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1

Introduction

Two and a half billion years ago life on Earth entered a new age. At that time the early biosphere consisted entirely of bacteria-like cells, churning through an anoxic, sulfurous ocean. Somewhere in this brew, a group of cells evolved a new form of energy industry, powered by the abundant sunlight and producing molecular oxygen as a by-product. The mutants began to spread, filling the ocean and atmosphere with oxidizing free radicals and gradually poisoning the planet for the anaerobic cells that had reigned since the beginning of life. By mastering this feat of oxygenic photosynthesis, the cyanobacteria came to rule the world, relegating the previously dominant anaerobes to fringe habitats and fundamentally transforming the geochemistry of planet Earth. The Great Oxygenation Event, as it is known, was probably the most far-reaching global change in Earth's history. And it had another momentous consequence: one cell's poison became another's food. A second group of opportunistic microbes evolved to exploit the growing supply of molecular oxygen, in the process developing a far more powerful molecular engine. This innovation, aerobic metabolism, drove the evolution of complex, multicellular life, which proliferated vigorously. Some 300,000 years ago that lineage spun off *Homo sapiens*.

It's been a long road from the Great Oxygenation Event to the current Anthropocene epoch. Perhaps 100 million years into the oxygen era, another evolutionary upheaval roiled the waters. In the blink of an eye, geologically speaking, global temperatures plunged and glaciers spread from the poles nearly to the equator, creating a "snowball earth" not seen before or since. The trigger, it now appears, was the proliferation of advanced eukaryotic algae, which produced dimethyl sulfide in such quantities that it nucleated a global cloud bank and tipped the earth system into a winter that lasted millions of years (Feulner et al. 2015).

Nor were such upheavals confined to Earth's microbial youth. Around 55,000 years ago—during a previous episode of rapid climate change—a band of early humans ventured out from their East African homeland and spread rapidly into Europe and across Asia. With little more than fire and crude stone tools, our ancestors overhunted, outcompeted, or displaced most other large land animals within a few centuries of arrival on every continent and island they encountered (Sandom et al. 2014). And our impacts have accelerated ever since. Within the lifetime of elderly people living today, humans have transformed the earth almost as profoundly as during the entire span since our departure from Africa more than 50,000 years ago. Like those first photosynthetic bacteria long before, *Homo sapiens* is now altering the composition of the atmosphere and climate in profound ways whose outcome we can only dimly foresee.

Why start a book about marine ecology with such ancient history? There are two reasons. First, these examples offer a vivid lesson about the central role of living organisms in the working of the earth system as a whole. The common thread running through them is that life has repeatedly and fundamentally transformed the atmosphere, the ocean, and the climate from the beginning of time. Consider what our planet's atmosphere and climate would be like in the absence of life (**table 1.1**).

TABLE 1.1 Influence of life on the geochemical composition of Earth's atmosphere

	Planetary atmospheres: Their composition			
	Venus	Mars	Earth without life	Earth as it is
Carbon dioxide	96.5%	95%	98%	0.03%
Nitrogen	3.5%	2.7%	1.9%	79%
Oxygen	trace	0.13%	0.0	21%
Argon	70 ppm	1.6%	0.1%	1%
Methane	0.0	0.0	0.0	1.7 ppm
Surface temperatures (°C)	459	-53	240 to 340	13
Total pressure (bars)	90	0.0064	60	1.0

Source: Lovelock (1995).

As late as the 1960s the scientific consensus was that Earth's atmosphere was produced passively by gases diffusing from the planet's interior, and that living organisms were passengers rather than drivers. This view was turned on its head by the atmospheric chemist James Lovelock and the evolutionary biologist Lynn Margulis, first in a series of journal articles (Lovelock and Margulis 1974) and culminating in Lovelock's famous (or infamous) book *Gaia: A New Look at Life on Earth* (Lovelock 1979), which argued that the atmosphere is "a dynamic extension of the biosphere itself." The Gaia hypothesis had its flaws. But it got right that Earth's atmosphere, and by extension global climate, are fundamentally influenced by metabolism of the living biosphere. These facts are now universally accepted (Kasting and Siefert 2002, Holland 2006).

