Ecological and Evolutionary Processes: Species Diversity and the Structure and Function of Ecosystems

Introduction

The vastness of the oceans once lulled world leaders, government resource managers, and citizens into believing that human activities could not degrade marine ecosystems or reduce historically rich harvests of fish and other seafoods. Over the past several decades, however, this view has rapidly eroded, yielding to the harsh reality that human activities are changing every aspect of Earth's interconnected biogeochemical cycles and ecosystems. Today, we hear a constant barrage of news about losses of habitat and biodiversity and how these threaten the structure and function of marine ecosystems. As ecosystems degrade, we risk losing the crucial services they provide, such as sequestering atmospheric carbon dioxide and thereby slowing its buildup and global warming impacts. Fisheries yields continue to decline and lists of threatened and endangered species grow longer each year. Coastal eutrophication is a common occurrence and changing the nature and structure of coastal and ocean habitats from the bottom-up at the same time overfishing and fisheries bycatch are decimating species at the higher trophic levels thereby altering traditional top-down controls on marine communities and ecosystems.

The health of many of the ocean's unique and vital ecosystems, such as tropical coral reefs and temperate oyster reefs, is in a rapid state of decline despite the diversity of programs being instituted to conserve these and other habitats. These efforts are often hampered, however, by a lack of knowledge about the genetic identity and the basic biology of the organisms comprising these systems and of the nature of their interactions. Even less is known about the responses of most marine organisms to variations in their physical environments that are moving beyond normal fluctuations with accelerating climate change and direct human alterations to marine systems. Efforts to mitigate the adverse impacts of habitat fragmentation will require an in-depth knowledge of dispersal and genetic connectivity among populations in isolated habitat patches. Yet much of the dispersal for benthic invertebrate occurs at the poorly understood larval stage, while even less is known about factors affecting the survival of early juvenile stages. Basic science research conducted by faculty in the Marine Sciences Program addresses fundamental questions in biology, ecology, population genetics, and evolution that have implications for developing more scientifically sound programs for the conservation of critical marine species, habitats and ecosystems and the restoration of degraded systems.

Faculty
Research related to species diversity and the structure and function of marine communities and ecosystems is conducted by many of the UNC Marine Sciences faculty in diverse systems. The efforts of faculty focused largely on microbially-mediated

processes are described elsewhere in this chapter. This section covers the research topics and accomplishments of five program faculty who work primarily with macro-organisms. These faculty members include the most recent additions to MASC: Bruno, Marko and Moran, as well as Lindquist and Peterson at IMS.

John Bruno studies the population and community biology of marine plant and invertebrate communities and addresses factors controlling site-to-site variations in species composition, impacts of large-scale disturbance on communities, including the understudied impact of diseases on populations. Peter Marko's research employs molecular phylogenetic and population genetic tools to study biogeography and ecological connectivity on spatial scales ranging from oceanic to estuarine basins. Amy Moran's work focuses in large part on understanding the significance of physiological and morphological characteristics of marine larvae within the context of variable environments affecting larval performance, post-settlement success and the evolution of life histories. Lindquist studies how the products of secondary metabolism in marine organisms affect species interactions, susceptibility to environmental stresses, and the evolution of life histories. Finally, Peterson's research broadly examines issues of ecosystem functions and services, connectivities among ecosystems, anthropogenic impacts on ecosystems and their services and marine conservation and resource management.

Faculty Research Activities

Figure 3.13a

John Bruno

• **Biodiversity and ecosystem functioning in marine ecosystems:** A major focus of the Bruno lab is to understand the role of species diversity in controlling a variety of marine ecosystem properties. The lab recently completed a series of experiments in North Carolina and Jamaica testing the hypothesis that algal species richness is directly related to primary productivity. Unlike work in terrestrial grasslands, they have not detected a significant effect of algal richness. Instead, species' identity appears paramount in controlling production. The lab is currently focusing on the role of diversity at higher trophic levels. For example, field and mesocosm experiments performed in 2004 indicate that predator diversity has striking effects on prey and plant biomass and composition. This project is funded by NSF and is being performed in collaboration with J. Emmett Duffy (VIMS).

