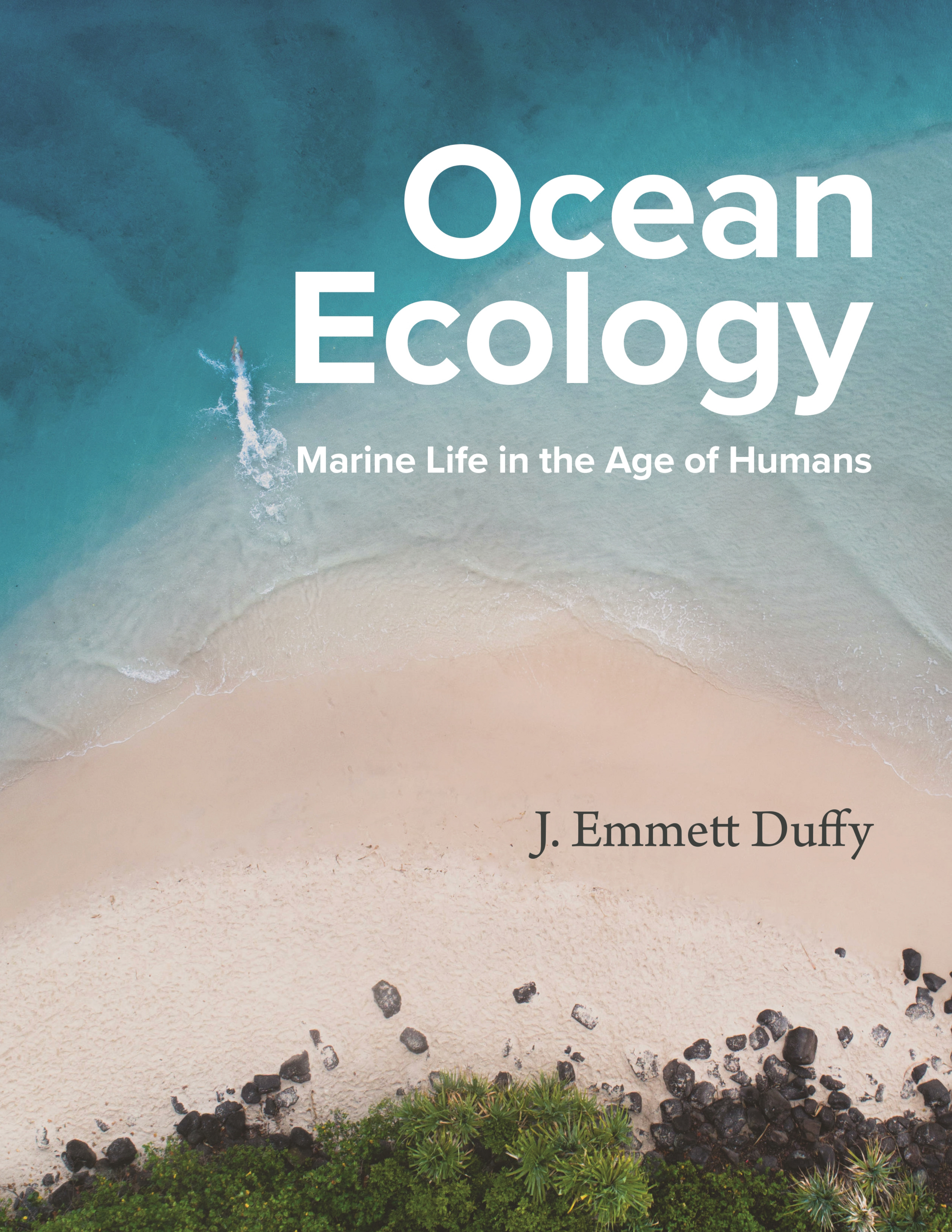

Ocean Ecology

Marine Life in the Age of Humans

J. Emmett Duffy

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Preface

When I entered grad school, I was required to enroll in physical oceanography. Completing the course meant resurrecting the calculus I'd learned in college and promptly forgotten. One day I confessed to my professor that I was struggling with the complex math. He seemed surprised, and said "But physics is simple—there are clear and consistent laws that can be described by equations. What's really complex is *your* field, ecology."

He was right. The difference between physics and biology stems from the extravagant variety and idiosyncrasy of life, Earth's most striking feature as well as the most formidable challenge to understanding how it works. The rules of life seem far fewer, and the exceptions more numerous, than those of physics. This book aims to put that diversity at the center of our understanding of the world ocean. It is organized around the conviction that biodiversity—the variety of life forms—is the heart of functioning ecosystems, and aspires to outline a coherent framework for understanding its drivers, dimensions, and functional roles in ecosystems.

This way of thinking is relatively new to ecology. Research on ecological structure—the distribution and abundance of species—has historically taken a separate path than that of systems ecology, meaning the emergent biogeochemical fluxes of energy and materials through a land- or seascape. These paths are the provinces of community ecology and ecosystem ecology, respectively—two separate nations, with distinct cultures, languages, and literatures, and little traffic across the gulf between. But that gulf may be yielding—a sort of revolution over the last two decades is building a bridge.

As a postdoc in the early 1990s, I was captivated by the first experiments exploring how species diversity influences ecosystem productivity, a topic that seemed a perfect marriage between the fascination of natural history and a profound scientific and societal challenge. I spent much of the next decade thinking about this problem and exploring it with experiments. Over that time I was struck by repeatedly hearing the same criticisms: that the experiments proliferating around this theme were simplistic (which largely was true, at least in the beginning) and were a distraction from more important processes driving ecosystems in the real world (which arguably was not). In fact, there are several reasons to suggest that biodiversity may in fact be more, not less, important in wild nature than in experiments. A decade later I believe that suggestion has been vindicated. Growing evidence shows that the kinds and numbers of species are just as important as major environmental gradients in mediating the way ecosystems work. Of course, the environment ultimately controls what kinds of organisms live in a system, so this dichotomy is somewhat artificial. But the biological composition of ecosystems also owes a lot to idiosyncrasies of evolutionary history and dispersal (or lack thereof), so similar environments in different regions can differ substantially in ecosystem processes. For example, prior to European colonization, northern North America lacked earthworms, which allowed accumulation of leaf litter and greatly altered soil properties.

The functional characteristics, or traits, of organisms determine how they affect ecosystem processes. Focusing on the roles of traits in ecological processes opens the door (with a very long hallway still ahead) to a unified functional ecology—from the biophysical processes that drive cellular metabolism, through interactions among species, to flows of materials through ecosystems. The central link and the central challenge to such unification is the diversity of life's functional capacity. Although clearly central to ecology, the challenge in integrating biological diversity into a unifying framework is idiosyncrasy, the seemingly infinite and unpredictable ways that organisms make a living. So addressing the specifics of major marine ecosystem types is unavoidable in understanding them.

Among the most comprehensive treatments of marine ecological processes, from individual to ecosystem level, at the graduate level was Ivan Valiela's book of that name, first published in 1984. In the preface to the second edition (1995), Valiela highlighted the impossibility of keeping track of the vigorous flood tide of scientific literature. That was over two decades ago (and he was hardly the first—even Charles Elton bemoaned the difficulty of keeping up in 1927). The situation is far more daunting today. One book and one author can't pretend to cover the whole of marine ecology more than superficially. Instead I propose a way of thinking about ocean life and a foundation of basic knowledge on which the rest can be built. I hope this will give students a framework for connecting the parts.

While working on this book, I've had to contemplate the possibility that scientific books may be fading into obsolescence in the internet age. I hope not. If anything, books—the right kinds of books—are more valuable than ever in the torrent of overwhelming information (not to mention disinformation), fragmentation, and eroding attention span endemic to the online media ecosystem, whatever its other benefits. I grew up in an age when books were central, even revered. Many of them changed my life. I can only hope that this one proves to be useful for someone else.

Acknowledgments

I owe a special debt to my PhD adviser, Mark Hay, who influenced me more than anyone outside my nuclear family. I arrived at the University of North Carolina's Institute of Marine Science as a PhD student only three years after Mark started as an assistant professor. The timing was fortuitous—his initial flurry of grant-writing was bearing fruit and there was suddenly a lot to do and few people to do it. Mark was a locomotive of energy and intellect, and it was exhilarating trying to keep up. We traveled all over the world together. Those were great years. I didn't fully appreciate until much later how fundamentally my worldview was shaped by the immersion, literally and figuratively, in so many regions of the ocean. One of Mark's many gifts was pushing me through long practice to unlearn the numbing, jargon-laden style so common in scientific writing. I have tried to employ that lesson here.

Dennis Taylor took a chance and hired me in my first permanent job during his brief but transformational tenure as director of the Virginia Institute of Marine Science, as he set it on the course toward a world-class institution. When I arrived at VIMS as a green assistant professor in 1994, my first assignment was a new graduate course in marine ecology cotaught with another new but more senior arrival, Hugh Ducklow. This was a stroke of luck. I'm a marine benthic community ecologist with a natural history bent, and Duck, as most call him, is a biological oceanographer with expertise in microbial ecology, ecosystem modeling, and a quantitative, global outlook. The two of us somehow welded together the poles of biological oceanography and benthic community ecology into a unique course, and we taught it together for the next 13 years. I not only gained a deep knowledge of the ocean as a global ecosystem but also learned from Hugh how to teach. To this day the way I approach the subject, including a strong focus on primary literature, owes much to his example during those early days as a deer in the headlights.

