

Behavioral Ecology of Mobile Animals: Insights from In Situ Observations

David B. Eggleston, William F. Herrnkind, and Anson H. Hines

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.

David B. Eggleston, North Carolina State University, Department of Marine, Earth and Atmospheric Sciences, Raleigh, North Carolina 27695-8208, USA. *William F. Herrnkind*, Florida State University, Department of Biological Science, Tallahassee, Florida 32306, USA. *Anson H. Hines*, Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, Maryland 21037, USA. **Correspondence:** D. Eggleston, eggleston@ncsu.edu.

Manuscript received 25 January 2012; accepted 5 March 2013.

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]).

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.

These scuba observations of spiny lobster migratory behavior, first described in the scientific literature by Herrnkind



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.

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 semi-field 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 non-gravid 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

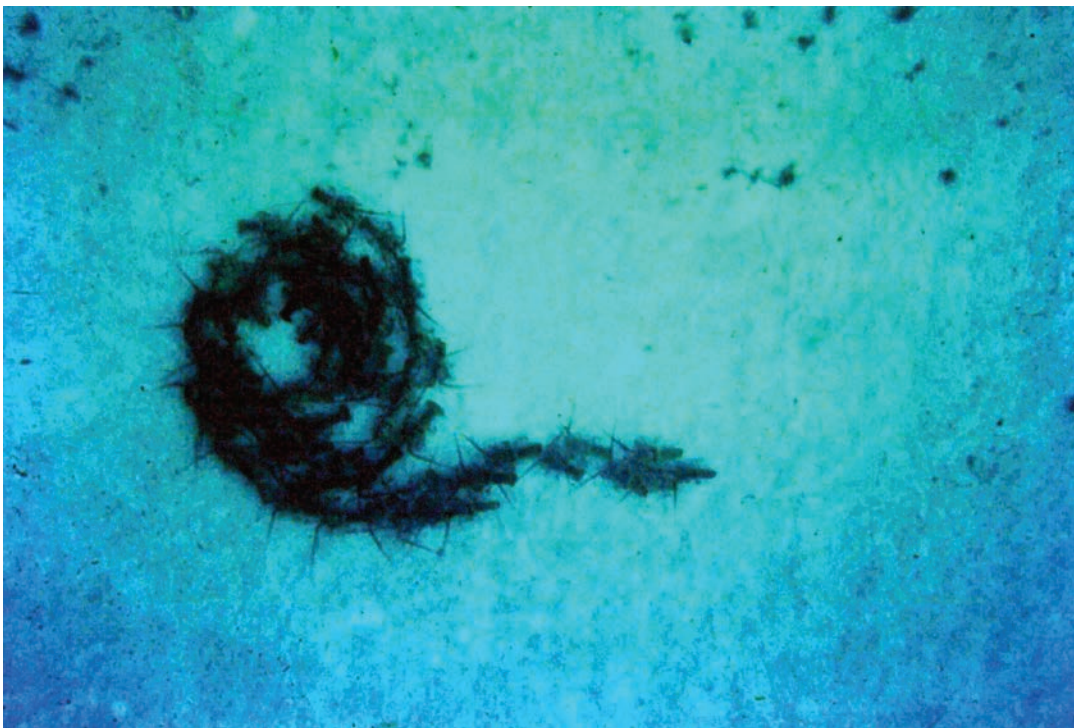


FIGURE 2. When threatened by predators (a descending diver in this case), a queue winds around the pirouetting lead lobster, quickly forming a stationary pod, all members directing their defensive antennae outward to confront attackers. Photo by W. Herrnkind.

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 capricus*) against tethered lobsters in the field, as well as against free-moving lobsters in large, seminatural enclosures (~40 m²) (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/m²) 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. foliatus* 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

