

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.

Jon D. Witman, Box G-W, Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912, USA. *Paul K. Dayton*, Mail Code 0227, Scripps Institution of Oceanography, La Jolla, California 92093-0227, USA. *Suzanne N. Arnold*, Darling Marine Center, University of Maine, 193 Clark's Cove Road, Walpole, Maine 04573, USA. *Robert S. Steneck*, Darling Marine Center, University of Maine, 193 Clark's Cove Road, Walpole, Maine 04573, USA. *Charles Birkeland*, Department of Biology, University of Hawaii at Manoa, Honolulu, Hawaii 96822, USA. **Correspondence:** J. Witman, Jon_Witman@brown.edu.

Manuscript received 25 January 2012; accepted 5 March 2013.

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

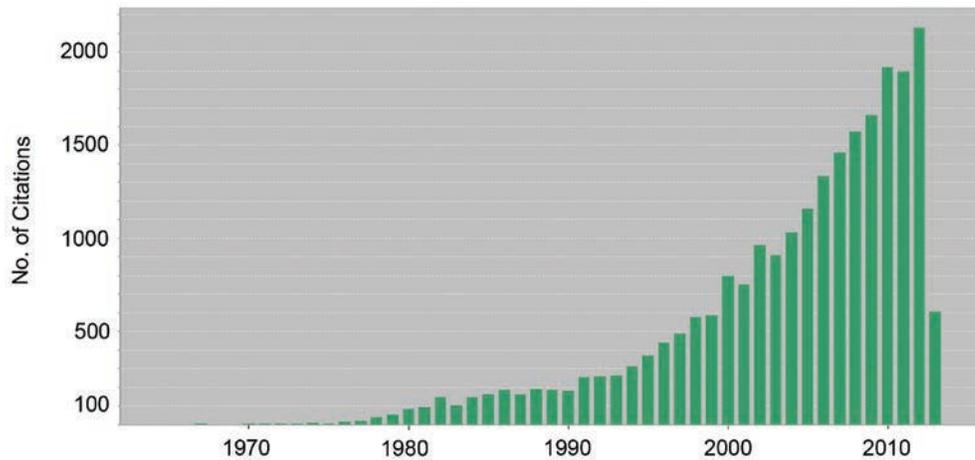


FIGURE 1. The use of scuba in the production of scientific papers in biology and oceanography has increased exponentially over the past few decades (data from ISI website).

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, *Sphyrna 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/m², 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 counter-intuitive 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; Futuyama 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.

