured brachyuran crabs and amphinomid worms *Pherecardia striata*. The polychaete worms are ~1 cm wide. Photo courtesy of V. W. Brandtneris.

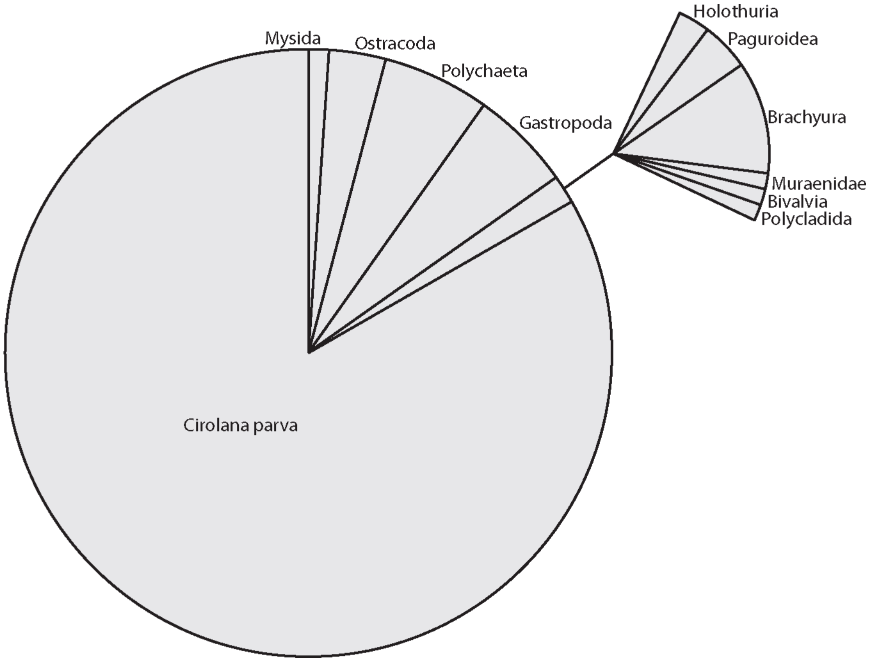

FIGURE 13. Small scavenger taxa and relative abundances captured in 55 baited traps set in pocilloporid framework on the Uva Island coral reef, Gulf of Chiriquí, Panama, 2–4 m depth.

polychaete worms, bivalve mollusks, and barnacles. Mobile crustaceans (e.g., trapeziid crabs and alpheid shrimps) and symbiotic fishes such as gobies and certain pomacentrids also increase circulation in the interbranch spaces of corals. Positive effects include increased availability of nutrients, dissolved oxygen, and food and dispersal of waste products, including reactive oxygen species generated during stress events. Overgrowth by fouling organisms can also be restricted by filter-feeding barnacles and shrimps and crabs that scrape coral surfaces.

Metazoan symbionts of corals employ diverse mechanisms to defend their host colony from corallivores. A serpulid polychaete worm thrusts an armed operculum and a scallop directs jets of water at attacking *Acanthaster*. Xanthid crabs employ a variety of agonistic responses toward sea stars, including pinching, clipping spines and tube feet, and body thrusts and dislodgment of large corallivores. Alpheid pistol shrimps direct aggressive snapping and water jets toward attacking corallivores. Gobies limit the grazing of chaetodontids probably by releasing an ichthyotoxic repellant.

Care should be exercised in establishing the identity of coral reef organisms in light of widespread species-specific interdependencies. For example, molecular genetic studies of the morphospecies of *Pocillopora damicornis* in the western Indian Ocean has shown the existence of two distinct species (Souter, 2010), and eight morphospecies of *Pocillopora* in the far eastern Pacific may in fact represent only three species (Pinzón and LaJeunesse, 2010). Other noted sibling species complexes are *Acanthaster planci* and *Spirobranchus giganteus*, representing four and 10–12 species respectively.

Sampling of cryptic reef scavengers in Australia and Panama suggests that this is a taxonomically diverse feeding group dominated by various crustacean orders, especially isopods. Mesoscavengers affect the rapid breakdown of reef carrion and particulate organic matter, driving nutrient recycling and coral reef primary production. Small, cryptic fish carnivores on eastern Pacific reefs (Panama and Colombia) were represented by 37 species in 20 families, and consisted of adult resident and immature transient members. Crustaceans ranked high in the diets of these fishes, as did other invertebrate taxa (e.g., polychaete worms, gastropod and bivalve mollusks, and cephalopods) and fishes. This cryptic carnivore guild likely exerts heavy consumer pressure on other cryptic metazoans, including biota recruiting to reefs via planktonic larval stages. Coral reef frameworks and associated habitats providing shelter can no longer be perceived as predator-free refuges.

From the variety of newly described coral–metazoan symbioses and a clearer understanding of functional interrelationships, it is apparent that small cryptic animals play numerous and essential ecological roles in many host corals. Their effects, both positive and negative, need to be understood with regard to the nature of key ecosystem processes and their influence on the dynamics of populations in reef systems and the diversity and structure of coral reef communities overall. The importance of understanding the various interactions and nuances involved in cryptic reef communities is critical in light of projected and unknown responses that are sure to accompany climate change impacts on coral reefs.

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Suzanne N. Arnold attended Bates College in Lewiston, Maine, and graduated in 1999 with a B.S. in biology. During her semester abroad she studied marine ecology in Zanzibar. It was this experience that spurred her interest in coral reef ecosystems and the people who are dependent on them. After completing her undergraduate degree, Susie worked as a Natural Resource Officer on Cape Cod and a Research Associate for a climate change mitigation consulting firm in Oregon, studied coral reefs and seamanship in Southeast Asia, and worked in Florida at Mote Marine Laboratory's Center for Tropical Research. In 2003, she relocated to the University of Maine's Darling Marine Center to do subtidal lobster and sea urchin research, and in 2007 received Master of Science degrees in marine biology and marine policy from the University of Maine. Susie is currently a Ph.D.

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Richard B. Aronson is professor and head of the Department of Biological Sciences at the Florida Institute of Technology. He received his A.B. from Dartmouth College in 1979 and his Ph.D. from Harvard University in 1985. His primary research focus is understanding how large-scale processes, including climate change, disease, overfishing and nutrient loading, control the geology and ecology of coral reefs on time scales ranging from decades to millennia. To that end, he has been coring reefs under water in Belize, Panama, and Jamaica for the past 15 years. A second area of interest is climate change in Antarctica and its implications for species invasion and community turnover. In 2004 Rich coauthored a report titled "Coral Reefs and Global Climate Change" for the Pew Center on Global Climate Change. He is past-president of the International Society for Reef Studies (ISRS). Rich is grateful for the support he has received from Smithsonian programs since 1986.