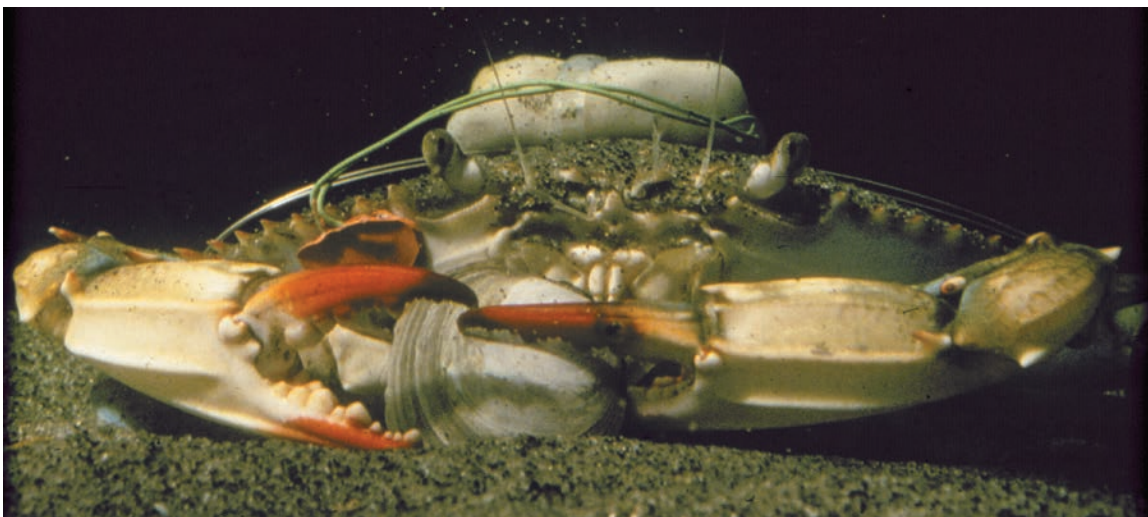


FIGURE 3. Biotelemetry tag attached to blue crab (*Callinectes sapidus*) eating a clam prey item. Photo by A. Hines.

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



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

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).

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

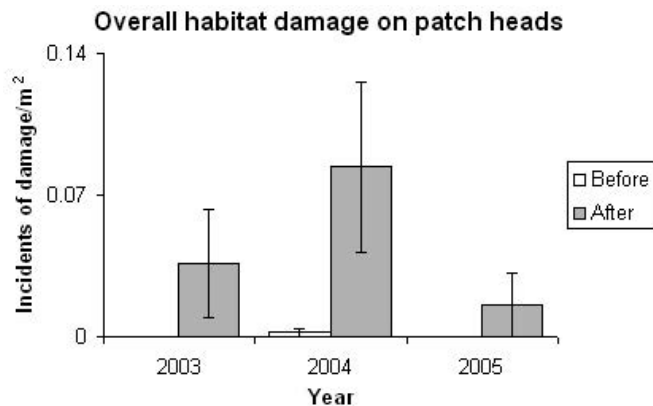


FIGURE 5. Incidents of habitat damage (e.g., broken corals and sponges, obvious anchor damage) per square meter from before and after the two-day mini-season for *P. argus* on patch coral heads in the lower Florida Keys during 2003–2005 (D. Eggleston, unpublished data).

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.

ACKNOWLEDGMENTS

We thank Michael Lang for his leadership in organizing the Smithsonian Scientific Diving Symposium, and his patience in serving as coeditor of these proceedings. We also thank several anonymous referees for reviews of a previous draft of this paper, and the Smithsonian Institution for sponsoring the Scientific Diving Symposium and these proceedings.

REFERENCES

- Albins, M. A., and M. A. Hixon. 2008. Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress Series*, 367:233–238. <http://dx.doi.org/10.3354/meps07620>.
- Alonzo, S. H., and R. R. Warner. 2000. Dynamic games and field experiments examining intra- and intersexual conflict: explaining counterintuitive mating behavior in a Mediterranean wrasse, *Symphodus ocellatus*. *Behavioral Ecology*, 11:56–70. <http://dx.doi.org/10.1093/beheco/11.1.56>.
- Anderson, M. B. 1994. *Sexual selection*. Princeton, N. J.: Princeton University Press.
- Appeldoorn, R. S. 1994. Spatial variability in the morphology of queen conch and its implication for management regulations. In *Queen conch biology, fisheries and management*, ed. R. S. Appeldoorn, and B. Rodriguez, pp. 145–158. Caracas: Fundación Científica Los Roques.
- Begon, M., C. R. Townsend, and J. L. Harper. 2005. *Ecology: From individuals to ecosystems*. 4th ed. Oxford: Blackwell Publishing.
- Behringer, D. C. 2003. The ecological ramifications of density and disease in the Caribbean spiny lobster *Panulirus argus*. Ph.D. diss., Norfolk, Va.: Old Dominion University.
- Bell, G. W., D. B. Eggleston, and T. G. Wolcott. 2003a. Behavioral responses of free-ranging blue crabs to episodic hypoxia. I. Movement. *Marine Ecology Progress Series*, 259:215–225. <http://dx.doi.org/10.3354/meps259215>.
- . 2003b. Behavioral responses of free-ranging blue crabs to episodic hypoxia. II. Feeding. *Marine Ecology Progress Series*, 259:227–235. <http://dx.doi.org/10.3354/meps259227>.
- Bellingham, J. G., and K. Rajan. 2007. Robotics in remote and hostile environments. *Science*, 318: 1098–1102. <http://dx.doi.org/10.1126/science.1146230>.
- Bill, R., and W. F. Herrnkind. 1976. Drag reduction by formation movement in spiny lobster. *Science*, 193:1146–1148. <http://dx.doi.org/10.1126/science.193.4258.1146>.
- Bouwma, P. E. 2006. Aspects of antipredation in *Panulirus argus* and *Panulirus guttatus*: Behavior, morphology, and ontogeny. Ph.D. diss., Florida State University, Tallahassee.
- Bricker, S., B. Longstaff, W. Dennison, A. Jones, K. Boicourt, C. Wicks, and J. Woerner. 2007. *Effects of nutrient enrichment in the nation’s estuaries: A decade of change*. NOAA Coastal Ocean Program Decision Analysis Series, No. 26.

