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REVIEW

Marine ecological research in seashore and seafloor systems: accomplishments and future directions

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ABSTRACT: Research in seashore and seafloor communities has contributed immensely to the conceptual growth of ecology. Here we summarize some of the most important findings and discuss needs and opportunities for future work. Disproportionately large numbers of the most influential contributions are derived from studies of rocky shores and coral reefs because aspects of these systems (accessibility) and of their most common species (sessile or weakly motile, high density, short generation time) make them well suited to manipulative experiments. Foremost among the research contributions from seashore and seafloor systems are increased understanding of (1) competition and consumer-prey interactions, (2) trophic cascades and other indirect species interactions, (3) the evolution of defense and resistance in consumer-prey systems, (4) the importance of propagule transport and recruitment variation to adult populations, (5) the impacts of physical disturbance, and (6) the generation and maintenance of species diversity on ecological time scales. We acknowledge the importance of manipulative experiments in the growth of marine ecology, but question whether a strict adherence to this approach will best serve future needs. Some of the most pressing needs for future knowledge are: (1) documenting the complex influences of spatial and temporal scales on ecological processes, (2) identifying the role of large, mobile predators in marine ecosystems, (3) understanding factors limiting marine autotrophs, (4) integrating historical biology and neontology, and (5) appreciating intersystem linkages. Increased attention to conducting arrays of experiments, taking measurements and observations, and documenting change at larger scales of space and time will provide insights that are unattainable by the commonly used methodological protocols. Novel approaches, including (1) evaluating and managing human disturbance for the joint purpose of conservation and learning, (2) developing stronger ties between scientists working in open-ocean and near-shore systems, and (3) developing collaborative projects among scientists in the academic, governmental, and private sectors are required to understand many of these processes.

KEY WORDS: Coral reefs · Ecological concepts · Kelp forests · Novel approaches · Rocky shores · Unconsolidated substrates

INTRODUCTION

The broad goal of ecological research is to understand the structure and dynamics of populations, communities, and ecosystems. Marine and estuarine systems associated with the seafloor, especially on coastal hard substrata, have contributed substantially to this agenda. Here we review important conceptual advances that are based on research in seashore and seafloor systems, the system-level characteristics and research approaches that have led to these contributions, the

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resulting strengths and limitations of current knowledge, and visions of what is both possible and necessary to move the field toward interesting and useful new horizons. Our focus is on spatial patterns and temporal dynamics of populations and communities, the processes that explain them, and the level of success that science can achieve in understanding and predicting those patterns and dynamics. This is not a comprehensive, in-depth review, but rather an overview, strongly influenced by our own experiences and perspectives. Despite our potentially non-representative viewpoints, however, the ideas expressed in this review have been exposed to and modified by extensive input from dozens of our colleagues in the field of ocean ecology.

Marine ecological systems associated with the seafloor occur from near the poles to the equator and from the intertidal zone to the deepest ocean bottom; thus, they are necessarily characterized by immense taxonomic and physical/chemical variation. This variation can be categorized in numerous ways. We divide it in the traditional fashion by substrate type—hard versus unconsolidated (soft)—because this is a recurrent and reasonably dichotomous distinction among marine benthic systems, and the methods used and many of the processes investigated segregate accordingly. Most work on population, community and ecosystem dynamics has come from studies in nearshore and estuarine environments, and our presentation is weighted accordingly.