Science is a community. It is rooted in personal interactions, diverse perspectives, debate, competition, collaboration, rivalries, and friendships. The knowledge and ideas that arise from that ecosystem are themselves like living entities that grow and evolve such that it is often difficult to trace where they came from. My thinking has been influenced, no doubt in ways I don't fully recognize, by the many colleagues, mentors, and students that have been my community over the years. There are too many to name individually, since I will surely overlook someone important, but in addition to those mentioned above, I must thank several formal and informal mentors, including Nancy Knowlton, Mark Bertness, Rick Grosberg, John Graves, and Seth Tyler. I also gratefully acknowledge several reviewers who provided thoughtful feedback on early chapters of this book and helped steer it clear of a treacherous fate. These include Mark Hay, Jennifer Ruesink, and especially Mark Carr and his students, who gave me a timely and invaluable reality check on how to serve the needs of young people starting out in the field. Michael Tennenbaum gave me the opportunity of a lifetime and challenged me to raise the bar as high as I can. And I am grateful to three institutions that sponsored the deep experiences of ocean life that I hope are reflected in the following pages: the Virginia Institute of Marine Science, the Smithsonian Institution, and the National Science Foundation. This is contribution 77 from the Smithsonian's MarineGEO and Tennenbaum Marine Observatories Network. Alison Kalett, my editor at Princeton University Press, first approached me with the idea for this book, expertly parried my initial skepticism, and kept me on course with sage advice at several key junctures in its (long) evolution—I am so happy we both stuck with it, and it has been a pleasure working with the staff of Princeton University Press. Thank you to Carmen Ritter, who drafted the glossary, and to Eleanor Cole, Leah Harper, and Michelle Rossman who shouldered much of the burden of organizing figures and permissions.

Finally, and in many ways most importantly, it's hard to imagine where I would be now or what I would be doing without my family. I had the good fortune that my childlike curiosity survived into adulthood and found a place to take root, thanks largely to my supportive parents. My spouse and son, Liz and Conor, have been the joy of my life and contributed to this book more than any of us know through the seemingly endless years of its gestation. "I could drink a case of you, darlin'."

Ocean Ecology

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

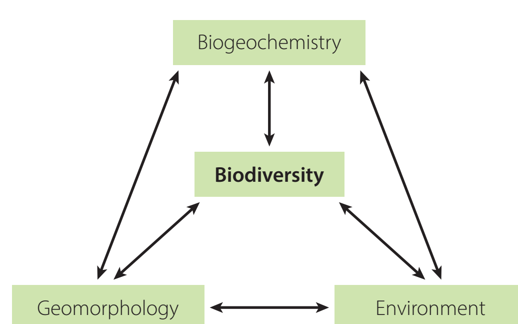

Figure 1.1. This book's framework for thinking about ecology.

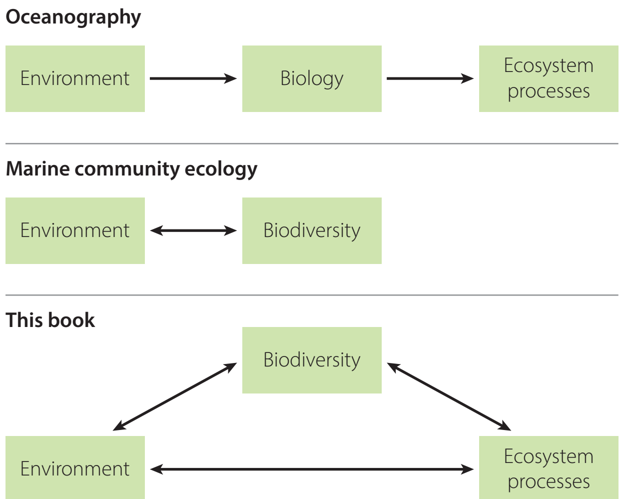

Figure 1.2. A simplified view of relationships among the environment, biological communities, and ecosystem processes in different traditions of marine science.

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.

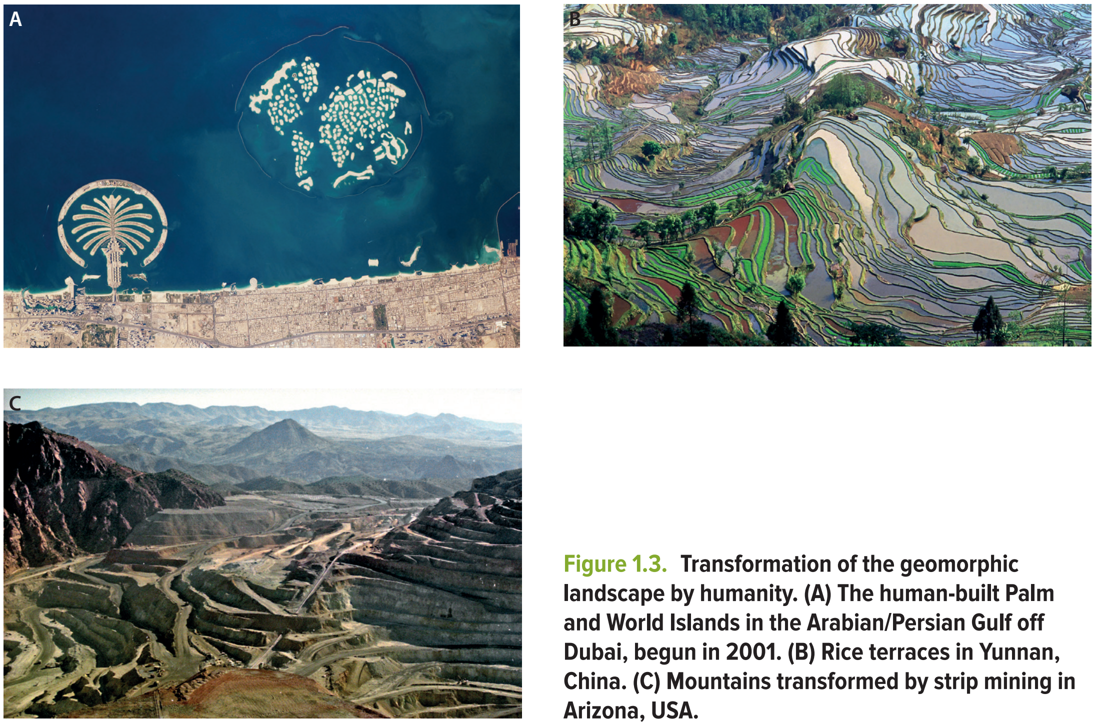

Figure 1.3. Transformation of the geomorphic landscape by humanity. (A) The human-built Palm and World Islands in the Arabian/Persian Gulf off Dubai, begun in 2001. (B) Rice terraces in Yunnan, China. (C) Mountains transformed by strip mining in Arizona, USA.

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, microelectronic 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

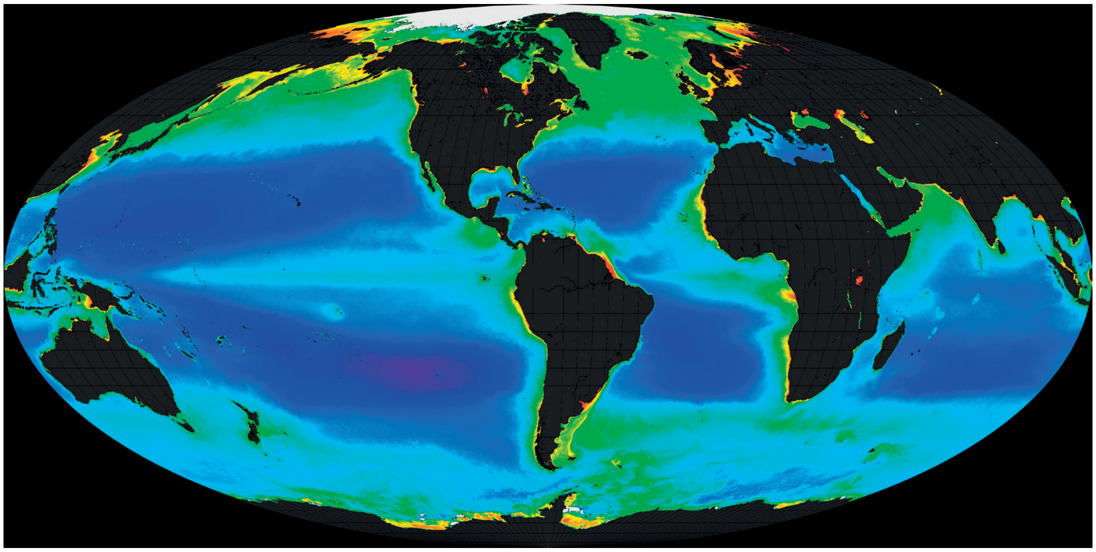

Figure 1.4. Distribution of primary producer biomass across the world ocean's surface. The image is a composite average of sea surface chlorophyll concentrations since the SeaWIFS satellite was launched in 1997. Chlorophyll concentrations range from very low (deep blue) in the open ocean to highest (red)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

2 Life in the Ocean

The Magnitude of Biodiversity

Life is our planet's most striking feature, what uniquely distinguishes it from the rest of the universe, and what drives the functioning of Earth's ecosystems. The diversity of life is staggering: roughly 1.9 million different kinds of organisms—species—have been described scientifically, at least 226,000 of which live in the ocean (Appeltans et al. 2012). But those are only a fraction of the number that remain unknown to science. Estimates of the total number of species on Earth differ widely, based variously on expert opinion, proportions of undescribed species in field samples, extrapolation from rates of new species descriptions, and macroecological scaling laws. Most estimates are in the range of 5–11 million eukaryotic species worldwide, 0.7–2.2 million of them marine (Costello et al. 2012, Appeltans et al. 2012, Pimm et al. 2014). The uncertainty is especially high for the ocean because most of it is unexplored and populated by tiny organisms that are difficult to sample. A survey of a small beach in Scotland sequenced DNA from sediments and detected 182 species of nematodes (roundworms) alone along an 800 m transect, which compares with ~450 species of nematodes previously described from the entire British Isles (Fonseca et al. 2010). More than 95% of the sequences did not match sequences in publicly available databases, and many are new to science. Similarly, DNA barcoding of invertebrate communities that colonized on settling plates at two well-studied sites on the east coast of the USA turned up over 2000 species, many of them new to science, and 22 phyla (Leray and Knowlton 2015).

Discovery of a new species of mammal or bird routinely generates press around the world, whereas we are still finding new groups of marine invertebrates at the deepest branches of the animal kingdom (i.e., phyla) (**figure 2.1**). Since 1983 these have included the Loricifera, tiny creatures nestling among sand grains; and Cycliophora, which make their living among the mouthparts of Norwegian lobsters (Kristensen 2002). And then there is the invisible world of microbes, which are key players in all marine ecosystems and whose almost unfathomable diversity is only now coming into view with the aid of modern genomics (chapter 10). Scaling laws applied to a comprehensive database of molecular sequences suggest there may be as many as a trillion species of microbes worldwide (Locey and Lennon 2016).