- Silver Spring, Md.: National Centers for Coastal Ocean Science. <http://ccma.nos.noaa.gov/publications/eutroupdate/>.
- Butler, M. J., A. B. MacDiarmid, and J. D. Booth. 1999. The cause and consequence of ontogenetic changes in social aggregation in New Zealand spiny lobsters. *Marine Ecology Progress Series*, 188:179–191. <http://dx.doi.org/10.3354/meps188179>.
- Butler, M. J., R. S. Steneck, and W. F. Herrnkind. 2006. Juvenile and adult ecology. In *Lobsters: Biology, management, aquaculture and fisheries*, ed. B. Phillips, pp. 263–309. Oxford: Blackwell Scientific Press. <http://dx.doi.org/10.1002/9780470995969.ch8>.
- Carpenter, S. R., K. L. Cottingham, and C. A. Stow. 1994. Fitting predator–prey models to time series with observation errors. *Ecology*, 75:1254–1264.
- Childress, M. J., and W. F. Herrnkind. 1997. Den sharing by juvenile Caribbean spiny lobsters (*Panulirus argus*) in nursery habitat: cooperation or coincidence? *Marine and Freshwater Research*, 48:751–758.
- . 2001. The guide effect influence on the gregariousness of juvenile Caribbean spiny lobsters. *Animal Behavior*, 62:465–472. <http://dx.doi.org/10.1006/anbe.2001.1760>.
- Clark, M. E., T. G. Wolcott, and A. H. Hines. 1999a. Foraging and agonistic activity co-occur in free-ranging blue crabs (*Callinectes sapidus*): Observations of animals by ultrasonic biotelemetry. *Journal of Experimental Marine Biology and Ecology*, 233:143–160. [http://dx.doi.org/10.1016/S0022-0981\(98\)00129-4](http://dx.doi.org/10.1016/S0022-0981(98)00129-4).
- . 1999b. Intraspecific interference among foraging blue crabs *Callinectes sapidus*: Interference effects of predator density and prey patch distribution. *Marine Ecology Progress Series*, 178:69–78. <http://dx.doi.org/10.3354/meps178069>.
- Clark, M. E., T. G. Wolcott, D. L. Wolcott, and A. H. Hines. 2000. Foraging behavior of an estuarine predator, the blue crab *Callinectes sapidus* in a patchy environment. *Ecography*, 23:21–31. <http://dx.doi.org/10.1111/j.1600-0587.2000.tb00257.x>.
- Clifton, H. E., C. Mahnken, J. Van Derwalker, and R. Waller. 1970. Tektite I. Man-in-the-sea project: Marine science program. *Science*, 168: 659–663. <http://dx.doi.org/10.1126/science.168.3932.659>.
- Cohen, D. M. 1977. Swimming performance of the gadoid fish *Antimora rostrata* at 2400 m. *Deep Sea Research*, 24:275–277. [http://dx.doi.org/10.1016/S0146-6291\(77\)80006-4](http://dx.doi.org/10.1016/S0146-6291(77)80006-4).
- Coleman, D. C., D. A. Crossley, Jr., and P. F. Hendrix. 2004. *Fundamentals of Soil Ecology*, 2nd ed. Burlington, Mass.: Elsevier Academic Press.
- Colin, P. L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environmental Biology of Fishes*, 34:357–377.
- Cooper, W. E., and W. G. Frederick. 2010. Predator lethality, optimal escape behavior, and autotomy. *Behavioral Ecology*, 21:91–96. <http://dx.doi.org/10.1093/beheco/arp151>.
- Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution*, 14:405–410. [http://dx.doi.org/10.1016/S0169-5347\(99\)01683-3](http://dx.doi.org/10.1016/S0169-5347(99)01683-3).
- Crawley, M. J. 1986. The population biology of invaders. *Philosophical Transactions of the Royal Society of London, B*: 314:711–731. <http://dx.doi.org/10.1098/rstb.1986.0082>.