Andrew C. Baker is a marine biologist whose research focuses on the effects of climate change on coral reefs. An assistant professor of marine biology and fisheries at the University of Miami's Rosenstiel School of Marine and Atmospheric Science, Andrew graduated with a Double First in natural sciences (zoology) from Cambridge University in 1993. After coming to the United States on a Fulbright Scholarship, he was a predoctoral fellow of the Smithsonian Tropical Research Institute in Panama (1995) and doctoral fellow of the Australian Museum (1997). He received his Ph.D. in marine biology from the University of Miami in 1999 and worked for the Wildlife Conservation Society (WCS), first at the New York Aquarium (1999–2000) and then in the Global Marine Program (2001–2005), where he was also a member of the adjunct faculty of Columbia University. In 2008 Andrew was awarded a Pew Fellowship in marine conservation for his work on reef coral symbioses and climate change.

Bill J. Baker holds a B.S. in chemistry from California Polytechnic State University, San Luis Obispo (1982) and a Ph.D. in chemistry from the University of Hawaii (1986). Bill is a University of South Florida professor of chemistry and director of the USF Center for Drug Discovery and Innovation. His research interests include analysis of secondary metabolites from marine invertebrates, macroalgae, and microorganisms; drug discovery, including tropical (malaria, leishmaniasis, dengue, influenza, river blindness), infective, proliferative, and neurodegenerative diseases and multidrug resistance; marine biotechnology; chemical ecology of marine organisms; biosynthesis of marine natural products; and agrochemical applications of marine natural products. Bill is a long-term Antarctic scientific diver and principal investigator. In 1998, the U.S. Board of Geographic Names designated Baker Point, Antarctica. Bill has served as 2007 president of the American Society of Pharmacognosy.

Charles H. Baxter's commitment to holistic biology has grown from a career of developing diverse interests in biology to becoming a naturalist and supporting students who ask questions of organisms in nature. Chuck taught biology at Stanford University and Hopkins Marine Station from 1961 to 1993. His areas of interest focused on the structure and function of animals, how they evolved, how they operated in natural systems, and how humans were impacting those systems. From 1988 to 1996 Chuck did benthic ecology in the Monterey Canyon with the Monterey Bay Aquarium Research Institute's remotely operated vehicle, and from 1996 to 2003 he did concept and content development for Sea Studios Foundation television production company. He has had a long-standing interest in and participated in ongoing collaborations on climate forcing of coastal communities and the biogeographic responses of species along the Pacific coast. Chuck received the 1993 Dinkelspiel Award for outstanding service to undergraduate education and the 2000 Naturalist of the Year Award from the Western Society of Naturalists.

Giacomo Bernardi obtained his Master's and Ph.D. in molecular biology from the University of Paris and a postdoc from Stanford University. His research on molecular ecology and speciation of marine fishes has a strong field component that includes much subtidal work. His diving experience started in his early teens and was centered in the Mediterranean and the Red Sea. Now with University of California, Santa Cruz, his current research is primarily done in southern Africa, the tropical eastern Pacific, and French Polynesia. He has used a variety of underwater methods, including saturation and technical diving, for his research. His commitment to underwater research translated to teaching a kelp forest ecology course in California and a subtidal field course that has been taught for the past ten years in Mexico, French Polynesia, and the Mediterranean.

Charles E. Birkeland earned his doctorate at the University of Washington, Seattle. From 1970 to 1975 he was a postdoc at the Smithsonian Tropical Research Institute in Panama, where he experimented with the effects of nutrient input on the reefs of the eastern Pacific in contrast to the reefs in the oligotrophic western Atlantic. From 1975 to 2000 he was at the University of Guam Marine Laboratory, and from 2000 through 2010 he was at the Hawaii Cooperative Fishery Research Unit (U.S. Geological Survey) at the Department of Biology, University of Hawaii at Manoa. His recent research focused mainly on coral reef communities, namely (1) how corals acclimatize (physiological or behavioral adjustment of individual colony) or adapt (genetic adjustment of population) to climate change, (2) why some reef communities recover from damage by human activities and others do not, and (3) how alien populations adjust their realized niche dimensions in their new habitats.

Deron E. Burkepile received his Bachelor's degree from the University of Mississippi in biology in 1999. In 2006, he received his Ph.D. under the direction of Dr. Mark Hay from Georgia Tech, where he examined the impacts of herbivorous fish species richness and identity on community structure of coral reefs. After finishing his Ph.D., Deron was a Brown Postdoctoral Fellow at Yale University, where he did research in Kruger National Park in South Africa on the role of different-sized guilds of mammalian herbivores (elephants versus zebra versus impala) in driving ecosystem function in African savannas. Deron is currently an assistant professor in biological sciences at Florida International University in Miami. His lab is currently working on projects examining how alterations to herbivore pressure and nutrient availability impact coral–microbe interactions and coral disease, and he continues to investigate the similarities and differences between marine and terrestrial grazing ecosystems.

Mark H. Carr is a professor in the Department of Ecology and Evolutionary Biology at the University of California, Santa Cruz. Mark received his Master's degree at Moss Landing Marine Laboratories and his Ph.D. at the University of California, Santa Barbara. Mark and his graduate students study the behavioral, population, and community ecology of temperate marine fishes and salmonids, including kelp forest and riparian ecosystems. Much of his basic ecological research is designed to inform management and conservation problems, including the design and evaluation of marine protected areas, the design of large-scale, long-term monitoring programs, and ecosystem-based fisheries management. Mark is a co–principal investigator with the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), a multicampus coastal marine research consortium. Mark is also a science advisor to California's Marine Life Protection Act and Ocean Protection Council, an editor for the Ecological Society of America (*Ecology*, *Ecological Monographs*), a member of the Society's Rapid Response Team, and an Aldo Leopold Leadership Fellow.

Kenneth E. Clifton began diving in 1974 as a skinny 15-year-old, exploring the kelp beds of Monterey. In 1976 Ken moved to La Jolla, where he undertook advanced diver and dive master training while earning a B.A. in biology from the University of California, San Diego. Ken then moved to UC Santa Barbara, receiving a Ph.D. in 1987 from Bob Warner's lab for studies of reef fish behavioral ecology. After a three-year stint studying gazelle foraging in East Africa, he returned to marine studies as a postdoctoral researcher with the Smithsonian Tropical Research Institute, working out of the San Blas field station for nearly five years. It was there that his work on the reproductive ecology of green seaweeds began. Ken remains an active research diver who continues to focus on the behavior, ecology, and life history of various marine organisms. He is currently an associate professor of biology at Lewis and Clark College in Portland, Oregon.