Biological diversity, often abbreviated as *biodiversity*, is usually defined as the variety of life forms at all levels, including genetic variation within species, among species, and among ecosystem types. A detailed account of the diversity of marine organisms is well beyond the scope of this book, but understanding how ecosystems work requires some knowledge of biodiversity. In this chapter we take a brief tour of the tree of life's major branches, their functional characteristics, and approaches to organizing that functional diversity. We review the evolutionary origins of diversity in chapter 3 and the processes that maintain diversity within communities in chapter 7. The influence of biodiversity on ecosystem processes is discussed in detail in chapters 8 and 9, and is a theme we return to regularly.

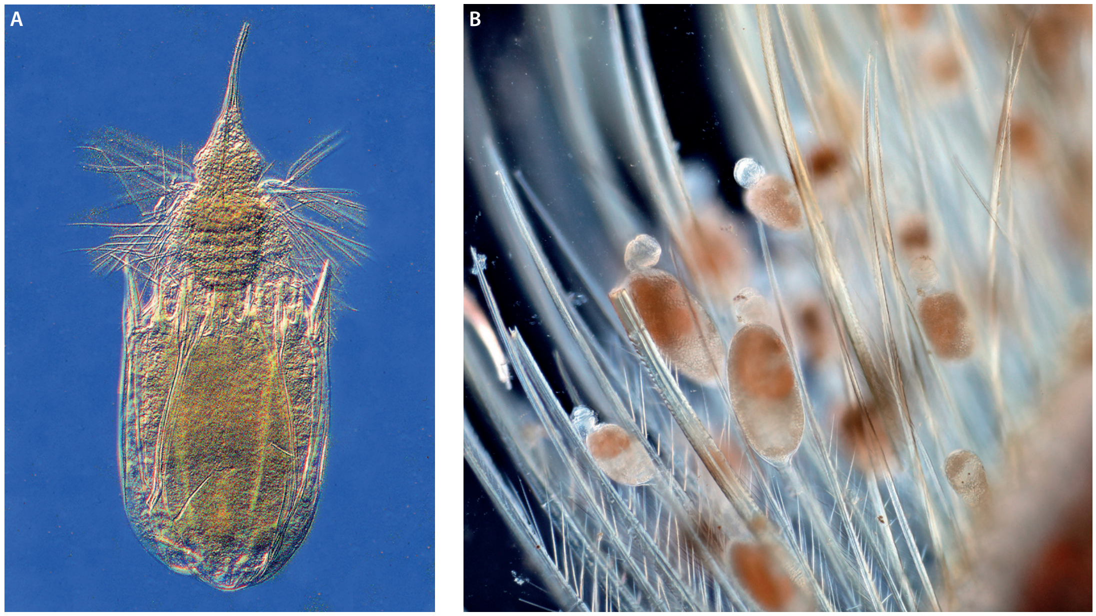

Figure 2.1. **New discoveries among the deep branches of life in the ocean. (A) *Nanaloricus mysticus*, phylum Loricifera, described in 1983. (B) A member of the phylum Cycliophora in its natural habitat, clinging to the mouth-hairs of a Norwegian lobster.**

Diversity on Land and Sea

Most animal species are found on land because most species of animals are insects, which are absent from the ocean. Beetles alone account for nearly a quarter of all eukaryotic species described so far. So species diversity is lower in the sea than on land. However, the great majority of terrestrial organisms, in both abundance and number of species, come from only three major groups: seed plants, insects, and vertebrates. Therefore, these three taxa, along with microbes, dominate the workings of terrestrial ecosystems. Terrestrial global change biology, for example, focuses largely on the biology of seed plants.

But among higher taxa, meaning the deep branches of the tree of life, the ocean is vastly more diverse than the land (**table 2.1**). Roughly 35 animal phyla are currently recognized, though the number changes occasionally as new phylogenetic analyses suggest that a taxon is more or less unique than previously believed. Only one of these phyla, the obscure velvet worms (Onychophora), lives only on land, and even this is an artifact of extinction in the sea since fossils remarkably similar to onycophorans are known from the 500-million-year-old marine sediments of the Burgess Shale. In contrast, nearly half the known phyla of animals occur only in the sea, and these include not only microscopic creatures like loriciferans and cycliophorans but also many of the ocean's major players and ecosystem engineers (**figure 2.2**). The echinoderms, for example, are exclusively marine and include the familiar sea urchins—important herbivores in benthic ecosystems worldwide—and the original keystone predator, the sea star *Pisaster ochraceous*. The sponges (Porifera) are sessile filter-feeders that arose from single-celled ancestors on a branch possibly separate from that of all other Metazoa (multicellular animals). These unique organisms include a few freshwater species, but in the ocean sponges have radiated into a diverse and abundant fauna. Sponges dominate many benthic communities, include large and important habitat-forming species, and dominate water-column biogeochemical processes in such systems by pumping huge volumes of seawater as they

TABLE 2.1 Diversity of marine and terrestrial animals at the deepest branches of life (phyla)

Exclusively marine	Marine & nonmarine	Exclusively nonmarine
Brachiopoda (lamp shells)	Acanthocephala	Micrognathozoa
Chaetognatha (arrow worms)	Annelida (segmented worms)	Onychophora (velvet worms)
Ctenophora (comb jellies)	Arthropoda (joint-legged animals)	
Cycliophora	Chordata (chordates)	
Dicyemida	Cnidaria (coelenterates)	
Echinodermata	Ectoprocta (bryozoans)	
Echiura	Entoprocta	
Gnathostomulida	Gastrotricha	
Hemichordata (acorn worms)	Mollusca (mollusks)	
Kinorhyncha	Nematoda (roundworms)	
Loricifera	Nematomorpha (horsehair worms)	
Phoronida	Nemertea (ribbon worms)	
Placozoa	Platyhelminthes (flatworms)	
Priapulida	Porifera (sponges)	
Sipuncula (peanut worms)	Rotifera (wheel animals)	
Xenacoelomorpha	Tardigrada (water bears)	
Total phyla: 17	**16**	**2**

Source: Norse (1993).

feed on suspended bacteria. There is nothing like them on land. Arrow worms (Chaetognatha) are an exclusively marine phylum of small, fanged predators common throughout the blue waters of the open ocean. The list goes on. At the higher taxonomic levels, then, the ocean is far more diverse than the land.

As is true of animals, the functional diversity of primary producers is much greater in the ocean than on land (**figure 2.3**). Nearly all terrestrial primary producers belong to a single clade derived in the distant past from green algae (the Embryophyta or "land plants"), whereas marine autotrophs come from all three of life's major domains—Archaea, Bacteria, and Eukarya—and comprise at least eight major divisions or phyla among eukaryotes alone. Marine primary producers range from photosynthetic bacteria of several kinds, through the smallest known eukaryotic organism *Ostreococcus tauri* (Prasinophyceae)—a tiny planktonic cell with a single mitochondrion and chloroplast (Courties et al. 1994)—to the giant kelp *Macrocystis pyrifer*a, which can reach a length of > 45 m and creates the physical habitat that supports rich coastal ecosystems in cooler waters of both the North and South Pacific (figure 2.3B). These divergent lineages are often lumped together as "algae," a disparate group that includes all aquatic phototrophs that are not flowering plants. Even flowering plants inhabit the margins of the ocean, having secondarily invaded the sea from terrestrial ancestors, and they are dominant producers along the coastal fringes (chapter 11).

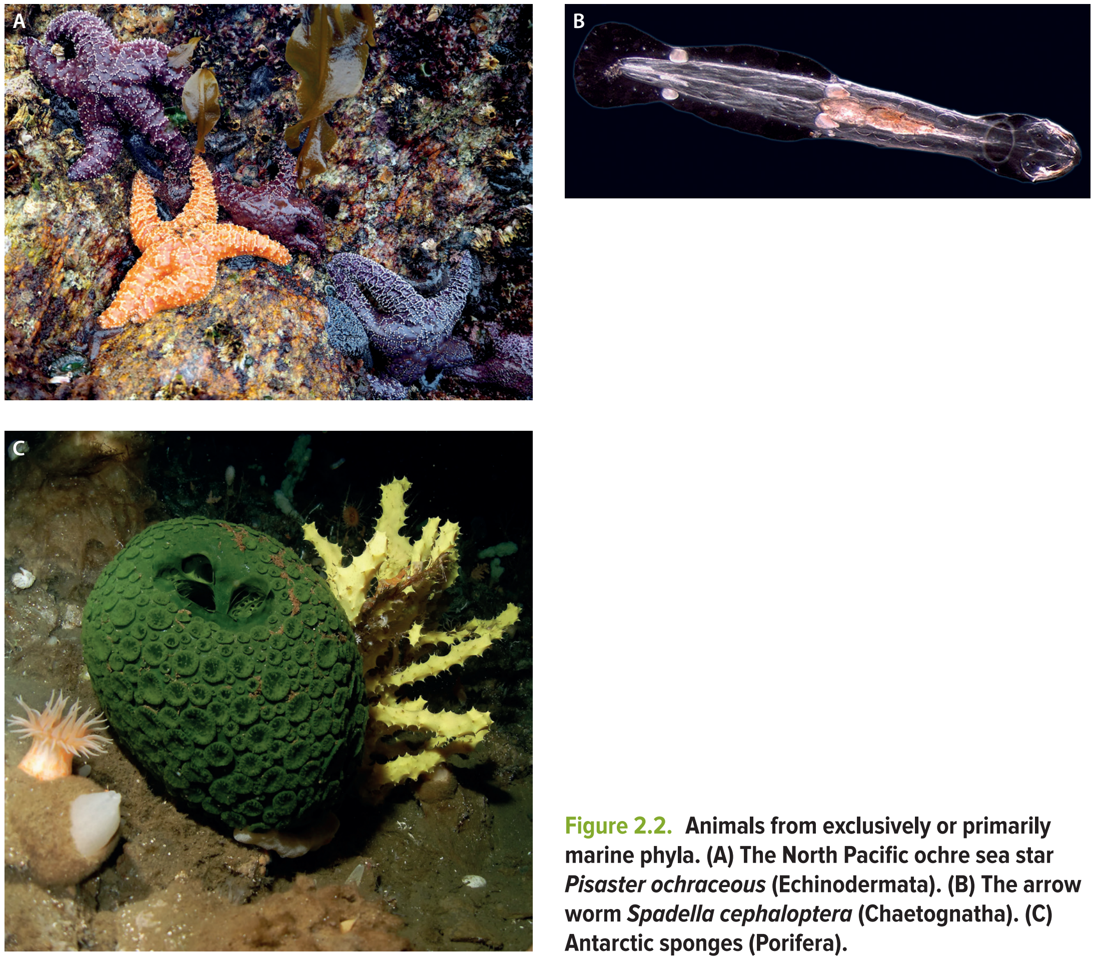

Figure 2.2. **Animals from exclusively or primarily marine phyla. (A) The North Pacific ochre sea star *Pisaster ochraceous* (Echinodermata). (B) The arrow worm *Spadella cephaloptera* (Chaetognatha). (C) Antarctic sponges (Porifera).**