Although each of these transitions in earth history could probably be linked to some environmental change, their far-reaching impacts were not predictable effects of environmental forcing. Instead, they involved intrinsic biological processes that spun off with their own momentum as a result of evolution and interactions among species (Falkowski et al. 2008). Similarly, at a much more local scale, organisms strongly influence one another's distributions, and thus the organization of communities, in ways only loosely related to the nonliving environment. The experiments on marine rocky shores in the 1960s that demonstrated this revolutionized ecology (Paine 1994, Bertness, Bruno, et al. 2014). We will see throughout this book that the pervasive consequences of biological interactions play out at local scales in shaping the organization of communities, just as they do at the scale of oceans and eons. Biodiversity, the interacting variety of living organisms, transformed the earth system. So the first lesson from these vignettes is that life is not just a passenger but also a driver of environmental processes—biology feeds back in powerful ways to shape the earth's abiotic environment.

The second theme illustrated by these examples is that life goes on. Even changes that seem catastrophic—that *are* catastrophic to those that experience them—eventually settle the ecosystem into a new groove around the altered conditions. Nature abhors a vacuum, as Aristotle first put it, and we can bet on the resilience of life to adapt and produce a productive, structured system in place of what was lost. This is not much comfort to those who depended on the former system, such as the Precambrian anaerobes sidelined in the Great Oxygenation Event, or modern societies that rely on predictable crop harvest and prices, or even those of us who simply love nature as it is. Change is hard. But it is inevitable.

These two themes offer both a cautionary tale and a ray of hope for the sobering challenges we face in the current Anthropocene age. The caution stems from the accelerating impact of humanity

on the distribution, abundance, and even existence of species, which will have far-reaching and still poorly understood consequences for the earth's ecosystems that support us. The hopeful message is that nature is resilient, with an inherent, vigorous capacity to recover even from major disturbances. This is reassuring since disturbances are a constant feature of the modern ocean. We can help it bounce back if we understand it. To be effective stewards of the earth and ocean, we need to understand how its parts fit together to make the system as a whole work. Building that understanding is the mission of this book.

A Framework for Functional Marine Ecology

Ecology is about understanding how living organisms interact with their environment. Its goals can be summarized in a few overarching questions: How does the environment influence the distribution and diversity of life? How do interactions among organisms modify those patterns? How do the groups of species that emerge from these interactions influence processing of energy and materials in ecosystems? And, finally, how do all those processes feed back to change the environment? Nearly every topic in ecology is a more specific derivation of one of these questions. But despite this superficial simplicity, ecology is the most difficult science. This is because it is, in essence, the study of everything. Ecology begins with energy from a star 150M km away, and follows that energy as it flows through biomolecules that mediate life processes, and interactions among species, to the metabolism of megacities built by technologically advanced humans. In the modern era, answering these questions requires every tool we can muster, from molecular probes of genomes to satellites that quantify biomass at a planetary scale. Because ecology is about interactions, everything is connected to everything else.

Organizing this sprawling domain poses big challenges. We need a framework to get hold of it. This book aims to advance such a framework for marine ecosystems. The basic argument is simple: ecosystems emerge from interactions among four major features of nature (**figure 1.1**), which are predictable in broad outline from biophysical principles. First, ecology begins with *geomorphology*: the shape of the rotating earth and the arrangement and composition of land masses on its surface. These factors constrain circulation of the ocean and atmosphere, which in turn create the climate and provide the physical template within which the other processes act. Second is the *abiotic environment*, largely defined by that geomorphic template and interacting with the sun's incoming radiation. The environment encompasses the solar and other energy that drives chemical and biological processes, the distribution of temperature that sets rates of those processes, and the distribution of water and chemical elements needed to create living biomass. Third is *biodiversity*, the constantly changing communities of living organisms that evolve and assemble in response to geomorphology and environmental forcing, and feed back to modify them. This network of diverse, interacting organisms is the heart of the dynamic earth system, comprising a sort of engine (Falkowski et al. 2008) that drives the fourth feature, *biogeochemistry*, the fluxes of energy and materials through the system.