STATE OF THE FIELD

Hard-substrate systems

Hard-substrate systems are common from the intertidal zone to the deep sea, and notably include intertidal rocky headlands, boulders, and limestone benches (Connell 1972, Sousa 1979, Underwood & Denley 1984), shallow subtidal rock walls (Witman 1987) and reefs (Connell et al. 1997), seamounts (Genin et al. 1986, 1989, Keating et al. 1987), and hydrothermal vents, where rocky crust is being actively formed (Grassle 1986, Tunnicliffe 1991). Our focus is mainly on shallow-water systems—rocky shores, coral reefs, and kelp forests. All 3 systems have been productive arenas for ecological research because they are comparatively easy to access and observe; many of the key organisms are abundant, sessile or weakly motile, and have short generation times; and some strong interactions among species tend to characterize specific systems (Paine 1980, Menge et al. 1994). This is not to say that all species are strong interactors (most may not be), but rather that at least some strong interactors have been found virtually everywhere scientists have looked for them in these habitats. The suite of characteristics of these hard-substrate systems in shallow water makes manipulative experiments both feasible and profitable, an approach that has come to dominate ecological research in hard-substrate systems in recent decades (Dayton & Oliver 1980, Paine 1994, Rafaelli & Hawkins 1996). Experimental manipulation is far more limited in the deep sea, but the development of manned and unmanned research submersibles has created new opportunity for exploring ecological dynamics in these systems (e.g. Thistle & Levin 1998).

A list of contributions from research in hard-substrate marine systems would be vast. One need only peruse titles from the general ecological and marine specialty journals to see this. Several recurrent themes emerge from the profusion of research. A substantial proportion of papers addresses pair-wise interactions among species or guilds of species. Most of them focus on competition (Connell 1983) or consumer-prey interactions (Schmitt 1987). Definitive evidence for the importance of both processes is provided by studies of numerous taxa in many areas of the world. A second theme concerns the indirect effects of apex consumers on lower trophic levels (Power et al. 1996). Indirect effects of apex predators typically play out in 1 of 3 ways—via trophic cascades, in which top consumers facilitate autotrophs by limiting populations of mid-level consumers (Fretwell 1987, Carpenter & Kitchell 1993); via preferential consumption of competitive dominants, which frees limiting resources and enhances diversity among competitors (Paine 1966, Connell 1978); or via positive species interactions including, especially, provision of biogenic habitat by 'bioengineers' (Jones et al. 1994). Studies built around the second of these processes provide important evidence for the Intermediate Disturbance Model of species diversity (Connell 1978, Lubchenco 1978, Sousa 1979). A third theme to emerge from research on coastal marine systems concerns the ecological and evolutionary roles of defense and resistance in consumer-prey interactions (Hay & Fenical 1988). Although there is empirical evidence of defense and resistance for a variety of trophic levels, geographic regions, and modalities of defense, the most well-developed findings concern the role of secondary plant metabolites in plant-herbivore interactions within tropical/subtropical reef systems. A final theme of conceptual importance is 'supply-side ecology'—the notion that dispersive life history stages (usually spores and larvae) significantly influence the population dynamics of adult stages in species with complex life cycles (Sale 1977, Doherty & Williams 1988, Roughgarden et al. 1988, Underwood & Fairweather 1989, Caley et al. 1996). Larval characteristics and physical transport processes are also important in explaining the rapid colonization of habitat patches in dynamically open systems, such as newly created hydrothermal vents (Mullineaux et al. 1995).

Soft-substrate systems

Unconsolidated sediments characterize the sea floor over a large fraction of the global ocean. Habitats range from intertidal sandy beaches and protected estuarine mudflats to deep-sea deposits. Physical regime and water depth, which in turn influence sediment disturbance and grain size, play dominant roles in establishing community composition and character in marine soft sediments (Hall 1994).

Study of the dynamics of soft-sediment populations and communities has an almost century-long history, dating from early Scandinavian pioneers. Some of the initial focus of this work addressed questions of the relationships between benthic invertebrate-prey resources and demersal fishes in the North Sea (Blegvad 1928). In the mid 20th century, other Scandinavian marine ecologists made important advances in relating reproductive modes and larval life histories to dispersal and recolonization dynamics of benthic invertebrates (Thorson 1950, Segerstråle 1962). Modern research has stressed experimental approaches in evaluating the roles of physical and biological disturbance in organizing soft-sediment systems (Woodin 1976, Elmgren et al. 1986, Hall 1994). By integrating fluid dynamics and sedimentology with ecology, much progress has been made in understanding recruitment dynamics of soft-sediment invertebrates (Eckman 1983, Nowell & Jumars 1984, Butman 1987, Olafsson et al. 1994). Interdisciplinary research also has characterized the significant historical focus on habitat relationships in soft-bottom environments (Snelgrove & Butman 1994).