- Dahlgren, C. P., and D. B. Eggleston. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology*, 8:2227–2240. [http://dx.doi.org/10.1890/0012-9658\(2000\)081\[2227:EPUOHS\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2000)081[2227:EPUOHS]2.0.CO;2).
- Davis, G. E. 1981. Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management. *U.S. National Marine Fisheries Service Fishery Bulletin*, 78:979–984.
- Davis, J. L. D., A. C. Young-Williams, R. Aguilar, B. L. Carswell, M. R. Goodison, A. H. Hines, M. A. Kramer, Y. Zohar, and O. Zmora. 2004a. Differences between hatchery-raised and wild blue crabs (*Callinectes sapidus*): Implications for stock enhancement potential. *Transactions of the American Fisheries Society*, 133:1–14. <http://dx.doi.org/10.1577/T03-004>.
- Davis, J. L. D., A. C. Young-Williams, A. H. Hines, and O. Zmora. 2004b. Fishery and population studies: Comparing two types of internal tags in juvenile blue crabs. *Fisheries Research*, 67:265–274. <http://dx.doi.org/10.1016/j.fishres.2003.11.005>.
- Dittel, A. I., A. H. Hines, G. M. Ruiz, and K. K. Ruffin. 1995. Effects of shallow water refuge on behavior and density-dependent mortality of juvenile blue crabs in Chesapeake Bay. *Bulletin of Marine Science*, 57:903–917.
- Dixson, D. L., P. L. Munday, and G. P. Jones. 2010. Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecology Letters*, 13:68–75. <http://dx.doi.org/10.1111/j.1461-0248.2009.01400.x>.
- Drazen, J. C., S. K. Goffredi, B. Schlining, and D. S. Stakes. 2003. Aggregations of deep-sea brooding fish and cephalopods on the Gorda escarpment: A reproductive hotspot. *Biological Bulletin*, 205:1–7. <http://dx.doi.org/10.2307/1543439>.
- Eggleston, D. B. 1995. Recruitment in Nassau Grouper, *Epinephelus striatus*: Post settlement abundance, microhabitat features, and ontogenetic habitat shifts. *Marine Ecology Progress Series*, 124:9–22. <http://dx.doi.org/10.3354/meps124009>.
- Eggleston, D. B., E. G. Johnson, G. T. Kellison, and D. A. Nadeau. 2003. Intense removal and non-saturating functional responses by recreational divers on spiny lobster *Panulirus argus*. *Marine Ecology Progress Series*, 257:197–203. <http://dx.doi.org/10.3354/meps257197>.
- Eggleston, D. B., and R. N. Lipcius. 1992. Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. *Ecology*, 73:992–1011. <http://dx.doi.org/10.2307/1940175>.
- Eggleston, D. B., R. N. Lipcius, L. Coba-Centina, and D. Miller. 1990. Shelter scaling regulates survival of juvenile spiny lobster, *Panulirus argus*. *Marine Ecology Progress Series*, 62:79–88. <http://dx.doi.org/10.3354/meps062079>.
- Eggleston, D. B., and C. P. Dahlgren. 2001. Distribution and abundance of Caribbean spiny lobsters in the Key West National Wildlife Refuge: relationship to habitat features and impact of an intensive recreational fishery. *Marine and Freshwater Research*, 52:1567–1576.
- Eggleston, D. B., and D. M. Parsons. 2008. Disturbance-induced spill-in of Caribbean spiny lobster to marine reserves. *Marine Ecology Progress Series*, 371: 213–220. <http://dx.doi.org/10.3354/meps07699>.