This framework is not revolutionary. Anyone can see that the environment influences the distribution and abundance of organisms. Physical forcing of communities and ecosystems was central to the development of ecology as a science (Elton 1927, MacArthur 1972) and especially in biological oceanography, which is arguably the most integrative field of ecology (Mann and Lazier 1996, A. R. Longhurst 2007). It's also widely recognized that the kinds of organisms in a system influence fluxes of matter and energy (Chapin et al. 2000). Where this book departs from many previous treatments of ecology is its emphasis on the links between the four components, the bidirectional

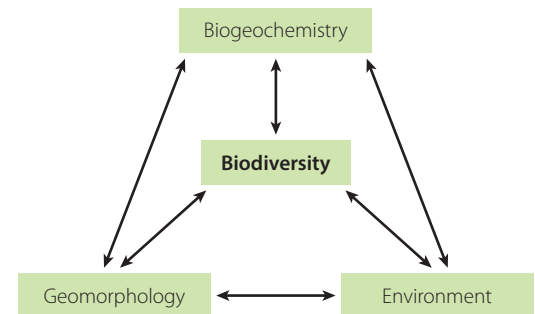


Figure 1.1. This book's framework for thinking about ecology.

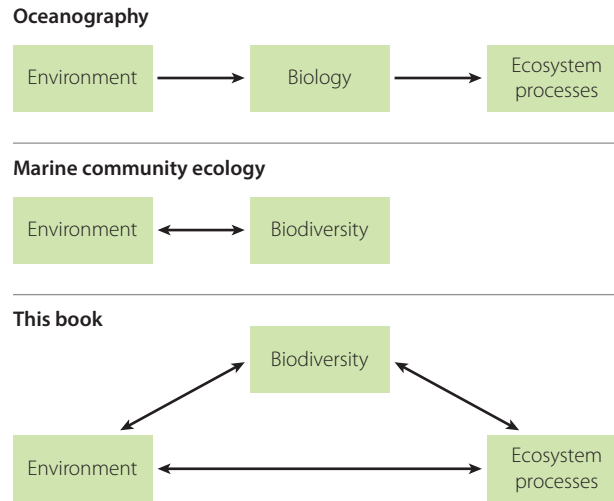


Figure 1.2. A simplified view of relationships among the environment, biological communities, and ecosystem processes in different traditions of marine science.

nature of these links, and the central role of biodiversity in the functioning of the ocean's ecosystems (**figure 1.2**). The vignettes that opened this chapter illustrate that environment, biodiversity, and biogeochemistry feed back intimately and strongly in both directions, and biodiversity is at their center (see figure 1.1). We will see that in modern times, as in early earth history, the kinds of organisms present are often just as influential as climate and resource supply in shaping the biomass, productivity, and cycling of materials through ecosystems, and that organisms fundamentally change—even create—the physical environment. Each of the links among these components is a two-way street. In modern parlance, an ecosystem is a *complex adaptive system*.

This ecological web is important to all of us because the earth is transitioning to a new geologic epoch, the Anthropocene (chapter 4). Human civilization grew up during the ~13,000-year Holocene epoch that followed the retreat of the last major ice sheets. The Holocene has been a period of climatic stability, which we take for granted. That stability is coming to an end, but it's less clear what will replace it. The profound changes in Earth's early history wrought by an evolving biosphere hold lessons for us in this new era.

Plan of the book

Following the functional framework outlined above, the book begins by introducing the main players in the ocean's ecosystems, approaches to organizing their diversity, and key features of their biology that drive ecosystem processes (chapter 2). We then consider geomorphology: the physical template defined by the earth's configuration of land and ocean, and how it has influenced the evolutionary history and current distribution of marine life (chapter 3). Having thus set the stage, we turn to the current Anthropocene epoch, and how marine ecology is changing in the modern ocean (chapter 4).

