

# Contents

## Preface xv

## Chapter 1: Introduction 1

---

### A Framework for Functional Marine Ecology 3

- Plan of the book 4
- Some recurrent themes 5
- Humans in marine ecosystems 6

### Ecology in Practice 6

- The central challenges of marine ecology 6
- The ocean and the shore 8
- The major patterns 9

## Chapter 2: Life in the Ocean 11

---

### The Magnitude of Biodiversity 11

### Diversity on Land and Sea 12

### Phylogenetic Classification of Marine Biodiversity 14

- The tree of life 18
- Phylogenetic relationships and tree thinking 20
- The web of life 21

### Functional Organization of Pelagic and Benthic Life 21

- Functional groups of pelagic life 22
- Functional groups of benthic life 30

### Marine Life in the Anthropocene 36

### Future Directions 37

### Summary 37

## Chapter 3: Geography of Marine Life 38

---

### A Short History of the Oceans and Continents 38

### Climate and Circulation of the World Ocean 40

- Geostrophic flow and the central ocean gyres 41
- Convergence zones and fronts 42
- Thermohaline circulation and the origins of deep water 43
- Coasts, shallows, and their consequences 44

### Major Patterns in the Distribution of Marine Life 44

- A conceptual framework for understanding biodiversity 44
- The spatial organization of diversity 45
- The latitudinal diversity gradient 47

The longitudinal diversity gradient	48
The depth diversity gradient	48
The role of bottom type	48
The Origin of Species	49
The ecology of speciation	49
Habitat area and geographic range	50
Habitat age	52
Temperature, energy, and metabolic rate	53
Body size	54
Life history and dispersal ability	54
Ecological specialization	55
Ecological opportunity and speciation	55
The Dispersal of Species	56
The Theory and Evidence for Island Biogeography	57
The End of Species: Extinction	58
Integrative Models of Marine Diversification	60
Biogeographic Classifications of the Ocean	61
The ecological geography of the sea	61
Marine ecoregions of the world	62
Large marine ecosystems	63
The Biogeography of Functional Traits	63
The Biogeography of Species Interactions	64
Biogeography of the Anthropocene Ocean	68
Climate warming and redistribution of global marine fauna	68
Tropicalization	70
The Arctic opening	70
The sixth mass extinction?	72
Future Directions	72
Summary	73

## Chapter 4: Introduction to the Anthropocene Ocean

74

---

First, the Good News	74
The Great Acceleration	75
Coal and climate change	78
Nitrogen: Detonator of the population explosion	79
The limits to growth	80
The Natural and Cultural History of <i>Homo Sapiens</i>	83
Ecology for the Anthropocene	84
Culture and the evolution of human society	84
Energetics and economics of <i>Homo sapiens</i>	86
The tragedy and triumph of the commons	86
The Anthropocene ocean	87
Ocean Warming	89
Warming effects on communities	90
Sea level rise	91
Ocean Acidification	92
Effects of acidification on organisms	92
Effects of acidification on communities	93

*Homo Sapiens: Top Predator of the Ocean* 95

The history and extent of fishing 95

The current state of marine fisheries 97

Ecosystem impacts of fishing 98

The future of fisheries 99

*Marine Biodiversity in the Anthropocene* 101

Species decline and extinction 101

Functional consequences of declining biodiversity 102

Marine globalization 103

Evolution in the domesticated ocean 104

Novel ecosystems 105

*Future Directions* 105

Science for solutions 105

Policy for solutions 106

Reasons for cautious optimism 108

*Summary* 110

---

**Chapter 5: Organisms**

112

*Building Blocks of Life* 113

Ecological stoichiometry 113

Nutrient uptake and use 115

Iron 117

*Powering Life* 117

Autotrophy 118

Heterotrophy 118

*Kinetics of Life* 120

*Dimensions of Life* 121

*Mechanics of Life* 124

*Coding Life* 126

Natural selection and adaptation 126

Genotype and phenotype 127

*Functional Ecology and the Niche* 128

Historical and modern concepts of the niche 128

Toward a trait-based ecology of marine organisms 129

*Functional Ecology of Marine Primary Producers* 131

Functional groups of phytoplankton 131

Functional groups of benthic macrophytes 133

*Macroecology* 133

*Organisms in the Anthropocene* 135

*Future Directions* 136

*Summary* 137

---

**Chapter 6: Populations**

138

*Development and Life History* 139

*The Problem of Larval Dispersal* 142

*Population Growth: A Brief Review* 144

*Growth of Age- and Stage-Structured Populations: Matrix Approaches* 147

<b>Demographic Models in Conservation and Management</b>	149
Maximum sustainable yield in fisheries	149
Strategic conservation of vulnerable life stages	151
Life history and the effectiveness of marine reserves	154
<b>Organismal Fitness and Adaptation to the Environment</b>	155
<b>Dispersal, Recruitment, and Metapopulations</b>	158
Tagging and tracking	159
Hydrodynamic simulation of larval movement	161
Larval behavior	161
Population genetic markers of dispersal and connectivity	162
Geochemical tags	164
<b>Macroecology of Populations</b>	165
Metabolic scaling and life history	165
Abundance and the energetic equivalence rule	166
The macroecology of range size	167
<b>Marine Populations in the Anthropocene</b>	168
<b>Future Directions</b>	169
<b>Summary</b>	170

## **Chapter 7: Species Interactions**

171

---

<b>Interactions among Species: General Considerations</b>	171
<b>Interactions between Competitors</b>	175
<b>Interactions between Plants and Herbivores</b>	176
Controls on herbivory: Plant traits	178
Controls on herbivory: Herbivore traits	179
<b>Interactions between Prey and Predators</b>	182
Controls on predation: Prey traits	182
Controls on predation: Predator traits	184
Parasitism and disease	184
Predation and community diversity	185
<b>Facilitation and Mutualism</b>	185
<b>Ecological Networks</b>	186
Functional traits as a lens into community organization	187
Traits in interaction networks	189
Emergent properties of ecological networks	189
<b>Ecological Interactions in the Anthropocene</b>	191
Changing species interactions in a changing climate	191
Food web decapitation and trophic skew	193
<b>Future Directions</b>	193
<b>Summary</b>	194

## **Chapter 8: Ecological Communities**

195

---

<b>What Is a Community?</b>	196
<b>Community Dynamics: A Conceptual Framework</b>	198
Ecological selection	199
Dispersal and metacommunities	200
Ecological drift	201

**Synthesis: Diversity in Ecological Communities** 203

- Neutral models and their assumptions 203
- The unified neutral theory of biodiversity 204
- Testing the neutral theory in nature 204
- Disturbance and diversity in communities 207
- The role of history 207
- Dispersal and species richness 209
- Metabolic theory and species diversity 210
- Space and species diversity 211

**Linking Communities to Ecosystems** 211

- Functional structure of communities 211
- Phylogenetic structure of communities 214

**Communities in the Anthropocene** 214

- Climate change and communities 214
- Marine defaunation and trophic skew 215

**Future Directions** 216

**Summary** 216

**Chapter 9: Ecosystems**

218

**History of the Ecosystem Concept** 219

- Evolution of the ecosystem concept 223
- Ecosystems as complex adaptive systems 224

**Primary Production** 225

- Light and photosynthesis 225
- Nutrient uptake and use 226

**Herbivory** 226

**Control of Biomass Distribution and Productivity in Marine Ecosystems** 228

- The green world hypothesis 228
- Bottom-up control of biomass and productivity by resources 229
- Top-down control of biomass and productivity by consumers 231
- Trophic cascades in the ocean 232
- Detritus-consumer interactions 233

**Functional Structure of Marine Ecosystems** 236

- Organismal traits in ecosystems 236
- The size spectrum 237
- The macroecology of trophic interactions 240

**Biodiversity and the Functioning of Ecosystems** 241

- Biodiversity and ecosystem functioning: Theory 241
- Biodiversity and ecosystem production: Empirical evidence 242
- Biodiversity and ecosystem stability 245

**Alternative Stable States and Regime Shifts in Complex Adaptive Ecosystems** 249

- Empirical evidence for regime shifts in marine ecosystems 251
- Mechanisms of marine regime shifts 251

**Applications of Marine Ecosystem Modeling in Fisheries and Management** 252

**Models of the Global Ecosystem** 255

Marine Ecosystems in the Anthropocene	257
Eutrophication	257
Defaunation and trophic skew	258
Future Directions	258
Summary	259

## Chapter 10: The Open Ocean

260

---

Physical Forcing of Pelagic Ecosystems	261
The global distribution of ocean productivity	261
Vertical structure of the pelagic water column	262
The spring bloom	265
High-nitrogen low-chlorophyll (HNLC) regions	266
Organisms and Traits	266
The phytoplankton: Major functional types	266
Grazers: Major functional types	268
Grazing	269
Structure and Organization of Pelagic Communities	269
Specialization and resource partitioning	270
Nonequilibrium dynamics	270
Chaos	271
Functioning of Pelagic Ecosystems	272
Pelagic food webs: The microbial loop	272
The biological pump and the global carbon cycle	273
Trophic control in pelagic ecosystems	274
The Deep Sea	276
Adaptations to life in the deep sea	276
Pelagic-benthic coupling	278
Deep-sea biodiversity	279
Chemosynthetic Ecosystems: Vents and Seeps	281
Hydrothermal vents	282
Cold seeps	283
Macroecology of the Open Ocean	284
Controls on biodiversity in the open ocean	284
Global controls on microbial diversity	286
Macroecology of open-ocean ecosystem processes	287
Deep-Sea Fisheries	288
The Open Ocean in the Anthropocene	289
Climate and the Anthropocene ocean	289
Ocean acidification	292
High-seas fisheries	292
Future Directions	293
Summary	294

## Chapter 11: Estuaries and Coastal Seas

296

---

The Edge of the Sea	296
Interacting ocean and continents	296
Estuaries	298

Coastal life and communities	300
Coastal ecosystem processes	302
<b>Rocky Shores</b>	<b>304</b>
Geomorphology and environment	305
Organisms and traits	305
Community organization and key interactions	306
Ecosystem processes and services	309
Rocky shores in the Anthropocene	309
<b>Sediment Bottoms</b>	<b>310</b>
Geomorphology and environment	310
Organisms and traits	311
Community organization and key interactions	313
Ecosystem processes and services	314
Sediment bottoms in the anthropocene	315
<b>Seagrass Meadows</b>	<b>317</b>
Geomorphology and environment	317
Organisms and traits	318
Community organization and key interactions	319
Ecosystem processes and services	321
Seagrass meadows in the Anthropocene	322
<b>Salt Marshes</b>	<b>325</b>
Geomorphology and environment	326
Organisms and traits	327
Community organization and key interactions	328
Ecosystem processes and services	330
Salt marshes in the Anthropocene	330
<b>Mangrove Forests</b>	<b>331</b>
Geomorphology and environment	332
Organisms and traits	332
Community organization and key interactions	333
Ecosystem processes and services	334
Mangrove forests in the Anthropocene	334
<b>The Seascape: Interactions among Habitats</b>	<b>335</b>
<b>Coastal Ecosystems in the Anthropocene</b>	<b>337</b>
Climate change and the coast	337
Decline of foundation species	338
Trophic skew	338
Nonnative and invasive species in coastal ecosystems	338
Coastal fisheries	340
Eutrophication and hypoxia	340
Multiple stressors in coastal ecosystems	341
Coastal anthropogenic biomes: Urbanized estuaries	343
<b>Future Directions</b>	<b>344</b>
<b>Summary</b>	<b>346</b>

## Chapter 12: Coral Reefs

347

---

<b>Geomorphology and Environment of Coral Reefs</b>	348
Geomorphology	348
Abiotic environment	351
<b>Organisms and Traits: Functional Diversity in Reef Ecosystems</b>	352
Biodiversity: Foundation species	352
Diversity and functional ecology of primary producers	354
Diversity and functional ecology of consumers	355
<b>Community Organization and Key Interactions</b>	357
Origin and maintenance of diversity in reef communities	357
Herbivory in reef ecosystems	360
Trophic cascades in reef ecosystems	361
Disease in reef ecosystems	362
Phase shifts and alternative stable states on coral reefs	363
Regional variation in coral reef dynamics	366
<b>Ecosystem and Biogeochemical Processes</b>	367
Coral reef production and nutrient cycling	367
Coral reef fisheries	368
<b>Coral Reefs in the Anthropocene</b>	369
Coral reefs in a warming ocean	371
Ocean acidification	372
Coral reef fisheries	373
The future of coral reefs	373
Strategic coral reef conservation and management	374
<b>Future Directions</b>	374
<b>Summary</b>	375

## Chapter 13: Ocean 2.0

377

---

<b>The Earth Is a Complex Adaptive System</b>	377
<b>Biodiversity Is as Important as Climate</b>	378
<b>Humans Are Now the Force of Nature</b>	378
<b>Apocalypse Not</b>	379
<b>But What about Nature?</b>	379
<b>Rays of Hope</b>	381

**Glossary** 383

**Literature Cited** 393

**Photo Credits** 429

**Index** 431

# 1

## Introduction

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

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

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

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

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

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

Source: Lovelock (1995).