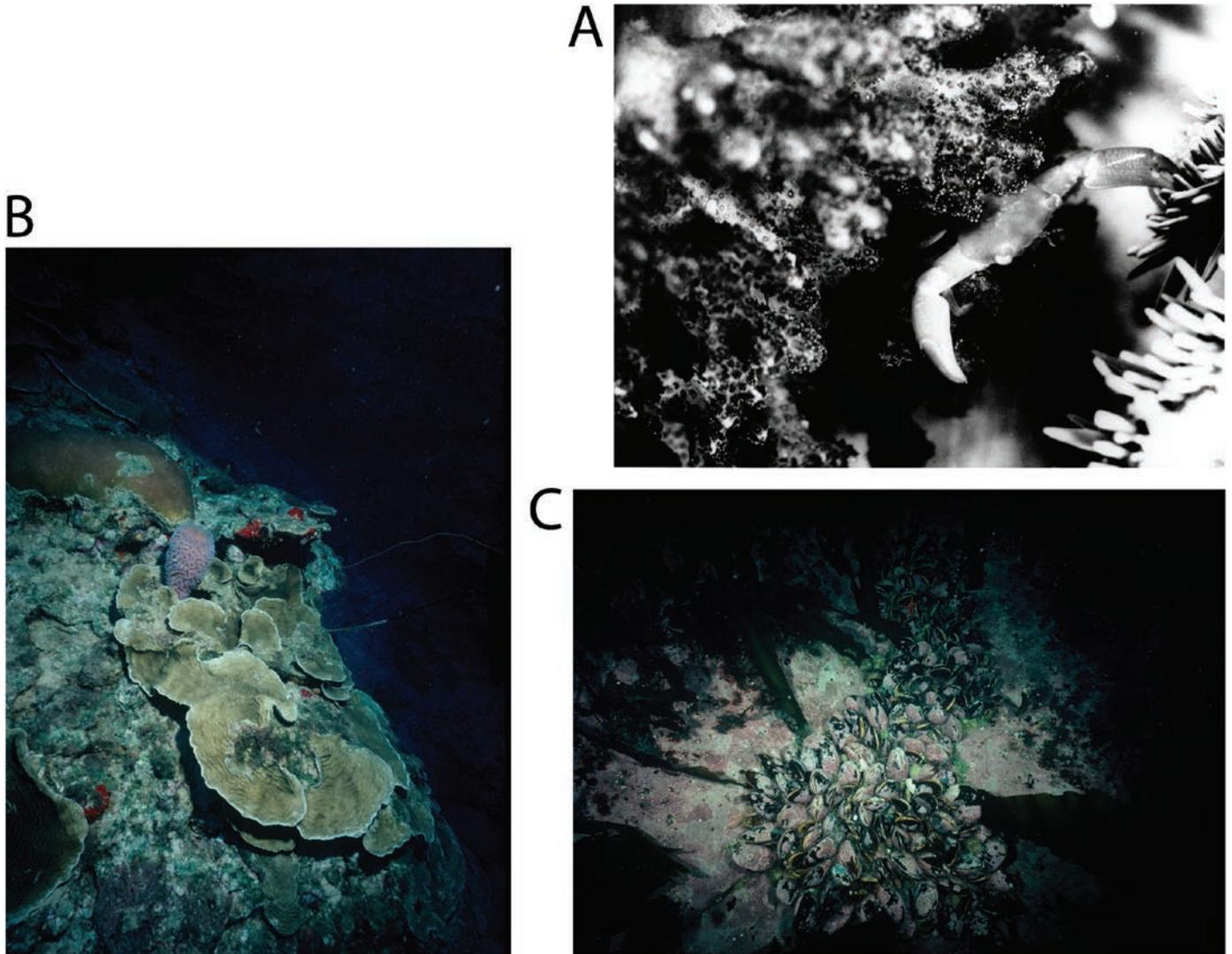


FIGURE 2. (A) *Trapezia* crab within a pocilloporid coral colony pinching a crown of thorns starfish *Acanthaster planci*, which deters it from consuming the coral. Red arrow points to chelae of *Trapezia* (photo from video by P. Glynn). (B) Foliose corals (*Agaricia* spp.) of the deep forereef slope 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.

ACKNOWLEDGMENTS

We thank Michael Lang, Susan Roberts, Phil Taylor, and Roberta Marinelli for their hard work in organizing “The

Revolution of Science through Scuba” symposium. We are grateful to the National Science Foundation (Biological Oceanography Program), the Smithsonian Institution, and the National Undersea Research Program (NOAA) for funding that made our research possible. This paper is dedicated to four outstanding pioneers in our field that inspired us and many others to do the best possible science in the ocean: Walter Adey, Peter Glynn, Jack Randall, and Bob Vadas.