The next set of chapters develops the key features and processes at successive levels of organization, from individual organisms to ecosystems. Building the bridges between these levels—from environment, through biodiversity, to biogeochemistry—requires mechanistic theory. At the cellular level, the metabolic theory of ecology seeks to explain major features of organismal function based on physical principles, focusing on how metabolism varies with energy input, temperature, and the fundamental organismal trait of body size (chapter 5). These principles help link environmental drivers through activities of individual organisms to their abundance and distribution in communities. Organisms adapt to their environment via growth, reproduction, and genetic change within populations, which can be described mathematically (chapter 6). The pool of species produced by this adaptive process over evolutionary time is then filtered to a set that co-occurs within a local area—the

community—via the processes of dispersal and deterministic interactions (ecological selection), with a background of random demographic drift (chapters 7, 8). Neutral theory provides a null model against which to explore the importance of biological interactions in structuring communities. Lastly, at the broadest scale of the ecological hierarchy, interacting communities of organisms influence the fluxes of materials and energy through ecosystems (chapter 9).

The final set of chapters applies the concepts developed in the earlier sections to the major ecosystem types of the world ocean, including the open pelagic ocean and the deep-sea floor (chapter 10), coastal and estuarine systems (chapter 11), and coral reefs (chapter 12). Each of these chapters is structured around the themes we began with, building on a template of geomorphology, major physical forcing, the characteristic functional types of organisms that dominate under those conditions, and the ecosystem processes that emerge from their interactions. Each chapter concludes with a discussion of how its themes are changing in the Anthropocene ocean, and a consideration of the way forward, asking: What are the major unanswered questions that need attention? What are the current challenges that we need to overcome? How can we apply what we've learned to practical problems in marine ecology?

Some recurrent themes

Several themes emerge from this conceptual framework that recur throughout the book. The first has already been mentioned: the central importance of biological diversity. The essence of life is its tendency toward continuous, self-generated, adaptive change (Szathmary and Maynard Smith 1995). A consequence of life's responses to the physical environment acting over eons of earth history has been proliferation into a spectacular range of forms, functionally differentiated and interacting—that is, biodiversity (chapter 2). That biological diversity is often as important as underlying abiotic processes in determining patterns of biomass, productivity, trophic structure, even the composition of the atmosphere and ocean. As one example, phytoplankton—the tiny single-celled algae that dominate open-ocean waters—are more heavily grazed, channel less biomass to detritus, and store less carbon in sediments than higher plants like seagrasses with their complex, largely inedible support structures (Cebrián and Lartigue 2004). This dichotomy in traits of primary producers is largely responsible for the profound differences in how pelagic versus benthic ecosystems work (Steele 1985, 1991).

A second, related theme is that functional biology, the physics and chemistry of how organisms work, is the link between different scales and components of ecosystems. Differences in the elemental composition and nutritional quality among types of plants strongly influence how energy and nutrients flow up the food chain, constraining everything else that happens in the ecosystem (Cebrián et al. 2009). In the ocean, the availability of one element in particular, nitrogen, varies systematically among types of plants and strongly affects the biomass of herbivores that eat them, and hence all food web processes. Such relationships illustrate that ecosystem structure and biogeochemical fluxes are closely linked to the functional biology of species. That functional diversity is shaped by environmental forcing (chapter 3), but it also evolves idiosyncratically and, as the opening vignettes emphasize, can feed back to change the environment substantially. Focusing on function emphasizes the connections between environmental conditions, diverse assemblages of interacting species, and the fluxes of energy and matter through ecosystems that result from their activities. This approach contrasts with many previous approaches to ecology, which either intentionally ignore species (Mann and Lazier 1996) or treat explanation of species richness as an end in itself, largely divorced from their functional characteristics (Ricklefs 1987, Hubbell 2001, Vellend 2016) (see figure 1.2). I am not criticizing those approaches—explaining diversity and ecosystem processes are challenging and important jobs in their own right, and I draw heavily on those syntheses. But the frontier that we focus on here is the links between community composition and biogeochemical fluxes. I attempt to keep that frontier in view throughout.