Mary-Alice Coffroth completed her undergraduate degree in biology at the College of William and Mary in Virginia. She obtained an M.S. and Ph.D. in biological oceanography from the Rosenstiel School of Marine and Atmospheric Science (RSMAS) at the University of Miami, where she did a large portion of her dissertation work at the Smithsonian Tropical Research Institute's (STRI) field station in San Blas, Panama. She continued to work at STRI as an NSF postdoc and then moved to the University at Buffalo, where she is now a professor. She continues to work and dive on reefs, with her work focusing on the establishment and maintenance of coral–algal symbioses.

James A. Coyer received a B.S. in biology from the University of Wisconsin-Eau Claire in 1970 and a Ph.D. in biology from the University of Southern California in 1979. Jim is Assistant Director of Appledore Programs at the Shoals Marine Laboratory (Cornell University/University of New Hampshire). His current research interests include phylogeny and phylogeography of *Fucus* spp. and *Zostera* spp. in northern Europe, the role of sea urchins in determining community structure in giant kelp forests off southern California, and the impact of introduced species on the kelp beds in the Gulf of Maine. Jim is coauthor of Shoals Marine Lab's *The Underwater Catalog: A Guide to Methods in Underwater Research*.

Paul K. Dayton started diving in the mid-1950s with homemade gear that should have killed him. He is now a marine ecologist at Scripps Institution of Oceanography. Interested in understanding the processes organizing marine ecosystems, Paul focuses his work on the evaluation of important interaction strengths in ecosystems and how they vary in space and time in relation to both ecological and physical forcing. He has studied marine systems along the eastern rim of the Pacific Ocean from the Arctic to the tip of South America and in McMurdo Sound, Antarctica. Paul has been awarded both the George Mercer and William Cooper awards from the Ecological Society of America, the E. O. Wilson Naturalist Award from the American Society of Naturalists, and the Ramon Margalef Prize in Ecology and Environmental Sciences in Barcelona. He is proud to have been recognized with a Scientific Diving Lifetime Achievement Award from the American Academy of Underwater Sciences.

David O. Duggins is a resident senior research scientist, marine technologist, and supervisor of marine operations at the University of Washington Friday Harbor Marine Laboratories (FHL). Dave holds a Ph.D. from the University of Washington. He initiated and supervises the FHL Science Outreach Partnership and served on the board of directors of the San Juan Nature Institute. His research interests are in benthic community ecology, particularly as it relates to intertidal and shallow subtidal habitats and population biology and biomechanics of kelps. He pioneered an experimental approach to the ecological role of sea otters in relation to sea urchins abundances in kelp forests.

David B. Eggleston is a professor of marine science at North Carolina State University, and director of NC State's Center for Marine Sciences and Technology in Morehead City, North Carolina. David began scuba diving in 1974, became an active scuba instructor with the Professional Association of Diving Instructors in Florida, and then integrated scuba into his academic research and education/outreach programs. David's areas of expertise are marine ecology and conservation, fisheries, and marine science education. David has won numerous awards for his research and teaching, such as an NSF Early Career Award and induction into the North Carolina Academy of Outstanding Teachers. He has published more than 90 scientific papers in peer-reviewed journals, logged more than 4,000 dives, and used scuba to help conserve and restore species and ecosystems in the Florida Keys, Bahamas, Caribbean, and North Carolina.

Michael S. Foster is professor emeritus at Moss Landing Marine Laboratories/San Jose State University. He received his B.S. from Stanford University and Ph.D. from UC Santa Barbara. His research interests center on the ecology of subtidal and intertidal reefs, especially the structure and dynamics of algal assemblages in kelp forests, rhodolith beds, and on rocky shores. He is an instructor with the National Association of Underwater Instructors, fellow of the California Academy of Sciences, a Fulbright Scholar, and recipient of the Scientific Diving Lifetime Achievement Award from the American Academy of Underwater Sciences.

Peter W. Glynn hails from Coronado Island, southern California. Peter graduated from Stanford University in 1963 with a Ph.D. in biological sciences. Peter's doctoral research at Stanford was performed at the Hopkins Marine Station (Pacific Grove) and involved the trophic relationships of an intertidal community; Donald P. Abbott served as his advisor. Following graduation he joined the Institute of Marine Biology, University of Puerto Rico (Mayagüez, 1960–1967), then moved to the Smithsonian Tropical Research Institute (Panama, 1967–1983). In 1983 Peter joined the faculty of the Rosenstiel School of Marine and Atmospheric Science, University of Miami, where he is currently a professor in the Division of Marine Biology and Fisheries. Peter's main research interests have centered on coral reef ecology, with specialization in biotic interactions (predation, mutualisms), coral community structure, species diversity, reef accretion and distribution, biogeography, and disturbances to reefs, especially coral reef bleaching and El Niño disturbances.

Steven H. D. Haddock is a research scientist at the Monterey Bay Aquarium Research Institute and an adjunct associate professor at the University of California, Santa Cruz. His work focuses on gelatinous plankton, in particular ctenophores and siphonophores, and on bioluminescence, a common property among these animals. He has been conducting blue-water dives as part of his research for the last 20 years, since learning from some of the pioneers of the technique. Some of his most enjoyable experiences have been night dives to study bioluminescence and Humboldt squid behavior, and diversity surveys of plankton in Pacific, Atlantic, and Mediterranean habitats. With John Heine he has written a book promoting blue-water diving as a unique and irreplaceable method of experiencing the open ocean and upper water column.

William M. Hamner obtained a B.A. in zoology from Yale (1961) and Ph.D. in zoology from UCLA (1965). Bill's dissertation and early research was on photoperiodic control of the annual testicular cycles of birds. He was assistant professor of zoology (1966–1972) and associate professor of zoology and environmental sciences (1972–1974) at UC Davis. From 1971 to 1972 he and a group of highly gifted graduate students spent 15 months in Bimini scuba diving in the Gulf Stream to investigate gelatinous zooplankton; the research was funded by NSF, Guggenheim, and the National Geographic Society. He was a principal research scientist at the Australian Institute of Marine Science (1974–1977) and adjunct professor (1978–1988) and professor (1988–2004) at UCLA. Bill is now a professor emeritus at UCLA and an adjunct senior scientist at Dauphin Island Sea Lab, University of South Alabama. Bill and Research Associate Peggy Hamner have investigated oceanic zooplankton using scuba in Australia, Palau, Antarctica, and the western north Pacific.

