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

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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,

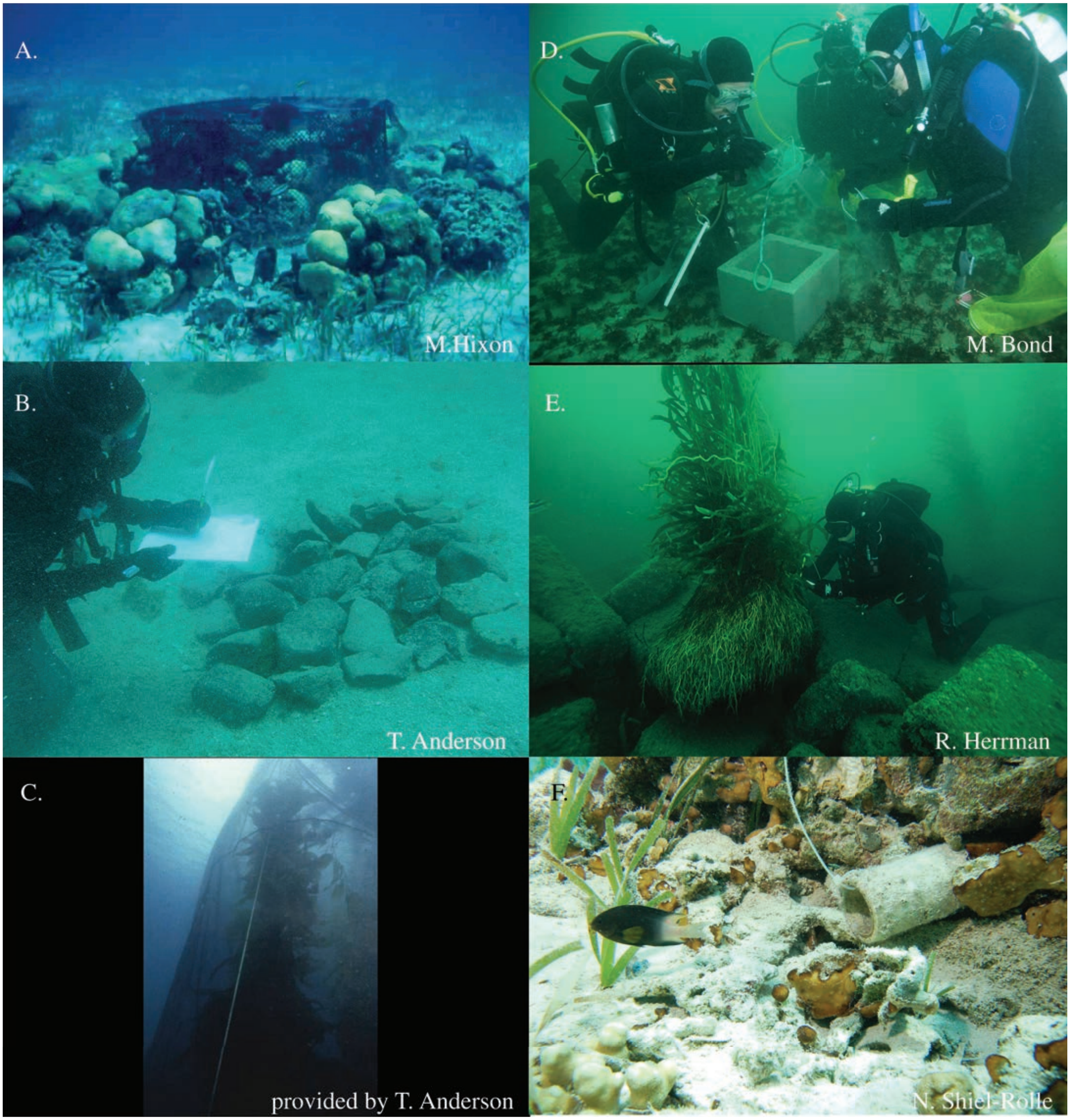

FIGURE 1. Habitat manipulations to create independent isolated experimental treatment levels (e.g., density levels, refuge availability) from natural substrata: (A) corals, (B) rock, (C) kelps; and artificial substrata: (D) cinder blocks, (E) concrete rubble, (F) tubes. (Photo credits given in each image.)