- Eggleston, D. B., D. M. Parsons, G. T. Kellison, G. R. Plaia, and E. G. Johnson. 2008. Functional response of sport divers to lobsters with application to fisheries management. *Ecological Applications*, 18:258–272. <http://dx.doi.org/10.1890/06-1409.1>.
- Ehrhardt, N. M., and V. Deleveaux. 1999. *Report on the 1999 Nassau grouper stock assessment in the Bahamas*. Miami: University of Miami.
- Etherington, L. L., and D. B. Eggleston. 2003. Spatial dynamics of large-scale, multi-stage crab dispersal: Determinants and consequences for recruitment. *Canadian Journal of Fisheries and Aquatic Sciences*, 60:873–887. <http://dx.doi.org/10.1139/f03-072>.
- Finn, J. K., T. Tregenza, and M. D. Norman. 2009. Defensive tool use in a coconut carrying octopus. *Current Biology*, 19: R1069–R1070. <http://dx.doi.org/10.1016/j.cub.2009.10.052>.
- Gebruk, A. V., E. C. Southworth, H. Kennedy, and A. J. Southward. 2000. Food sources, behavior and distribution of hydrothermal vent shrimps at the Mid-Atlantic Ridge. *Journal of the Marine Biological Association of the U.K.*, 80:485–499. <http://dx.doi.org/10.1017/S0025315400002186>.
- Gillanders, B. M., K. W. Abel, J. A. Brown, D. B. Eggleston, and P. F. Sheridan. 2003. Evidence for connectivity between juvenile and adult habitat for mobile marine fauna: Important component of nurseries. *Marine Ecology Progress Series*, 247:281–295. <http://dx.doi.org/10.3354/meps247281>.
- Haaker, P. L., D. O. Parker, K. C. Barsky, and C. S. Y. Chun. 1998. Growth of red abalone, *Haliotis rufescens* (Swainson), at Johnsons Lee, Santa Rosa Island, California. *Journal of Shellfish Research*, 17:747–753.
- Hamner, W. M., and B. H. Robison. 1992. *In situ* observations of giant appendicularians on Monterey Bay. *Deep Sea Research*, 39:1299–1313. [http://dx.doi.org/10.1016/0198-0149\(92\)90070-A](http://dx.doi.org/10.1016/0198-0149(92)90070-A).
- Hansell, M., and G. D. Ruxton. 2008. Setting tool use within the context of animal construction behaviour. *Trends in Ecology and Evolution*, 23:73–78. <http://dx.doi.org/10.1016/j.tree.2007.10.006>.
- Hargeby, H., G. Andersson, I. Blindow, and S. Johansson. 1994. Trophic web structure in a shallow eutrophic lake during a dominance shift from phytoplankton to submerged macrophytes. *Hydrobiologia*, 279/280:83–90. <http://dx.doi.org/10.1007/BF00027843>.
- Heatwole, H., and R. Levins. 1972. Trophic structure stability and faunal change during recolonization. *Ecology*, 53:531–534. <http://dx.doi.org/10.2307/1934248>.
- Herrnkind, W. F. 1969. Queuing behavior of spiny lobsters. *Science*, 164:1425–1427. <http://dx.doi.org/10.1126/science.164.3886.1425>.
- . 1974. *In situ* approach to marine behavioral research. In *Experimental marine biology*, ed. R. Mariscal, pp. 55–98. New York: Academic Press.
- . 1980. Movement patterns in palinurid lobsters. In *The Biology and Management of Lobsters: Volume 1: Physiology and Behavior*, ed. J. Cobb and B. Phillips, pp. 349–407. New York: Academic Press.
- . 1983. Movement patterns and orientation of Crustacea. In *Biology of Crustacea: Volume 5: Behavior and Ecology of Crustacea*, ed. F. Vernberg and W. Vernberg, pp. 41–105. New York: Academic Press.