• **Coral reef ecology and conservation**: The Bruno lab is also focused on untangling the many factors causing the global decline in reef-building corals. For example, they are using mesocosm and field experiments to test the hypothesis that nutrient pollution and increasing sea surface temperatures

Figure 3.13b

have increased the severity of coral disease by making coral hosts more susceptible and/or by making bacterial and fungal pathogens more virulent. They have recently begun to compliment this experimental approach with correlative analysis of regional data on coral disease dynamics, water shed model, and Pathfinder satellite SST data. Preliminary analysis indicates that coral disease outbreaks are highly correlated with the recent thermal history of a reef (e.g., the frequency of temperature stress anomalies). This research (funded by NSF) is being performed in collaboration with C.D. Harvell, S. Ellner, and G. Smith at field sites in Akumal, Mexico, the Florida Keys, Jamaica and Moorea.

Niels Lindquist: The conceptual underpinning for much of the Lindquist group research is the impact of bioactive secondary metabolites on ecological interactions and evolutionary processes.

• **Defensive strategies of marine cnidarians:** Jellyfish and gorgonians (Fig. A) possess different defensive strategies: nematocysts and distasteful secondary metabolites, respectively. With Jay Stachowicz (UC Davis), we have discovered that, among hydroids, nematocysts and distasteful lipophilic compounds occur (inset) as alternative defenses that are equally effective against fish. Urchins readily consume nematocyst-defended hydroids but not chemically-defended species and were shown to strongly influence the diversity and abundance of hydroids in NC and FL. Our research has also identified an intriguing biogeographic pattern with the Atlantic and Pacific being rich and depauperate, respectively, in chemically defended hydroid species.

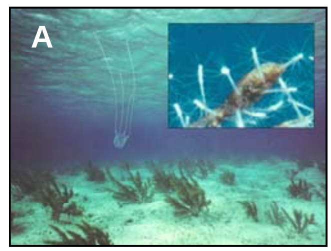


Figure 3.14a

• **Symbioses:** The vast majority of described symbioses are associations of macroorganisms with microorganisms, the later providing novel biochemical services that increase host fitness. Results of two projects, one recently published and one under review, represent the 1st and 2nd examples from the marine environment of symbiotic microbes producing chemical defenses that protect the host from predators. The first study found that larvae of the bryozoan, *Bugula neritina*, are defended from predators by secondary metabolites called bryostatins and confirmed that these compounds are produced by a bacterial symbiont. The 2nd example involves unique symbioses between a complex of related coral-reef isopods and microbial episymbiont communities dominated by unicellular cyanobacteria (Fig. B). The isopods consume their photosymbionts and "cultivate" them by inhabiting exposed sunlit substrates, a behavior made possible by symbiont production of a chemical defense repulsive to fishes. Defensive symbioses are possibly quite common and important in marine environments but largely unrecognized.