REFERENCES

- Addicott, J. F. 1984. Mutualistic interactions in population and community processes. In *A new ecology: Novel approaches to interactive systems*, ed. P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, pp. 437–456. New York: John Wiley and Sons.
- Allredge, A. L., and J. M. King. 1977. Distribution, abundance and substrate preference of demersal reef zooplankton at Lizard Island lagoon, Great Barrier Reef. *Marine Biology*, 41:317–335. <http://dx.doi.org/10.1007/BF00389098>.
- Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nystrom. 2004. Confronting the coral reef crisis. *Nature*, 429:827–833. <http://dx.doi.org/10.1038/nature02691>.
- Bellwood, D. R., T. P. Hughes, and A. S. Hoey. 2006. Sleeping functional group drives coral-reef recovery. *Current Biology*, 16:2434–2439. <http://dx.doi.org/10.1016/j.cub.2006.10.030>.
- Bertness, M. D. 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. *Ecology*, 66:1042–1055. <http://dx.doi.org/10.2307/1940564>.
- Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology and Evolution*, 9:191–193. [http://dx.doi.org/10.1016/0169-5347\(94\)90088-4](http://dx.doi.org/10.1016/0169-5347(94)90088-4).
- Birkeland, C. 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *Proceedings of the Third International Coral Reef Symposium*, 1:331–336.
- Boucher, D. H., S. James, and K. H. Keeler. 1982. The ecology of mutualism. *Annual Review of Ecology and Systematics*, 13:315–347. <http://dx.doi.org/10.1146/annurev.es.13.110182.001531>.
- Brandt, M., J. D. Witman, and A. I. Chiriboga. 2012. Influence of a dominant consumer reverses at increased diversity. *Ecology*, 93:868–878.
- Bruno, J. F., J. D. Fridley, K. D. Bromberg, and M. D. Bertness. 2005. Insights into biotic interactions from studies of species invasions. In *Species invasions: Insights into ecology, evolution and biogeography*, ed. D. F. Sax, J. J. Stachowicz, and S. D. Gaines, pp. 13–40. Sunderland, Mass.: Sinauer Associates, Inc.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, 18:119–125. [http://dx.doi.org/10.1016/S0169-5347\(02\)00045-9](http://dx.doi.org/10.1016/S0169-5347(02)00045-9).
- Buss, L. W., and J. B. C. Jackson. 1979. Competitive networks: Non-transitive competitive relationships in cryptic coral reef environments. *American Naturalist*, 112:127–154.
- Butler, M., R. S. Steneck, and W. Herrnkind. 2006. The ecology of juvenile and adult lobsters. In *Lobsters: The biology, management, aquaculture and fisheries*, ed. R. Phillips, pp. 263–309. Oxford: Blackwell Publishing Ltd. <http://dx.doi.org/10.1002/9780470995969.ch8>.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, 42:710–723. <http://dx.doi.org/10.2307/1933500>.
- Darwin, C. 1909. *The Voyage of the Beagle*. The Harvard Classics, Vol. 29. New York: P.F. Collier & Son Company.
- Dayton, P. K. 1971. Competition, disturbance and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*, 41:351–389. <http://dx.doi.org/10.2307/1948498>.
- . 1973. Two cases of resource partitioning in an intertidal community: Making the right prediction for the wrong reason. *American Naturalist*, 107:662–670. <http://dx.doi.org/10.1086/282865>.
- . 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs*, 45:137–159. <http://dx.doi.org/10.2307/1942404>.
- . 2003. The importance of the natural sciences to conservation. *American Naturalist*, 162(1):1–13. <http://dx.doi.org/10.1086/376572>.
- Dayton, P. K., R. J. Rosenthal, L. C. Mahen, and T. Antezana. 1977. Population structure and foraging biology of the predaceous Chilean asteroid *Meyenaster gelatinosus* and the escape biology of its prey. *Marine Biology*, 39:361–370. <http://dx.doi.org/10.1007/BF00391939>.