- . 1985. Evolution and mechanisms of mass single-file migration in spiny lobster: Synopsis. *Contributions to Marine Science*, 27:197–211.
- Herrnkind, W. F., M. J. Childress, and K. L. Lavalli. 2001. Defense coordination and other benefits among exposed spiny lobsters: Inferences from mass migratory and mesocosm studies of group size and behavior. *Marine and Freshwater Research*, 52:1113–1124. <http://dx.doi.org/10.1071/MF01044>.
- Herrnkind, W. F., and W. C. Cummings. 1964. Single file migrations of spiny lobster, *Panulirus argus* (Latreille). *Bulletin of Marine Science of the Gulf and Caribbean*, 14(1):123–125.
- Herrnkind, W. F., and R. McLean. 1971. Field studies of orientation, homing, and mass emigration in the spiny lobster, *Panulirus argus*. *Annals of the New York Academy of Sciences*, 188:359–377. <http://dx.doi.org/10.1111/j.1749-6632.1971.tb13109.x>.
- Herrnkind, W. F., J. Vanderwalker, and L. Barr. 1975. Population dynamics, ecology and behavior of spiny lobster, *Panulirus argus*, of St. John, U.S. Virgin Islands: Habitation and pattern of movements. Results of the TEKTITE Program, Volume 2. *Bulletin of the Natural History Museum of Los Angeles County*, 20:31–45.
- Hilborn, R., and C. J. Walters. 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. New York: Chapman and Hall.
- Hines, A. H. 1982. Coexistence in a kelp forest: Size, population dynamics, and resource partitioning in a guild of spider crabs. *Ecological Monographs*, 52:179–198. <http://dx.doi.org/10.2307/1942610>.
- . 2007. Ecology of juvenile and adult blue crabs. In *The Blue Crab* *Callinectes sapidus*, ed. V. S. Kennedy and L. E. Cronin, pp. 565–654. College Park, Md.: Maryland Sea Grant College, Publication UM-SG-TS-2007-01.
- Hines, A. H., A. M. Haddon, and L. A. Wiechert. 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Marine Ecology Progress Series*, 67:105–126. <http://dx.doi.org/10.3354/meps067105>.
- Hines, A. H., W. C. Long, J. R. Terwin, and S. F. Thrush. 2009. Facilitation, interference, and scale: The spatial distribution of prey patches affects predation rates in an estuarine benthic community. *Marine Ecology Progress Series*, 385:127–135. <http://dx.doi.org/10.3354/meps08055>.
- Hines, A. H., and G. M. Ruiz. 1995. Temporal variation in juvenile blue crab mortality: Nearshore shallows and cannibalism in Chesapeake Bay. *Bulletin of Marine Science*, 57:884–901.
- Hines, A. H., T. G. Wolcott, E. González-Gurriarán, J. L. González-Gurriarán, and J. Friere. 1995. Movement patterns and migrations in crabs: Telemetry studies of juvenile and adult behavior in *Callinectes sapidus* and *Maja squinado*. *Journal of the Marine Biological Association of the U.K.*, 75:27–42. <http://dx.doi.org/10.1017/S0025315400015174>.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist*, 93:45–159.
- Jackson, J. B. C. 2008. Ecological extinction and evolution in the brave new ocean. *Proceedings of the National Academy of Sciences*, 105:11458–11465. <http://dx.doi.org/10.1073/pnas.0802812105>.
- Johnson, B. M., and S. R. Carpenter. 1994. Functional and numerical responses: a framework for fish-angler interactions? *Ecological Applications*, 4:808–821.
- Kitchell, J. F., ed. 1992. *Food web management: A case study of Lake Mendota*. New York: Springer-Verlag.
- Kitchell, J. F., and S. R. Carpenter. 1993. Variability in lake ecosystems: Complex responses by the apical predator. In *Humans as components of ecosystems*, ed. M. McDonnell and S. Pickett, pp. 111–124. New York: Springer-Verlag.
- Konstantinou, H., and D. C. Shen. 1995. The social and reproductive behavior of the eyed flounder, *Bothus ocellatus*, with notes on the spawning of *Bothus lunatus* and *Bothus ellipticus*. *Environmental Biology of Fishes*, 44:311–324.
- Krebs, J. R., and N. B. Davies. 1993. *An introduction to behavioural ecology*. Oxford: Wiley-Blackwell Publishing.
- Lavalli, K., and W. F. Herrnkind. 2009. Collective defense by spiny lobster (*Panulirus argus* Latreille, 1804) against triggerfish (*Balistes capriscurus* Gmelin, 1788): Effects of number of attackers and defenders. *New Zealand Journal of Marine and Freshwater Research*, 43:15–28. <http://dx.doi.org/10.1080/00288330909509978>.
- Logan, C. A. 2010. A review of ocean acidification and America's response. *BioScience*, 60:819–828. <http://dx.doi.org/10.1525/bio.2010.60.10.8>.
- Mackie, G. O., and C. E. Miller. 1983. Use of Pisces IV submersible for zooplankton studies in coastal waters of British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, 40:763–776. <http://dx.doi.org/10.1139/f83-099>.
- MacLennan, D. N., and E. J. Simmonds. 1992. *Fisheries acoustics*. London: Chapman and Hall.
- Madin, L. P. 1974. Field observations on the feeding behavior of salps (Tunicata: Thaliacea). *Marine Biology*, 25:143–147. <http://dx.doi.org/10.1007/BF00389262>.