The third recurrent theme is a special case of the importance of biology in the earth system mentioned above. This is the pervasive impact of the global keystone species *Homo sapiens*, which has made us a force of nature with a vastly outsized influence on Earth's ecosystems, including the world ocean (chapter 4). The ocean and especially the coastal zone is a very different world than the one that my grandparents were born into. Some estimates suggest we've lost two-thirds of the world's salt marsh and seagrass cover since measurements began (Lotze et al. 2006, Waycott et al. 2009) and a third of global mangrove area (Spalding 2010), and coral reefs face existential threats (Hughes, Barnes, et al. 2017). Like it or not, we are now the stewards of our planetary ecosystem. The future of all species, including our own, depends on our actions, and the next few decades will make or break their fate and our own. This is far more than an academic issue. We depend intimately on the ocean. Over a third of the world's population lives in coastal regions and islands that make up less than 5% of Earth's land area. The global ocean economy was valued by the OECD (2017) "very conservatively" at \$1.5 trillion, and provided 31 million full-time jobs in 2010, mainly in capture fisheries but with a substantial component in coastal tourism. Marine fisheries in 2013 provided 17% of the global population's supply of animal protein, and are especially important in coastal and small-island states of the developing world (FAO 2016). These and other services are degrading in the face of overfishing, pollution, and climate change, potentially threatening food security and human and environmental health (Millennium Ecosystem Assessment 2006b).

Humans in marine ecosystems

Humans have left a mark on ecosystems nearly from the day our ancestors ventured out of Africa millennia ago. In coastal regions, even small populations with simple technology quickly depleted the most easily accessible marine animals (Wing and Wing 2001). But human populations and impacts have exploded since the mid-twentieth-century "Great Acceleration" (chapter 4), altering all the major components of the earth system: the environment, biodiversity, biogeochemical fluxes, and even geomorphology in the case of coral reefs, river deltas, and heavily populated estuaries (**figure 1.3**). Humanity's rise has reached the status of a major historical event in earth history, comparable in scale to glaciations or tectonic movements. This is mainly a consequence of mobilizing huge quantities of fossil carbon formerly sequestered beneath Earth's surface and using it to power widespread land use change to support a growing human population and standard of living (Steffen et al. 2007). Humans have changed the rules of the game. Our understanding of how the natural world works was historically based on patterns in nature that developed over the long sweep of evolutionary time. Those expectations may no longer be valid because the systems we live in today are out of whack, far from the quasi equilibrium driven by the geography and environment of evolutionary history. Adapting the science of ecology to the human-dominated world is a central challenge for both basic and applied science.

Ecology in Practice

The central challenges of marine ecology

This book is motivated by the premise that major advances in marine ecology will be made at the interfaces between traditions and approaches—theory and natural history, benthic and pelagic, community and ecosystem, molecular and earth system—and between these historically basic fields of science and the applied fields of fisheries and environmental management and social sciences. Linking these approaches and perspectives brings a fuller toolbox than any individual tradition has been accustomed to using, and benefits from a range of advances in technology and data science. It is early days for this integration, but I hope that readers, especially students, are inspired to think in such terms about how to bridge boundaries.