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

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

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

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

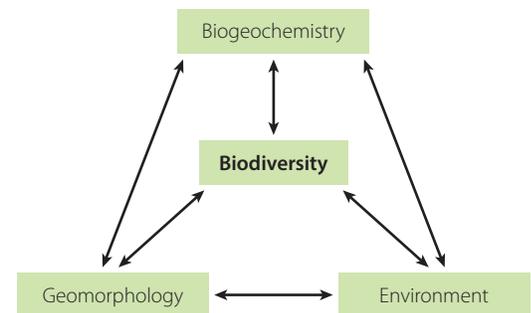
on the distribution, abundance, and even existence of species, which will have far-reaching and still poorly understood consequences for the earth's ecosystems that support us. The hopeful message is that nature is resilient, with an inherent, vigorous capacity to recover even from major disturbances.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

## A Framework for Functional Marine Ecology

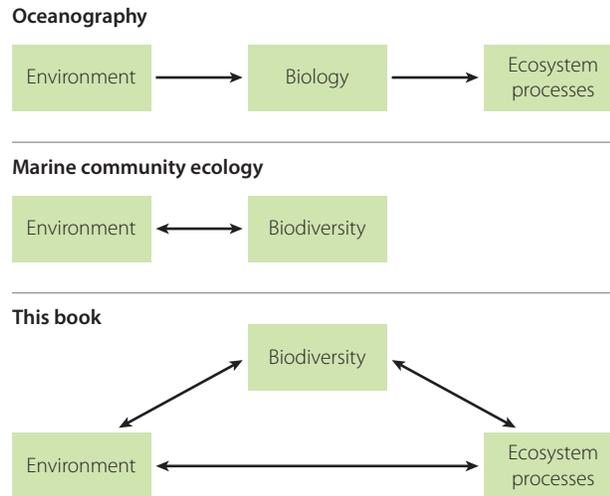
Ecology is about understanding how living organisms interact with their environment. Its goals can be summarized in a few overarching questions: How does the environment influence the distribution and diversity of life? How do interactions among organisms modify those patterns? How do the groups of species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

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

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



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



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

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

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

### Plan of the book

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

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

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

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

### Some recurrent themes

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

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

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

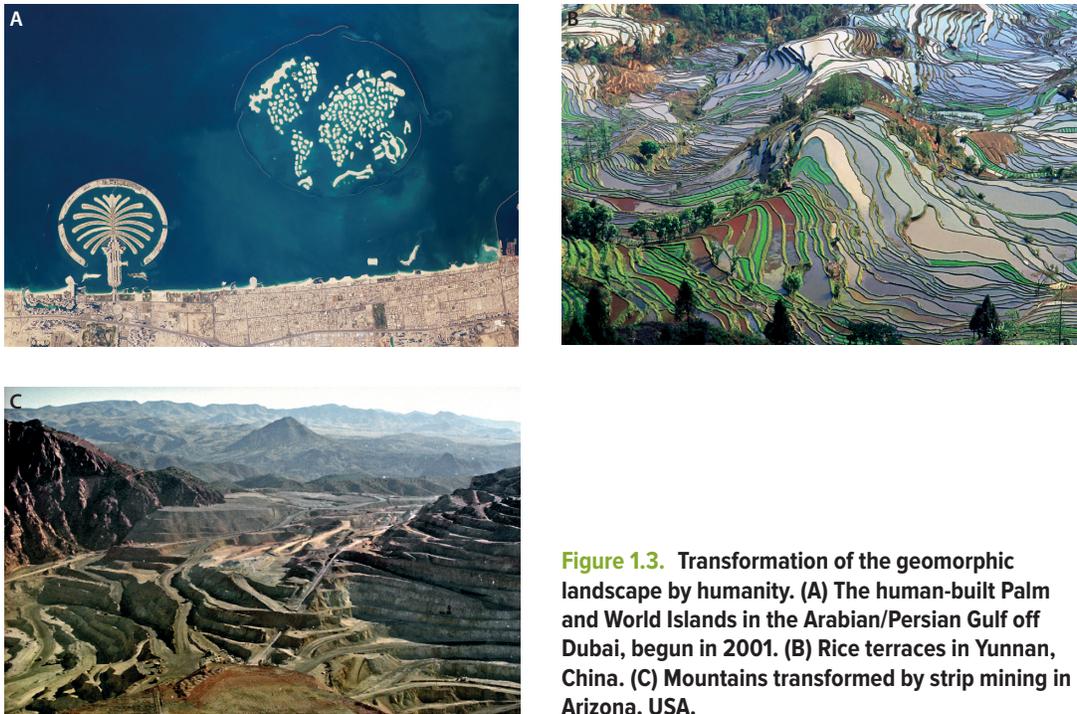
## Humans in marine ecosystems

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

## Ecology in Practice

### The central challenges of marine ecology

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



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

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

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

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

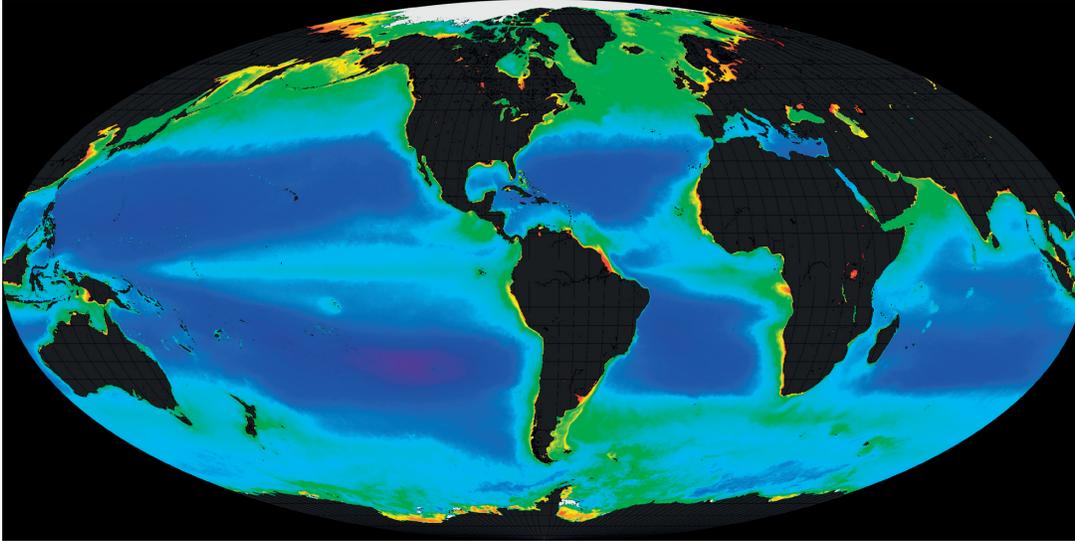
unlimited opportunities for seeking and testing those general rules. The best example of such a fundamental law is the theory of natural selection—it is simple enough to state briefly in plain language and to be understood by most anyone, yet powerful enough to capture the central mechanism that has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

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

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

## The ocean and the shore

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



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

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

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

## The major patterns

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

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

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

## Index

A page number followed by f refers to a figure and a page number followed by t indicates a table.