- Dayton, P. K., and M. J. Tegner. 1984. The importance of scale in community ecology: A kelp forest example with terrestrial analogs. In *A new ecology: Novel approaches to interactive systems*, ed. P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, pp. 457–481. New York: John Wiley & Sons.
- Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Journal of Applied Ecology*, 8:309–322.
- Elton, C. 1927. *Animal ecology*. London: Sidgwick and Jackson, Ltd.
- Eschmeyer, W. N., R. Fricke, J. D. Fong, and D. A. Polack. 2010. Marine fish diversity: History of knowledge and discovery (Pisces). *Zootaxa*, 2525:19–50.
- Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. *Ecological Monographs*, 65:75–100. <http://dx.doi.org/10.2307/2937159>.
- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. *Science*, 185:1058–1060. <http://dx.doi.org/10.1126/science.185.4156.1058>.
- Estes, J. A., J. Terbourgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitich, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soule, R. Virtanen, D. A. Wardle. 2011. Trophic downgrading of planet Earth. *Science*, 333:301–306. <http://dx.doi.org/10.1126/science.1205106>.
- Forsman, Z. H., and C. Birkeland. 2009. *Porites randalli*: A new coral species (Scleractinia, Poritidae) from American Samoa. *Zootaxa*, 2244:51–59.
- Futuyma, D. J., and M. Slatkin. 1983. *Coevolution*. Sunderland, Mass.: Sinauer Associates, Inc.
- Glynn, P. 1976. Some physical and biological determinants of coral community structure in the Eastern Pacific. *Ecological Monographs*, 45:431–456. <http://dx.doi.org/10.2307/1942565>.
- Grabowski, J. H., A. R. Hughes, and D. L. Kimbro. 2008. Habitat complexity influences cascading effects of multiple predators. *Ecology*, 89:3413–3422. <http://dx.doi.org/10.1890/07-1057.1>.
- Grabowski, J. H., and D. L. Kimbro. 2005. Predator-avoidance behavior extends trophic cascades to refuge habitats. *Ecology*, 86:1312–1319. <http://dx.doi.org/10.1890/04-1216>.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control and competition. *American Naturalist*, 94:421–425. <http://dx.doi.org/10.1086/282146>.
- Hamner, W. M., and J. H. Carleton. 1979. Copepod swarms: attributes and role in coral reef ecosystems. *Limnology and Oceanography*, 24:1–14. <http://dx.doi.org/10.4319/lo.1979.24.1.0001>.
- Hamner, W. M., L. P. Madin, A. L. Alldredge, R. W. Gilmer, and P. P. Hamner. 1975. Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology and behavior. *Limnology and Oceanography*, 20:907–917. <http://dx.doi.org/10.4319/lo.1975.20.6.0907>.
- Hixon, M. A. 1997. Effects of reef fishes on corals and algae. In *Life and death of coral reefs*, ed. C. Birkeland, pp. 230–248. New York: Chapman and Hall. http://dx.doi.org/10.1007/978-1-4615-5995-5_10.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia: Or, why are there so many kinds of animals? *American Naturalist*, 93:145–159. <http://dx.doi.org/10.1086/282070>.
- Jayawardene, D., M. J. Donahue, and C. Birkeland. 2009. Effects of frequent fish predation on corals in Hawaii. *Coral Reefs*, 28:499–506. <http://dx.doi.org/10.1007/s00338-009-0475-y>.
- Jennings, S., and N. V. C. Polunin. 1995. Biased underwater visual census biomass estimates for target-species in tropical reef fisheries. *Journal of Fisheries Biology*, 47:733–736. <http://dx.doi.org/10.1111/j.1095-8649.1995.tb01938.x>.
- Johnson, D. S., and A. F. Skutch. 1928. Littoral vegetation on a headland of Mt. Desert Island, Maine. I. Submersible or strictly littoral vegetation. *Ecology*, 9:188–215. <http://dx.doi.org/10.2307/1929354>.
- Jones, C. G., J. H. Lawton, and M. Shackak. 1994. Organisms as ecosystem engineers. *Oikos*, 69:373–386. <http://dx.doi.org/10.2307/3545850>.
- Lang, J. C. 1973. Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. *Bulletin of Marine Science*, 23:260–279.