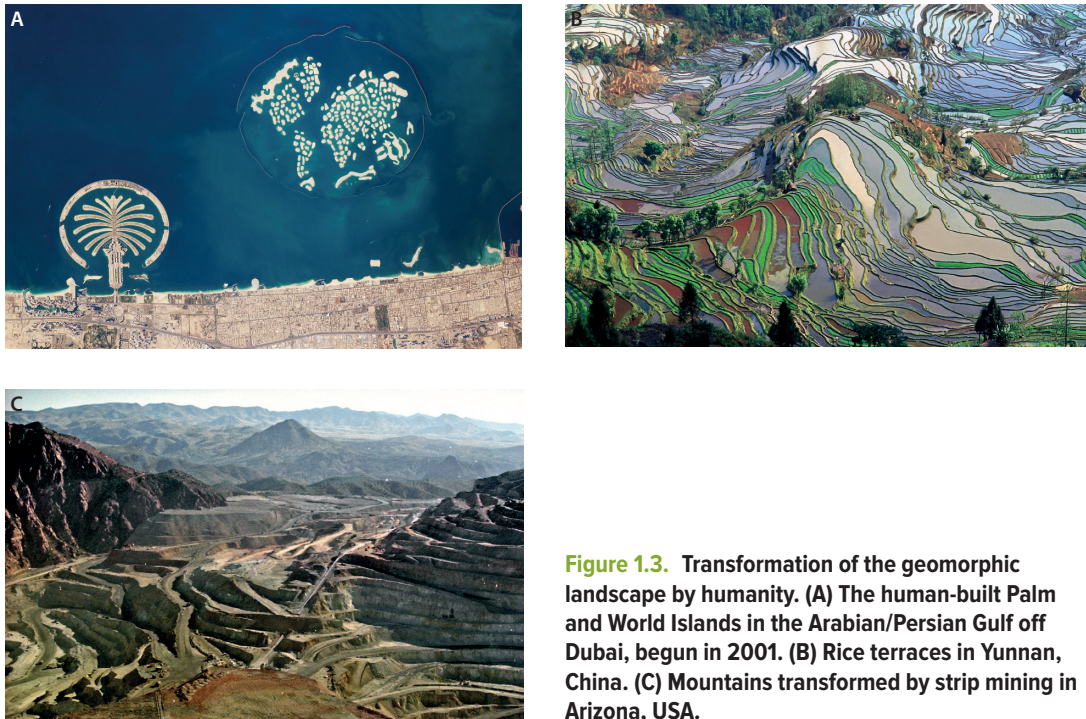


Figure 1.3. Transformation of the geomorphic landscape by humanity. (A) The human-built Palm and World Islands in the Arabian/Persian Gulf off Dubai, begun in 2001. (B) Rice terraces in Yunnan, China. (C) Mountains transformed by strip mining in Arizona, USA.

Complexity and contingency are inescapable in ecology, more so than in the physical sciences. That complexity is both exhilarating and intimidating, and stems primarily from biological diversity. The first spark of life has flourished into a variety of forms that we are still struggling mightily to get a handle on. Physics has a canon of field theories, chemistry has its periodic table, but it sometimes seems that biology has 10 million special cases. Or maybe 100 million; we're still not sure.

Fortunately, the situation is not so overwhelming as it may seem. Two features of life provide handles for taming this complexity. First, organisms are biophysical entities, composed of the same chemical elements and subject to the same physical laws as the rest of the universe (chapter 5). While the diversity of organisms is great, the ways they work are constrained within well-defined limits. This opens the door to general theory in ecology. Second, because all species radiated from a single origin, they share many characteristics, and the more recently a species arose, the more similar it is to its siblings in form and function. This means that, functionally, there are fewer types of life forms than there are species. This phylogenetic legacy often allows generalizations about how whole lineages of organisms function. All diatoms, for example, require silica to build their opaline shells, and all sea turtles need to come ashore to lay eggs.

Nevertheless, inherent tensions remain in ecology. Perhaps the central one is between holistic and reductionist approaches. Getting to know wild organisms and understanding what they do, that is, natural history, is the raw material of ecology at all levels. Personally, I have always loved identifying organisms, watching them, and figuring out how they make a living. Those details are critical to understanding organisms and their interactions, which are in turn critical to managing and conserving life. But seeing the forest that emerges from these trees—the ecosystem—can also require backing away from the details. Considering a system as a whole reveals that it is more than the sum of its parts. That is, ecosystems have emergent properties (chapter 9). I take it as given that the purpose of science is to seek and synthesize general rules of cause and effect about how the world works. My approach to ecology, which guides the organization of this book, seeks the generalities, the rules that transcend the details of natural history to explain why disparate organisms are built and behave as they do and how they interact to produce the emergent features of communities and ecosystems. In this context, the good news about the dizzying complexity of ecology is that it provides nearly

unlimited opportunities for seeking and testing those general rules. The best example of such a fundamental law is the theory of natural selection—it is simple enough to state briefly in plain language and to be understood by most anyone, yet powerful enough to capture the central mechanism that has produced the living world (chapters 5, 6). I strive throughout the book to link such underlying principles. Some arise from basic math and physics, such as the laws of thermodynamics and mass balance. Some can be expressed by simple equations, such as logistic population growth. Others are more multifaceted, such as the metabolic theory of ecology and ecological stoichiometry (chapter 5). My treatment of such theory usually includes minimal mathematics. This does not reflect a lack of appreciation for rigorous theory, but rather that I don't think intuitively in mathematical terms and, in my experience, neither do most students in ecology. I refer interested readers to other excellent sources for an entrée into the mathematics of ecology (Gotelli 2008).