- abiotic environment: biodiversity and, 2, 378;  
components of, 3
- abundance, scaling with body mass, 166–67, 237,  
238f, 240, 241f
- acidification. *See* ocean acidification; volcanic vents
- Acropora*: dozens of coexisting species of, 205;  
white-band disease of, 185, 362–63, 370, 375
- Acropora cervicornis*. *See* staghorn coral
- Acropora millepora*: acidification affecting larval  
settlement of, 93–94; heritable heat tolerance in,  
127–28
- Acropora palmata*. *See* elkhorn coral
- active continental margins, 297
- active metabolic rate, 120
- adaptation, 126, 128, 135
- age classes, 145; in field populations, 147; Leslie  
matrix and, 147–48; reproductive values of, 146
- age-structured populations, 147–48
- Agulhas current, 41
- algae: defenses against herbivores, 177–78, 179, 181f,  
186; as disparate group, 13, 20, 22; functional  
classification of, 32, 33f; as most of ocean's  
primary producers, 225; seagrass competition  
with, 319–21, 320f; in sediment, 32; viruses  
infecting, 25; vulnerability to grazing, 32, 34f.  
*See also* crustose coralline algae; ephemeral  
algae; filamentous (turf) algae; macroalgae;  
perennial algae; phytoplankton
- algal matrices, 354f, 355. *See also* filamentous (turf)  
algae
- Allee effect, 251, 286
- allometric equations, 121
- allometric exponent, 121, 122f
- allometric scaling laws, 123–24. *See also* metabolic  
scaling
- allometry, 121; macroecology and, 134
- allopatric speciation, 49, 50
- alpha diversity ( $\alpha$ ), 45
- alternative stable states, 208, 249–52; on coral reefs,  
363, 365–66, 365f, 366f; in marine fisheries,  
250–51, 250f; rapid shifts among, 224; rarity of  
evidence for, 380; on temperate rocky reefs, 181
- ammonium, in seawater, 115, 116, 226
- amphipods: direct development of, 18, 140;  
nonconsumptive effects of predators on, 182;  
overgrazing stressed kelps, 302; *Phronima*, 23f;  
on seagrass blade, 227f; species-area relation-  
ship, 46f
- anglerfish, 277, 278f
- anoxic sediment layer, 30
- anoxic sediments: coastal, 310, 314, 328, 332, 333; of  
cold seeps, 283
- Antarctic: circumpolar current and, 39; predation of  
king crab in, 88f, 91, 215
- Anthropocene epoch, 1, 2–3, 4; beginning of, 75–76;  
biodiversity and, 36–37, 101–5, 135; central  
challenges for, 111; coastal ecosystems in, 337–44;  
coral reefs in, 369–74, 370f, 372f; earth system  
status in, 75, 77f; evolution driven by human  
impact in, 135; fossil fuels and, 78; humanity as  
major force of nature in, 74; hybridization  
increasing in, 21; industrial fixation of nitrogen  
and, 79–80, 80f; mangroves in, 334–35; rocky  
shores in, 309–10; salt marshes in, 330–31;  
seagrass meadows in, 322–23, 325; sediment  
bottoms in, 315–17, 316f; species interactions  
in, 191–93; technological innovation and, 84.  
*See also* Great Acceleration
- Anthropocene ocean: biogeography of, 68–72, 69f,  
71f; cautious optimism about, 108–10, 109f;  
ecosystems in, 257–58; human impacts on, 87,  
88f, 89; marine organisms in, 135–36; marine  
populations in, 168; predicted species  
distributions in, 69–70, 69f
- antitropical distribution patterns, 60
- apparent competition, 173, 173f
- aquaculture: disease in marine organisms and, 101,  
104–5; evolutionary changes caused by, 104–5;  
global growth of, 340, 341f; hybridization resulting  
from, 21; integrated, 106; management of, 101;  
mangrove forests cleared for, 334–35; of oysters,  
339; prospects if better planned and managed,  
340; of shrimps, 77f, 334, 340
- aragonite, 372
- Archaea, 19–20, 19f; metabolic characteristics of, 25,  
26, 27t; at methane seeps, 283–84; picoplanktonic,  
22; primary producers among, 225
- Arctic opening, 70–72, 78
- Arctic sea ice extent, 78, 79f
- arrow worms (Chaetognatha), 12, 14f
- artificial reefs, 344
- artificial structures, 105, 343–44
- ascidians, ocean warming and nonnative species of, 103
- Asian clam (*Corbula amurensis*), 342–43, 342f
- assemblage, 197
- Atlantic menhaden (*Brevoortia tyrannus*), 162, 162f
- Atlantic Ocean: ancient separation from Indian and  
Pacific Oceans, 39; Caribbean as biodiversity  
hotspot in, 60; passive continental margins of,  
297; species richness in, 52; trait differences on  
two sides of, 63–64. *See also* North Atlantic
- atmosphere of Earth, with or without life, 2, 2t
- atolls, 347; Enewetak, 222, 222f, 223, 350; evolution  
of, 350, 350f
- ATP, 115, 118
- autotrophy, 26, 27t, 118
- bacteria: on algal turfs of reefs, 355; chemoautotro-  
phic, 26, 27t, 282–83; consuming phytoplankton  
primary production, 272; latitudinal diversity  
gradients of, 286–87; of mesopelagic zone,  
264; ocean warming and, 215; picoplanktonic,  
22; primary producers among, 225. *See also*  
cyanobacteria
- Bacteria, 19–20, 19f
- Baltic Sea: collapse of cod population in, 252, 276;  
as estuary, 298; productivity enhanced by  
eutrophication of, 341
- Banks, Joseph, 260
- barnacles: experiments with competition between,  
174–75, 174f, 176, 304; life histories of, 139f, 149f;  
neutral theory vs. determinism and, 205, 206
- barrier reef, 350, 350f
- basal metabolic rate, 120, 121, 123
- bathypelagic zone, 263f, 264–65
- Becking, Lourens, 286
- behavior: human, 108; phenotypic plasticity of, 128;  
in predator-prey interactions, 182–84
- Belize Barrier Reef, 370–71
- benthic biomass, deep-sea global distribution of,  
276, 277f
- benthic ecosystems: altered by acidification, 94;  
changed by eutrophication, 258; coastal, 300,  
302–3; defined, 21; marine ecology of, 8, 9;  
organic enrichment and, 315–16, 316f
- benthic organisms: functional groups of, 30–36;  
invertebrates with pelagic larvae, 201; reef fishes  
with benthic egg guarding, 54–55, 55f
- benthic substrata, 30. *See also* sediments
- benthopelagic animals, 278
- Bertness, Mark, 328
- beta diversity ( $\beta$ ), 45; reduced by ocean warming, 103
- biodiversity: acidification and, 94–95; in the Anthro-  
pocene, 36–37, 101–5, 135; central importance  
of, 5; conceptual scheme for processes in,  
44–45, 45f; in coral reef communities, 347, 351,  
357–60; in deep sea, 48, 265, 279–80, 280f,  
284–88, 285f; defined, 11; diseases exacerbated  
by decline in, 341, 343; driving ecosystem  
processes, 378; ecosystem functioning and,  
241–45, 243f; in framework for thinking about  
ecology, 3–4, 3f, 4f; functional classification of,  
14, 18, 21–28, 30–36; functional consequences  
of decline in, 102–3; global hotspot of, 48;  
human dependence on, 36–37; human impacts  
on, 36, 72, 258–59; integrative models of, 60;  
interaction strength in tropical communities  
and, 68; magnitude of, 11; major patterns in,  
44–48; of marine vs. terrestrial animals, 12–13,  
13t, 14f; of marine vs. terrestrial primary  
producers, 13, 15f; phylogenetic classification  
of, 14, 18–21, 19f; planetary boundary for, 103;  
regime shifts promoted by low values of, 252;  
resource availability and, 284–86, 285f; spatial  
organization of, 45–46, 46f; stability of  
ecosystems and, 245–48, 369; vertical and  
horizontal components of, 232, 232f, 246.  
*See also* diversity in communities; functional  
diversity; species richness
- biogeochemical processes, 3, 4, 5, 6; coastal zones  
and, 303; of coral reef ecosystems, 367–68;  
microbial biosphere and, 293; in sediment  
bottoms, 310, 314, 315, 321
- biogeography, 38; of Anthropocene ocean, 68–72,  
69f, 71f; biodiversity and, 44–48; classification  
of coastal regions in, 62–63, 62f; classification  
of pelagic ocean in, 61–62, 61f, 63; community  
structure and, 208–9; earth history and, 38–40,  
39f; fisheries management and, 63; of functional  
traits, 63–64, 66f; ocean circulation and, 40–44;  
pressing questions in, 72–73; rocky shore species  
and, 308; of species interactions, 64, 66–68, 67f.  
*See also* dispersal; island biogeography; theory of

- biological accommodation, 280  
biological oceanography, 8–9  
biological pump, 273–74, 273f; climate warming and, 26, 290, 291, 292; metazoan heterotrophs and, 28; midwater fishes and, 28, 273; organismal processes involved in, 237; tropicalizing plankton and, 70, 73  
bioluminescence, 23f, 277  
biomass production: control of, 228–36; as 10% of animal's ingested energy, 237–38; as yield in fisheries, 117. *See also* primary producer biomass  
biomass pyramids, 239–40, 239f  
biomes: anthropogenic, 106; of Longhurst's scheme, 61–62, 63  
bioturbation, 314, 315; by crabs in mangrove forests, 333  
birds: as bycatch in fisheries, 201; salt marsh habitat for, 328; seabirds rescued by dispersal, 201; waterfowl feeding on seagrass, 321  
bivalves, marine: coastal, in MEOW provinces, 63; as concentrators of heavy metals, 343; epifaunal, 34; evolutionary radiation after origin of siphon, 56; infaunal, 33, 34, 312, 312f, 313, 314; latitudinal diversity gradient and, 60; ocean acidification and, 135; temperature influence on speciation in, 53–54; at vents and seeps, 281, 283, 284. *See also* clams; mussels in salt marshes; mussels on intertidal shores; oyster reefs; oysters  
Black Sea: low-diversity regime shifts in, 252; pelagic food web of, 250f, 251; trophic cascade in, 251, 274, 275, 276  
bleaching of corals, 370, 370f, 371, 372f, 374; affecting different types differently, 353; flattened reefs in Caribbean and, 363; risk of extinction and, 102; thermal tolerance and, 121  
blooms of algae and phytoplankton: with chemically noxious properties, 257–58, 266, 341; decline of seagrass and, 323f, 324, 325; in freshwater ecosystems, 232; invasive zooplankton in Black Sea and, 275, 275f, 276; spring bloom, 265–66, 278, 279; stimulated by iron, 266. *See also* eutrophication  
bluefin tuna, 97–98, 102, 140  
blue ling (*Molva dipterygia*), 289  
blue whale, 23f, 28, 264f  
body size: of benthic organisms, 30, 32f; biological pump and, 274; carbon flux to deep sea and, 287; classes of plankton and, 22, 22t; consumer-prey interactions and, 182, 183f, 184; declining due to human impact, 89, 193; declining with food scarcity in deep sea, 276; ecosystem processes and, 237–40; extinction vulnerability and, 59, 101–2; future development of theory based on, 136; of harvested fish, 95, 96f, 98, 104, 156–57, 157f, 193; home range size and, 167, 167f; interaction strengths and, 189, 190, 190f, 193; of keystone species, 102; larval mortality and, 141f; as master trait, 121; metabolic scaling as function of, 121–24, 122f, 123f, 165–66; of pelagic organisms, 22–24, 24f; sensory functions affected by transitions in, 124; speciation and, 54; species richness and, 210; temperature-mediated changes in, 90, 215; trophic level of fish and, 144, 144f; vulnerability to exploitation and, 65. *See also* cell size of phytoplankton  
body velocity, and temperature effect on predation, 191–92  
bottom type, and species composition, 48  
bottom-up control, 113f, 229–31, 230f, 231f, 233; in estuarine ecosystems, 302; of fish biomass, 276; of hydrothermal vent communities, 283; as incomplete analysis of mangroves, 333; salt marsh ecosystems and, 330  
Briggs, John, 60  
brittle stars (Ophiuroidea), 286  
brooding. *See* direct development  
brown web, 235, 236  
buoyancy in seawater, 124–25; of bloom-forming algal cells, 266  
butterflyfishes (Chaetodontidae), 202, 202f, 364, 364f  
bycatch in fisheries, 97, 98, 100, 106; in deep sea, 289; of seabirds, 201; of sea turtles, 151–52, 153  
calcareous algae, 32, 33f. *See also* crustose coralline algae  
calcareous organisms, and ocean acidification, 93, 94–95, 135–36  
calcium carbonate: of corals, 350, 351–52, 351f, 371, 372; ocean acidification and, 92f, 93, 135; as plant defense against herbivores, 178  
California halibut (*Paralichthys californicus*), 155  
carbonate precipitation at seeps, 284  
carbon content, 113–14  
carbon cycle: biological pump and, 273–74, 273f; destabilized by fossil fuel consumption, 78; phytoplankton in, 267; sediment processes and, 314  
carbon dioxide (CO<sub>2</sub>): atmospheric rise in, 78, 78f; biological pump and, 273, 273f; diffusing into ocean surface, 289; emissions from mangrove clearance, 335; ocean acidification and, 92–95, 92f; phytoplankton species composition and, 237; trend since 1972 predictions, 81f, 82  
carbon export to deep ocean: diel vertical migration and, 273; phytoplankton species composition and, 237; whales and, 29. *See also* export of production to deep ocean  
carbon fixation by photosynthesis, 118  
carbon sinks: mangrove production and, 334; salt marshes as, 330  
carbon storage in sediments or soil: from mangroves, 335; from seagrasses, 321–22, 322f; from terrestrial and marine ecosystems, 322f; trophic skew and, 338  
Caribbean as biodiversity hotspot, 60  
Caribbean reefs: biodiversity in communities of, 357; bleaching of corals on, 371, 372f; carbonate thickness in, 350; compared to Indo-West Pacific, 366–67; decline of, 370–71, 370f; diseases with impacts on, 362–63 (see also *Diadema antillarum*); flattening of, 363; loss of carbonate structure on, 372; non-stony corals on, 354; overgrown by sponges on overfished reefs, 360–61. *See also* Jamaican coral reefs  
carnivores: ecosystem energy pathways and, 113f; nutrition of food chosen by, 182  
carpet-of-mouths hypothesis, 142–43  
carrying capacity (*K*): body mass and, 166; regime shifts in predator-prey systems and, 251  
catch-share programs, 100–101  
cell size of phytoplankton: diversity of, 285, 285f; as fundamental trait, 132–33, 132f, 267; responses to physical forcing and, 267; in warming ocean, 291, 292  
centers of accumulation, 60  
centers of origin, 60  
centers of overlap, 60  
central ocean gyres, 40f, 41–42, 41f; oligotrophic systems of, 228, 261, 276; warming-induced decline of phytoplankton biomass in, 291  
*Challenger* expedition, 48, 261, 279  
chaos, 271  
chaotic dynamics, 269, 271, 293  
chemical cues: amphipod reaction to fish predation and, 182; for larval settlement, 163, 163f; *Phaeocystis* colony formation and, 179  
chemical defenses of plants and algae, 178; of bloom-forming algae and phytoplankton, 257, 266, 341; of coral reef algae, 355, 359, 360; of host plants of mesograzers species, 179, 181f, 186; induced in marine algae, 179  
chemoautotrophs, unicellular, 23, 24f, 26, 27t, 225  
chemosynthetic ecosystems, 281–84, 281f  
chicken bones, 76, 104  
chlorophyll: iron required for synthesis of, 117; primary producer biomass and, 9f  
chlorophyll *a*, 25, 118, 119  
chlorophyll *b*, 25–26  
chlorophyll *c*, 26  
chlorophyll maximum, 61, 263, 335  
circumpolar current, 39, 63  
clades, 18f, 20  
clams: Asian clam invasion, 342–43, 342f; at hydrothermal vents, 281, 283  
Clements, Frederic, 196  
climate: biogeography and, 38; biological pump and, 274; ocean circulation and, 40–41  
climate change: biotic homogenization driven by, 103–4; communities and, 214–15; coral reef conservation and, 374; disease in marine organisms and, 307, 341; ecosystem models and, 254; evolution in response to, 158; during Last Glacial Maximum, 70; novel ecosystems resulting from, 257; species interactions and, 191–92; as threat to economic worldview, 86. *See also* climate warming  
climate variation: fishery yield stabilized by diversity and, 247; regime shifts in pelagic systems and, 249  
climate warming, 78, 78f; Anthropocene ocean and, 289–92; biogeographic reorganization and, 68–71; communities and, 90–91; coral diseases and, 364; in ecosystem modeling of primary production, 254; eutrophication and, 341; low-oxygen zones due to, 316; mangroves and, 332, 333, 335; metabolic balance of ocean and, 287; metabolic models and, 135; with most heat absorbed by ocean, 90; salt marsh ecosystems disturbed by, 331; seagrass ecosystems and, 322–23. *See also* climate change; ocean warming; sea level rise  
climax community, 197, 220, 253  
clownfish (*Amphiprion percula*), 163  
CO<sub>2</sub>. *See* carbon dioxide (CO<sub>2</sub>)  
coast: cultural eutrophication on, 79; development on, 322, 323, 330, 340; extending from waterline to continental shelf, 296; interactions among habitats on, 335–36; oceanography of, 296–97; vegetation protecting against storms and erosion on, 321, 330, 334  
coastal biome, 62  
coastal boundary layer, and local retention of larvae, 161