The invisible life of the ocean—the microbes—are in a class by themselves. The term *microbes* refers to prokaryotes and single-celled eukaryotes (**figure 2.4**). Microbes make up the bulk of the marine biosphere's living biomass and species diversity and by far the greatest functional diversity of metabolic pathways that underlie biogeochemical processes. Biological oceanography has been transformed in the last few decades by the discovery of the vast abundance, diversity, and ecological importance of these very small organisms. The most striking example is the picoplanktonic cyanobacterium *Prochlorococcus*, the most abundant photosynthetic organism on Earth, making up 30%–60% of total phytoplankton biomass throughout the *oligotrophic* open ocean. But microbes also include a plethora of ancient lineages of Bacteria, Archaea, eukaryotes invisible to microscopy, parasitic flagellates that infect nearly all major taxa in the plankton, and an abundant community of even smaller viruses (**box 2.1**). Most of the organisms in this microbial menagerie are smaller than the phytoplankton captured in nets, and thus were underestimated or missed entirely by traditional sampling methods. This world first came to light in 2003 when shotgun genome sequencing was applied to water samples collected from the Sargasso Sea, producing more than 1800 species of planktonic microbes, many of them only distantly related to previously known lineages (Venter et al. 2004).

Phylogenetic Classification of Marine Biodiversity

Species can be classified either phylogenetically, according to common ancestry (who they are), or functionally (what they do). The two approaches coincide to some degree because closely related species also tend to be functionally similar—for example, all diatoms are unicellular, photosynthetic

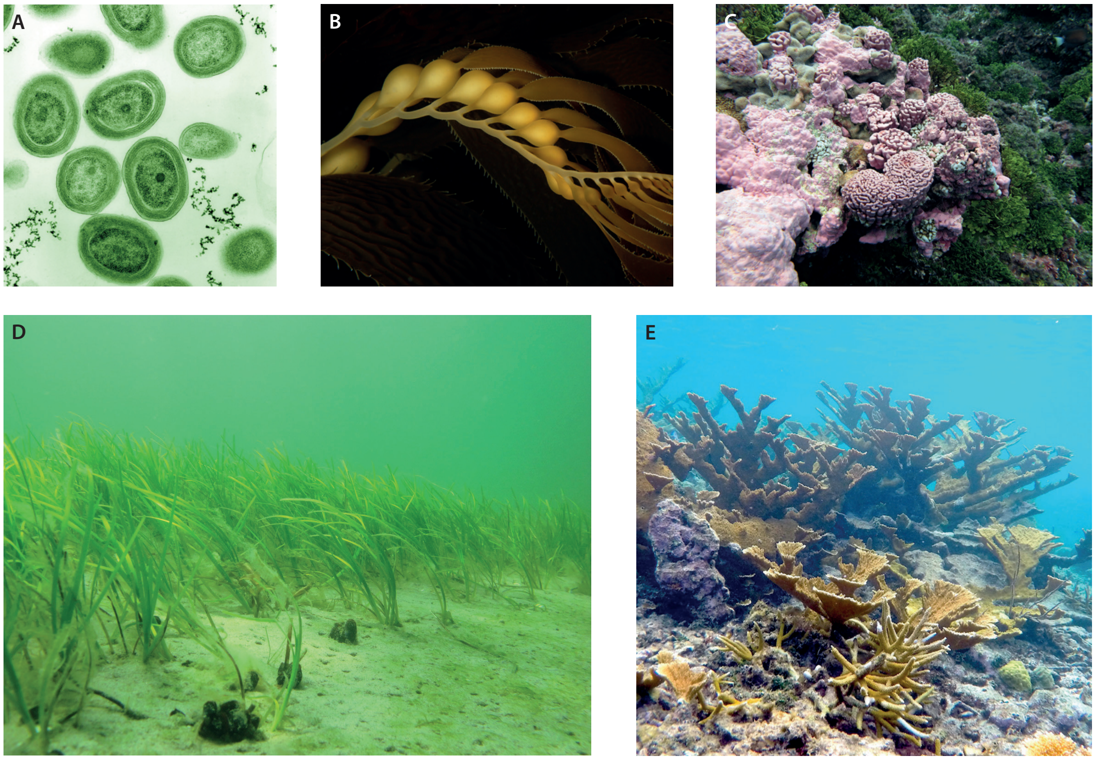

Figure 2.3. The diversity of marine primary producers. (A) The picoplanktonic cyanobacterium *Prochlorococcus*, dominant primary producer of the oligotrophic ocean. (B) The giant kelp *Macrocystis pyrifera*, world's largest marine plant. (C) A crustose coralline alga, characteristic of highly grazed habitats. (D) The seagrass *Zostera marina*, most widespread marine macrophyte in shallow water. (E) The reef coral *Acropora palmata*, former foundation species of shallow reefs throughout the tropical West Atlantic. Reef corals derive most of their nutrition from symbiotic algae, so are functionally plants.

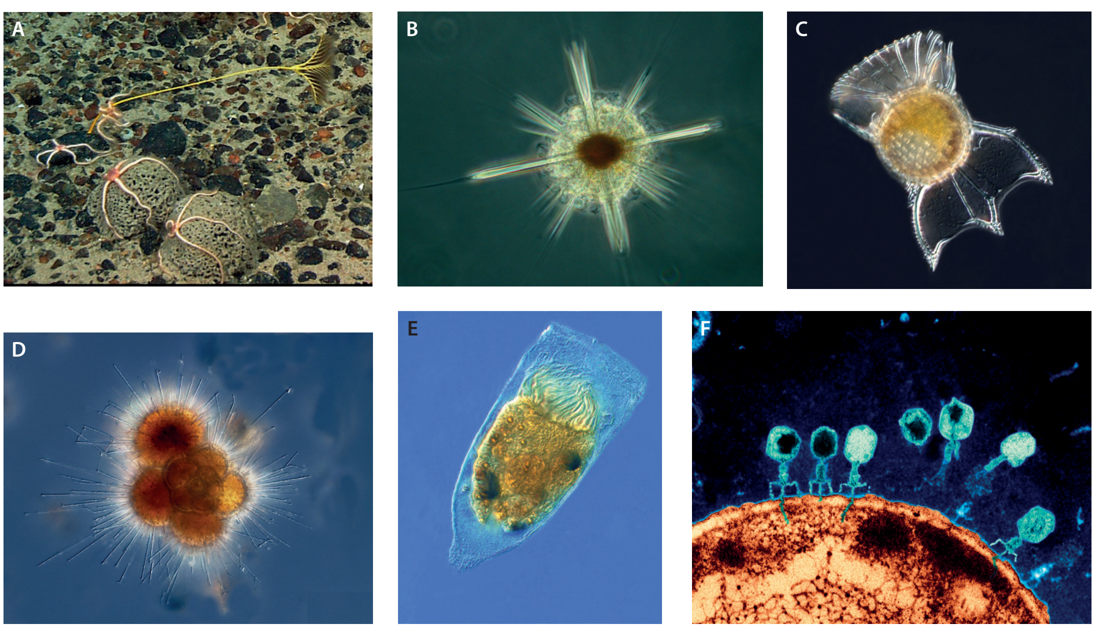

Figure 2.4. The diverse microbial life of the ocean. (A) Giant xenophyophore protists on the deep-sea floor, providing habitat for brittle stars. (B) A planktonic radiolarian. (C) The dinoflagellate *Ornithocercus*. (D) A planktonic foraminiferan. (E) A tintinnid ciliate. (F) Viruses at the surface of a host cell.

Box 2.1. Invisible ocean: Discovery of a new microbial world

Early in the twenty-first century the developing genomic revolution blew the lid off the classical view of the ocean's pelagic ecosystems, revealing a staggering diversity and abundance of tiny, previously unknown organisms. The first milestone came with a comprehensive inventory of microscopic organisms in seawater using *metagenomics*, that is, characterization of genetic material from bulk environmental samples rather than by sampling individual species. In the early 2000s researchers used the new technique of whole-genome shotgun sequencing to census the microbial communities in surface waters from the Sargasso Sea off Bermuda. In this approach, a