Listing the major contributions of soft-sediment investigations to our general understanding of the dynamics of natural systems is necessarily idiosyncratic. Nevertheless, many people would include the following facets. (1) The study of soft-sediment benthic communities as a function of water depth has revealed the maintenance of extremely high species diversity at great depths, with diversity increasing with global area of habitat despite the low rates of energy provision (Grassle 1989). Although the mechanisms responsible for these depth-related patterns are still in question, this work has produced many conceptual contributions to theories of biodiversity maintenance (Rex et al. 1993, Pineda & Caswell 1998). Research on evolution and maintenance of coral diversity has had similarly large impacts on understanding biodiversity (Connell 1978, Hughes 1989, Jackson 1991, Karlson & Cornell 1998). (2) Predation by crustaceans and fishes has been shown to reduce density of soft-sediment invertebrates in many shallow habitats that lack such structural barriers to foraging as aquatic vegetation or shell debris (Peterson 1979, Oliver & Slattery 1985, Olafsson et al. 1994, but see Rafaelli & Hall 1992). (3) Important demonstrations of tri-trophic interactions have emerged from estuarine experiments, showing that fish, wading bird, and shorebird predation is often directed preferentially towards predatory crustaceans, large predatory polychaetes, or small demersal fishes, thereby releasing population controls on their smaller invertebrate prey (Kneib & Stiven 1982, Commito & Ambrose 1985, Wilson 1986, Kneib 1988). (4) The strong interactions significant to soft-sediment community dynamics do not generally include interspecific competition, but instead involve either predation and physical disturbance of the sediments or transformation of the physical habitat by creating an emergent or seabed structural habitat (Nowell & Jumars 1984, Peterson 1991, Hall 1994). (5) Food limitation is generally important to both main functional groups of basal consumers in soft sediments—deposit and suspension feeders (Levinton & Lopez 1977, Peterson & Black 1987). Seasonal food availability contributes on a large scale to temporal dynamics by inducing pulses of reproductive activity and settlement, but on local scales it is growth rate not abundance that responds most commonly to competition for food in this system (Wildish & Kristmanson 1997).

DEVELOPMENT OF INNOVATION

Ecologists may differ greatly in their personal lists of the most interesting conceptual developments in understanding the dynamics of benthic/demersal marine ecosystems. Regardless of one's perspective, it is easy to embrace the view that marine ecology has long been and continues to be a productive area of scientific research, and thus that external guidance, infrastructural changes, and imposition of new visions represent unnecessary interference with a successful formula. Under this philosophy, an effective strategy for funding agencies might be simply to let science proceed in the future as it has in the past, banking on the expectation that continued productivity by a renewable resource of imaginative scientists will provide the substrate for intellectual growth through individual and collaborative creativity and original syntheses of accumulating knowledge. A critic of this philosophy, on the other hand, could reasonably make the following argument: while history clearly indicates past successes (as briefly discussed above) and staying the course promises even more in the future, the very methods that have led to these successes and the conceptual themes that have emerged from them condition our thinking, constrain our creativity, and inhibit our capacity for innovation. We believe that there is truth in both perspectives, that these views are not mutually exclusive, and that an effective agenda for research should thus contain elements of each philosophy. Our major motivation for writing this paper is to address issues that emerge under the latter view and thereby encourage marine ecologists to consider honestly and thoughtfully how they may break through constraints of vision that they may not even recognize exist. What, then, would we like to know about seashore and seafloor systems and what opportunities exist for facilitating the novel research needed to obtain that knowledge?

Critical gaps in understanding

This section identifies important issues that are still poorly understood. With each, we discuss opportunities for catalyzing novel and recent developments in technology that offer hope of progress.