How to balance holistic versus reductionist approaches? The art of ecology, in practice, is resolving the tension between generality and specificity, which amounts to an optimization problem. The solution depends on the question at hand. How much do we have to know about the system in order to characterize it at the necessary resolution? Optimizing the trade-off between generality and specificity depends on the goal and involves both empirical considerations and values. For conservation of an endangered species, it's important to know everything we can about its natural history, so we strive for specificity—studying the minute details of species biology and distribution, which are key to effective conservation and management. In contrast, if we want to answer the general question of why habitat fragmentation consistently reduces diversity across a wide range of ecosystems, we need to identify general principles. What is the sweet spot between the explanatory power of a model—meaning any proposed explanation, whether expressed mathematically or not—and the effort and resources required to evaluate it? In statistics, this optimization is a formal process that compares alternative models by weighing explanatory power against the cost in numbers of parameters used (Burnham and Anderson 2002). In ecology generally, the approach is more informal but the goal is the same. Since time, funding, and human capacity are limited, striking a balance between the explanatory power of our model and the cost of constructing that model becomes a serious, practical issue. Stated briefly, the central challenge is to achieve Einstein's somewhat cheeky recommendation: "Everything should be made as simple as possible, but not simpler."

How do we achieve that balance? There are no shortcuts. Historically, ecology was the province of field naturalists working with their wits and ordinary tools at hand. The field has evolved rapidly, and answering the questions posed above now requires bringing to bear the full panoply of approaches in modern biology, from molecular reconstruction of evolutionary history to large- and small-scale experimental manipulation of living communities in their natural habitats, to biogeographic analysis, micro-electronic physiology, and remote sensing applied to the physical drivers that act on scales of global spaces and eons—simulation models that strain even the colossal computational power of modern computers. Nevertheless, the single most critical tools for understanding how living things interact with their environment remain the human brain and senses. To deeply understand the ocean and its life, you have to plunge in and open your eyes. Only with the understanding that comes from careful observation will the shiny products and data streams of the modern age mean anything of importance.

The ocean and the shore

The very different traditions of biological oceanography (of pelagic systems) and what is usually called marine ecology (of benthic systems) have themselves been shaped strongly by the environment. Studies of pelagic and benthic systems use different methods, which have led to different cultures of research and to focus on different questions. Planktonic communities are mixed suspensions of tiny organisms, and directly observing them in their natural habitats is very challenging. Access to the open ocean requires big ships, and constraints of both shipboard work and the small sizes of