Catherine Drew Harvell received her Ph.D. from the University of Washington in 1985. After receiving NATO and NSF postdoctoral fellowships she joined the faculty of Cornell University in 1986 as a professor of ecology and evolutionary biology. Drew is recognized for chairing both the World Bank Targeted Research Program on Coral Disease and the National Center for Ecological Analysis and Synthesis (NCEAS) Program on the Ecology of Marine Disease. Drew's analyses and papers have led to the now-widespread acceptance that diseases in marine ecosystems are important, particularly in the very climate-sensitive coral reef ecosystems. Drew has worked for many years on coral reefs in the Mexican Yucatan and Florida Keys and, more recently, in Hawaii, Palau, the Philippines, and Australia. She has been a sabbatical fellow at NCEAS and vice president of the Society of American Naturalists, is a senior scientist at The Kohala Center in Hawaii, and serves on the editorial board of *Annual Reviews of Ecology, Evolution and Systematics*.

William F. Herrnkind received his B.S. in biology in 1961 from the State University of New York at Albany. His scientific diving career began in 1961 at the University of Miami Marine Laboratory (now Rosenstiel School of Marine and Atmospheric Science), where he earned his M.S. and Ph.D. In 1967, as an assistant professor at Florida State University (FSU), he initiated research using scuba and other underwater technologies to study mass single-file migrations by spiny lobster, which he first witnessed in the field as a graduate student. This propelled his career research on behavior and ecology of spiny lobsters and other crustaceans. Bill taught animal behavior and invertebrate zoology and created educational outreach programs at the FSU Marine Laboratory, which he directed from 1981 to 1985. Bill was instrumental in establishing FSU's first scientific diving program for safety and training. Florida State University awarded him several prizes for both teaching and outreach, as well as a named professorship for academic excellence. Bill retired in 2007.

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Mark A. Hixon was introduced to scuba by Lloyd Bridges (via TV's *Sea Hunt*), Jacques Cousteau (also via TV), and Bill Brisby (his high school marine biology teacher). Starting with undersea research as an undergraduate in the early 1970s, Mark has used scuba to study kelp forest fishes in California (based at UC Santa Barbara) and a variety of coral reef fishes in a broad range of Pacific and Atlantic locations (based at the University of Hawaii, University of the Virgin Islands, James Cook University, and Oregon State University). An endowed professor at the University of Hawai'i at Manoa, Mark is past chair of both the Marine Protected Areas Federal Advisory Committee (for the National Oceanic and Atmospheric Administration and the Department of the Interior) and the Ocean Sciences Advisory Committee for the National Science Foundation. He currently studies the invasion of Atlantic coral reefs by Pacific lionfish.

Sally J. Holbrook is a professor of ecology in the Department of Ecology, Evolution and Marine Biology at the University of California, Santa Barbara. She is co–principal investigator of two NSF Long Term Ecological Research (LTER) programs: the Moorea Coral Reef LTER and the Santa Barbara Coastal LTER. Sally is a member of the NSF LTER Network Executive Committee, is a coorganizer of the international Coral Reef Environmental Observatory Network (CREON; www.coralreefeon.org), is the faculty director of the Santa Cruz Island Natural Reserve of the UC Natural Reserve System, and has served on the editorial board of the Ecological Society of America. Her research explores factors that influence population and community dynamics on subtidal temperate and tropical marine reefs. She has a particular interest in the role of biotic interactions and resource constraints, and in the links between individual-, population-, and community-level responses to short- and long-term environmental drivers.

Nicholas A. Kamenos received a B.Sc. (Hons) in marine biology from the University of Wales, Bangor, in 2000 and his Ph.D. in marine biology from the University of London in 2004. Nick is a research fellow in the School of Geographical and Earth Sciences and honorary lecturer in the School of Life Sciences at the University of Glasgow. His research interests include investigating relationships between global change (e.g., climate variability and ocean acidification) and marine ecosystems; development of ultra-high-resolution paleoclimatic and paleoecological proxies for the Holocene; and investigating if and how fisheries affect the expected responses of marine ecosystems to global change.

Brenda Konar is a professor in the School of Fisheries and Ocean Sciences at the University of Alaska Fairbanks (UAF). She holds a Ph.D. from the University of California, Santa Cruz. Her research expertise is in phycology, biodiversity, and nearshore and benthic ecology. She teaches the UAF scientific diving course at Kasitsna Bay and is a principal researcher in NaGISA, a Census of Marine Life Program. Brenda's current research includes mapping and characterization of Alaska's unexplored Arctic coastal rocky habitats (funded by NOAA/OE); epifaunal communities in the Chukchi and Beaufort Seas (funded by BOEMRE); and kelp forest interaction webs in the Aleutian archipelago, namely patterns and mechanisms of change following the collapse of an apex predator (funded by NSF).

Michael A. Lang is senior fellow at The Ocean Foundation and multiterm president of the American Academy of Underwater Sciences (AAUS). He was recruited as Smithsonian scientific diving officer in 1990, concurrently served as director of the pan-institutional Marine Science Network from 1998 to 2011, and as National Science Foundation Polar Programs Diving Officer from 2001 to 2011. Michael was a staff marine biologist at San Diego State University from 1982 to 1989. He is the 1991 DAN/Rolex Diver of the Year and recipient of the 2000 Undersea and Hyperbaric Medical Society's Craig Hoffmann Diving Award, the 2008 AAUS Conrad Limbaugh Scientific Diving Leadership Award, the 2009 Diving Equipment and Marketing Association's Reaching Out Award and Diving Hall of Fame admission, and the Academy of Underwater Arts and Sciences 2010 NOGI Award for Science. Michael received his D.Phil. in environmental physiology from the Norwegian University of Science and Technology in Trondheim and pursues research interests in polar regions, marine conservation, and diving safety.

Howard R. Lasker is a marine ecologist whose research focuses on Caribbean octocorals as an instrument for studying the processes controlling coral reef cnidarians. A theme in much of his research is the manner in which colonization interacts with morphology and reproduction in controlling population dynamics. Much of his research has been conducted at the Smithsonian Tropical Research Institute in Panama. He has also worked at a variety of other Caribbean sites ranging from Belize to the

Bahamas, as well as on the Great Barrier Reef. His current research focuses on the reproduction and population connectivity of gorgonians in the Bahamas. All of his work involves extensive use of scuba. Howard received B.S. and M.S. degrees from the University of Rochester and a Ph.D. from the University of Chicago. He currently is professor of geology and director of the Graduate Program in Evolution, Ecology, and Behavior at the University at Buffalo.