- coastal ecosystems, 44, 302–4; in the Anthropocene, 337–44; climate of adjacent continent and, 297; human dependence on, 6; less nutritious higher plants in, 231; materials delivered by the land to, 296; restoration of, 323–25, 323f, 324f; sea level rise and, 323; services to humans from, 303–4; summary of, 346; trophic cascades in, 234f, 302. *See also* mangroves; rocky intertidal communities; salt marshes; seagrasses; sediment bottoms
- coastal infrastructure: anthropogenic biomes and, 106; global increase in jellyfish and, 105; of urbanized estuaries, 343–44
- coastal marine communities: homogenization of, 103; invaded by nonindigenous species, 103, 104f; trophic skew in, 193, 193f. *See also* coastal ecosystems
- coastal marine organisms, and island biogeography, 58
- coastal regions: with high productivity, 261; MEOW biogeographic realms of, 62–63, 62f; oceanography of, 44
- coastal squeeze, 323, 330
- coastal upwelling, 44, 62, 261, 297, 298f, 299, 305
- coccolithophorid phytoplankton, 135, 136, 267, 267f, 292
- cod (*Gadus morhua*): Baltic Sea collapse of, 252, 276; North Atlantic fisheries for, 64, 65, 252; tropicalization and, 70
- coexistence of competing species: differences in dispersal ability and, 202, 202f; ecological drift and, 203; neutral theory and, 205; stable or unstable, 176. *See also* niche differentiation; niche partitioning
- cognitive psychology, 381, 382
- cold seeps, 281f, 283–84
- comb jellies. *See* ctenophores
- commerce: globalized, 72; homogenization of ocean driven by, 103; invasive species facilitated by, 339; transport of nonnative species by, 71
- communities: accidents of history vs. environmental forcing and, 72; in the Anthropocene, 214–15; climate warming and, 90–91; concepts of, 196–98; defining variables of, 195; definitions of, 197–98; ecosystems and, 211, 213–14; functional structure of, 211, 213; functional traits and, 187–89, 211, 213–14; history and geography in structuring of, 197; number and kinds of species in, 195–96; ocean acidification and, 93–95; ocean warming and composition of, 192; pelagic, 269–71; phylogenetic structure of, 214; with similar composition in similar habitats, 197. *See also* diversity in communities; rocky intertidal communities
- community assembly, 199–200, 200f, 201
- community dominant, 173, 175
- community dynamics, 198–203. *See also* dispersal; ecological drift; ecological selection; speciation
- community metabolism, 222
- community modules, 173, 173f
- community organization: functional traits and, 187–89, 211, 213–14; in mangroves, 333; in rocky intertidal communities, 2, 9, 306–8, 308f, 309f; in salt marshes, 328–29; in seagrass meadows, 319–21, 320f; in sediment bottoms, 313–14; of sediment fauna subject to organic enrichment, 315–16, 316f; species interactions and, 2, 9. *See also* community structure
- community structure: climate change and, 121, 291; deterministic interactions and, 205; ecosystem functioning and, 218. *See also* community organization
- competition: climate warming causing shift to facilitation from, 192; interspecific, 175–76; in mangrove forests, 333; natural selection and, 126; in salt marshes, 328, 329, 330; specialists vs. generalists and, 55; speciation and, 49–50, 51, 53, 55; three possible outcomes of, 176; Tilman's resource-ratio theory of, 176
- competitive exclusion: accelerated by herbivorous snail, 175; chaotic dynamics and, 269, 271; despite long-distance dispersal, 50; disturbances maintaining higher diversity and, 207, 280; limited by larval dispersal, 201; nonequilibrium dynamics and, 270–71; paradox of the plankton and, 198, 269–70; resource partitioning and, 269, 270; on rocky intertidal shores, 174–75, 174f, 306–7; selective predator with effect on, 185. *See also* niche differentiation
- competitive exclusion principle, 176, 270
- complementarity: diverse prey community and, 246; productivity of diverse species and, 242. *See also* niche partitioning
- complex adaptive systems: of biosphere containing humanity, 84, 85, 379; earth system as, 377, 378; ecosystem as, 4, 224–25, 236; in ecosystem model of phytoplankton, 255; unpredictable but resilient, 377
- connectivity: genetic markers of, 162, 164; geochemical tracers and, 164; larval dispersal and, 159, 169
- Connell, Joseph, 174–75, 176, 207, 304, 306
- conservation: cautious optimism about, 108–10, 109f; community interactions applied to, 345; of coral reefs, 374, 375; ecosystem approach in, 257; elasticity analyses and, 151–52, 154, 154f; evidence-based, 381; life histories and, 151–55; local engagement in management and, 106, 110; of mangroves, 231; marine ecoregions classification and, 62, 63; nonconsumptive effects of predators and, 184; of seagrass ecosystems, 231, 322–23, 323f, 325; social-cultural institutions and, 106
- consumer-prey interactions: diverse prey assemblages and, 246, 248f; as function of three processes, 121; stoichiometric mismatch in, 115, 115f; temperature and, 121; warming-related life history changes and, 91
- consumers, major energy pathways of, 112, 113f
- consumption, in energy budget, 118, 120f
- continental shelves: of active and passive margins, 297; coastal ocean extending to edge of, 296; disproportionate significance of, 296; organic matter delivered to, 303; trophic cascades over, 274
- continents, history of, 38–40, 39f
- convergent fronts, 42–43, 42f
- Cook, James, 260, 347
- copepods: biogeographic patterns in functional traits of, 64; biological pump and, 274; calanoid, 268, 272; climate warming and, 68–69, 70, 90; as macroplankton, 22; meiofaunal, 33; as mesoplankton, 22; population growth under food-poor conditions, 146–47, 147f; resilient pattern of species diversity in, 271; sensitivity of life stages to temperature, 166; trade-off between egg size and number in, 140, 141f
- coral gobies (*Gobiodon*), 51, 51f
- coral larvae: crustose coralline algae and, 93–94, 161; inhibited by degradation of reefs, 365; ocean acidification and, 93–94, 372; from robust source reefs, 374; sensory biology of, 163, 163f; specific species of macroalgae and, 163
- coral reef food web, simulated species removals in, 190
- coral reefs: abiotic environment of, 351–52; in the Anthropocene, 369–74, 370f, 372f; biodiversity of, 347, 351, 357–60; chemically defended organisms on, 186; conservation and management of, 374, 375; cyanobacteria on, 178; dead zones in, 341; diseases with impacts on, 362–64, 362f; diversity in Atlantic vs. Pacific, 208; ecosystem services to humans from, 371; of Enewetak Atoll, 222, 222f, 223, 350, 367; evolution of, 350, 350f; fisheries on, 253, 368–69, 369f, 373; future of, 373–74, 380–81; geomorphology of, 348–51, 349f, 350f; halos of grazed areas surrounding, 177, 177f, 319; healthy vs. degraded algal-dominated, 163, 163f, 363, 365–66, 365f, 366f; herbivorous fishes on, 179, 248, 355–56, 356f, 365, 368–69, 373, 375; human impacts on, 367; intermediate disturbance hypothesis and, 207, 208f; legacy of Pleistocene ice ages in, 208; mangrove interactions with, 334; near urban centers, 337; ocean acidification and, 372; ocean warming and, 371, 372f; as oligotrophic systems, 218, 222, 228, 351, 352, 368; paradox of low fisheries yields in, 253; paradox of productivity of, 347, 352, 367; plastic pollution on, 364; primary producers of, 222, 354–55, 354f; promising topics for research on, 374–75; regional variation in, 366–67; in state of crisis, 363, 369–71, 370f; summary of, 375–76; transition from kelp forests to, 192; trophic cascades on communities of, 361–62; uncertain role of algal proliferation on, 375. *See also* Caribbean reefs; crustose coralline algae; filamentous (turf) algae; Great Barrier Reef; Jamaican coral reefs; reef communities; reef fishes
- corals: acidification altering communities of, 94; anatomy and physiology of, 351f, 352; communities supporting better condition of, 110; of deep sea, 278f, 289, 292; as dominant coastal primary producers, 301; double blow to calcification of, 93; facilitation by fire corals, 186; fishes feeding on live corals, 179; as foundation species, 102–3, 301, 352; functional classification of, 353–54, 353f; hermatypic, 347; heterotrophic capacity of, 352; hybridization among, 21; Indo-Pacific species distributions of, 39–40, 57; life history matrices for, 148–49, 149f, 150–51, 152t; local vs. regional control of diversity and, 212–13, 212f; loop diagrams of life histories, 149f; maintained by herbivore functional diversity, 246, 248; as net producers due to symbiotic algae, 296; neutral theory and, 205, 206f; restoration projects for, 109f; seagrasses reducing disease prevalence in, 336; symbiotic algae of (*see* zooxanthellae); thermal tolerances of, 121; threatened species of, 102; trait-based approaches to, 137. *See also* *Acropora*; bleaching of corals; coral larvae; holobiont, coral-algal
- Coral Triangle, 48, 350; biodiversity in, 357; distributions of species in, 57; diversity of seagrasses in, 318; as evolutionary center of origin, 60. *See also* Indo-West Pacific reefs