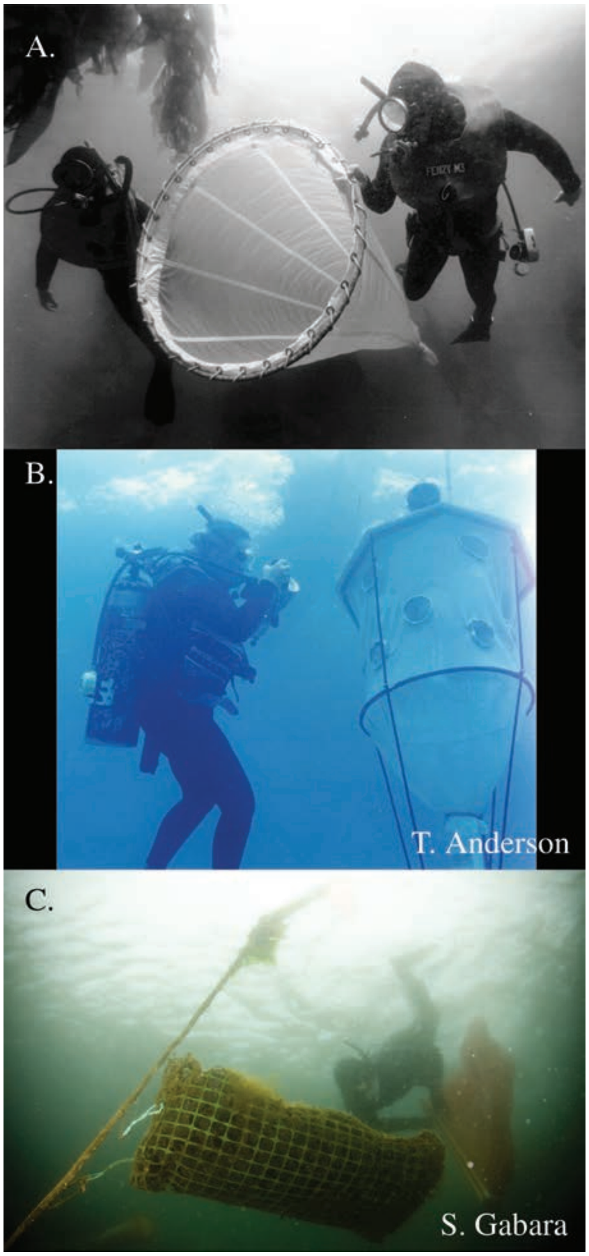

FIGURE 2. Devices for collecting larvae using scuba. (A) Plankton nets, (B) light traps, and (C) SMURFs (see text). (Photo credits: A, reprinted from Hobson and Chess, 1976; B, C, as given in each image.)

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.