Scale. This is an older issue (Dayton & Tegner 1984, Levin 1992), although it is as topical and elusive now as ever before. Some of the questions pertaining to scale are: (1) Over which dimensions of space and time do the most significant organizing processes operate? (2) Can measurements to understand these processes be scaled accordingly, or must they be? and (3) What are the patterns of generality and variation within and across processes and ecosystems? These important questions have led to considerable debate. Their relevance to ecology also transcends coastal and seafloor marine ecosystems. We see several opportunities for increased understanding of questions of scale and, as in the past, work on benthic/demersal marine systems could play a leading role. One such opportunity is the use of meta-analyses to evaluate patterns across multiple studies (Gurevitch & Hedges 1999). An emerging scientific culture of ecological synthesis needs to be cultivated and supported. The rich informational base from past research in benthic/demersal systems seems ripe for such an approach, and recent examples are exciting and encouraging (Menge et al. 1994, Caley et al. 1996). A second opportunity is conducting experimental studies on varying spatial and temporal scales (Thrush et al. 1997a,b). This has always been possible, but is rarely done. Long-term data sets, sometimes even utilizing historical, archaeological or paleontological information, have provided novel temporal perspectives on marine systems (Simenstad et al. 1978, White 1987, Allen & Smith 1988, Dayton 1989, Baumgartner et al. 1992, Connell et al. 1997, Jackson 1997, Dayton et al. 1999). A third opportunity comprises the potential use of new technology in Geographic Information System (GIS) mapping and analysis and in satellite imagery to investigate ecological processes on larger spatial scales than was possible heretofore.

Large, mobile predators. Understandably, ecologists have focused attention on those species they could most easily manipulate, i.e. small to moderately sized organisms that do not wander widely and are abundant in small areas amenable to experimentation. This selectively excludes certain groups of species from study, thus providing a potentially biased picture of important patterns and processes in benthic/demersal systems. Scientists have speculated about the ecological roles of such highly mobile groups as marine mammals, birds, and large fishes, but have not known how to incorporate them adequately into compelling evaluations. This problem is exacerbated by the fact that prevailing standards of scientific rigor (which emphasize experimental manipulation, replication, and local controls) that are often achievable in studies of relatively small-bodied, sessile or weakly mobile species (Paine 1994) are difficult or impossible to meet in addressing such questions for large, highly mobile components of the ecosystem. Furthermore, many scientists who study mobile marine vertebrates assume a strong bottom-up view of ecosystem dynamics, thereby creating a perspective of 'response to' rather than 'effect on' their environment as the domain of inquiry. New approaches—ranging from technological to conceptual to philosophical—are needed for research on these species. Natural history observations, usually obtained opportunistically, often are a source of significant insight into the ecological roles of these elusive creatures. Recent advances in the development of instruments for tracking and measuring the behavior and physiology of large, mobile marine vertebrates promise new insights into such questions as where and how they forage (Gentry & Kooyman 1986, Block et al. 1993, Davis et al. 1999). Further understanding of their roles in community organization and dynamics could be obtained in 4 ways: (1) excluding them from areas where they are otherwise abundant, (2) protecting them in areas where they are otherwise rare or have become rare due to exploitation, (3) tracking long-term changes in populations and communities in response to intentional management actions, and (4) using historical data from archaeology or paleontology to infer relationships between community structure and the presence-absence of large mobile predators. Using marine reserves for large-scale experiments is a useful approach for studying some species. Because of the dramatic impacts of fishing, especially on seafloor communities in the coastal zone (Dayton et al. 1995), the use of reserves as an adaptive management experiment is especially promising (Lauck et al. 1998).

Limiting factors on autotrophs. Plants have long commanded particular attention in ecological studies because of their pre-eminence in controlling the flux of energy and nutrients and because of their importance as 'ecosystem engineers' (sensu Jones et al. 1994) in providing or modifying structural habitat for other organisms. Four factors are thought to limit marine plant populations—physical disturbance, herbivory, light, and nutrients. While there is abundant evidence for each, a broad synthesis of their joint influence is lacking for 2 main reasons: first, past studies have tended to focus on single factors; second, methodological differences among different investigators have made geographic and taxonomic contrasts difficult to interpret. Both problems are technically resolvable—the first by conducting multi-factorial experiments and the second by establishing a programmatic infrastructure wherein similar approaches are used to study different areas and different species.