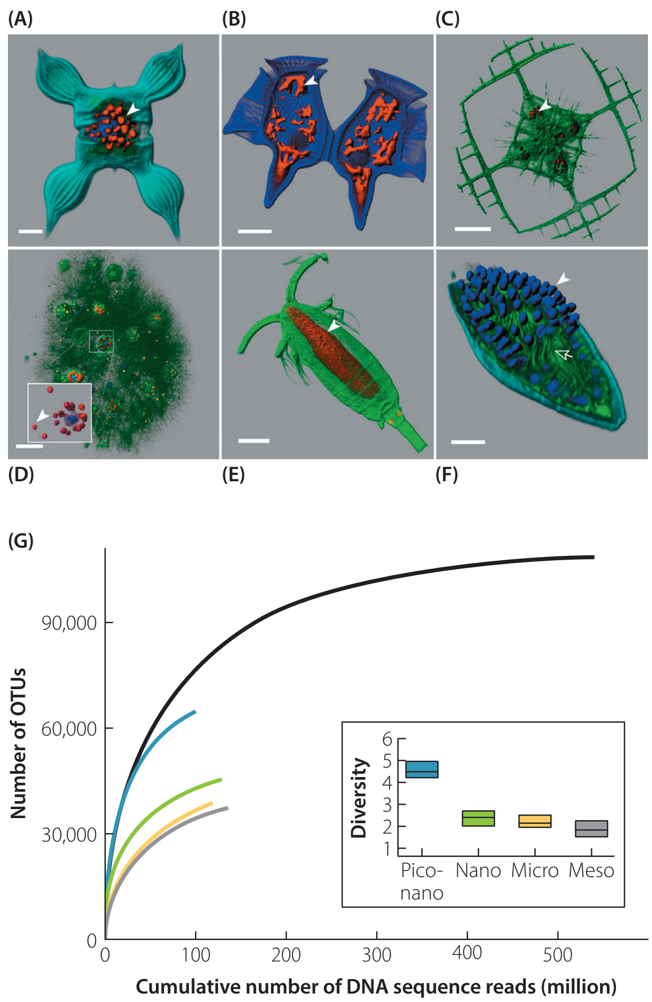

Figure B2.1.1. **(A) A diatom *Chaetoceros bulbosus* (Stramenopila), with chloroplasts shown in red (scale = 10 µm). (B) A heterotrophic dinoflagellate with kleptoplasts in red (scale = 20 µm). (C) An Acantharian with endosymbiotic cells of the haptophyte alga *Phaeocystis* in red (scale = 50 µm). (D) A colonial network of Rhizarians with captive dinoflagellate symbionts (scale = 50 µm). (E) A copepod with gut colonized by parasitic dinoflagellates in red (scale = 100 µm). (F) Cross section of a dinoflagellate infected with parasitoid alveolates (blue spots) (scale = 5 µm). (G) Rarefaction curves of number of operational taxonomic units (OTUs) with increasing number of samples, and Shannon diversity (inset) for each size fraction of plankton (after de Vargas et al. 2015).**

genomic sample is broken up into random fragments and sequenced; then powerful computer algorithms reassemble the fragments into coherent genome sequences by matching them along areas of overlap. The Sargasso Sea census revealed at least 1800 *operational taxonomic units* (OTUs, or putative species), including 148 previously unknown bacterial types, and over a million new genes (Venter et al. 2004). Molecular explorers then turned to deep ocean environments, first in the North Atlantic and waters around hydrothermal vents, finding that bacterial communities in these habitats were up to two orders of magnitude more diverse than any previously reported. Most samples were dominated by a few common and abundant types, as is true of nearly all ecological communities (chapter 7), but beyond these were a long list of thousands of species represented by only a few sequences each. Many of the latter were radically different from previously known lineages and apparently very ancient, and were dubbed the "rare biosphere" (Sogin et al. 2006).

The next major exploration of the ocean's invisible biosphere targeted pelagic communities worldwide, in both the surface and deeper ocean. The Tara Oceans expedition launched a sailing schooner that sampled 68 sites around the world. The voyage yielded more than 40 million gene sequences from the ocean's smallest organisms (viruses, prokaryotes, and small eukaryotes) and revealed no end in sight for the diversity of marine microbial life (figure B2.1.1). Samples of the intermediate plankton size range, from the smallest eukaryotic protists to the smallest animals, produced ~150,000 putative species, about a third of which could not be assigned to any known higher taxon (de Vargas et al. 2015). As is also common among larger animals and plants, community composition of the more than 35,000 species most strongly followed gradients in temperature, but in contrast to larger organisms there was little clear differentiation among geographic regions (Sunagawa et al. 2015).

Ocean metagenomic studies have since moved beyond the description of diversity to catalog the types and frequencies of interactions involving the microbial menagerie—the ocean's "interactome" (Lima-Mendez et al. 2015). The Tara expedition samples revealed a rich range of interactions (figure B2.1.2). Among the surprises was the commonness of parasitism, even among the tiniest protists and copepods: the largest number of interactions involved Syndiniales, a group of parasitic and symbiotic dinoflagellates that infected nearly all taxa of both protists and metazoans (mostly copepods) in these samples. Viruses were also abundant and highly host-specific. These results suggest a much more intricate and specialized interaction web than previously suspected, implying that parasitism exerts a profound and previously underappreciated impact on plankton dynamics and therefore on biogeochemical cycles.

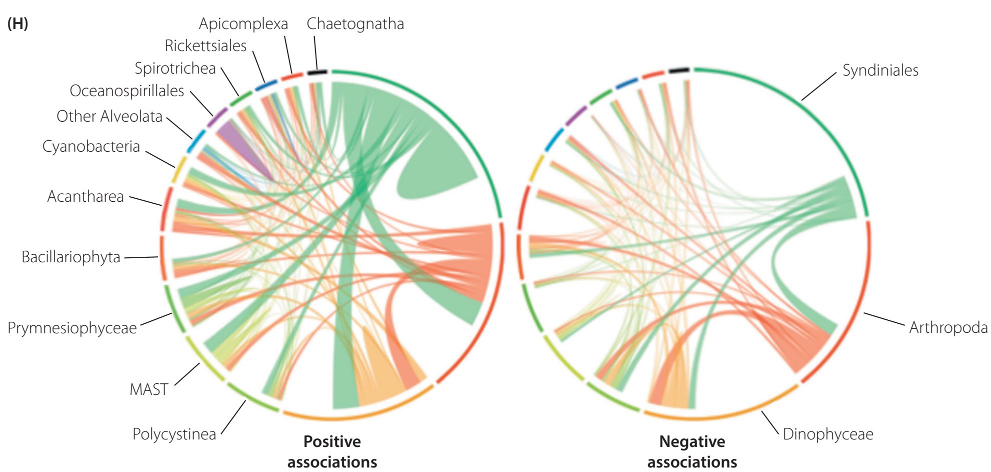

Figure B2.1.2. The interactome of the open pelagic ocean. Figures show links among the top 15 taxa as colored segments, where links connecting two segments indicate co-occurrence (left) or mutual exclusion (right). Thickness of the connector reflects the number of links between the species within each category, and color reflects the partner taxon with the most total links (after Lima-Mendez et al. 2015).

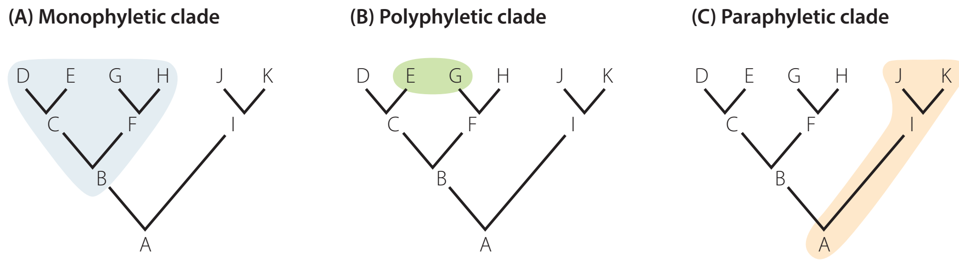

Figure 2.5. Schematic phylogenetic trees, showing (A) a natural group (monophyletic clade) of species defined by shared lines of evolutionary descent, and (B, C) two types of nonnatural groups.

organisms with a siliceous shell. But the converse is less reliable: functionally similar species are not always closely related. As noted above, unicellular, photosynthetic organisms (phytoplankton) include a highly diverse collection of prokaryotic and eukaryotic lineages that diverged early in earth history. Here we review the major branches in the tree of life before turning to functional approaches for classifying marine organisms.

The tree of life

Because all life forms arose from a single origin early in Earth's history, they are related by a pedigree, or family tree of species, known as a *phylogeny* (**figure 2.5**). A phylogeny summarizes the lines of descent and thus the evolutionary relationships among the entities at the tips, whether they be species or genes (D. A. Baum et al. 2005). The common ancestry of all species has two implications for ecology. First, the pattern of ancestral relationships defines a natural, hierarchical classification of life. This classification begins with domains or kingdoms, which represent the earliest branching trunks of the evolutionary tree and extend to closely related species as the twigs at its tips. Reconstructing that pattern of branching and using it to classify life is the province of *phylogenetic systematics* (Nei and Kumar 2000, Wiley and Lieberman 2011). The second consequence of life's common ancestry is that evolutionary divergence among species is roughly proportional to the time since they were separated, and therefore recent common ancestry of species implies some similarity in their biology. Indeed, it is surprisingly common for ecologically important traits to be conserved at very deep branches in the tree of life. For example, all peracarid crustaceans—the amphipods, isopods, and their kin, which include over 10,000 species—have direct development, hatching into benthic juveniles without a planktonic stage. This conserved development mode has large consequences for demography, population genetic structure, ecological interactions, and evolutionary processes. Similarly, feeding mode (e.g., carnivory, herbivory, planktivory) is typically conserved at the level of taxonomic family or even higher levels in many fishes and invertebrates. Such evolutionary conservatism can have far-reaching consequences for ecosystems. A global meta-analysis of marine herbivory shows that the strongest predictors of grazer impacts on plants are producer taxonomic order and morphology (which are related), whereas, surprisingly, there is little or no effect of latitude, temperature, or nutrients (Poore et al. 2012). This phylogenetic conservatism of ecological traits has generated an active field of comparative methods and phylogenetic community ecology (Webb et al. 2002, Srivastava et al. 2012). Despite (or perhaps because of) this progress, it is important to emphasize that ancestry is not destiny—many taxa of organisms show strong phylogenetic conservatism in their traits, but these are nevertheless poor predictors of ecological interactions (Losos 2011). Trait-ecology relationships need to be tested, not assumed.