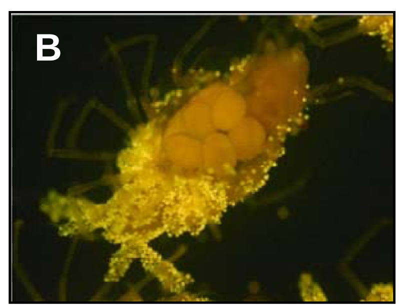


Figure 3.14b

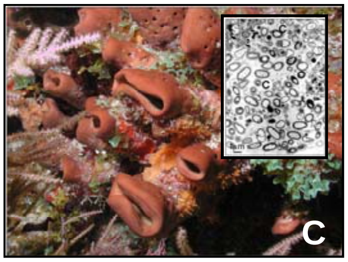


Figure 3.14c

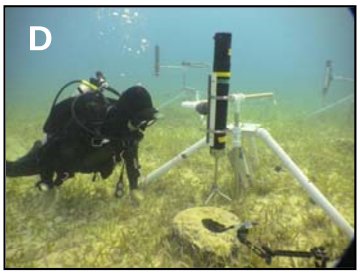


Figure 3.14d

• **Sponge impacts on coral reefs:** Sponges (Fig. C) are another group of marine invertebrates that can host abundant communities of microbes (TEM inset) known to produce some of the bioactive secondary metabolites isolated from sponges and to possibly mediate important N transformations, such N_2 fixation. Sponges may substantially influence levels and speciation of N in reef water because of their great abundance and unparalleled ability to filter seawater. *In situ* measurements of sponge pumping rates by video techniques and with ADVs (with Jim Hench, Fig. D) found some species filtering up to 50,000 L of seawater per L of tissue per d. Sponge abundance on Caribbean reefs has likely been increasing as important spongviores, such as turtles and urchins, have been decimated by overfishing and disease, respectively. Sponges can harm reef corals through direct contact, by the release of allelochemicals and possibly indirectly, for example, by remineralization of PON/DON to DIN that stimulates the growth of macroalgae and coral pathogens. Studies with Martens (UNC), Hench (Stanford) and Hentchel (U. Würzburg) are focused on: (i) the flux of nutrients, oxygen, and bioactive metabolites from sponges; (ii) the breadth of N conversion mediated by sponges and associated microbes, (iii) identifying microbes involved in important N transformations, and (iv) coral-sponge-urchin interactions.

Peter Marko. Research in the Marko lab addresses fundamental questions about how historical biogeographic and contemporary ecological together shape patterns of organismal diversity in the world's oceans. Projects cover a range of subjects, from studies of species' distributional changes over geological time to molecular forensic analysis of wildlife products from the sea. Research is currently funded by two NSF grants. Current areas of emphasis in the lab include the following:

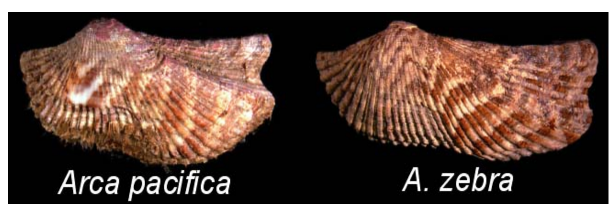
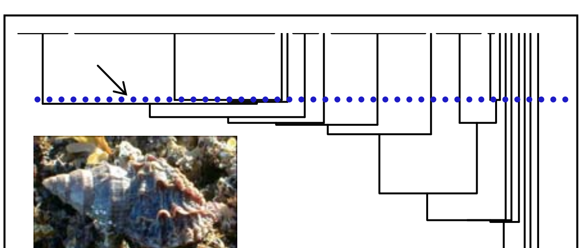


Figure 3.15

• **Speciation history of benthic marine faunas:** This work focuses on the nature and role of historical barriers involved in species formation in the sea. (Figure 3.15). Projects involve molecular phylogenetic and paleontological studies of "geminate" species found on either side of the Isthmus of Panama (Figure 3.15), and similar research into the phenomenon of "transient" allopatric isolation on linear coastlines that lack obvious contemporary barriers to dispersal and gene flow.



Coalescence of gene copies indicate high haplotype diversity at the peak of the last major glacial (~20 kyr ago). In the northeastern Pacific, this pattern

• **Late Pleistocene demographics of marine species living at high latitudes**: Research in our lab has demonstrated the existence of high-latitude glacial refugia on the west coast of North America. Several species showing strong population genetic signatures of persistence (see Figure 3.16) throughout late Pleistocene glacial cycles include taxa consumed by ancient coastal people, indicating the existence of coastal refugia that could have sustained early human colonists entering North America from Asia. We are currently expanding this work to other taxa, in order to reconstruct the biogeographic history of the entire community.

Figure 3.16

• **Larval dispersal and population connectivity:** Lab members are currently involved in several population genetic projects involving a wide range of taxa such as demersal finfish, pelagic sharks, and benthic invertebrates (see section on connectivity).