- cordgrasses. See *Spartina* cordgrasses  
Coriolis force, 40–42, 40f  
crabs: European green crab (*Carcinus maenas*), 310;  
king crab (*Paralomis birsteinii*), 88f, 91, 215; in  
mangrove forests, 333; predatory, using seagrass  
near oyster reefs, 336; in salt marshes, 329  
critical depth, 265  
cross-habitat diversity gradient, 54  
crown-of-thorns starfish (*Acanthaster planci*), 361–62,  
365, 370f, 374  
crustaceans: euphausiid (krill), 22, 264f, 268, 272, 274;  
mesograzing, 179; zooplanktonic, top-down  
control of diatoms by, 233. See also amphipods;  
copepods; crabs  
crustose coralline algae, 15f, 88f; acidification and,  
93–94, 372; coral larvae settling on, 372; grazing  
intensity and, 360; on hot tropical shores, 304;  
overgrown by fleshy seaweeds, 93, 94; on  
temperate rocky reefs, 181  
cryptic species, 156, 205  
ctenophores, top-down control of zooplankton by,  
233, 234f, 275, 275f  
cultural eutrophication, 79  
cyanobacteria: avoided by herbivores, 214; on coral  
reefs, 178, 355; as dominant primary producers  
of ocean, 268–69; fossils similar to, 311; of  
harmful algal blooms, 341; origin of chloroplasts  
and, 19; origin of oxygenic photosynthesis and,  
1; in sediment, 32; stromatolites built by, 348.  
See also *Prochlorococcus*  
Cyclophora, 11, 12f  
cytometric diversity of phytoplankton, 285, 285f
- damsel-fishes: Caribbean (*Stegastes partitus*), 155, 156f;  
on coral reefs, 355, 362, 369; species interactions  
stabilizing populations of, 248  
dark reaction, 118  
Darwin, Charles, 49–50, 60, 126, 155, 245, 260; coral  
reefs and, 347, 350, 358, 367  
dead zones, low-oxygen, 110, 257, 316, 340–41  
decomposers, and energy pathways, 113f  
decomposition: nitrate accumulation from, 115–16;  
quality of primary producers and, 115, 115f,  
116f  
deep scattering layer, 28, 264  
deep sea, 276–80; adaptations to life in, 276–77, 278f;  
biodiversity in, 48, 265, 279–80, 280f, 284–88,  
285f; dead zones in, 316, 341; detritus as main  
food source in, 235, 278–79; episodic food  
sources in, 279; fisheries of, 288–89, 290, 292;  
global distribution of benthic biomass in, 276,  
277f; limited knowledge of, 276; pelagic-benthic  
coupling in, 278–79, 279f; scarcity of food in,  
276; seagrass detritus in, 321; seasonality of  
material flux to, 278–79, 279f; volume of, 276  
defaunation, 215, 258  
democracy, 378  
demographic modeling. See matrix population models  
demographic parameters, and metabolic allometry,  
166–67  
demographic transition, human, 168  
depensation, 251  
deposit-feeders, 312, 312f, 313, 314, 315; detritivores  
as, 236; macrofauna as, 33–34; in salt marshes,  
328  
depth diversity gradient, 48  
deserts: of deep sea, 277, 281; of open ocean, 42, 222,  
261, 347, 352, 367. See also oligotrophic systems  
determinism: in community structure, 205, 206, 207;  
ecosystem processes and, 225  
detritivores, 113f, 236; of deep-sea benthos, 277;  
increased by nutrient enrichment, 341; limited  
by nitrogen availability, 115; nutrition of food  
chosen by, 182  
detritus, 235–36, 235f; aggregates of, 235; on algal  
turfs of reefs, 355; in coastal systems dominated  
by higher plants, 231; consumers of, 233, 235–36  
(see also detritivores); declining exponentially  
with depth, 264, 264f, 278; defined, 233; from  
epipelagic ecosystem, 264; grazed in seagrass  
meadows, 319; from kelps of rocky coasts, 181,  
232; from mangrove production, 333, 334;  
morphous vs. amorphous, 235, 235f; pathways  
of, 235–36, 235f; as primary deep sea food source,  
235, 278–79; in reef fishes' diet, 359; in salt  
marshes, 325, 328, 330; from ungrazed seagrass,  
317, 321  
development, 139. See also life histories  
*Diadema antillarum* (long-spined sea urchin), 175,  
184–85, 362, 362f, 363, 373, 375  
diatoms: biological pump and, 274; conditions  
favoring, 267, 267f; disfavored by ocean warming,  
292; epiphytic on seagrasses, 319; functional  
differentiation from dinoflagellates, 270; ocean  
acidification affecting iron use of, 292; responding  
to day length more than temperature, 192; in  
sediment, 32; silica cell wall as defense of, 268;  
Si:N ratios and, 129, 130; species composition  
associated with nutrient availability and, 286;  
in spring bloom, 266; top-down control by  
crustacean zooplankton, 233; trans-Arctic  
invasion of North Atlantic by, 71, 88f; warming  
of polar waters and, 26  
dilution hypothesis, 364  
dinoflagellates: conditions favoring, 267, 267f;  
functional differentiation from diatoms, 270; of  
red tides, 266. See also zooxanthellae  
direct development (brooding), 140, 141–42; of  
peracarid crustaceans, 18, 140  
directional selection, 156–57, 157f  
discrete rate of increase: of population, 146, 148,  
152t; of trait or gene, 146  
disease in humans: declining biodiversity and, 341,  
343; seagrasses reducing prevalence of, 336  
disease in marine organisms, 184–85; aquaculture as  
risk for, 101, 104–5; climate change and, 341; coral  
reefs impacted by, 362–63; coral species threatened  
by, 102; in seagrass meadows, 320–21, 322–23;  
seagrass role in reducing prevalence of, 336;  
transported with nonnative oysters, 339; unan-  
swered questions about, 375; warming favoring  
the spread of, 91, 102, 192, 322–23  
disease organisms, as keystone species, 173, 175, 362,  
364  
disequilibrium in community ecology, 207  
dispersal: across Arctic Ocean, 198; artificial structures  
as barrier to, 344; composition of communities  
and, 45, 45f, 198; distance variation between types  
of organisms, 158–59, 158f, 164; genetic markers  
of, 162, 164; global microbial diversity and, 286;  
human impact on barriers to, 72; in integrative  
models of biodiversity, 60; latitudinal diversity  
gradient and, 60; local community diversity  
and, 200–201; marine reserves and, 154; in  
metacommunity, 201; in metapopulations, 138;  
rescue effect of, 201; species richness and, 209–10,  
209f; theory of island biogeography and, 57–58,  
57f. See also larval dispersal  
dispersal ability, 56–57; coexistence of ecologically  
equivalent species and, 202, 202f; genetic  
structure in reef fishes and, 54–55, 55f, 57;  
geographic range size and, 167; speciation and,  
50, 51, 54–55, 55f, 57  
dispersal filter, 200, 200f  
dissolved organic carbon (DOC), 273f, 354  
dissolved organic matter (DOM): absorbed by  
corals, 352; Bacteria and Archaea feeding on, 25;  
in detritus formation, 235; in pelagic ecosystem  
processes, 129f; in sediments, 30, 32  
disturbance: coral disease outbreaks and, 363, 364;  
deep-sea biodiversity and, 280, 285; diversity in  
communities and, 207, 245–46; reef community  
diversity and, 358; to salt marsh ecosystems, 331.  
See also intermediate disturbance hypothesis  
diversification rate hypothesis, 53  
diversity in communities, 203–11; adaptation to  
environmental change and, 225; disturbance  
and, 207, 245–46; local vs. regional control of,  
212–13, 212f; metabolic theory and, 210–11;  
neutral theory of, 204–6; ocean warming and,  
214–15; predation affecting level of, 175, 185;  
productivity and, 368; regional enrichment and,  
209–10, 209f. See also biodiversity  
diversity minimum, estuarine, 299, 299f  
DNA sequencing: reconstruction of phylogeny from,  
20–21. See also metagenomics  
DOC. See dissolved organic carbon  
DOM. See dissolved organic matter  
domestication of marine species, 104–5, 158. See also  
aquaculture  
domestication of the ocean, 104–5  
donor-controlled systems, 235  
downwelling at convergent front, 42, 42f  
dugongs, 302, 319, 321, 323, 355  
dynamic equilibrium model, 207
- EAF (ecosystem approach to fisheries), 63, 100  
East Indies. See Coral Triangle  
EBFM (ecosystem-based fisheries management),  
100, 106  
echinoderms, 12, 14f; ocean acidification and, 135.  
See also sea urchins; starfish  
ecological drift, 45, 45f, 198, 201, 203, 359. See also  
neutral theory  
ecological economics, 80, 108  
ecological efficiency, 237–38  
ecological engineering: in coastal communities  
dominated by macrophytes, 302; in sediment  
communities, 314  
ecological extinction, 102, 258  
ecological opportunity hypothesis, 55  
ecological selection, 45, 45f, 198, 199–200; in coral  
reef communities, 357, 359–60; in rocky intertidal  
communities, 206; sympatric speciation and, 50  
ecological speciation, 50, 51  
ecological stoichiometry, 115, 115f, 116f  
ecology: adapted to human-dominated world, 6;  
complexity in, 7–8; framework for thinking  
about, 3–4, 3f, 4f; human sciences essential  
to, 84  
economic growth, 380. See also economics  
economics: conservation goals and, 110; ecological,  
80, 108; energy use and, 77f, 84, 85f;  
evidence-based understanding of, 381; ignoring