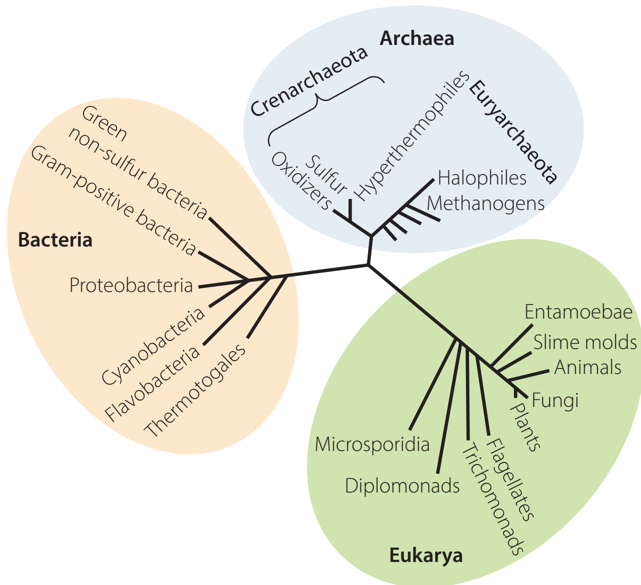

Figure 2.6. The tree of life, showing its three main branches. These contain 92 named phyla of Bacteria, 26 phyla of Archaea, and the eukaryotic supergroups.

With the advent of modern DNA sequencing and *metagenomics*, the tree of life has been revealed in much finer resolution. Life is now recognized as having three main trunks or domains, the Bacteria, Archaea, and Eukarya (**figure 2.6**), which diverged very early in earth history. One of the most important events in late twentieth-century biology was the discovery, hidden among the Bacteria, of a formerly unrecognized deep branch of life, the Archaea—organisms superficially similar to Bacteria in being tiny cells lacking nuclei, but otherwise as different genetically and metabolically from Bacteria as either is from animals or plants. Many of the genes and metabolic pathways of Archaea are closer to those of eukaryotes than of Bacteria and, uniquely among living organisms, their cell membranes contain ether lipids. Archaea include many of the key players in ocean ecosystems, occurring throughout the ocean water column and sediments, but they are especially important in chemically extreme environments, such as low-oxygen zones, sulfide-rich sediments, hydrothermal vents, and chemical hot springs (Woese et al. 1990, Offre et al. 2013). These *extremophile* Archaea greatly expand the metabolic capacity of the biosphere over that attributable to Bacteria and eukaryotes. They include organisms that produce methane and that inhabit hot springs and nearly salt-saturated waters, and cells that metabolize metal ions, methane, and even elemental hydrogen.

Bacteria and Archaea are the oldest life forms on earth. In addition to their lack of nuclei and other intracellular infrastructure, they share the curious ability to transfer genes among unrelated organisms, which shuffles genetic material, and associated physiological and metabolic capacity, among lineages. Such *horizontal gene transfer* among Bacteria is one reason for the frightening spread of antibiotic resistance among human pathogens in hospitals. It has also played a central role in developing the collective metabolic capacity of the ocean *microbiome* (Falkowski et al. 2008). The promiscuity of horizontal gene transfer probably also facilitated a key event in life's early history when entire bacterial cells were engulfed by, and incorporated as permanent symbionts within, cells of Archaea. The symbiotic bacteria eventually became completely integrated into their host cells—we now know them as mitochondria—enabling a powerful new form of energy metabolism that greatly increased efficiency of energy production. These early cellular chimaeras were the ancestors of the first eukaryotes, and their energetic superiority enabled them to flourish and diversify as the third domain of life (Lane 2015). Another such symbiotic event involved capture of photosynthetic cyanobacteria by early eukaryotes, which were permanently integrated as chloroplasts. Over subsequent eons, many genes of the originally free-living symbionts were lost, while others were transferred permanently to the host's genome, blurring the distinction between host and symbiont. Such horizontal gene transfer is a standard mode of evolution among Bacteria and Archaea, and was long thought to be restricted to these relatively simple organisms. In contrast, the genetic material of eukaryotes is isolated within a membrane-bound nucleus, and their cells are far more complex structurally than those of Bacteria and Archaea. Yet genomic studies provide growing evidence that horizontal gene transfer from prokaryotic symbionts to eukaryotic hosts has been common and has had major consequences (Boto 2010), for example, in allowing certain herbivorous insects to tap new food sources and become major crop pests (Moran et al. 2008).

The Eukarya include virtually all living things with which most people are familiar and are traditionally divided into four kingdoms: plants, animals, fungi, and protists. Another major outcome of the molecular revolution of recent decades has been recognition that single-celled eukaryotes, formerly lumped into the grab bag of "Protozoa," constitute a highly diverse collection of lineages, as different from one another as humans are from jellyfish (figures 2.4, 2.6). Recognition of this deep diversity required the erection of a large number of new phyla of single-celled organisms, collectively known as protists (Caron et al. 2012, Forster et al. 2016). These developments highlight the point that the living world is and always has been microbial—large, complex animals like *Homo sapiens* are anomalies.

Phylogenetic relationships and tree thinking

How is the tree of life reconstructed? Classification of life by genealogical relationships is based on two premises: (1) the natural unit of classification is a *monophyletic* group or *clade* (from the Greek *klados*, "branch"), that is, a group that contains an ancestral species and all its descendants; and (2) these monophyletic groups are defined in practice by shared derived characters (*synapomorphies*), which provide evidence of common ancestry. A phylogenetic tree is thus a set of hierarchically nested groups, or clades (see figure 2.5). By contrast, early taxonomic classifications grouped species by characteristics that are superficially similar but not inherited from common ancestors (e.g., Linnaeus's taxon "Vermes" for many unrelated wormlike animals). The Vermes is an example of a *polyphyletic* group, one that includes descendants of multiple unrelated ancestors. Another example is "algae," which includes members from the Bacteria and several unrelated protist groups. The second type of artificial taxonomic group is the *paraphyletic* taxon, which includes some but not all descendants of a common ancestor. An example is "fishes," which excludes the terrestrial vertebrates that evolved from fishes and are nested within that clade. The traditional group "Protozoa" is also paraphyletic because it excludes the animals and fungi that evolved from protists.

How do we identify shared derived characters? Because the ancestors of most life forms are long extinct and cannot be directly observed, genealogical relationships must be reconstructed using the indirect evidence still available to us. This comes from fossils, which are fragmentary and generally available only for groups with mineralized skeletons, and from the DNA sequences of living organisms. DNA preserves a record of ancestry, but it is obscured by evolutionary processes over the long period of time since divergence. Thus, some ingenuity is required to extract the signal of common ancestry from the noise of subsequent random mutations and adaptations. Reconstructing a phylogenetic tree starts with collecting data on characters, a generic term for any observable feature of an organism, which can include morphology, biochemistry, or behavior. The most valuable characters are in DNA sequences, which provide rich quantities of data and for which models of evolution are well worked out. In essence, phylogeny reconstruction compares the sequences of bases in the DNA of species under the assumption that the differences among them have accumulated via random mutation over time. Mutated sequences that are shared among species, and that differ from those of other species, are considered evidence of common ancestry. To analyze that evidence, models of evolutionary change in sequences are applied to the distribution of character states (base sequences, in the case of DNA) among species, which groups them into hierarchical patterns of genealogical relationships. A central principle guiding phylogenetic reconstruction is *parsimony*: given a choice between evolutionary scenarios, the one that requires the fewest evolutionary changes in the observed data is preferred.

The web of life

Divergence of lineages from a common ancestor over Earth's history has created a branching pattern of relationships among lineages and species—a tree of life. But those branches are not forever separate from one another. In some cases, lineages fuse with one another partially and exchange genes even among rather distantly related evolutionary branches, as mentioned above, forming what is more accurately a web of life than a tree. Such horizontal gene transfer is common among prokaryotes, but it also occurs more often than previously appreciated among eukaryotic lineages (Andersson 2005). In some types of organisms, exchange of genetic material across species, known as *hybridization*, is fairly common. For example, hybridization among species is routine in oak trees, which have nevertheless retained their integrity as species for millions of years. Among marine animals, hybridization and genetic introgression among species appears to be especially widespread in reef corals, some of which are better thought of as *syngameons*—complexes of partially interfertile species that regularly exchange genes (van Oppen et al. 2001, Ladner and Palumbi 2012). Hybridization is important for a couple of reasons. First, genes obtained by hybridization increase the functional capacity of a lineage, with important consequences for its physiology, species interactions, and ecosystem processes. Second, the distinctness of individual species is often maintained as much by their use of different habitats and geographic separation as it is by their intrinsic behavior and physiology. But in the Anthropocene, human activities are transporting and mixing species that were formerly separated, and the rate of hybridization is increasing dramatically as a result. That hybridization has consequences for conservation and management of populations in the modern ocean, for example, as aquaculture species escape into the field.

Functional Organization of Pelagic and Benthic Life

Ecosystem processes are the outcome of what species do. Process-oriented ecology therefore requires organizing biodiversity by the functions that organisms perform. An individual organism works as an integrated whole; but, like a machine, examining its parts helps us understand how it works. Those parts include any characteristic of the organism, whether morphological, biochemical, physiological, or behavioral, and are referred to as traits. A *functional trait* is any characteristic of an organism that influences its fitness by affecting growth, reproduction, or survival (Violle et al. 2007). Functional traits include fundamental characteristics common to all organisms, such as body size, fecundity, and rates of metabolism and growth, as well as more specific characteristics—ability to fix nitrogen, produce defensive chemicals, and so on. We can further distinguish two types of traits: *effect traits* influence what species do, including their use of energy and resources, growth rates, and interactions with other species, whereas *response traits* affect how species respond to environmental forcing (Lavorel and Garnier 2002).

The functions that organisms perform are of course also shaped by the environments where they live. The major dichotomy among marine ecosystems is between the pelagic realm, where organisms are suspended in the open, three-dimensional water column, and benthic systems, where life is concentrated around organisms anchored to the two-dimensional seabed. The physical conditions of these realms favor different functional types of organisms and thus differences in ecosystem processes. Below we outline pelagic and benthic functional diversity.