Historical biology. Ecologists working on marine benthic/demersal systems seem to have taken an unusually strong existential/neontological view of the world, thus endeavoring to understand the workings of marine systems from the perspective of extant species characteristics and community composition, with relatively little thought given to history that extends beyond individual memory. Important new insights can be obtained when ecologists expand their time scales to include evolutionary processes and historical events (Simenstad et al. 1978, Jackson 1991, Steinberg et al. 1995). This goal is best achieved by ecologists joining forces with biogeographers, historians, archaeologists and paleontologists. The knowledge of recent historical status of community composition and population abundance can help discriminate between climatic explanations for change such as climatic regime shifts (Anderson & Piatt 1999) and human exploitation or habitat modification (Martin 1973). In addition, evaluation of longer histories of community composition provides insight into the evolutionary conditions and interactions that shaped the species that we study today. Use of molecular genetic techniques offers special promise in defining the geographical dimensions of populations and taxonomic relationships among species. This molecular approach will also help define the spatial structure of exploited populations, which is certain to improve management and clarify relationship between the openness of populations and diversity maintenance especially critical to understanding the deep sea (Powers et al. 1990). More work at the interface of ecology and evolution promises exciting new discoveries (Palumbi 1992).

Linkages among ecosystems. Most prior research on marine benthic/demersal systems has proceeded by identifying or defining specific systems and attempting to understand organizational processes within each. One notable exception is 'supply-side ecology' (Gaines & Roughgarden 1987, Roughgarden et al. 1988), wherein the oceanic realm is recognized as a potential transport vector for the dispersive life-history stages of otherwise sessile and weakly motile species. Presently, this is an area of active research in marine ecology. Similar interactions between the physical transport vectors such as internal waves and benthic organisms and communities have been responsible for remarkable new discoveries on subtidal rock walls (Witman et al. 1993) and coral reef environments (Leichter et al. 1996). Otherwise, the nature and importance of linkages among various marine and even terrestrial ecosystems are poorly known. Coastal benthic/demersal systems are especially interesting in this regard because they are juxtaposed with the land on one side and the open sea on the other, and in both cases significant linkages between systems occur via physical (oceanic, atmospheric, riverine) and biological (mobile species) transport mechanisms (Polis et al. 1997, Paerl et al. 1998). New opportunities for the study of such processes are available with recent developments in isotopic analyses, remote sensing, satellite imagery, GIS technology, and instrumentation for tracking animals at sea.

OPPORTUNITIES AND CHALLENGES

As is true for any successful endeavor, one challenge faced by benthic/demersal ecologists is to shed the constraints of tradition—not absolutely, for the value of small-scale manipulative experiments has not and may never run its course, but sufficiently to recognize other needs, to more freely explore opportunities, and perhaps even to rethink the standards of scientific inference. While admittedly something of a potpourri, we urge that programmatic infrastructures be implemented to emphasize or take advantage of the following issues:

Effects of human exploitation

Human activities perturb natural ecosystems on scales than cannot be achieved for the purpose of learning alone. For instance, there is little doubt that fisheries have dramatically affected fish stocks and marine communities (Dayton et al. 1995, Botsford et al. 1997, Pauly et al. 1998). While most emphasis has been on simply documenting the effects of fishing on fishes, the fact that so many coastal fish stocks have been depleted provides numerous opportunities for understanding their ecological roles. Marine reserves, to the extent that they protect fish stocks from depletion and enhance their recovery, also should be looked to as important research opportunities (e.g. Alcala & Russ 1990, Lauck et al. 1998).