- Leonard, G., P. Ewanchuk, and M. D. Bertness. 1999. How recruitment, interspecific interactions and predation control species borders in a tidal estuary. *Oecologia*, 118:492–502. <http://dx.doi.org/10.1007/s004420050752>.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology*, 23:399–418. <http://dx.doi.org/10.2307/1930126>.
- Mauzey, K. P., C. Birkeland, and P. K. Dayton. 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound Region. *Ecology*, 49:603–619. <http://dx.doi.org/10.2307/1935526>.
- May, R. M. 1981. Patterns in multi-species communities. In *Theoretical ecology: Principles and applications*, 2nd ed., pp. 197–227. Sunderland, Mass.: Sinauer Associates, Inc.
- McClanahan, T. R., N. A. Muthiga, A. T. Kamukuru, H. Machano, and R. Kiambo. 1999. The effect of fishing and marine protected areas on the coral reefs of northern Tanzania. *Biological Conservation*, 89:161–182. [http://dx.doi.org/10.1016/S0006-3207\(98\)00123-2](http://dx.doi.org/10.1016/S0006-3207(98)00123-2).
- Moody, K., and R. S. Steneck. 1993. Mechanisms of predation among large decapod crustaceans of the Gulf of Maine coast: Functional versus phylogenetic patterns. *Journal of Experimental Marine Biology and Ecology*, 168:111–124. [http://dx.doi.org/10.1016/0022-0981\(93\)90118-8](http://dx.doi.org/10.1016/0022-0981(93)90118-8).
- Ong, L. 2007. The ecological importance of parrotfish as bioeroders and sediment producers in Hawaii and their conservation within small marine protected areas. Ph.D. diss., University of Hawaii at Manoa, Honolulu.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist*, 100:65–75. <http://dx.doi.org/10.1086/282400>.
- Palma, A. T., R. S. Steneck, and C. Wilson. 1999. Settlement-driven, multiscale demographic patterns of large benthic decapods in the Gulf of Maine. *Journal of Experimental Marine Biology and Ecology*, 241:107–136. [http://dx.doi.org/10.1016/S0022-0981\(99\)00069-6](http://dx.doi.org/10.1016/S0022-0981(99)00069-6).
- Peckarsky, B. L., P. A. Abrams, D. I. Bolnick. 2008. Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator–prey interactions. *Ecology*, 89:2416–2425. <http://dx.doi.org/10.1890/07-1131.1>.
- Popper, K. R. 1959. *The logic of scientific discovery*. London: Hutchinson and Co.
- Porter, J. W., and K. G. Porter. 1977. Quantitative sampling of demersal plankton migrating from different coral reef substrates. *Limnology and Oceanography*, 22:553–556. <http://dx.doi.org/10.4319/lo.1977.22.3.0553>.
- Power, M. E. 1992. Top-down and bottom-up forces in food webs: Do plants have primacy? *Ecology*, 73:733–746. <http://dx.doi.org/10.2307/1940153>.
- Randall, J. E. 1965. Grazing effects on sea grasses by herbivorous reef fishes in the West Indies. *Ecology*, 46:255–260. <http://dx.doi.org/10.2307/1936328>.
- Sala, O. E. 2001. Price put on biodiversity. *Nature*, 412:34–36. <http://dx.doi.org/10.1038/35083676>.
- Sandin, S. A., S. M. Walsh, and J. B. C. Jackson. 2010. Prey release, trophic cascades, and phase shifts in tropical nearshore marine ecosystems. In *Trophic cascades: Predators, prey, and the changing dynamics of nature*, ed. J. Terborgh and J. A. Estes, pp. 71–90. Washington, DC: Island Press.
- Siddon, C. E., and J. D. Witman. 2004. Behavioral indirect interactions: Multiple predator effects and prey switching in the shallow rocky subtidal. *Ecology*, 85:2398–2945. <http://dx.doi.org/10.1890/03-0519>.
- Steneck, R. S. 2006a. Is the American lobster *Homarus americanus* overfished? A review of overfishing with an ecologically-based perspective. *Bulletin of Marine Science*, 78:607–632.
- . 2006b. Possible demographic consequences to intraspecific shelter competition among American lobsters. *Journal of Crustacean Biology*, 26:628–638. <http://dx.doi.org/10.1651/S-2753.1>.
- Steneck, R. S., and M. N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. *Oikos*, 69:476–498. <http://dx.doi.org/10.2307/3545860>.
- Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J. Tegner. 2002. Kelp forest ecosystem: Biodiversity, stability, resilience and their future. *Environmental Conservation*, 29:436–459. <http://dx.doi.org/10.1017/S0376892902000322>.
- Steneck, R. S., and L. Watling. 1982. Feeding capabilities and limitations of herbivorous molluscs: A functional group approach. *Marine Biology*, 68:299–319. <http://dx.doi.org/10.1007/BF00409596>.
- Steneck, R. S., and C. J. Wilson. 2001. Long-term and large scale spatial and temporal patterns in demography and landings of the American lobster, *Homarus americanus*, in Maine. *Journal of Marine and Freshwater Research*, 52:1302–1319. <http://dx.doi.org/10.1071/MF01173>.
- Thomsen, M. S., A. Altieri, B. Wernberg, F. Tuya, D. Gulbransen, K. McGlathery, M. Holmer, and B. R. Silliman. 2010. Habitat cascades: The conceptual context and global relevance of facilitation cascades via habitat formation and modification. *Integrative and Comparative Biology*, 50:158–175. <http://dx.doi.org/10.1093/icb/icq042>.
- Thorson, G. 1957. Bottom communities (sublittoral or shallow shelf). In *Treatise on marine ecology and paleoecology*, ed. J. W. Hedgpeth and H. S. Ladd, pp. 461–534. Geological Society of America, Memoirs 67. Baltimore: Waverly Press.
- . 1971. *Life in the sea*. New York: McGraw-Hill.
- Tittensor, D. P., B. Worm, and R. A. Myers. 2009. Macroecological changes in exploited marine ecosystems. In *Marine macroecology*, ed. J. D. Witman and K. Roy, pp. 310–337. Chicago: University of Chicago Press. <http://dx.doi.org/10.7208/chicago/9780226904146.003.0012>.
- Vermeij, G. J. 1983. Intimate associations and coevolution in the sea. In *Coevolution*, ed. D. J. Futuyma and M. Slatkin, pp. 311–327. Sunderland, Mass.: Sinauer Associates, Inc.
- Wahle, R. A., and R. S. Steneck. 1991. Recruitment habitats and nursery grounds of the American lobster (*Homarus americanus* Milne Edwards): A demographic bottleneck? *Marine Ecology Progress Series*, 69:231–243. <http://dx.doi.org/10.3354/meps069231>.
- . 1992. Habitat restrictions in early benthic life: Experiments on habitat selection and in situ predation with the American lobster. *Journal of Experimental Marine Biology and Ecology*, 157:91–114. [http://dx.doi.org/10.1016/0022-0981\(92\)90077-N](http://dx.doi.org/10.1016/0022-0981(92)90077-N).
- Wallace, A. R. 1858. On the tendency of varieties to depart indefinitely from the original type. *Journal of the Proceedings of the Linnean Society (Zoology)*, 3:53–62.
- Wells, R. J. D., R. S. Steneck, and A. T. Palma. 2010. Three-dimensional resource partitioning between American lobster (*Homarus americanus*) and rock crab (*Cancer irroratus*) in a subtidal kelp forest. *Journal of Experimental Marine Biology and Ecology*, <http://dx.doi.org/10.1016/j.jembe.2010.01.008>.
- Witman, J. D. 1985. Refuges, biological disturbance, and rocky subtidal community structure in New England. *Ecological Monographs*, 55:421–445. <http://dx.doi.org/10.2307/2937130>.
- . 1987. Subtidal coexistence: Storms, grazing, mutualism, and the zonation of kelps and mussels. *Ecological Monographs*, 57:167–187. <http://dx.doi.org/10.2307/1942623>.
- Witman, J. D., and P. K. Dayton. 2001. Rocky subtidal communities. In *Marine community ecology*, ed. M. D. Bertness, S. D. Gaines, and M. Hay, pp. 339–366. Sunderland, Mass.: Sinauer Associates, Inc.
- Witman, J. D., and K. Roy. 2009. Experimental marine macroecology. In *Marine macroecology*, ed. J. D. Witman and K. Roy, pp. 341–356. Chicago: University of Chicago Press. <http://dx.doi.org/10.7208/chicago/9780226904146.003.0013>.
- Witman, J. D., and K. D. Sebens. 1992. Regional variation in fish predation intensity: A historical perspective in the Gulf of Maine. *Oecologia*, 90:305–315. <http://dx.doi.org/10.1007/BF00317686>.
- Wulff, J. L., and L. W. Buss. 1979. Do sponges help hold coral reefs together? *Nature*, 281:474–475. <http://dx.doi.org/10.1038/281474a0>.