Functional groups of pelagic life

The open ocean is home to a wider range of life forms than anywhere else on Earth (figures 2.3, 2.4, 2.7). Biological oceanographers have traditionally classified them from a functional perspective, mainly because of sampling logistics, since different size classes of plankton are caught with different gear. Plankton sampling relies mostly on nets, and the larger eukaryotic algal cells and small invertebrates they retain are often referred to as *net plankton*, in contrast to the smaller microbes that can be captured only on very fine filters. Today plankton are still categorized mainly by body size (**table 2.2**). The *picoplankton* comprise cells 0.2–2 μm in size and include the smallest eukaryotes, but mainly prokaryotes, including the dominant phytoplankton of the open ocean, the cyanobacterium *Prochlorococcus*. Most ocean Bacteria and Archaea fall within the picoplankton size class, which contains a large part of the ocean's biomass and phylogenetic and metabolic diversity. Picoplanktonic eukaryotes are also diverse, phylogenetically and functionally, comprising many lineages of photosynthetic and heterotrophic protists, primarily bacterivores, that are important links in the *microbial loop*, discussed in chapter 10 (Massana 2011). The *nanoplankton* (2–20 μm) include both phototrophic and heterotrophic eukaryotes, at the smallest limit of resolution by light microscopy. Photosynthetic flagellates in the nanoplankton size range are major components of many plankton communities, particularly under stratified, low-nutrient conditions where their high surface-to-volume ratio and the mobility conferred by the flagellum provide an advantage over other phytoplankton types in accessing scarce nutrients. The *microplankton* (20–200 μm) include many of the familiar taxa of the classical net phytoplankton, such as diatoms and larger dinoflagellates. The *mesoplankton* (0.2–2 mm) are at the low end of the metazoan size range, notably the small copepods historically considered the major herbivores of the open ocean. The *macroplankton* (> 2 mm) include larger copepods, krill, and the gelatinous animals, such as medusae, ctenophores, and salps (**figure 2.7**).

Size classes of organisms generally correspond roughly to functional groups because body size strongly affects biological rates and modes of life. Functional groups may include phylogenetically distinct species that perform similar processes, such as the several unrelated photosynthetic lineages lumped as algae. But functional groups often correspond to distinct phylogenetic lineages (i.e., higher taxa). Among primary producers, examples include nitrogen-fixers or diazotrophs (certain lineages of cyanobacteria), silica producers (diatoms), and calcifiers (coccolithophorids). Functional groupings are more subjective than phylogenetic classifications since species may be grouped quite differently depending on the traits of interest. But most functional schemes group species by some combination of body size and metabolic capacity.

TABLE 2.2 Size-based classification of plankton

Group	Size (ESD)	Major taxa
Macroplankton	> 2 cm	Metazoans: pteropods, chaetognaths; euphausiids, medusae, ctenophores, salps, pyrosomes, amphipods
Mesoplankton	0.2–20 mm	Metazoans: copepods, cladocerans, ostracods, chaetognaths, pteropods, heteropods
Microplankton	20–200 μm	Protists: foraminifera, ciliates; metazoans: rotifers, copepod nauplii
Nanoplankton	2–20 μm	Small protists: diatoms, flagellates, pyrrophytes, chrysophytes, chlorophytes, xanthophytes
Picoplankton	0.2–2 μm	Bacteria, cyanobacteria, Archaea, chrysophytes, smallest protists
Femtoplankton	< 0.2 μm	Viruses

Note: ESD = equivalent spherical diameter.

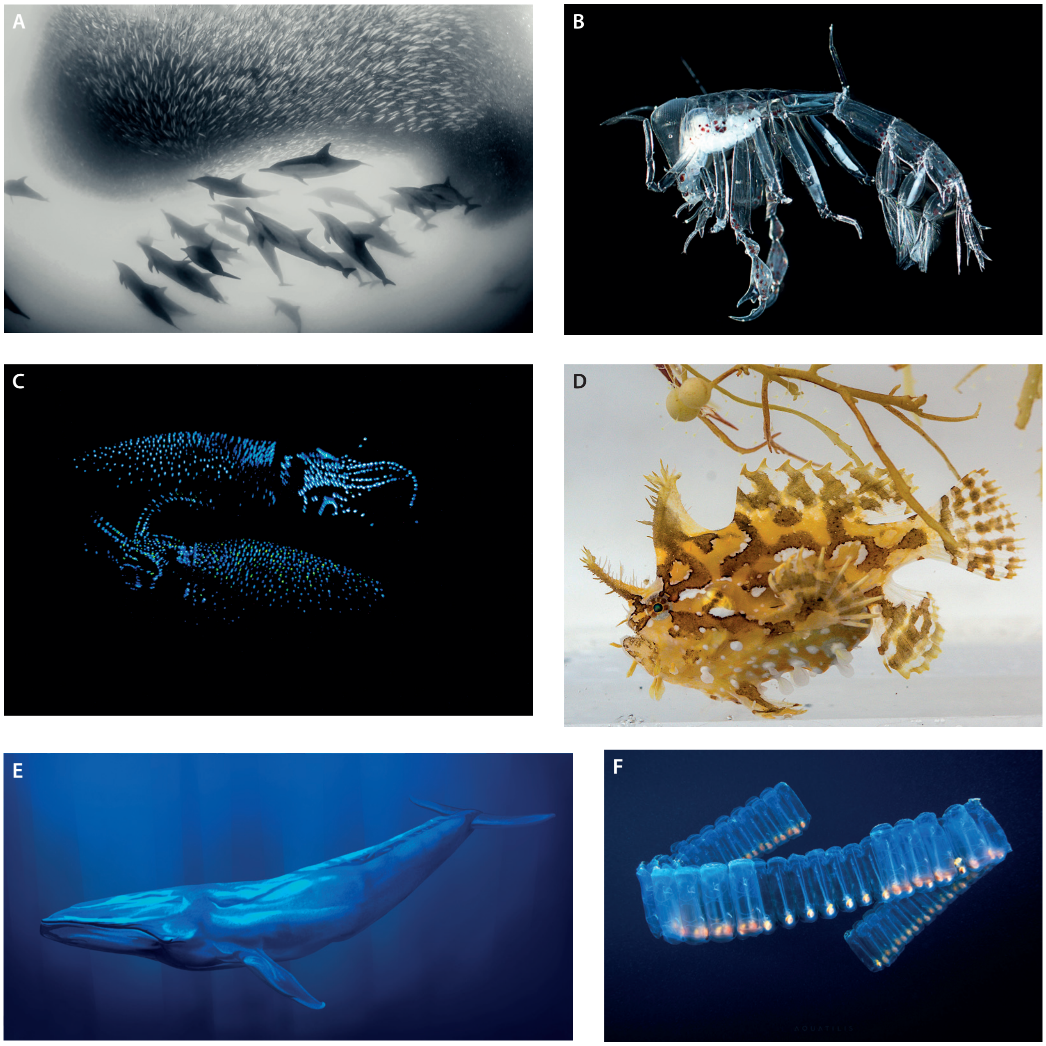

Figure 2.7. Some organisms of the open ocean. (A) A "bait ball" of planktivorous fishes, schooling tightly in response to feeding dolphins. (B) The pelagic amphipod *Phronima*, which associates with salps; *Phronima* was the model for the creature in the 1986 movie *Alien*. (C) The bioluminescent display of the mesopelagic firefly squid (*Watasenia scintillans*). (D) A sprig of pelagic *Sargassum* with associated Sargassum frogfish endemic to these oceanic rafts of seaweed. (E) A blue whale, largest animal that has ever lived. (F) A chain of colonial salps, suspension-feeding lower chordates.

One useful system divides pelagic life into major groups based on body size and mode of nutrition and metabolism (**figure 2.8,** Andersen et al. 2016). These include molecular life (viruses), heterotrophic bacteria, unicellular phototrophs, unicellular chemoautotrophs, unicellular eukaryotic heterotrophs (including *mixotrophs*), multicellular heterotrophs (e.g., copepods), visually foraging poikilotherms (fishes and cephalopods), and homeotherms (birds and mammals). These are described briefly below. Most of these categories are also taxonomic groups, illustrating the often close correspondence between taxonomic and functional classifications. This scheme aims to separate groups at characteristic sizes that represent physical and physiological transition points between different ways of making a living. For example, the tiny, simple cells of bacteria obtain their nutrition by absorbing dissolved substances across the cell membrane, but this mechanism is inadequate for slightly larger eukaryotic cells. Size is the main factor in this classification because it is a master variable of sorts, strongly influencing resource encounter rate, capacity for diffusive uptake and