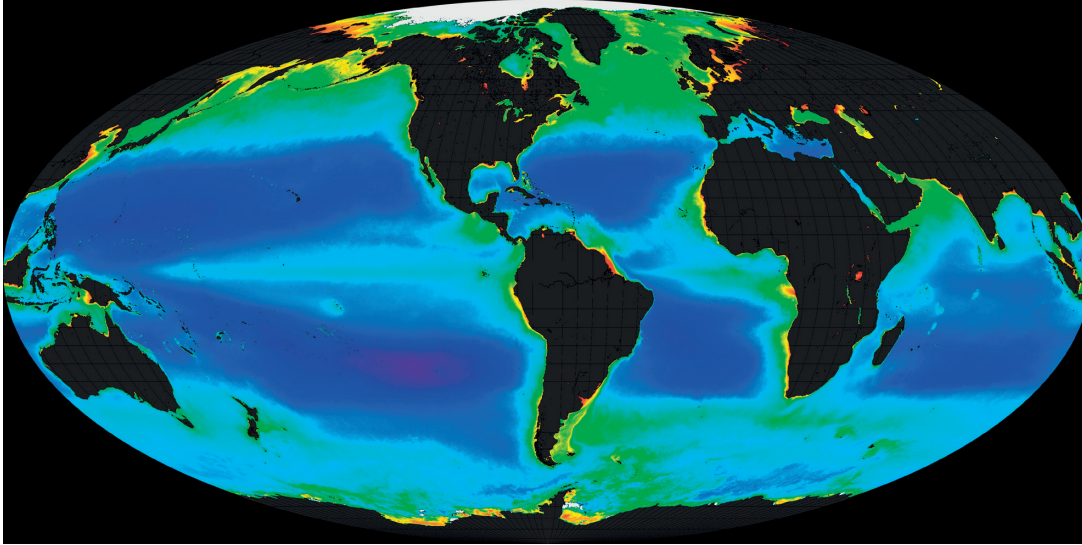


Figure 1.4. Distribution of primary producer biomass across the world ocean's surface. The image is a composite average of sea surface chlorophyll concentrations since the SeaWiFS satellite was launched in 1997. Chlorophyll concentrations range from very low (deep blue) in the open ocean to highest (red) in the most productive coastal areas.

plankton favor a focus on aggregate properties, such as bulk chlorophyll as a measure of producer biomass. Importantly, both the dynamic, physically forced nature of pelagic systems and those logistical constraints have encouraged a culture of multidisciplinary collaboration in oceanography. Biological oceanography thus focuses primarily on questions about ecosystem-level processes involving broad functional groups on large, regional scales. For example, how does physical forcing interact with nutrient concentrations to explain global and regional patterns of phytoplankton biomass and production (chapter 10)? The triumph of this approach is vividly illustrated by the view from space of the distribution of the ocean's primary producers (**figure 1.4**), which can now be reproduced surprisingly accurately by models (Follows et al. 2007).

Benthic marine ecology has had a different flavor, traditionally practiced by lone naturalists and steeped in place-based knowledge. Benthic ecosystems are dominated by seaweeds and sessile invertebrates that are attached and visible to the naked eye, fostering a focus on detailed observation and experimentation. Benthic marine ecology thus developed around questions about interactions among species on organismal scales: How do competition and predation influence local diversity and species composition? Which species are most important to community organization and why? Much of the pioneering work on processes of community organization in ecology as a whole emerged from experimental research in marine benthic communities, particularly those of rocky intertidal shores (Paine 1994, Bertness, Bruno, et al. 2014). In recent years, the approaches of biological oceanography and benthic community ecology have begun to converge, to the benefit of both. I hope this book helps advance that convergence.

The major patterns

Marine ecology was born early in the twentieth century from the need to understand and manage fisheries (Petersen 1918). The natural focus was what controls the productivity of plants, the forage animals that sustain fish, and the fish themselves. With the benefit of detailed modern knowledge (see figure 1.4), we have been able to address more specific questions: Why is primary production concentrated at high latitudes and along coastlines? Why do some regions of the ocean

rich in nitrogen support so little phytoplankton biomass? How important are predators compared with inorganic nutrients in controlling plant biomass, and what factors influence the relative strengths of these controls? How can coral reefs, with little visible plant biomass, support such an abundance of large fish? Conversely, why do many coastal systems, such as seagrass beds, support luxuriant plant biomass that goes largely uneaten? The answers to these questions require understanding how environment, resources, and traits of plants and consumers interact. We address them in this book, and we offer important questions that have not yet been answered.

As change in the ecosystems accelerates during the Anthropocene, a new set of questions is redirecting our attention from the mythical pristine systems that traditionally occupied marine ecology to those that we see plainly all around us, transformed by the footprint of humanity. How common are alternative stable states in marine ecosystems and how can we recognize them? What features of the human-dominated seascape are favorable versus detrimental for marine life, and how do we maximize the favorable aspects? Increasingly, the most pressing questions are at the interface of natural and social science, involving the ecology of the keystone species *Homo sapiens*: What policy measures most effectively mold human behavior to sustainable practices, locally and globally? How do we take advantage of human nature to achieve desirable ends? And how do we coevolve our social contracts and our relationships with nature toward a world that is just and fair for all? Answering these questions will require entrepreneurial, solution-oriented attention. This book aspires to provide a foundation for addressing them.

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