Harilaos A. Lessios received his Bachelor's degree from Harvard University in 1973 and his Ph. D. from Yale University in 1979. Haris has worked at the Smithsonian Tropical Research Institute (STRI) ever since, rising to the rank of senior scientist. Since 2007 he has also been an adjunct professor at the Department of Biology at McGill University. He also served as deputy director and director of marine research at STRI. Most of his field work was done in the San Blas Archipelago on the Caribbean coast of Panama, and in recent years he has been concentrating on questions of speciation and molecular evolution of marine organisms with special emphasis on sea urchins. He has published approximately 70 papers in peer-reviewed journals, and is a fellow of the American Association for the Advancement of Science. He was the editor of the proceedings of the eighth International Coral Reef Symposium, held in Panama in 1996.

Don R. Levitan is a professor in the Department of Biological Science at Florida State University. Don is interested in the ecology and evolution of marine invertebrates. His work examines the interaction of ecology, behavior, and water flow on shaping the evolution of reproductive strategies and patterns of speciation. He addresses these topics by integrating field work with molecular analyses and theory. Before entering graduate school, he taught diving and how to use scuba as a research tool in the Florida Keys and the U.S. Virgin Islands. Spending time under water taught Don to appreciate the biology of an organism in the context of the environment in which it lives. His current field sites are in the cold waters off of British Columbia, Canada, where he studies the evolution of gamete traits in sea urchins, and in the warm waters of the Caribbean, where he examines reproductive isolation and speciation in corals.

Mark M. Littler and **Diane S. Littler** are marine scientists who have developed a unique collaborative relationship. Diane is formerly a Research Associate at the Smithsonian Institution and an Adjunct Research Scientist at Harbor Branch Oceanographic Institute, Florida Atlantic University. Mark is formerly a Senior Scientist at the National Museum of Natural History. Diane and Mark each have more than 30 years of scuba experience on coral reefs, with more than 195 papers and books published in a wide range of disciplines. Their research has taken them around the world in search of unexplored marine habitats, often to areas of exceptional diversity or places in danger of biodegradation. These include Southern California, the Pacific and Atlantic coasts of Panama, the Sea of Cortez, the Galapagos Islands, the Mediterranean Sea, Morocco, Western Sahara, the Seychelles Archipelago, the Australian Great Barrier Reef, the Hawaiian Islands, Palau, Guam, Tahiti, the Cook Islands, American Samoa, Great Astrolabe Reef, Fiji, the Solomon Islands, Papua New Guinea, French Guiana, and many island nations of the Caribbean. Mark and Diane's recent research has focused on relative dominance theory, functional morphology, and complex top-down versus bottom-up interactions in coral reef systems. Other active research includes monographic, floristic, and phylogenetic systematics; seaweed experimental taxonomy; and biodiversity, ecology, and conservation of tropical marine ecosystems. Their series of user-friendly field guides is now focused on the unique and rich flora of Panama, both Caribbean Panama (San Blas Islands, Isla Escudo de Veraguas, and Bocas del Toro) and Pacific Panama (Archipelago de las Perlas, Gulf of Panama, Gulf of Chiriquí, and Coiba National Park).

Ian G. Macintyre is a research scientist in the Department of Paleobiology in the National Museum of Natural History. He received his B.Sc. from Queen's University, Ontario, Canada, in 1957 and his Ph.D. from McGill University, Montreal, Canada, in 1967. He joined the Smithsonian staff in 1970 after three years of research at Duke University Marine Laboratory. He is a carbonate petrologist and sedimentologist with a multidisciplinary interest in the postglacial history of coral reefs, submarine lithification, skeletal mineralogy of reef organisms, bioerosion, and Holocene sea level history. Ian developed the first submersible hydraulic drill used in the study of reef history. It enabled him, and subsequently many others, to collect cores from reefs at their entire depth range. In 1996 he received the Darwin Medal from the International Society for Reef Studies. Ian was an original member of the scientific team that established Smithsonian's research activities in Belize in 1972.

Laurence P. Madin is the executive vice president and director of research, and a senior scientist, at the Woods Hole Oceanographic Institution (WHOI) in Woods Hole, Massachusetts. Previously Larry has been chair of the WHOI Biology Department and director of the WHOI Ocean Life Institute. Larry received his A.B. from the University of California, Berkeley and his Ph.D. from UC Davis, and has been at WHOI since 1974. His principal research interests are in the biology of oceanic and deep-sea zooplankton, particularly medusae, siphonophores, ctenophores, and pelagic tunicates. Larry has been a diver since 1970, and was among the first biologists to use scuba and submersibles for the in situ study of oceanic plankton. He has participated in more than 70 research cruises. Larry holds an adjunct appointment at the Monterey Bay Aquarium Research Institute, and is a member of the American Geophysical Union, Association for the Sciences of Limnology and Oceanography, Sigma Xi, and several advisory boards.

Daniel P. Malone is a data analyst and field ecologist with an M.S. in marine science working at the University of California, Santa

Cruz, as a part of the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO). Dan has used scuba for research in African Rift Valley lakes, on coral reefs in the Caribbean and Pacific, under Antarctic ice, and in California kelp forests. During the past 15 years he has been involved with long-term monitoring studies of kelp forest ecosystems, including restoration projects on artificial reefs, kelp forest related fisheries, shore-based impacts to kelp forests, and other projects. His current research activities include integrating a variety of collected data to monitor and evaluate the performance of California's expanding network of marine protected areas, and a study that combines oceanographic modeling and genetic parentage analysis to examine the connectivity of fish populations living in kelp forests.

Roberta L. Marinelli is the director of the Wrigley Institute for Environmental Studies at University of Southern California and the former program director for the Antarctic Organisms and Ecosystems Program in the Antarctic Sciences Division at the National Science Foundation. Previously she was an associate professor at University of Maryland's Center for Environmental Science, where her research included the ecology and biogeochemistry of nearshore and continental shelf environments with funding from the National Science Foundation, the Office of Naval Research, and Maryland Sea Grant. Her projects have taken her to the Pacific Northwest, the southeastern USA, and the shores of Nova Scotia.

Adam G. Marsh received his Ph.D. in marine science from the University of Maryland in 1989 while working at the Chesapeake Biological Laboratory, Solomons Island, Maryland. Recognizing the oncoming revolution in cell and molecular biology at that time, he pursued postdoctoral research appointments in cell biology, molecular biology, immunology, and molecular ecology. In 2000 he was hired as an assistant professor at the University of Delaware School of Marine Science, where he is currently an associate professor. He has been involved with Antarctic research since 1994 and has logged more than 100 dives under the sea ice at McMurdo Station. He has authored more than 50 peer-reviewed journal publications, holds one U.S. patent with a second patent now pending, and is the cofounder of a biotech startup focusing on microbial gene and protein bioengineering under harsh/extreme bioreactor conditions.