- Magnuson, J. J. 1991. Fish and fisheries ecology. *Ecological Applications*, 1(1):13–26.
- Marx, J. M., and W. F. Herrnkind. 1985. Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for young juvenile spiny lobsters, *Panulirus argus*. *Bulletin of Marine Science*, 36:423–431.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- McMullin, E. R., D. C. Berkquist, and C. R. Fisher. 2000. Metazoans in extreme environments: Adaptations of hydrothermal vent and hydrocarbon seep fauna. *Gravitational and Space Biology Bulletin*, 13:1–23.
- McNamara, J. M., and A. I. Houston. 1986. The common currency for behavioral decisions. *American Naturalist*, 127:358–378.
- Miller, J. W., J. VanDerwalder, and R. Waller, eds. 1971. *Tektite I. Scientists-in-the-Sea*. Washington, D.C.: U.S. Government Printing Office.
- Mintz, J. D., R. N. Lipcius, D. B. Eggleston, and M. S. Seebö. 1994. Survival of juvenile Caribbean spiny lobster: Effects of shelter size, geographic location and conspecific abundance. *Marine Ecology Progress Series*, 112:255–266. <http://dx.doi.org/10.3354/meps112255>.
- Moorman, M. C., D. B. Eggleston, C. B. Anderson, A. Mansilla, and P. Szjener. 2009. The implications of North American beaver and trout invasion on native diadromous fish in the Cape Horn Biosphere Reserve, Chile. *Transactions of the American Fisheries Society*, 138:306–313. <http://dx.doi.org/10.1577/T08-081.1>.
- Naud, M.-J., R. T. Hanlon, K. C. Hall, P. W. Shaw, and J. N. Havenhand. 2004. Behavioral and genetic assessment of reproductive success in a spawning aggregation of the Australian giant cuttlefish, *Sepia apama*. *Animal Behavior*, 67:1043–1050. <http://dx.doi.org/10.1016/j.anbehav.2003.10.005>.
- Nemeth, R. S. 2005. Recovery of a U.S. Virgin Islands red hind spawning aggregation following protection. *Marine Ecology Progress Series*, 286:81–97. <http://dx.doi.org/10.3354/meps286081>.
- Nemeth, R. S., E. Kadison, S. Herzlieb, J. Blondeau, and E. A. Whiteman. 2006. Status of a yellowfin (*Mycteroperca venenosus*) grouper spawning aggregation in the U.S. Virgin Islands with notes on other species. *Proceedings of the Gulf and Caribbean Fisheries Institute*, 57:541–558.
- Nevitt, G., N. D. Pentcheff, K. J. Lohmann, and R. K. Zimmer. 2000. Den selection by the spiny lobster *Panulirus argus*: testing attraction to conspecific odors in the field. *Marine Ecology Progress Series*, 203:225–231.
- Norman, M. D., J. Finn, and T. Tregenza. 2011. Dynamic mimicry in an Indo-Malayan octopus. *Proceedings of the Royal Society of London, B*, 268:1755–1758. <http://dx.doi.org/10.1098/rspb.2011.1708>.
- Orth, R. J., and J. van Montfrans. 1987. Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Marine Ecology Progress Series*, 41:283–294. <http://dx.doi.org/10.3354/meps041283>.
- Palma, A., and R. S. Steneck. 2002. Does variable coloration in juvenile marine crabs reduce risk of visual predation? *Ecology*, 82:2961–2967. [http://dx.doi.org/10.1890/0012-9658\(2001\)082\[2961:DVCIJM\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2001)082[2961:DVCIJM]2.0.CO;2).
- Pardieck, R. A., R. J. Orth, R. J. Diaz, and R. N. Lipcius. 1999. Ontogenetic changes in habitat use by postlarvae and young juveniles of the blue crab. *Marine Ecology Progress Series*, 186:227–238. <http://dx.doi.org/10.3354/meps186227>.
- Parsons, D. P., and D. B. Eggleston. 2005. Indirect effects of recreational fishing on spiny lobster behavior (*Panulirus argus*). *Marine Ecology Progress Series*, 303:235–244. <http://dx.doi.org/10.3354/meps303235>.
- . 2006. Human disturbance, natural predators and unobserved mortality in a spiny lobster, *Panulirus argus*, fishery. *Journal of Experimental Marine Biology and Ecology*, 334:196–205.
- Pile, A. J., R. N. Lipcius, J. van Montfrans, and R. J. Orth. 1996. Density-dependent settler–recruit–juvenile relationships in blue crabs. *Ecological Monographs*, 66:277–300. <http://dx.doi.org/10.2307/2963519>.
- Post, E., N. C. Stenseth, R. O. Peterson, J. A. Vucetich, and A. M. Ellis. 2002. Phase dependence and population cycles in a large-mammal predator–prey system. *Ecology*, 83:2997–3002.
- Ratchford, S. G., and D. B. Eggleston. 1998. Size- and scale-dependent chemical attraction contribute to an ontogenetic shift in sociality. *Animal Behavior*, 56:1027–1034. <http://dx.doi.org/10.1006/anbe.1998.0869>.
- Reyns, N. B., and D. B. Eggleston. 2004. Environmentally controlled, density-dependent secondary dispersal in a local estuarine crab population. *Oecologia*, 140:280–288. <http://dx.doi.org/10.1007/s00442-004-1581-8>.
- Rindone, R. R., and D. B. Eggleston. 2011. Predator–prey dynamics between recently established stone crabs (*Menippe* spp.) and oyster prey (*Crassostrea*