- biophysical constraints, 86; in natural history of humans, 86
- Ecopath mass balance model, 253
- Ecopath with Ecosim (EwE), 253–54
- ecoregions classification, 62–63, 62f
- ecosystem approach to fisheries (EAF), 63, 100
- ecosystem-based fisheries management (EBFM), 100, 106
- ecosystem engineering by humans, 85, 378
- ecosystem functioning, 218
- ecosystem modeling: in fisheries management, 252–55, 253f, 254f; future of, 259; of global ecosystem, 255–57, 256f
- ecosystems: in the Anthropocene, 257–58; biodiversity and, 241–48; communities and, 211, 213–14, 224–25; as complex adaptive systems, 4, 224–25, 236; conceptual history of, 219–25; control of biomass and productivity in, 228–36, 258; functional traits and, 128, 129f, 211, 213, 236–37; irreversible transitions in, 380–81; Odum's engineering metaphor for, 222, 222f; organismal traits in, 236–37; predictability of major properties of, 293; resilience of, 380–81; risk assessment for, 257; terrestrial, 12, 13t, 293
- ecosystem services to humans, 218; coastal, 303–4
- ecotypes, 50, 51; of *Prochlorococcus*, 256f, 270
- eelgrass (*Zostera marina*): beneficial nutrient enrichment in meadows of, 341; coastal sediment conditions and, 251; food web of animals supported by, 187, 187f; genetic diversity of, 325; legacy of glaciation and invasion on, 40; length of shoots in, 318; organic carbon stored in sediment by, 322; trophic cascades involving, 302, 324–25, 324f; wasting disease in 1930s and, 175, 321, 322–23; wide range of salinity tolerance in, 318. *See also* seagrasses
- eelgrass, Japanese (*Zostera japonica*), 339, 340f
- effect traits, 21, 215–16
- Ekman transport, 41, 44, 349–50
- elasticity, 148, 152t; management uses of, 151–52, 154, 154f
- electrical circuit approach to ecosystems, 222, 223, 223f
- elemental composition of organisms, 113–15, 114f. *See also* stoichiometry
- elkhorn coral (*Acropora palmata*), 15f; beginning to revive, 381; threatened status of, 88f, 102; white-band disease of, 185, 362–63, 370, 375
- El Niño event of 1982–1983, 371
- Elton, Charles, 120, 238
- emergent properties: climate change effects on ecosystems and, 257, 293; of ecological networks, 189–91; of ecosystems, 7, 218, 219, 224; in ecosystem simulations, 255; of food webs, 186, 187. *See also* complex adaptive systems
- endemicity, 44, 45; within MEOW realms and provinces, 63; modern extinctions and, 59; of remote islands, 58
- endosymbiosis, in origin of eukaryotic cell and mitochondrion, 56
- end-Permian mass extinction, 58
- end-to-end ecosystem models, 254–55, 254f
- energetic equivalence rule, 166–67, 190; population-level interaction strengths and, 190; species richness and, 210; trophic levels and, 240, 241f
- energy: as central human resource, 86; in early ecosystem studies, 222–23, 223f; major pathways of producers and consumers of, 112, 113f; metabolism and, 117; mostly lost to animal's respiration and excretion, 237–38; species diversity and, 210–11; species-energy hypotheses and, 54, 210–11, 285–86; stored in carbon-carbon bonds, 114
- energy budget of organism, 118, 120f
- energy use by humans: economic activity and, 77f, 84, 85f; human life history traits and, 168. *See also* fossil fuels
- Enewetak Atoll: drilling to volcanic basement of, 350; Odum study at, 222, 222f, 223, 367
- Enteromorpha*, 310
- environmental filtering, 200, 200f
- environmental forcing vs. accidents of history, 72
- environmental niche models, 69–70, 69f, 106; climate change and, 158
- ephemeral algae: eutrophication and, 258, 310, 324; facilitation by herbivores feeding on, 302; on rocky shores, 307, 310; seagrasses and, 324–25; traits of, 133
- epifauna, 30, 34; damaged by fishing machinery, 99; seagrass providing habitat for, 321
- epipelagic zone, 263–64, 263f
- epiphytic algae on seagrasses, 319, 324
- equalizing mechanisms, and unstable coexistence, 176
- equilibrium. *See* nonequilibrium processes
- Estes, James, 181, 232
- estuaries, 298–300; bottom-up control in, 302; circulation patterns of, 298f, 299; dead zones in, 341; defined, 298; diversity gradients in, 299, 299f; dominant primary producers of, 300; fauna of sediment bottom in, 312f; invasive species in, 339, 340f, 342–43, 342f; oyster reefs in, 299, 338; of passive continental margins, 297; primary and secondary production in, 302–3, 303f; reorganized by nonnative species, 339, 340f; salt marshes in, 326; seagrasses in, 317, 318, 324–25; sea level rise and, 323; trophic cascades in, 276, 324–25; urban centers and, 337, 343–44
- estuarine fish species, functional traits predicting demographic changes in, 189
- Eukarya, 19, 19f, 20; endosymbiotic origin of, 56; primary producers among, 225
- euphausiid crustaceans (krill), 22; biological pump and, 274; deep foraging by whales and, 264f; as herbivores of plankton, 268; in pelagic food web, 272
- European green crab (*Carcinus maenas*), 310
- eurythermal species, 121, 291
- eutrophication, 257–58, 340–41; in Black Sea, 275; climate warming and, 341; coastal community composition and, 309–10; as control on seagrass distribution, 251; disturbing salt marsh ecosystems, 331; ephemeral algae and, 310; nitrogen availability and, 309–10, 324; trophic cascades in coastal ecosystems and, 302, 324–25. *See also* blooms of algae and phytoplankton
- evidence-based approach, 381–82
- evolution: coastal geography and, 44; human-induced, 98, 104–5, 135, 158, 168, 169–70; in urbanized environments, 344. *See also* natural selection
- EwE (Ecopath with Ecosim), 253–54
- excretion: by heterotrophs, 116, 118. *See also* fecal pellets
- exploitative competition, 126, 173, 173f, 176
- export of production to deep ocean, 226, 228; by biological pump, 273–74, 273f; microbial loop and, 267. *See also* carbon export to deep ocean
- extended phenotype, 83
- extinction: abiotic forcing vs. organismal traits and, 73; body size and, 136; climate warming and, 103; ecological, 102, 258; ecological specialization and, 55; functional redundancy and, 246; human impacts and, 36, 58, 59; in integrative models of biodiversity, 60; latitudinal diversity gradient and, 53, 60; of marine species in modern times, 59, 101–2, 102f; predicted in Anthropocene ocean, 69–70, 69f; prevented by rescue effect, 201; solar energy and, 54; temperature in fossil record and, 124; theory of island biogeography and, 57–58, 57f, 59; two distinct syndromes of, 58–59. *See also* mass extinctions
- extinction debt, 103
- extremophile Archaea, 19
- facilitation, 185–86, 186f, 189; in coastal communities, 302; by foundation species, 185–86, 189, 304; in mangrove forests, 333; in rocky intertidal communities, 307; in salt marsh communities, 329, 330; in sediment communities, 314; stressful environments causing shift to, 192
- fecal pellets: of metazoan heterotrophs, 28, 274; of zooplankton, 235, 237, 273, 278
- fecundity: age-specific, 145, 147, 148; larval dispersal and, 142–43; scaling with body mass, 166
- fertilization of ocean with iron, 107, 266
- filamentous (turf) algae, 178, 179, 222, 354–55, 354f, 356; epiphytic on seagrasses, 319; fishes excreting nutrients absorbed from, 367; keeping pace with herbivory, 360; mass die-off of *Diadema* and, 362, 362f
- fire corals, 186
- fisheries, marine: alternative stable states in, 250–51, 250f; biomass production in, 117; bottom-up control of yield in, 230, 231f; coastal, 340; coastal and estuarine productivity of, 302, 303f, 304, 326, 326f; on coral reefs, 253, 368–69, 369f, 373; current state of, 97–98; of deep sea, 288–89, 290, 292; directional selection in, 156–57, 157f; diversity enhancing stability of yield in, 246, 247, 247f; economic and nutritional importance of, 6, 95, 368; economic and nutritional losses in, 98, 100; ecosystem impacts of, 98–99; eutrophication enhancing productivity of, 341; exploitation rates in, 97–98, 97f, 100; “fishing down the food web” in, 215; future of, 99–101; hope for sustainable future in, 108, 109–10; human evolutionary pressure in, 104–5; human impacts on, 95, 96f, 97, 135f, 193, 337; illegal fishing in, 110; mangrove contribution to production in, 334, 336; ocean warming and, 91, 291; precipitous decline in, 89; of rocky subtidal habitats, 309; salt marsh ecosystems and, 330; seagrasses supporting services to, 321; shifting baseline and, 87; supported by soft sediments, 315; trophic cascades induced by, 361–62; tropicalization and, 70; upwelling systems that sustain high levels of, 228. *See also* bycatch in fisheries; industrial fishing
- fisheries management, 97–98; challenges of Anthropocene and, 106, 108; coral reef resilience and, 373–74; in developing tropical nations, 373; ecosystem focus in, 257; energy and element budgets in, 117; food webs used in, 186–87, 187f; future of, 99–101; good governance and, 381–82; Hjört-Cushing match-mismatch hypothesis and, 169; inflated Chinese catch statistics and, 252;

- fisheries management (*continued*)  
large marine ecosystems in, 63; modeling in, 252–55, 253f, 254f; nonlinear responses and, 99; specific production (P/B) and, 151; weakness of genetic approaches to, 165
- fishes: artificial structures providing nursery for juveniles of, 344; biomass increasing with species diversity of, 244, 245f; body size and vulnerability to exploitation of, 65; mangroves providing habitat for juveniles of, 333, 336; as nekton, 28; as paraphyletic group, 20; productivity boosted by interactions among habitats of, 336; seagrass providing habitat for juveniles of, 321, 336; size spectra of, 135f, 239; thriving when protected, 381; trait-based approaches to, 137. *See also* reef fishes
- fishes, herbivorous, 35–36; behavioral responses to predators and, 184; on coral reefs, 179, 248, 355–56, 356f, 365, 368–69, 373, 375; feeding on macroalgae, 179, 215, 360; functional groups of, 179; ocean warming and, 192, 215; in rocky intertidal communities, 305; on seagrass meadows, 319, 322
- fishes, predatory: acidification and, 94; amphipod reaction to chemical cues from, 182; migrating from protection of coral reefs to seagrass beds, 335; top-down control of coastal ecosystems by, 325
- fish larvae: planktotrophic, seasonality of recruitment, 169; recruitment variability based on size of, 141, 142; sensory biology of, 163, 163f; warming-related life history changes in, 192
- fitness: ecological selection and, 199; life history traits and, 127; natural selection and, 126; quantitative definition of, 155; reduced by competition, 175; species interactions and, 129
- Flavobacterium columnare*, 105
- fleshy seaweeds: *Diadema* mass die-off and, 362, 362f; favored in biotic homogenization, 104; low grazing on reefs and, 360; shifts toward dominance by, 94, 103
- flowering plants, 13, 30; detritus-based food web and, 235, 303; as dominant primary producers of estuaries, 300; herbivore effects on, 34f; low nutritional quality of, 115, 131, 301–2; low vulnerability to herbivory, 231, 301–2. *See also* macrophytes; mangroves; marsh grasses; seagrasses
- food chain: classical pelagic food chain, 267, 272, 272f, 291; energy and element budgets for, 117; modules of, 173f
- food supply to humans, 81f, 82
- food webs, 173f, 186–87; detritus-based, 235; early example based on eelgrass, 187, 187f; interaction strengths in, 189; ocean warming and, 291; simulations of, 189–91 (*see also* ecosystem modeling); supporting North Sea herring, 187, 188f; vulnerable to loss of well-connected species, 189–90
- foraminifera: of deep-sea benthos, 280, 286; planktonic, with faster speciation at high temperatures, 53f, 54
- fossil fuels: catalyzing Great Acceleration, 78; economic activity and, 84; as existential threat to coral reefs, 370, 371; human development supported by, 6, 74–75, 75f, 77–78; nitrogen oxides from combustion of, 79, 80f; trend in extraction since 1972 predictions, 81f, 82; unsustainable consumption rate of, 74, 86, 378. *See also* climate change; climate warming; ocean acidification
- fouling species: characteristic suite of, 344; interaction pathways in seagrass beds and, 320f; nonnative ascidians, 103; nonnative invertebrates in harbors, 343; temperature effect on consumer pressure on, 66, 192
- foundation species, 30, 34, 180–81; alternative ecosystem states on temperate rocky reefs and, 181; Anthropocene transition from, 36; artificial structures reducing establishment of, 344; calcareous, ocean acidification and, 93; coastal macrophytes as, 296, 300, 301; corals as, 102–3, 301, 352; declining due to human impact, 191, 337, 338; dependent on predator control of herbivores, 302; facilitation by, 185–86, 189, 304; large impacts on communities by, 190–91, 193; management of nutrient loading and, 343; nontrophic interactions and, 189; often declining fastest, 102–3; of salt marshes, 325, 327, 329; of sediment bottoms, 314
- fringing reefs, 350, 350f
- functional biology, 5
- functional diversity, 5; in ecosystem modeling, 228; ecosystems stabilized by, 246; extinction risk and, 59, 73; of herbivores, 227, 227f; species richness and, 241–42
- functional groups, 128; fates of primary production and, 230–31; of herbivores, 179; of phytoplankton, 131–33, 132f; species diversity and, 242; trophic structure and, 211, 213; of vent communities, 283
- functional groups, benthic, 30–36; herbivory and, 131; of macrophytes, 133
- functional groups, pelagic, 21–28, 129f; body size and, 22–24, 24f; nutrition and metabolism of, 23, 24f, 25–28, 27t
- functional redundancy, 246
- functional traits: biogeography of, 63–64; bridging levels of organization, 133–34, 187; community organization and, 187–89, 211, 213–14; defined, 21; ecosystem processes and, 128, 129f, 211, 213, 236–37; effect traits, 21, 215–16; in interaction networks, 189; limiting similarity in, 187–89, 188f; in models of global change, 106; predictions based on study of, 136; responses to environmental forcing and, 189; response traits, 21, 215–16; trade-offs in, 128, 131, 136–37; trait-based ecology and, 129–31. *See also* functional groups; phylogenetic conservatism of traits; traits
- fundamental niche, 129, 199, 199f
- Gaia hypothesis, 2, 221
- gamete recognition proteins, 50
- gamma diversity ( $\gamma$ ), 45
- gas hydrates, 284
- GDP (gross domestic product), 77f, 84, 85f
- General Ecosystem Model, 255–57
- genetic drift: connectivity among populations and, 164; environmental disturbances and, 201
- genotype, 127
- geochemical tracers, 164–65, 165f
- geoengineering, 107
- geographic range size. *See* range size
- geomorphology, 3; of coral reefs, 348–51, 349f, 350f; human transformation of, 6, 7f; of mangroves, 332; of rocky shores, 305, 306f; of salt marshes, 326–27, 327f; of seagrass meadows, 317–18
- Georges Bank haddock, 250–51, 250f
- geostrophic flow, 40f, 42; trades biome and, 61
- giant kelp (*Macrocystis pyrifera*), 13, 15f, 30, 181
- glacial isostatic adjustment, 91
- glaciations: Antarctic, 39; in Pleistocene ice ages, 39, 39f, 40
- Gleason, Henry, 197
- Global Fishing Watch, 110
- globalization, 103–4
- global warming. *See* climate warming
- Gorgonian corals, 354
- governance, 381–82
- gray whales, 29, 29f, 159–60
- grazers: benthic, 34–36; in coastal ecosystems, 302; harmful algal blooms and, 257–58; micrograzers of phytoplankton, 268; pelagic ecosystems and, 274; pelagic functional types of, 268–69; on spring bloom, 265, 266. *See also* herbivores
- grazing: ecosystem pathway of, 113f; eutrophication and, 310; highest on nutrient-rich microalgae, 131, 230–31; inhibited by acidification, 94; intensified around artificial structures, 105, 344; lowest on higher plants, 131, 231; macroalgal functional groups and, 133, 134f; in marine vs. terrestrial ecosystems, 125–26; in modern vs. historical seagrass ecosystems, 321; overgrazing caused by trophic skew, 338; on phytoplankton, 268, 269; rapid turnover of primary production by, 228, 228f; in salt marshes, 329, 330; stronger at low latitudes, 66, 67f; top-down control by, 226–27, 228, 228f. *See also* herbivory
- Great Acceleration, 6, 76–82; decrease in extreme poverty since, 380; indicators of, 76, 77f; industrial-scale fishing in, 95
- great auk, 88f, 101
- Great Barrier Reef: bleaching of corals on, 371, 373, 374; coexistence of ecologically equivalent fish species on, 202, 202f; crown-of-thorns starfish on, 361–62; decline of coral cover on, 370f; disease linked to terrestrial runoff and, 363; dozens of coexisting *Acropora* species on, 205; herbivore abundance and algal proliferation on, 375; herbivores controlling algae on, 360, 361f; microhabitats and diets of herbivorous fishes on, 359; resilient source reefs in, 374; seen from space, 349f, 350; semisynchronous mass spawning of corals on, 143–44; signs of some recovery on, 373; weak top-down forcing on, 362
- Great Barrier Reef Marine Park Act, 100
- Great Oxygenation Event, 1, 2
- green algae (Chlorophyceae), 26
- greenhouse effect, 78
- greenhouse gases: climate warming and, 289; increasing since early human history, 75, 76f; methane as, 284; reaching equilibrium only after decades, 95. *See also* carbon dioxide (CO<sub>2</sub>)
- green web, 235, 236
- green world hypothesis, 228–29, 229f, 232
- gross primary production: defined, 118; highest on coral reefs, 367–68
- Gulf Stream, 41, 297
- gyre circulation, 40f, 41–42. *See also* central ocean gyres
- Haber-Bosch process, 79
- habitat: conservation strategies based on life histories and, 154–55; deep-sea heterogeneity of, 280; human impact on, 337–38; provided by seagrasses, 321; species richness and age of, 52, 52f