George I. Matsumoto is a senior educational and research specialist at Monterey Bay Aquarium Research Institute. He received his Ph.D. from UCLA. His research interests are open ocean and deep sea communities; ecology and biogeography of open ocean and deep sea organisms; functional morphology; and natural history and behavior. He manages several education and outreach programs, including collaborations with the Monterey Bay Aquarium Research Institute's sister organization, the Monterey Bay Aquarium (MBA). Dr. Matsumoto served on the Digital Library for Earth System Education (DLESE) Steering Committee and the 2004 NSF Committee of Visitors for Geoscience Education, and is currently serving on the National Ocean Studies Board and the national advisory boards for the Center for Microbial Oceanography: Research and Education (C-MORE) and the Centers for Ocean Sciences Education Excellence (COSEE). He was originally certified by the UC Berkeley Scientific Diving Program and used scuba extensively for his Ph.D. research. He still dives for both research and enjoyment, including volunteering for feeding shows in the MBA kelp forest tank.

James B. McClintock is the Endowed University Professor of Polar and Marine Biology at the University of Alabama at Birmingham (UAB). Jim received his B.S. degree from the University of California, Santa Cruz (UCSC) in 1978 and his doctoral degree from the University of South Florida in 1984. In 1987, after completing an NSF Postdoctoral Fellowship at UCSC, he joined the faculty of the Department of Biology at UAB. He became a full professor at UAB in 1997 and Endowed University Professor of Polar and Marine Biology in 2003. Jim's research focuses on aspects of marine invertebrate nutrition, reproduction, and primarily, chemical ecology. He has published more than 230 peer-reviewed scientific publications. In 2001 he was selected as the winner of the Wright A. Gardner Award for the most outstanding scientist in the state of Alabama. He is an elected fellow of the American Association for the Advancement of Science. In 1998 the United States Board on Geographic Names designated the geographic feature McClintock Point in honor of his contributions to Antarctic science.

Mónica Medina obtained her undergraduate degree in biology from Universidad de Los Andes in Colombia. However, her fascination with the sea took her to an internship at the Naos Marine Laboratory at the Smithsonian Tropical Research Institute in Panama. Subsequently, she obtained her Ph.D. in marine biology at the University of Miami. Mónica did postdoctoral work at the Marine Biological Laboratory in Woods Hole, Massachusetts, and at the California Academy of Sciences in San Francisco. She spent several years at the Joint Genome Institute as a research scientist. In 2005, she became founding faculty of the new campus of the University of California, Merced. She currently studies the genomics of coral reef symbioses and the evolution of metazoan biomineralization.

Jessica U. Meir is a comparative physiologist interested in the physiology and adaptations of animals in extreme environments. Jessica is currently an assistant professor of anesthesia at Harvard Medical School and a former NSF-funded postdoctoral researcher at the University of British Columbia, where she researched hypoxia tolerance in the high-flying bar-headed goose. She received her Ph.D. at the Scripps Institution of Oceanography studying diving physiology of marine mammals and birds. Jessica's work focused on blood oxygen transport and depletion in diving emperor penguins in the Antarctic and elephant seals in California. Jessica received her bachelor's degree in biology at Brown University and master's degree from the International

Space University in France. Before pursuing her Ph.D. she worked as a scientist for human physiology space research at NASA's Johnson Space Center, coordinating, supporting, and training astronauts for experiments on the U.S. Space Shuttle and International Space Station.

Amy L. Moran is professor at University of Hawaii at Manoa's Biology Department and Marine Biology program. Prior to 2013 she worked in the Department of Biological Sciences at Clemson University for eight years as a researcher and teacher of marine biology, invertebrate biology, and Antarctic science and at the Department of Marine Sciences at the University of North Carolina at Chapel Hill. Amy did postdoctoral work on marine invertebrate ecology and physiology at the University of Southern California and the University of Washington. Her research focuses on adaptive responses of marine invertebrate animals to environmental change, with particular emphasis on the early and most vulnerable life history stages—eggs, embryos, and larvae. Her work has taken her to the tropics, the Antarctic, and many temperate parts of the world to examine closely related animals living in contrasting and often extreme habitats.

Mark R. Patterson is professor of marine science at the College of William and Mary, Virginia Institute of Marine Science. Mark holds an A.B., A.M., and Ph.D. in biology from Harvard University. He directs the Autonomous Systems Laboratory, where free-swimming robots are designed and built. His research interests are grounded in the interdisciplinary fields of marine ecology and biomechanics. Mark uses autonomous underwater vehicles to make new discoveries such as coherent structures of lowered oxygen over coral reefs, how krill swarms in the Antarctic appear on high frequency side scan sonar, and how to identify fishes from their side scan sonar images using neural network processing. He also applies chemical engineering theory to the allometry of metabolism of lower invertebrates and algae.

Valerie J. Paul is currently director of the Smithsonian Marine Station at Fort Pierce in Florida. She received her B.A. from the University of California, San Diego in 1979 with majors in biology and studies in chemical ecology and her Ph.D. in marine biology in 1985 from the Scripps Institution of Oceanography. Valerie joined the faculty of the University of Guam Marine Laboratory in 1985, serving as director of the laboratory from 1991 to-1994 and as full professor from 1993 to –2002. Valerie's research interests include marine chemical ecology, marine plant–herbivore interactions, coral reef ecology, and marine natural products. She was elected a fellow of the American Association for the Advancement of Science in 1996 and was elected and served as chairperson of the Marine Natural Products Gordon Research Conference in 2000. Valerie currently serves on the editorial boards of the journals *Coral Reefs* and *Journal of Natural Products*. Valerie and her collaborators have published more than 190 research articles in journals and books.

Joseph R. Pawlik received his B.S. in biology from the University of Minnesota, Twin Cities (1982), and his Ph.D. in marine biology from Scripps Institution of Oceanography, UC San Diego (1988). Joe is a professor in the Department of Biology and Marine Biology at the University of North Carolina, Wilmington, where he teaches an undergraduate course in invertebrate zoology and directs a research program involving undergraduate and graduate students. He and his collaborators have authored more than 100 publications in the scientific literature, primarily on the ecology of invertebrates on Caribbean coral reefs.