- virginica*). *Journal of Experimental Marine Biology and Ecology*, 407(2): 216–225. <http://dx.doi.org/10.1016/j.jembe.2011.06.018>.
- Sobel, J., and C. P. Dahlgren. 2004. *Marine reserves: A guide to science, design and use*. Washington, D.C.: Island Press.
- Spanier, E., J. S. Cobb, and M. Clancy. 1994. Impacts of remotely operated vehicles (ROVs) on the behavior of marine animals: An example using American lobsters. *Marine Ecology Progress Series*, 104:257–266. <http://dx.doi.org/10.3354/meps104257>.
- Starck, W. A. 1968. A list of fishes of Alligator Reef, Florida with comments on the nature of the Florida reef fish fauna. *Undersea Biology*, 1:4–40.
- Starr, R. M., D. S. Fox, M. A. Hixon, B. N. Tissot, G. E. Johnson, and W. H. Barss. 1996. Comparison of submersible-survey and hydroacoustic-survey estimates of fish density on a rocky bank. *Fishery Bulletin U.S.*, 94:113–123.
- Stephens, D. W., and J. R. Krebs. 1968. *Foraging theory. Monographs in behavior and ecology*. Princeton: Princeton University Press.
- Stoner, A. W. 1997. The status of queen conch, *Strombus gigas*, research in the Caribbean. *Marine Fisheries Research*, 59:14–22.
- Stoner, A. W., and M. Ray-Culp. 2000. Evidence for Allee effects in an over-harvested marine gastropod: Density-dependent mating and egg production. *Marine Ecology Progress Series*, 202:297–302. <http://dx.doi.org/10.3354/meps202297>.
- Tagatz, M. E. 1968. Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. John's River, Florida. *Fishery Bulletin*, 67:17–33.
- Taylor, J. C., D. B. Eggleston, and P. S. Rand. 2006. Nassau grouper (*Epinephelus striatus*) spawning aggregations: Hydroacoustic surveys and geostatistical analysis. In *Emerging technologies in reef fisheries management*, ed. J. C. Taylor, pp. 18–25. Seattle: NOAA Professional Paper NMFS 5.
- Todd, P. A., R. A. Biers, R. J. Ladle, and F. Middleton. 2006. Phenotype-environment matching in the shore crab (*Carcinus maenas*). *Marine Biology*, 148:1357–1367. <http://dx.doi.org/10.1007/s00227-005-0159-2>.
- Uiblein, F., P. Lorange, and D. Latrouite. 2003. Behavior and habitat utilization of seven demersal fish species on the Bay of Biscay continental shelf, NE Atlantic. *Marine Ecology Progress Series*, 257:223–232. <http://dx.doi.org/10.3354/meps257223>.
- Van Engel, W. A. 1958. The blue crab and its fishery in Chesapeake Bay. Part 1. Reproduction, early development, growth, and migration. *Commercial Fisheries Review*, 20:6–17.
- Verity, P. G., M. L. Alber, and S. B. Bricker. 2006. Development of hypoxia in well-mixed estuaries in the southeastern USA. *Estuaries and Coasts*, 29:665–673.
- Walsh, M. R., S. B. Munch, S. Chibe, and D. O. Conover. 2006. Maladaptive changes in multiple traits caused by fishing: Impediments to population recovery. *Ecology Letters*, 9:142–148. <http://dx.doi.org/10.1111/j.1461-0248.2005.00858.x>.
- Webb, J. K., D. A. Pike, and R. Shine. 2010. Olfactory recognition of predators by nocturnal lizards: Safety outweighs thermal benefits. *Behavioral Ecology*, 21:72–77. <http://dx.doi.org/10.1093/beheco/arp152>.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology and Systematics*, 15:393–425.
- Whitfield, P. E., T. Gardner, S. P. Vives, M. R. Gilligan, W. R. Courtenay, G. C. Ray, and J. A. Hare. 2002. Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. *Marine Ecology Progress Series*, 235:289–297. <http://dx.doi.org/10.3354/meps235289>.
- Whitfield, P. E., J. A. Hare, A. W. David, S. L. Harter, R. C. Muñoz, and C. M. Addison. 2007. Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the Western North Atlantic. *Biological Invasions*, 9:53–64. <http://dx.doi.org/10.1007/s10530-006-9005-9>.
- Wolcott, T. G. 1995. New options in physiological and behavioral ecology through multi-channel telemetry. *Journal of Experimental Marine Biology and Ecology*, 193:257–275. [http://dx.doi.org/10.1016/0022-0981\(95\)00121-2](http://dx.doi.org/10.1016/0022-0981(95)00121-2).
- Wolcott, T. G., and A. H. Hines. 1989. Ultrasonic biotelemetry of muscle activity from free-ranging marine animals: A new method for studying foraging by blue crabs (*Callinectes sapidus*). *Biological Bulletin*, 176:50–56. <http://dx.doi.org/10.2307/1541888>.
- . 1990. Ultrasonic telemetry of small-scale movements and microhabitat selection by molting blue crabs. *Bulletin of Marine Science*, 46:83–94.
- . 1996. Advances in ultrasonic biotelemetry for animal movement and behavior: The blue crab case study. In *Methods and techniques of underwater research*, ed. M. A. Lang and C. C. Baldwin, pp. 229–236. Nahant, Mass.: American Academy of Underwater Sciences.
- . 2004. Migration of adult blue crabs to spawning grounds: Mechanisms and routes. In *Chesapeake Bay fisheries research program symposium report 2003*, ed. D. Orner, pp. 17–24. Annapolis, Md.: NOAA Chesapeake Bay Office.
- Zeidberg, L. D., and B. H. Robison. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *Proceedings of the National Academy of Sciences*, 104:12948–12950. <http://dx.doi.org/10.1073/pnas.0702043104>.
- Zimmer-Faust, R. K., J. E. Tyre, and J. F. Case. 1985. Chemical attraction causing aggregation in the spiny lobster, *Panulirus interruptus* (Randall), and its probable ecological significance. *Biological Bulletin*, 169:106–118. <http://dx.doi.org/10.2307/1541391>.