- habitat area: speciation and, 50, 52; species richness and, 211; theory of island biogeography and, 57–58, 57f. *See also* species-area relation (SAR)
- habitat complementarity, 335–36
- habitat fragmentation: extinction driven by, 59, 72; metapopulations and, 159; speciation and, 357
- habitat selection, and speciation, 50, 51
- Halimeda*, 178
- Hardin, Garrett, 86
- hard substrata, 30; human infrastructure used as, 105
- Hardy, Alistair, 187, 188f
- herbivores: ammonium and urea excreted by, 226; of coastal benthic systems, 302; on coral reefs, 355–56, 356f, 360–61, 361f, 373, 375 (*see also* fishes, herbivorous; sea urchins); ecosystem energy pathways and, 113f; functional diversity of, 227, 227f; functional groups of, 179; grazing pelagic primary production, 268, 269; interactions between plants and, 176–79, 181f; latitudinal trends in impact of, 67–68, 67f; limited by nitrogen availability, 115, 115f; in mangrove forests, 333; nutritional quality of primary producers and, 115, 115f, 116f; range expansion due to tropicalization and, 70, 71f; in seagrass meadows, 319–21, 320f; stoichiometry of food choice by, 182; temperature-mediated increase in consumption by, 191, 193–94; in transition between coral- and algal-dominated states, 360, 362. *See also* fishes, herbivorous; grazers
- herbivory: plant defenses against, 177, 178, 268 (*see also* chemical defenses); plants' phylogenetic conservatism and, 214; plant stoichiometry and, 194; vigorous on coral reefs, 347; warming temperatures and, 192, 193. *See also* grazing
- hermatypic corals, 347
- Hessler, Robert, 279–80
- heterotrophic bacteria, 23, 24f, 25
- heterotrophs: metazoan invertebrate plankton, 28; multicellular, 23, 24f, 28; nitrogen from excretion by, 116, 226; unicellular eukaryotic, 23, 24f, 26–27
- heterotrophy, 118, 120
- higher plants. *See* flowering plants
- high-nitrogen low-chlorophyll (HNLC) regions, 107, 117, 266, 292
- Hilborn, Ray, 100
- historical processes, 72, 197, 198, 207–9. *See also* biogeography
- Hjört, Johan, 169
- Hjört-Cushing match-mismatch hypothesis, 169
- holistic vs. reductionist approaches, 7–8
- holobiont, coral-algal, 347, 351f, 352, 367
- Holocene epoch, 4, 377
- homeothermic megafauna, 23, 24f, 28–30, 29f
- homeothermic vertebrates, interaction strengths of, 193
- homogenization of ocean life, 103–4
- Homo sapiens*: dependence on the ocean, 6; evolving in response to niche construction, 85; as keystone species, 108, 345, 378; natural and cultural history of, 83–84; origin of, 1; outsized influence on Earth's ecosystems, 1, 6; as top predator of ocean, 87, 292; ultrasociality of, 84, 378. *See also* human society
- horizontal gene transfer, 19–20, 21, 25
- HSS (Hairton, Smith, and Slobodkin), 228–29
- Hubbell, Stephen, 201, 203, 204
- human behavioral and social ecology, 108
- human society: advancement in well-being of, 74–75, 378, 379; continuing dependence on biological communities, 378; energy use by, 84, 85f, 86; extinctions driven by, 36, 58, 59; impacts on natural world, 337; trends in socioeconomic development, 77f; tribal and emotional motivations in, 378, 382. *See also* *Homo sapiens*
- Hutchinson, G. E., 130, 195, 198, 357; deep-sea biodiversity and, 280; on disequilibrium, 207, 271; niche definition of, 128–29. *See also* paradox of the plankton
- Huxley, Julian, 121
- hybrid end-to-end ecosystem models, 254–55
- hybridization, 21
- hydrothermal vents, 281–83, 281f; global distribution of, 282, 282f; whale carcasses and, 29
- hyperdiverse tropical forests, 204
- Hypnea*, facilitated by *Sargassum*, 185–86, 186f
- hypoxic regions. *See* dead zones, low-oxygen
- hysteresis, 249, 250f, 251; in Black Sea, 275; in coral reef communities, 365, 365f
- indirect interactions, 173
- Indo-West Pacific reefs: Caribbean reefs compared to, 366–67; dilution hypothesis and coral disease in, 364; diversity in, 366–67; soft corals in, 354. *See also* Coral Triangle
- Indo-West Pacific region, 350, 357
- induced defenses of plants, 178–79
- industrial agriculture, 85
- industrial fertilizer, 229
- industrial fishing, 72, 88f, 95, 97; government subsidies for, 109; seafloor destruction caused by, 98–99, 289, 292; trawling of seabed in, 292, 295, 315, 316–17, 337
- Industrial Revolution, 74, 75, 76, 78, 79, 86
- infauna, 30, 33–34, 312, 313–15; increased by nutrient enrichment, 341; larvae of invertebrates of, 313–14; macroinfauna, 32f, 33–34; regime shifts and, 252; seagrass providing habitat for, 321; sediment grain size diversity and, 280. *See also* meiofauna
- innovation. *See* technological innovation
- instantaneous increase: of population, 146, 153f, 165–66; of trait or gene frequencies, 155
- insurance hypothesis, 246, 247
- integrated polyculture systems, 106
- interaction filter, 200, 200f
- interaction modules, 173, 173f
- interaction networks. *See* networks, ecological
- interaction strengths, 171, 172f, 173, 193–94; defined, 190; in food webs, 186; organismal traits as predictors of, 189; population-level, 190, 190f; in rocky shore communities, 190, 190f; temperature-mediated changes in, 191–92
- interactome, 17, 17f
- interference competition, 126; among infaunal species, 313
- intermediate disturbance hypothesis, 207, 208, 208f, 270; mixing of water column and, 285. *See also* disturbance
- International Convention on the Conservation of Antarctic Marine Living Resources, 100
- interspecific competition, 175–76
- intertidal zone, 297–98; mangroves and, 331–32; rocky shore community interactions in, 171, 172, 173; salt marshes and, 325, 327
- intrinsic growth rate of population ( $r$ ), 146, 153f, 165–66
- invasions of nonnative species, 338–39, 339f; of Antarctic shelf by king crab, 88f, 91, 215; Arctic opening and, 71; by Asian clam in San Francisco Bay, 342–43, 342f; in Black Sea, 275, 275f, 276; coastal patterns of, 103, 104f; commercial shipping as driver of, 103; in earlier earth history, 338–39; in estuaries, 339, 340f, 342–43, 342f; extinctions driven by, 59; favored by globalization, 103; fisheries-related, 103; by fleshy algae favored by acidification, 94, 136; increasing diversity in some areas, 72; low-diversity regime shifts triggered by, 252; ocean warming and, 103; often lower in food chain, 104; by pathogens, 184; predicted in Anthropocene ocean, 69–70, 69f; on rocky shores, 310; trophic skew exacerbated by, 193, 338; by weedy species, 338. *See also* nonnative species
- inverted biomass pyramids, 151
- iron: Caribbean vs. Pacific reefs and, 367; fertilization of ocean with, 107, 266; limiting primary production, 117, 266, 367; ocean acidification and, 292; phytoplankton growth and, 114; wind-borne, 291, 293, 367
- island area and age, and species richness, 52, 52f
- island biogeography, theory of, 57–58, 57f; extinction due to habitat loss and, 59; human impacts on diversity and, 72; neutral theory and, 203, 204
- Isthmus of Panama: allopatric speciation and, 49; origin of, 39, 297; vicariance across, 57
- IUCN Red List, 101, 102f, 136, 257, 371
- Jamaican coral reefs, 148–49, 150–51, 152t; beginning to come back, 373, 381; decline of, 363, 365
- Japanese eelgrass (*Zostera japonica*), 339, 340f
- jellyfish, global increase in, 105
- kelps: climate warming and acidification and, 338; fishing as cause of overgrazing in, 338; giant kelp (*Macrocystis pyrifera*), 13, 15f, 30, 181; high-latitude forests of, 300, 338; life histories of, 139f; predator diversity affecting productivity of, 242, 244f; on rocky shores, 181, 301, 304; in trophic cascade, 179, 180f, 181, 232, 249; vulnerable to human disturbance, 103; warming-related transition to coral reefs from, 192; warm-temperature stress leading to herbivore outbreak in, 302
- key innovations, diversification stimulated by, 56
- keystone predation, 173, 173f
- keystone species, 173; disease organisms as, 173, 175, 184, 307, 362, 364; *Homo sapiens* as, 108, 345, 378; human impacts on, 72, 191; with large impacts on communities, 190–91, 193; often declining fastest, 102; sea star *Pisaster ochraceus*, 12, 14f, 68, 91, 173, 175, 304, 306–7
- killer whales: expanded into Hudson Bay, 71–72; trophic cascade beginning with, 180f, 181, 232
- king crab (*Paralomis birsteini*), 88f, 91, 215
- Kleiber, Max, 121
- krill. *See* euphausiid crustaceans
- Kuroshio Current, 41, 297
- Labyrinthula zosterae*, 320–21, 323
- lakes, regime shifts in, 251, 252
- landscapes of fear, 177f, 183–84
- large-bodied species: ecological extinction of, 258; human impact falling on, 337, 338, 378. *See also* body size