John S. Pearse's undergraduate studies at the University of Chicago (1955–1958) led to Stanford University and marine biology. John's doctoral work examined reproductive timing of marine invertebrates at McMurdo Station, Antarctica. A faculty position at the American University of Cairo (1964–1967) allowed him to continue that work in the Red Sea. In 1968 he joined Wheeler North's program at California Institute of Technology to examine reproductive biology of sea urchins in kelp beds of southern California. He joined the faculty of the University of California, Santa Cruz in 1971 and began research in nearshore ecology. Research and teaching programs took him back to the Antarctic as well as to Bermuda and around the tropical western Pacific. Among his awards, he is most proud of teaching awards from the American University of Cairo and the University of California, Santa Cruz; but he feels the wonderful creatures in his field courses deserve the credit. John retired in 1994 but continues to teach, conduct research, and write as a professor emeritus.

Daniel C. Reed received his Ph.D. in biological sciences at the University of California in 1989. Dan is currently a research biologist in the Marine Science Institute at the University of California, Santa Barbara, and the lead principal investigator of the Santa Barbara Coastal Long Term Ecological Research Program funded by the National Science Foundation. His primary research interests pertain to the ecology of coastal marine ecosystems and the ecological and physical processes that structure them. Much of Daniel's work has focused on determining the mechanisms that allow these systems to recover from natural disturbance and then applying this knowledge to restoration programs designed to mitigate impacts caused by human disturbance. Giant kelp forests and sea grass beds have been the focal ecosystems for most of Dan's research, which includes studies on dispersal, recruitment, reproduction, population dynamics, community ecology, primary production, and trophic interactions.

Rafael Riosmena-Rodríguez is professor and leader of the Marine Botany Research Group of Universidad Autónoma de Baja California Sur in La Paz, Baja California Sur, Mexico. He obtained his Ph.D. from La Trobe University in 2002. Professor Riosmena is deeply interested in understanding the role of marine plants and algae in coastal habitats and their evolutionary significance. His research includes systematics, biogeography, and ecology of marine plants from subtropical habitats. Rodrigo is an expert in rhodoliths, free-living forms of nongeniculate coralline red algae (Corallinaceae, Rhodophyta) that form extensive beds over broad latitudinal and depth ranges with wide morphological variations in response to physical factors.

Raphael Ritson-Williams is a research technician who has been conducting research at the Smithsonian Marine Station at Fort Pierce since 2002. He recently became a Ph.D. candidate at the University of Hawaii at Manoa. He is interested in the evolutionary ecology of coral reefs. Especially important are the processes that promote reef recovery after a disturbance. Raphael's research expertise is in marine chemical ecology and larval ecology, both of which contribute to coral recruitment, which can increase reef resilience. At the University of Hawaii he studies population genetics to better understand the role of individual variation and resistance in response to stress. This research will help illuminate how natural and anthropogenic disturbance can shape genetic diversity of coral populations.

Susan J. Roberts became the director of the National Research Council's Ocean Studies Board in 2004. She received her Ph.D. in marine biology from the Scripps Institution of Oceanography, where she studied the biochemistry of fish muscle and discovered a symbiotic bacterium in the gills of the deep sea bivalve *Xylophaga washingtona*. She was a postdoctoral fellow at UC Berkeley in developmental biology and then moved east to take a position at the National Cancer Institute. In 1998 Susan joined the staff of the Ocean Studies Board, where she has directed a variety of ocean policy studies on topics such as marine protected areas, fisheries science and management, and coastal processes. She is a past president of the Washington, D.C. chapter of the Association for Women in Science and a fellow of the Washington Academy of Science.

Laura Rogers-Bennett received her B.A. from the University of New Hampshire after conducting subtidal research with Dr. Larry Harris. She completed an M.S. at the University of Massachusetts Boston by working with green sea urchins in nearshore kelp beds. After moving to California, she completed her Ph.D. in ecology at the University of California (UC), Davis, and two postdoctoral fellowships, one at the UC Santa Cruz Institute of Marine Science and the other at the University of Washington Friday Harbor Laboratories. Laura is a senior biologist with the California Department of Fish and Game and a research associate at UC Davis at the Bodega Marine Lab. The work in her lab focuses on processes that impact marine populations and communities and how to apply findings to resource assessment, fishery management, and marine conservation. Laura has been an active research diver for more than 30 years, co-teaches the research dive classes at UCD, and is chair of the UCD diving control board.

Russell J. Schmitt is a professor of ecology in the Department of Ecology, Evolution, and Marine Biology at the University of California, Santa Barbara. Russ is the lead principal investigator of the NSF Moorea Coral Reef Long Term Ecological Research (LTER) site and is an associate investigator on the Santa Barbara Coastal LTER. Russ directs the Coastal Research Center of UC Santa Barbara's Marine Science Institute, is a scientific advisor to the California Coastal Commission on mitigating effects of the San Onofre Nuclear Generating Station on marine resources, and founded the UC-wide graduate training program in coastal toxicology. His research interests bridge population and community ecology. He explores the dynamics and regulation of subtidal reef populations as well as the interplay between direct and indirect species interactions in shaping the structure and dynamics of reef communities. All of Russ's field research has involved scientific diving.

Kenneth P. Sebens is currently director of the University of Washington's (UW) Friday Harbor Laboratories (since 2005) and A. O. Dennis Willows Director's Endowed Professor of biology in the UW Department of Biology in Seattle. Ken received his B.A. from the University of Connecticut in 1972 and his Ph.D. from the University of Washington in 1977. He was previously at Harvard University, Northeastern University, University of Massachusetts Boston, and the University of Maryland. He conducts research on marine subtidal benthic populations and communities in both temperate and tropical locations. One ongoing project is an investigation of community and population dynamics and long-term change in rocky subtidal habitats in Massachusetts. He has authored more than 80 peer-reviewed publications. Support for Ken's research includes continuous funding from the National Science Foundation (since 1979) and facilities support from the National Oceanic and Atmospheric Administration and the Smithsonian Institution.

Diana L. Steller is a research biologist, lecturer, diving safety officer at Moss Landing Marine Laboratories and member of the board of directors of the American Academy of Underwater Sciences. Diana holds a B.A. in aquatic ecology from the University of California, Santa Barbara (1988), an M.S. in marine biology from Moss Landing Marine Laboratories (1993), and a Ph.D. in ecology and evolutionary biology from the University of California, Santa Cruz (2003). She has been working and teaching in the Gulf of California for the past twenty years. Her research interests include the ecology of temperate reefs and subtropical carbonate rhodolith beds with an emphasis on macroalgal ecology, algal physiology, and species interactions. Diana is particularly interested in the role that macroalgae play as a substrate and food resource in subtidal communities and in how algal dynamics influence community dynamics.