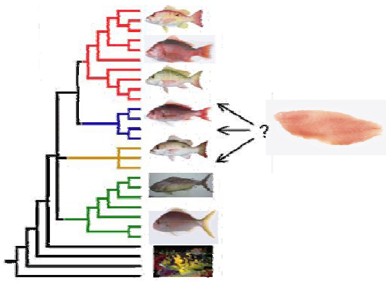


Figure 3.17

• **Forensic analysis of wildlife products:** Molecular forensic analysis provides an opportunity to compare policy with practice in the harvest, distribution, and marketing of natural marine resources. A recent publication from our lab demonstrates that overharvesting and bycatch of Red Snapper (*Lutjanus campechanus*) has resulted in widespread product mislabeling in the US market, which distorts the public's perception of the true abundance of this species. Lab members are currently working with local schools to develop molecular biology labs involving forensic questions, as well as with several media outlets to raise public awareness about the relationships between overfishing, mislabeling, and environmentally conscious consumer choices.

Amy Moran

Despite the fundamental importance of larvae in the life cycles of organisms, the factors controlling larval success or failure in the ocean are one of the great 'black boxes' of marine science. The majority of marine animals have a larval stage of development that is free-living, long-lived, and intermediate between the egg and the adult stages. Human activities in the sea are triggering a rapid and unprecedented decline in the natural resources of the ocean; for many species the impact of human activities and environmental degradation on the adult life history stages are fairly well understood, but very little is known of the fate of larval stages. In the Moran laboratory, we study the physiological and morphological adaptations of larvae and juveniles to different environmental conditions, and the implications of these for larval survival, dispersal, and recruitment into adult populations. Our research also focuses on identifying the fundamental evolutionary and ecological forces that have driven the tremendous diversity of life history modes seen today among marine organisms.

Research in the Moran laboratory currently has three primary branches:

(i) Understanding the physiological and ecological factors that are important to larval and juvenile survival and growth in the ocean. Our physiological data show that larvae from many invertebrate phyla are highly resistant to low-food levels and even to complete starvation, and that larval durations (and hence dispersal) under low-food conditions may be more than three times greater than estimates from most other studies in which larvae are fed *ad libitum*.

(ii) Determining the role of physical dispersal of planktonic, free-living larvae in connecting populations of benthic marine species. We have developed nontoxic, permanent, physical markers which can be used to label larvae from several invertebrate phyla for direct measurements of dispersal in the field. These markers have been used to label and release millions of scallop larvae in the field to characterize the dispersal shadow of a commercially-important marine mollusc (*Argopecten irradians*, the bay scallop).

(iii) Integrating the two previous branches with phylogenetic data and information from the fossil record to form a historical perspective on how life histories have evolved in a broad spectrum of marine taxa. We have reconstructed the evolution of egg size and larval development in a group of marine bivalves (Arcidae) relative to the rise of the Isthmus of Panama and associated environmental changes. These data demonstrated that when oceanic productivity increases, marine organisms evolve smaller eggs and larvae that are more reliant on exogenous phytoplankton foods.

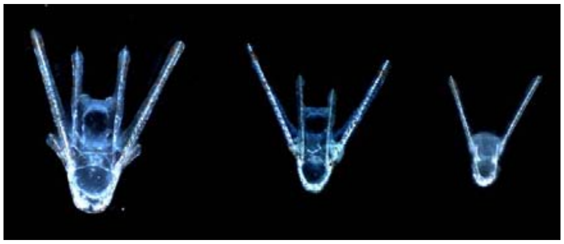


Figure 3.18: Echinoderm larvae from full-sized eggs (left), eggs that have been experimentally halved (middle), and quartered (right) by blastomere separation. Data from our group demonstrate that, surprisingly, maternally-supplied nutrients contained in the egg do not affect a larva's ability to resist starvation in the absence of phytoplankton food.