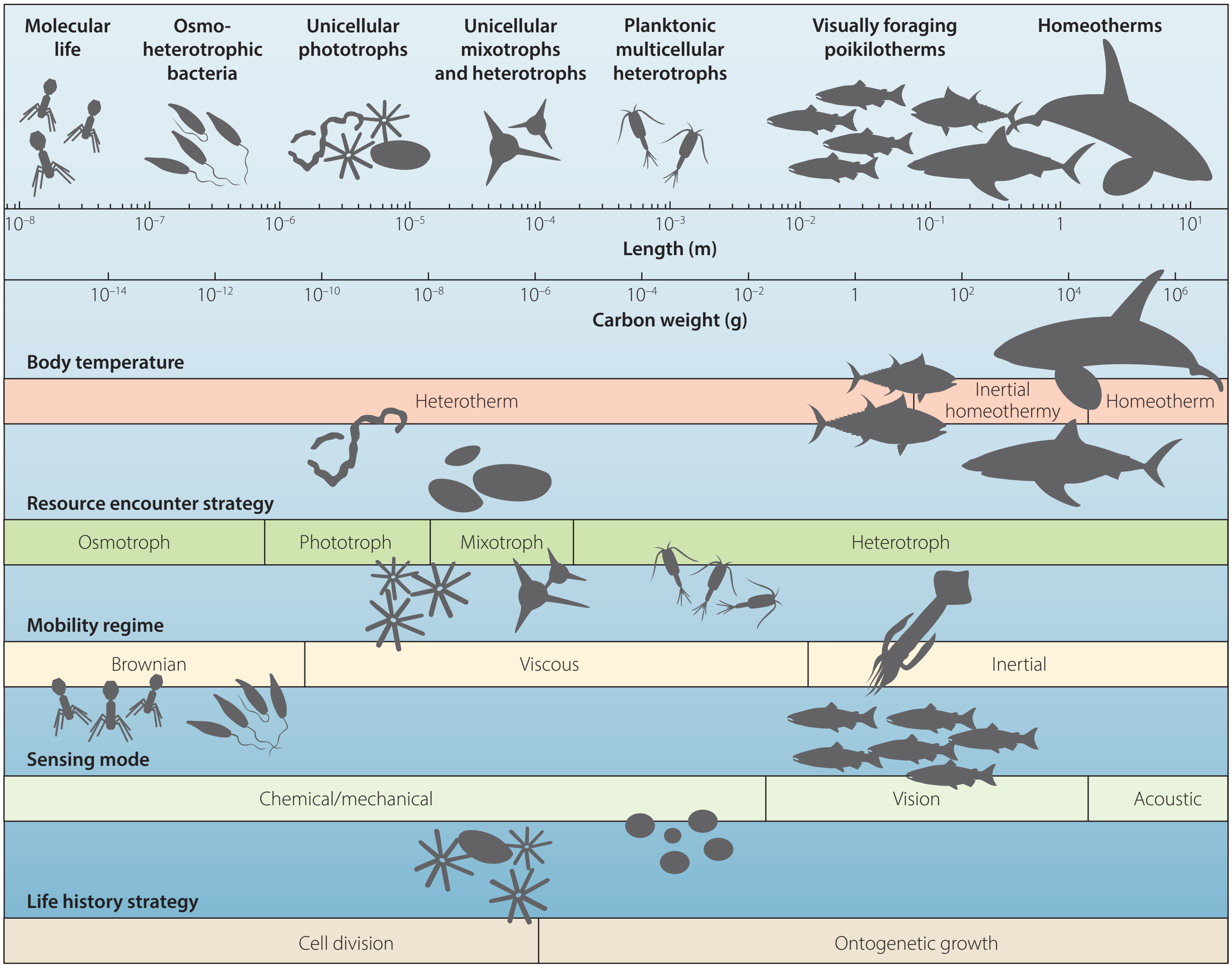

Figure 2.8. Dimensions of ocean life. The continuum in body size among pelagic marine organisms and the major transitions in their functional characteristics along that continuum (after Andersen et al. 2016).

photosynthesis, mobility, sensory capacity, body temperature, and life history strategy. Therefore, measuring the size of an organism allows a rough estimate of its metabolic rates, feeding rate, swimming speed, and sensory range (Andersen et al. 2016). Below we consider each of these groups in more detail.

Molecular Life: Viruses

Viruses are familiar as disease agents of humans and animals, but until a few decades ago their importance in the ocean was largely unappreciated. Early studies revealed millions of viruses per milliliter of seawater, many of them infecting phytoplankton, and experimental addition of viruses to seawater depressed primary production by an order of magnitude (Suttle 2007). Viruses are highly diverse as well. In 2002 a group of researchers applied shotgun sequencing to 200 liters of seawater collected off southern California and found a stunning 3000–7000 types of viruses, most of which were new to science (Breitbart et al. 2002). Since then, numerous studies have shown that viruses are the most abundant life forms (viruses straddle the line between highly complex biomolecules and extremely simple organisms) in the oceans, often averaging 10 million per milliliter in surface waters. Because most marine viruses are *phages* (i.e., parasites of bacteria, including prokaryotic phytoplankton), they profoundly influence the dynamics and activity of phytoplankton and bacterial populations and thus ocean biogeochemical cycles (Breitbart 2012). Moreover, because both viruses and their bacterial hosts have very short generation times, these organisms and the interactions among them evolve rapidly. Viruses drive evolution in their prokaryotic hosts through selection for resistance against viral attack, and also facilitate horizontal transfer between bacteria of metabolic genes encoding important ecological and biogeochemical processes, thus manipulating bacterial metabolism (Breitbart 2012). Viruses that infect algae are now understood to be major influences on the dynamics of marine phytoplankton biomass and production, reducing bacterial biomass by 20%–40% per day (Suttle 2007), strongly reducing marine primary production, and likely causing the sudden crashes often observed in phytoplankton blooms. Viruses are also highly host-specific, even specializing on particular genetic strains within host species, so they have strong impacts on phytoplankton community structure (Short 2012).

Heterotrophic Prokaryotes

Bacteria and Archaea are ubiquitous and ecologically important in all marine (and other) ecosystems. These prokaryotes are morphologically simple, lacking nuclei or organelles, but metabolically quite diverse and sophisticated (see next section). Both groups obtain nutrition by absorbing organic compounds from the medium across their cell wall. Thus, they feed on dissolved organic matter but can also use particulate matter by releasing enzymes that break down such particles outside the cell. Many bacteria also require inorganic nutrients and may compete with phytoplankton for these resources (Amin et al. 2012). Heterotrophic bacteria rapidly consume dissolved organic matter leaked by healthy growing phytoplankton cells and regenerate inorganic nutrients in the process, some of which are taken up by the phytoplankton cells. Bacteria may form physically intimate associations with phytoplankton cells that facilitate such exchanges. As a result, abundance and production of Bacteria in marine waters are generally closely correlated with the abundance of phytoplankton.

Unicellular Phototrophs

The vast majority of Earth's habitable living space is open-ocean water. Primary producers occur only in the upper sunlit layers of the ocean, and the dominant types are single-celled organisms that spend their lives suspended in the surface waters, collectively called *phytoplankton*. The phytoplankton comprise a diverse collection of mostly ancient microbial lineages. Much of that diversity has come to light only recently because prokaryotes and tiny eukaryotes are not captured by typical plankton nets and have not yet been successfully cultured (see box 2.1). Thus, they were unknown prior to the advent of metagenomic methods that can characterize DNA sequences from environmental samples containing many types of organisms, such as water from the open ocean. A major discovery of recent decades was that a large proportion of the open ocean's primary production is performed by picoplankton, notably the widely distributed cyanobacterium *Prochlorococcus marinus* (see figure 2.3A), one of the smallest primary producers and thought to be the most abundant organism on Earth—yet it was only discovered in 1986 (Chisholm et al. 1988).

The phylogenetic diversity of marine primary producers entails comparable diversity in biochemistry, function, and ecology, much of it ancient. Major clades of primary producers that diverged hundreds of millions of years ago retain strong and consistent differences in functional traits, including photosynthetic capacity and nutrient kinetics, that influence ecological and biogeochemical processes. This phylogenetic conservatism of function is a phenomenon we revisit repeatedly, emphasizing the importance of phylogenetic tree thinking mentioned above. Eukaryotic phytoplankton are dominated by two major clades with distinct photosynthetic structures (plastids), which were acquired independently by incorporating different prokaryotic symbionts early in the history of life (Quigg et al. 2003). While both groups use chlorophyll *a* as the main molecule for capturing solar energy, the green superfamily uses chlorophyll *b* as an *accessory pigment* in photosynthesis, and includes the green algae (Chlorophyceae), the ancestors of land plants. Fossil evidence suggests that this green group dominated the ocean during the Paleozoic era. The second, red superfamily uses chlorophyll *c* as an accessory pigment and includes the many benthic red and brown macroalgae (seaweeds) of nearshore ecosystems, as well as planktonic diatoms, haptophytes, and some dinoflagellates. The red clade expanded to dominate the ocean after the end-Permian mass extinction. Despite their great age, the two clades still differ consistently in stoichiometry and the efficiency of nutrient use. Interestingly, stoichiometries of the major nutrients carbon, nitrogen, and phosphorus in the red and green clades primarily reflect those of their ancestral host cell lineages, whereas trace element composition reflects those of their plastids, originally acquired from bacterial symbionts (Quigg et al. 2003). These differences can have substantial ecological and biogeochemical consequences. For example, greater stratification of polar waters is expected with climate warming and is likely to favor diatoms as a result of their lower N:P requirements compared with the other dominant phytoplankter of high latitudes, *Phaeocystis*. The siliceous shells of diatoms cause them to sink faster than *Phaeocystis*, so a shift to diatom dominance in warmer polar waters would likely strengthen the *biological pump*, exporting more nitrogen out of surface water into the deep ocean (Arrigo 2005).

Unicellular Chemoautotrophs

Most primary producers use the energy in sunlight to convert carbon dioxide and water into organic compounds via the process of oxygenic photosynthesis. These organisms are called phototrophs. But phototrophy is only one form (by far the dominant one) of *autotrophy*, the production of living organic matter from nonliving sources. Autotrophic carbon fixation can also be accomplished using energy stored in the chemical bonds of various inorganic compounds, notably ammonia, hydrogen sulfide, and reduced metals such as iron and manganese (**table 2.3**). These pathways of production that use chemical energy, rather than light, are known as *chemosynthesis* and the organisms that use them are *chemoautotrophs*. The reduced compounds they use as energy sources are generally stable only in low-oxygen conditions, so chemoautotrophs are restricted to specialized niches, such as organic-rich sediments and the oxygen minimum zones of the deep ocean water column. On a global scale, such chemoautotrophs contribute only about 1% of net aquatic primary production, estimated at 0.77 Pg C yr^{-1}, compared with a total of around 50 Pg C yr^{-1} by oxygenic phototrophs (Raven 2009, Middelburg 2011). About half of chemoautotrophic production is accomplished by nitrifying Archaea and Bacteria that fix carbon using the energy obtained by reducing ammonium to nitrate. Despite its relatively small global contribution, chemoautotrophy can be an important source of organic carbon in organic-rich coastal sediments, hydrothermal vents, and the deep ocean water column, and the total contribution of organic carbon to the world ocean by chemoautotrophs is comparable to that supplied by rivers (Middelburg 2011).

Unicellular Heterotrophs

Heterotrophic eukaryotes in the nanoplankton size range, primarily small flagellates and ciliates, are often referred to as microzooplankton and are major consumers of both bacteria and picophytoplankton. These single-celled consumers have much faster population growth rates than larger invertebrate grazers and can therefore respond quickly to blooms of their algal prey. Comparative studies and extrapolations from lab experiments show that nanoflagellates consume bacteria at roughly the same rate they are produced, on average, although there is considerable variation across systems, in part because nanoflagellates appear often to be under strong top-down control by their own predators. Heterotrophic protists are also key controls on pelagic producers, consuming 60%–70% of primary production in ocean surface waters on average (Calbet and Landry 2004).

Another major mode of life among heterotrophic protists is parasitism. Parasites were largely overlooked for much of the history of ecology and oceanography. But recent metagenomic studies show that they are abundant and diverse in ocean plankton and likely have large impacts on popula-