Robert S. Steneck is a professor in the School of Marine Sciences at the University of Maine Darling Marine Center. He received a B.Sc. in biology/geology from Baldwin-Wallace College in 1973, an M.S. in botany and plant pathology from the University of Maine in 1978, and a Ph.D. in earth and planetary sciences from the Johns Hopkins University in 1982. Bob received a Pew Fellowship in marine conservation in 1998 and is a fellow of the American Association for the Advancement of Science. The focus of Bob's research is in situ ecology. His research interests are the structure and function of coastal marine ecosystems in the Gulf of Maine and the Caribbean. With his students Bob has explored kelp forest ecosystems, studying lobsters, sea urchins, and fish stocks. He has also worked extensively throughout the Caribbean and tropical Pacific studying coral reefs from biological and geological perspectives.

Tanya L. Streeter is a ten-time world record freediver, television presenter, and environmentalist. Born and raised in Grand Cayman and educated at Brighton University in England, Tanya's 10 freediving world records span six years and seven disciplines, including five absolute and two current world records. In 2003 *Sports Illustrated* called her "The World's Most Perfect Athlete." In her quest to change the global misperception of her sport, Tanya has subjected herself to clinical physiological studies before, during, and after dives to facilitate a better understanding of freediving and safety. Her collaborations as an adventure and wildlife television presenter include series with the BBC, Animal Planet, and National Geographic. Tanya is a spokesperson for The Whale and Dolphin Conservation Society, The Coral Reef Alliance, Bite-Back (shark protection), and World Society for the Protection of Animals (WSPA); she is also patron to the Scuba Trust (a disabled diver charity).

Phillip R. Taylor is the University of Southern California's executive director of research advancement and federal relations and the former head of the Ocean Section in the National Science Foundation's (NSF) Ocean Sciences Division. He received a Ph.D. from the University of California, Irvine, in ecology and evolutionary biology based on research on California coastal systems pertaining to the biological interactions and physical processes controlling the composition of species assemblages on shorelines. Following time in the professorate at the University of the Virgin Islands, a term as a visiting scientist at the Smithsonian's National Museum of Natural History, and further research on the role of grazers in the control of community structure in Caribbean coral reef and mangrove ecosystems, Phil joined the NSF as a rotator in biological oceanography in 1985 and became director of the Biological Oceanography Program in 1988.

Karen B. Van Hoesen became a certified diver at age 17 and a diving instructor with the National Association of Underwater Instructors in 1983 while teaching diving at University of California, Davis. Her interest in diving physiology and medicine prompted her to attend Duke University Medical School and subsequently to collaborate with the Divers Alert Network and Duke Hyperbaric Center. She was the recipient of the Our World Underwater Scholarship in 1988. Karen is currently a clinical professor of medicine in emergency medicine at the University of California, San Diego (UCSD), and is board certified in both emergency medicine and undersea and hyperbaric medicine. She is also the director of the UCSD Diving Medicine Center and UCSD Undersea and Hyperbaric Medicine Fellowship. Karen is recognized as one of the world's leading authorities on diving medicine. She loves opening up the underwater world to others and teaching all aspects of diving medicine, safety, and appreciation of the underwater environment.

Steve V. Vollmer received his Ph.D. from Harvard University in evolutionary biology. His research group at Northeastern University's Marine Science Center in Massachusetts studies the evolutionary ecology of marine organisms, especially reef-building corals. Steve's research has focused on how evolution shapes the genetic architecture of coral populations and species. The current focus of his lab is on the genetic bases of innate immunity, pathogen recognition, and host resistance in reef corals. Steve has a long-standing relationship with the Smithsonian Institution; his coral research is based at the Smithsonian Tropical Research Institute in Panama, where he worked as a Smithsonian Marine Science Network and Hoch Fellow from 2004 through 2010.

James M. Watanabe received his Ph.D. in zoology from University of California, Berkeley. His background and research interests lie in the fields of invertebrate zoology and marine ecology, with particular emphasis on kelp forests and rocky intertidal communities. Jim has conducted research on the distribution and abundance of kelp forest invertebrates, the dynamics of sea urchin-mediated deforestations, and the physiological ecology of kelp (*Macrocystis pyrifera* and *Pterygophora californica*). These studies have focused on predator–prey interactions, interspecific competition, and the effects of disturbance on marine organisms. He is also interested in the statistical problems of detecting changes in natural populations through time. Jim's primary responsibility at Stanford University's Hopkins Marine Station is undergraduate teaching. During winter, spring, and summer quarters he teaches subjects ranging from introductory biology and invertebrate zoology to kelp forest ecology, experimental design, and statistics. His courses attempt to nurture an appreciation for the natural world through accumulation of detailed knowledge and hands-on experience.

Jon D. Witman grew up near the broad horizon of the ocean, which sparked his interest in large-scale marine ecology. Jon's exposure to marine ecology began at Sandy Hook Marine Lab, New Jersey, where he studied the impacts of sewage dumping on marine life. After an independent study (University of Otago, New Zealand) he took two years off from university to explore the relatively pristine coral reefs of Fiji and the New Hebrides Islands. These contrasting early experiences shaped Jon's present view of anthropogenic impacts in the oceans and the need for conservation. Jon conducted a Ph.D. in subtidal ecology in the Gulf of Maine (University of New Hampshire, 1984). A postdoc at Northeastern University's Marine Science Center led to an assistant professorship there. Jon is currently a professor of biology at Brown University. His research interests include the effects of large-scale processes on local communities, benthic–pelagic coupling, biodiversity, and supply-sided and trophic ecology.

REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

ALL MANUSCRIPTS ARE REVIEWED FOR ADHERENCE TO THE SISP MANUSCRIPT PREPARATION AND STYLE GUIDE FOR AUTHORS (available on the "Submissions" page at www.scholarlypress.si.edu). Manuscripts not in compliance will be returned to the author. Manuscripts intended for publication in the Contributions Series are evaluated by a content review board and undergo substantive peer review. Accepted manuscripts are submitted for funding approval and scheduling to the Publications Oversight Board.

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FIGURE CAPTIONS should be provided in a separate MS Word file.

FIGURES (e.g., photographs, line art, maps) should be numbered sequentially (1, 2, 3, etc.) in the order called out; be placed throughout text, not at end of manuscript; have all components of composites lettered with lowercase letters and described in the caption; include a scale bar or scale description, if appropriate; include any legends in or on the figure rather than in a caption.

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Figures must be original and submitted as individual TIFF or EPS files. Resolution for art files must be at least 300 dpi for grayscale and color images and at least 1200 dpi for line art. Electronic images should measure no more than 100% and no less than 75% of final size when published. JPG files will not be accepted. Color images significantly increase costs so should be included only if required. Funding for color art is subject to approval by SISP and the Publications Oversight Board.

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