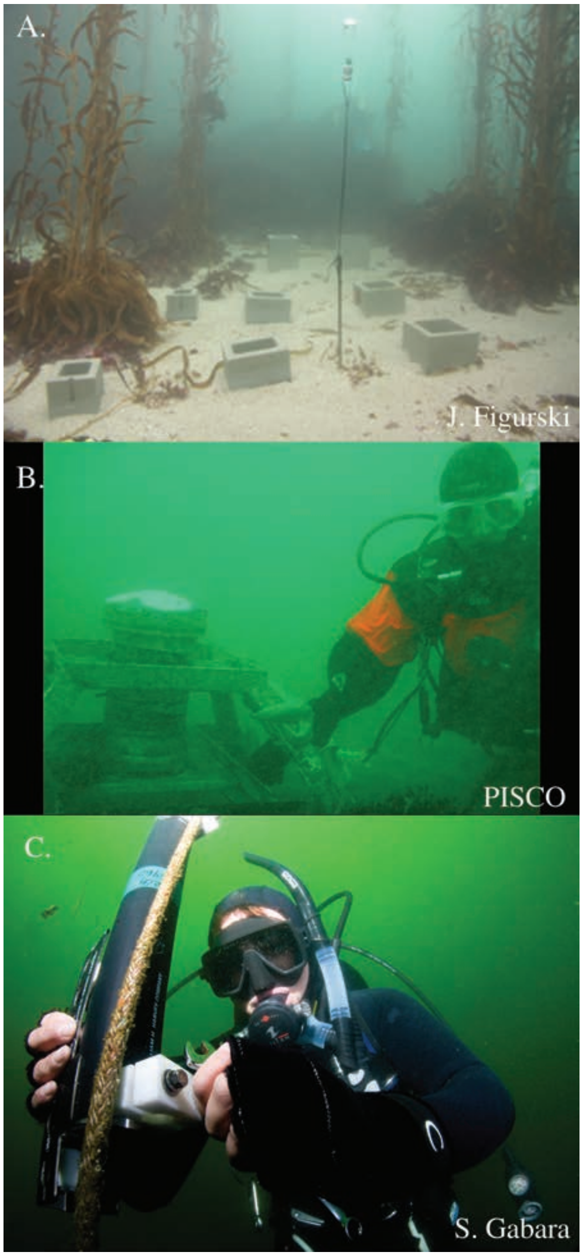

FIGURE 3. Deployment and maintenance of oceanographic instruments using scuba. (A) Swell gauges, (B) current meters, and (C) thermistors. (Photo credits given in each image.)