Long-term, large spatial-scale studies

The vast majority of even the best research on marine benthic/demersal systems has been done over a period of just a few years at 1 or 2 sites. Benthic ecologists must expand their efforts to encompass longer and larger scales (Brown 1995). Some work of this nature has been done (e.g. Connell et al. 1997), mostly through the initiative of individual investigators rather than as a consequence of programmatic infrastructures. The few data available are sufficient to demonstrate that these approaches produce important insights not otherwise attainable (see Brown & Heske 1990 for a terrestrial example, Estes et al. 1998 for a marine example).

Population consequences

Most experimental studies in marine benthic/demersal communities have emphasized mechanisms and processes, but few have expanded these mechanisms and processes to demonstrate population-level effects. The main reason for this failure is that the research is not conducted for sufficiently long periods or/and over sufficiently large areas. Since species and populations are the essential currency of applied ecology and the grist of evolution, future research is needed to bridge this gap from the qualitative to the quantitative. Furthermore, innovations to our understanding of the generation of population and even community dynamics can come from studies relating individual behavioral or physiological responses to environmental forcing: rarely do such studies make the connections between the individual and the population, despite a potential for enhancing predictive capacity by uncovering the underlying mechanisms for population and community change (Bertness 1992, Wootton 1993, Micheli 1997).

Developing stronger working relationships between scientists and managers

Several of the challenges identified in this review are not easily addressed solely within the province of basic research. However, researchers working in collaboration with regulatory and management agencies could address some of them. There has been an appeal by many scientists for application of the principles of ecosystem management; yet the protocols for applying this approach to marine ecosystems are undefined (Botsford et al. 1997). An example of the potential utility of merging science and management is the development of marine protected areas for the joint purpose of conserving exploited populations, assessing population-to-ecosystem-level impacts of fisheries, and determining the roles of large predatory fishes in benthic/demersal communities. While fishing is perhaps the most well known agent of anthropogenic influence on marine ecosystems, eutrophication is another process that is dramatically transforming estuarine and shallow coastal systems in some parts of the world (Turner & Rabalais 1994, Nixon 1995, Paerl et al. 1998). Much research has been devoted to understanding the effects of nutrient loading on phytoplankton (without yet adequate understanding of the dynamics of nuisance blooms). Yet the food-chain consequences of nutrient loading, and how change in productivity and composition of the microalgal assemblage alters the composition, production, interactions and dynamics of consumers at higher trophic levels are unknown (Paerl et al. 1998). The use of environmental management on the scales of watersheds for large-scale experiments, with resource managers working in conjunction with marine ecologists, holds tremendous promise for answering important questions about system dynamics and the sustainability of ecosystem services.

Biodiversity

Biodiversity has emerged as a powerful scientific and social allegory, largely because species and populations are being lost at alarmingly high rates from many terrestrial systems (Soulé & Sanjayan 1998). The oceans are a paradox in this regard (Roberts & Hawkins 1999). On the one hand, some of the strongest evidence for changes in biodiversity comes from the fossil record of marine species (Sepkoski et al. 1981), thus demonstrating that the sea is not invulnerable to mass extinction. On the other hand, while presently species are being lost at high rates from some terrestrial systems, few marine species are known to have become extinct during the 20th century (Carlton 1993). Reasons for this apparent discrepancy are intriguing and warrant further evaluation by marine ecologists. Are recent extinctions of marine species in fact rare, or is it simply that the taxonomy of so many of these species remains to be properly described? In addition, understanding the role of biodiversity looms as a major challenge. Given the apparent redundancy of species within functional groups in many marine benthic/demersal systems, what significance does that diversity have to the dynamics and sustainable functioning of any given system? Answers to these questions are important for assessing environmental impacts, designing relevant monitoring programs, and managing the health of marine ecosystems.

Research funding to study marine ecosystems is never sufficient to assess all component species, so the degree to which species can be pooled by taxonomic/functional group without loss of important information about the state and dynamics of the system has critical implications to the conduct of science. Answers to this problem should also help shed light on why some systems seem so readily invaded by exotics, and might help define and protect ecosystem integrity and sustainability—perhaps the greatest challenge of the 21st century (Carlton 1989).

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