Because free-living larvae are found in almost every marine phylum, work in the Moran laboratory utilizes a wide range of organisms including molluscs, echinoderms, and polychaetes. We also study larvae of related organisms that develop in very different environments, from tropical seas to the Antarctic Ocean. This work is currently funded by two grants from NSF.

Charles Peterson

The Peterson research collaborations address many aspects of marine conservation ecology from an interdisciplinary ecosystem context. Peterson's research approaches involve experimental manipulation (including use of management actions as experiments), synthesis and analysis of large data bases, and conceptual development of the role of interdisciplinary processes in ecology. The current research projects span many issues of significance in conservation ecology and basic community ecology, including especially: coupled geological-biological research on how changing the sedimentary environment of sandy beaches affects habitat value and use; development and application of ecosystem-based approaches to oyster reef restoration; ecological and economic valuation of the ecosystem services provided by oyster reefs; development of new ecosystem-based understanding of direct and indirect ecotoxicological impacts of oil spills and petroleum hydrocarbon releases in the marine environment; assessing the consequences of estuarine eutrophication on habitat value and production of higher trophic levels; and developing an ecosystem-based approach to fisheries management incorporating marine protected areas in an interdisciplinary context. Peterson not only conducts basic research in conservation ecology but he also works in environmental and fisheries management to bring rigorous science to the decision-making process and to facilitate quasi-experimental evaluation of adaptive management actions.

Major collaborations presently include:

• **Application of disturbance theory and development of animal-sediment interactions to understand ecological impacts of and recovery from beach nourishment**: With increasing rates of sea-level rise and increasing storm climates under conditions of global warming, efforts to combat shoreline erosion are greatly intensifying. In collaboration with John Wells and other sedimentary geologists, Peterson's group is using beach fill projects as experiments to evaluate how the intensity and duration of ecological impacts can be explained by effects of modifying the sedimentary environment. This research also involves tank mesocosms, designed to reproduce the physical environment of the swash zone of the beach. Effects on invertebrate prey and predatory shorebirds, surf-fishes, and crabs are being investigated in this project. See Figure 3.19.

Figure 3.19

• **Oyster reef services to the ecosystem and oyster restoration**: One of the major causes of the decline in water quality and fish nursery habitats in the world's estuaries can be traced to loss of filtration and of biogenic reef habitat historically provided by oysters. Peterson's group conducts restorations of oyster reef habitat in ways that vary key aspects of the restoration so as to test experimentally how those factors influence restoration success. T his work also involves collaboration with natural resource economists to develop both ecological and economic valuation of oyster reef services to the ecosystem. The approach of quantifying ecosystem services of estuarine habitats allows habitat restoration to be used as quantitative mitigation to compensate for habitat losses. This research requires interdisciplinary collaboration among all four basic sciences because relating habitat structure to function requires inclusive understanding of ecosystem processes (See Figure 3.20).

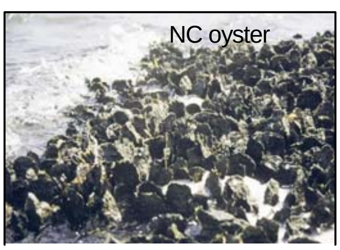


Figure 3.20

Future Directions

The complexities of species interactions and of physical and biological controls on biogeochemical cycles and ecosystems continue to motivate us to collaborate with researchers in other disciplines, both within the UNC marine science group and with scientists at other US and foreign institutions. These synergistic interactions have substantially increased our understanding of marine diversity, biogeochemical cycles, factors structuring marine communities and ecosystems, and quantifying the goods and services provided by marine ecosystems. The five faculty members in this Ecology and Evolution section, collaborate with physical oceanographers, coastal geologists, microbiologists, biogeochemists, numerical modelers, and economists. These associations expand the scope and impact of our research for the state of North Carolina, the U.S. and other nations. Among the various working groups, the members' scientific interests and applied goals are connected by the openness of marine systems and by the fact that lines on maps do not stop the movement of ocean currents and the species they carry.