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

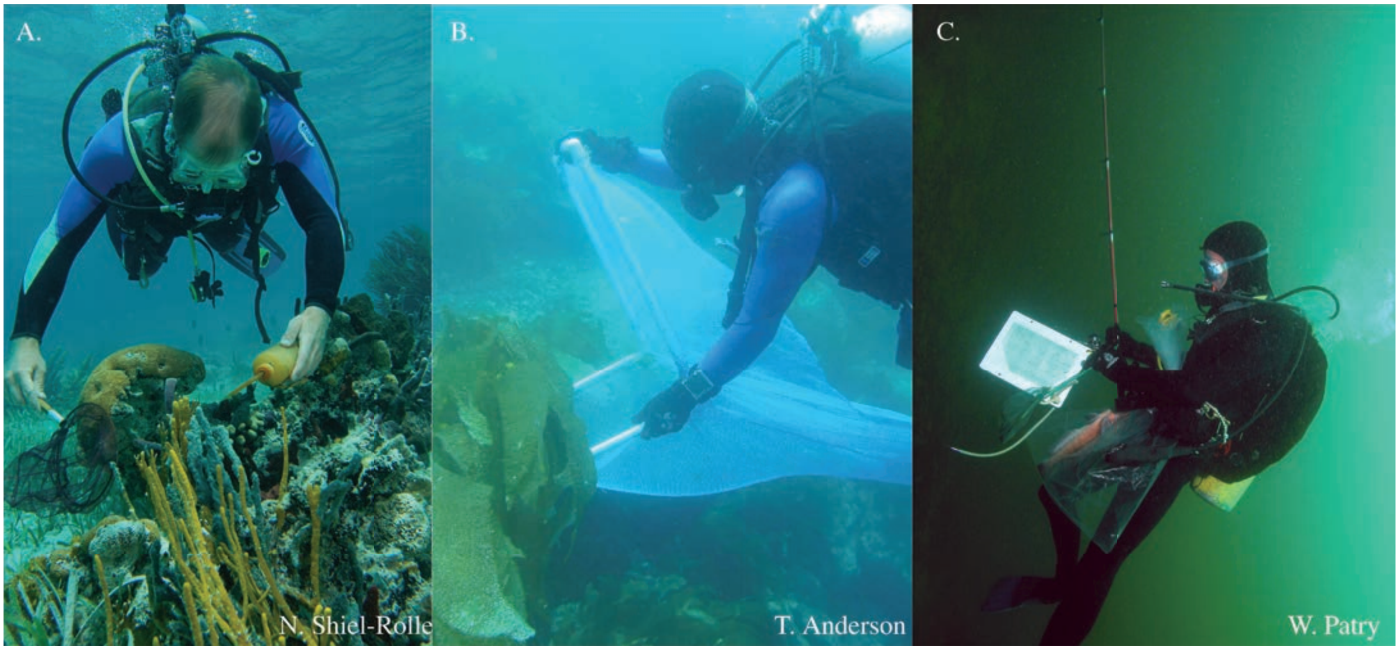

FIGURE 4. Methods for collecting reef fish using scuba. (A) Hand-netting while using anesthesia (clove oil), (B) BINCKE (Benthic Ichthyofauna Net for Coral / Kelp Environments), and (C) hook and line. (Photo credits given in each image.)

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).

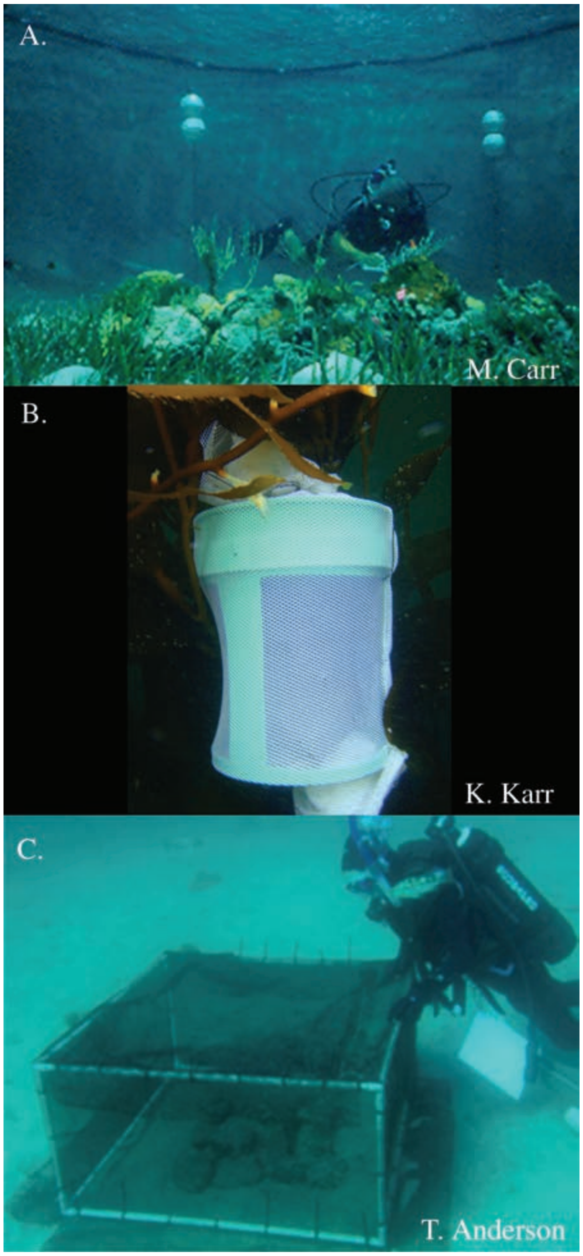

FIGURE 5. Predator exclusion cages used to study the role of predation in structuring communities. (A) Netting surrounding a patch reef to exclude piscivorous reef fish, (B) enclosure placed in the *Macrocystis* canopy to enclose juvenile rockfish (*Sebastes* sp.) and exclude their predators, and (C) 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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