- large marine ecosystems (LMEs), 63  
larval choice of habitat, sensory cues for, 163, 163f  
larval dispersal, 158–59; behavioral strategies and, 161, 162, 164; of benthic invertebrates, 201; as bet-hedging, 142; as a central theme in ecology, 138; connectivity and, 159; distances of, 158–59; as enduring problem in ecology, 142–44, 169; habitat complementarity and, 336; hydrodynamic simulation of, 161; methods for studying, 159; oceanography integrated with research on, 169; from rocky shore communities, 305–6; selection for high fecundity and, 142–43  
larval populations on rocky shores, 305–6, 307; energy of water movement and, 308, 309f  
latitudinal bands, 44  
latitudinal diversity gradient, 47, 47f; debate about causes of, 72; diversification rate hypothesis and, 53–54; in fossil marine bivalves, 60; habitat area and, 50, 52, 211; interaction of temperature and area in, 211; speciation and, 49, 50, 52, 53, 54; summary of factors driving, 73  
latitudinal trends: in life history related to temperature, 64, 66f; in plant defenses, 178; in species interactions, 64, 66–68, 67f  
lecithotrophy, 140  
Lefkovich matrix, 148, 149f, 152t  
Leibig's law of the minimum, 226  
Leopold, Aldo, 378  
Leslie, Patrick H., 147  
Leslie matrix, 145f, 147–48  
lettuce coral (*Agaricia*), 151, 370  
life histories, 139–42; of clonal invertebrates and plants, 148; conservation and, 151–55, 168; of coral species, 353–54, 353f; in deep sea, 277; evolutionary change and, 155; fish using multiple habitats during, 336; loop diagrams of, 148, 149f; marine protected areas and, 154; metabolic scaling and, 165–66; phenological mismatch and, 192; trade-offs in, 140–41, 141f. *See also* phenological mismatch; phenology  
life history traits, 127–28  
life history transitions: elasticity of population growth rate and, 148, 152t; Lefkovich matrix and, 148  
life tables, 145, 145f, 146–47, 147f; modeling with limited data from, 152, 154f  
lifetime reproductive output, 145–46; of industrialized humans, 168  
light, and photosynthesis, 225–26  
light reactions, 118  
limited access privilege programs (LAPPs), 100–101  
limiting similarity, 187–89, 188f  
*The Limits to Growth*, 80–82, 81f, 86  
Lindeman, Raymond, 219, 220f, 222, 223, 330  
lionfish, 104  
*Littorina littorea*, 310  
local richness, 199  
local saturation vs. regional enrichment, 209–10, 209f  
loggerhead turtles, fishing impacts on, 151–52, 153  
logistic population growth, 144, 145  
Longhurst, Alan, 61–62, 63, 97, 100, 265, 272  
longitudinal diversity gradient, 48, 60  
long-spined sea urchin. *See Diadema antillarum*  
loop diagrams, 148, 149f  
Loricifera, 11, 12f, 33  
lottery hypothesis, 202, 205, 359  
Lovelock, James, 2  
Lubchenko, Jane, 175  
Lyell, Charles, 350  
MacArthur, Robert, 57, 64, 197, 245, 280, 358, 359  
macroalgae, 15f, 30, 32, 33f, 34f; blooms of, 257, 258; coral larvae oriented to specific species of, 163; on coral reefs, 355, 360; defenses against microbial pathogens of, 179; detritus-based food web and, 235; dominating reefs with high river runoff, 352; functional groups of, 133, 134f; on healthy vs. degraded coral reefs, 163, 163f, 363, 365–66, 365f, 366f; herbivore intimidation by predators and, 182; herbivore pressure on artificial structures and, 105; herbivorous fishes feeding on, 179, 215, 360; high-latitude forests of, 300; life histories of, 139, 139f; on rocky shores, 301; sponges in mutually beneficial relationship with, 354. *See also* algae; ephemeral algae; kelps; perennial algae; seaweeds  
macroecological scaling, of community interactions, 190, 190f  
macroecology, 133–35; of open ocean, 284–88, 288f; of populations, 165–68; of trophic interactions, 240, 241f  
macroepifauna, 34  
macroinfauna, 33–34  
macrophytes: benthic, 30–32, 33f, 34f, 133; of coastal ecosystems, 296, 300–302, 301t, 303; as foundation species, 301; lake-water sediment and, 251. *See also* flowering plants; macroalgae; seaweeds  
macroplankton, 22, 22t, 28  
Magnuson-Stevens Fishery Conservation and Management Act, 99, 100, 257  
management: large strongly-interacting species and, 191; marine ecoregions classification and, 62–63; population genetic markers and, 164. *See also* fisheries management  
manatees, 302, 319, 321, 355, 373  
mangroves, 331–35; in the Anthropocene, 334–35; basic features of, 331–32; cleared for aquaculture, 340; as coastal primary producers, 296; community organization and key interactions in, 333; conservation of, 231; detritus-based food web and, 235; ecosystem processes in, 334; ecosystem services provided by, 334; estuarine habitats dominated by, 299, 300; expanding into salt marshes, 335; fish production associated with, 334, 336; as foundation species, 102–3; geomorphology and environment of, 332; global distribution of, 317f; historical focus on bottom-up control in, 333; latitudinal distributions compared to salt marsh habitat, 325, 331; lower nutritional quality of, 115, 131, 231; near urban centers, 337; organisms and traits of, 332–33; physiological adaptations of, 332; plant species in, 331, 331f; prop roots of, 332, 333; in shallow, soft sediment environments, 300, 300f, 301; yield in fisheries near to, 326f; zonation of, 332  
mantis shrimps, reef-dwelling, 57  
Margalef, Ramon, 220, 267, 270, 272, 285  
Margulis, Lynn, 2  
marine ecology: contrasted with biological oceanography, 4f, 8, 9; historically local focus of, 345; origins and motivation for, 95, 117  
Marine Ecoregions of the World (MEOW), 62–63, 62f  
marine mammals: body size and vulnerability to exploitation of, 65; extinction risk among, 59, 136; overharvesting of, 338; trophic cascades and, 274. *See also* sirenians; whales  
marine protected areas, 109, 109f, 110, 377; life histories and, 154  
marine snow, 235, 278, 279  
marine spatial planning, 100, 106  
marsh grasses, 131, 296, 299, 300, 300f, 301. *See also* salt marshes  
Martin, John, 107, 117  
mass balance, 117, 118  
mass balance models, 252–55, 253f, 254f; of Black Sea, 275  
mass extinctions: defined, 101; ecological opportunity and, 55–56, 56f; during most of earth history, 58–59; not yet happening, 379–80; sixth, 59, 72, 101  
matrix population models, 145f, 147–49, 149f, 152t; evolution and, 155; habitat protection and, 154; in sea turtle conservation, 153, 153f  
maximum sustainable yield (MSY), 97, 97f, 98, 99, 100, 149, 151  
May, Robert, 271  
Mayr, Ernst, 49  
mean temperature of the catch (MTC), 70  
megafauna, threatened, 108, 109f  
meiofauna, 30, 32–33, 32f, 35f, 312, 313, 314  
Menge, Bruce, 307, 308f  
menhaden spawning, 162, 162f  
MEOW (Marine Ecoregions of the World), 62–63, 62f  
meroplankton, 139  
mesograzers, 179, 181f, 186; mutualistic, 319, 320f; in seagrass meadows, 319, 320f, 321  
mesopelagic zone, 263f, 264  
mesoplankton, 22, 22t, 28  
mesopredators: on coral reefs, 362; trophic skew causing eruption of, 338  
metabolic balance of open ocean, 287, 288f  
metabolic ecology, 117, 124; balance between photosynthesis and respiration and, 287; climate warming and, 135; different components of metabolism and, 166; macroecology and, 134; species diversity and, 210–11; temperature effects on communities and, 216; trophic level and life history in, 240  
metabolic rates: of deep-sea animals, 287; higher in warm places and times, 121; low in deep sea, 277; speciation and, 53–54; specific production (P/B) and, 151  
metabolic scaling: of abundance with body mass, 166–67, 237, 238f, 240, 241f; with body mass and temperature, 121–24, 122f, 123f; deep-sea ecosystems and, 287; herbivore effects on plant biomass and, 194; life history syndromes and, 165–66; of metabolic components with temperature, 166  
metabolic scope, 120–21  
metabolic theory of ecology. *See* metabolic ecology  
metabolism, 117; aerobic, 1; of heterotrophs, 118, 120, 120f; of plants vs. herbivores, 125, 125f  
metacommunities, 201, 345; of coexisting reef fish species, 202; neutral theory of biodiversity and, 204  
metagenomics, 16–17, 16f, 19; parasitic plankton and, 26–27, 184; phytoplankton and, 25; of species interactions, 17, 17f  
metapopulations, 138; conceptual framework for, 159, 159f; genetic markers and, 164; geochemical tracers and, 164  
metazoan heterotrophs. *See* multicellular heterotrophs  
meteorite strike, end-Cretaceous, 58–59

- methane clathrates, 284  
methane ice worm, 281f, 284  
methane seeps, 281f, 283–84  
microalgae: of algal turfs, 376; detritus from, 236;  
high rate of grazing on, 131, 230–31; nutrient  
content of, 259; of sediment bottoms, 311, 315.  
*See also* phytoplankton  
microbes: in algal turfs of reefs, 355; aquaculture  
driving pathogenicity in, 104–5; as detritivores,  
236; diversity of, 14, 15f; genomic studies of, 14,  
16–17, 16f, 17f; number of species on Earth, 11;  
pathogenic, 184–85; sediment-dwelling, 31f, 32;  
suggested defenses of macroalgae against, 179. *See  
also* Archaea; bacteria; disease in marine organisms  
microbial communities, replacing foundation  
species, 103, 338  
microbial diversity, global controls on, 286–87  
microbial loop, 272–73, 272f; defined, 272;  
phytoplankton size structure and, 267;  
picoplanktonic eukaryotes in, 22; picoplank-  
tonic production passing through, 132, 269  
microbial mats: foundation species yielding  
dominance to, 103; on sediments, 311  
microbiome of ocean, and horizontal gene transfer,  
19–20  
microplankton, 22, 22t  
microzooplankton: grazing by, 268, 269, 272–73,  
293; ignorance about basic physiology of, 293  
mid-ocean ridges, 282, 282f  
midwater fishes, 264; biological pump and, 28, 273;  
Hawaiian monk seal preying on, 274  
migration of large marine vertebrates, 159–60, 160f  
*Mismanagement of Marine Fisheries* (Longhurst), 100  
mitochondrion, endosymbiotic origin of, 56  
mixed layer, 263; four main biomes and, 61–62  
mixotrophs, 23, 24f  
modules, sets of species as, 173, 173f  
mollusks: deep-sea diversity of, 286; expansion  
through Arctic into Atlantic, 71; mesograzing,  
179; ocean acidification and, 135; range size and  
speciation in, 52, 53f; vulnerable to human  
disturbance, 103. *See also* bivalves, marine  
monophyletic clade, 18f, 20  
monsoon, 61  
mortality rate, scaling with body mass and  
temperature, 166  
MSX, 339  
multicellular heterotrophs, 23, 24f, 28  
mussels in salt marshes, 328, 329  
mussels on intertidal shores, 189, 198, 304, 307,  
308; invasive *Mytilus galloprovincialis* in Africa,  
310; predation on (*see Pisaster ochraceus*)  
mutation rates: solar energy and, 54; temperature  
and, 53, 53f  
mutualistic mesograzers, 319  
NADH, 118  
nanoflagellates, 267; controlling bacteria in water  
column, 272  
nanoplankton, 22, 22t  
natural history: fundamental importance to ecology  
of, 7, 83, 359, 378; generalities that transcend the  
details of, 7–8, 187, 214; of humans, 83–84, 86,  
106, 378  
natural selection, 8, 126–27, 155–58; at different life  
stages, 151; directional selection, 156–57, 157f;  
ecosystem processes and, 224; stabilizing  
selection, 155–56, 156f. *See also* evolution  
nekton, 28; trophic diversity in Gulf of Mexico and,  
213  
nematodes: of deep-sea benthos, 287; meiofaunal,  
33, 35f, 313  
net plankton, 22, 272  
net primary production (NPP): defined, 118; of  
different plant communities, 301t; herbivore  
biomass correlated with, 230, 230f; human  
appropriation of, 79; low on coral reefs, 368;  
magnitudes and fates of, 116f; by marine phyto-  
plankton, 225. *See also* primary production  
network-based ecosystem models, 186  
networks, ecological, 186–91; loss of strongly-  
interacting species in, 189–91; nontrophic  
interactions in, 189; in rocky intertidal zone,  
189; topologies of, 171, 172f, 186, 189. *See also*  
food webs; interaction strengths  
neutral theory, 203–6; deterministic interactions  
and, 205, 206; ecological drift and, 203; habitat  
area and, 211; lottery hypothesis in, 202, 205,  
359. *See also* ecological drift; neutral theory of  
biodiversity and biogeography  
neutral theory of biodiversity and biogeography, 58,  
203, 204–6; island theory and, 57. *See also*  
neutral theory  
new production, 116, 226, 228  
niche: concepts of, 128–29; defined, 130, 199, 199f;  
dimensions of, 128–30, 130f, 176  
niche construction by humans, 85  
niche differentiation: coexistence of competing  
species and, 174–75, 176, 198; ecological  
selection and, 200; in phytoplankton, 130, 130f,  
198; vulnerability to selective grazing and, 270.  
*See also* specialization  
niche partitioning, 357; efficient processing of  
ecosystem resources and, 242; by photopigment  
diversity, 119; of reef fishes, 358–59, 358f.  
*See also* complementarity; resource partitioning  
nitrate: new production fueled by, 226, 228; reduced  
in nitrogen cycle, 117; in seawater, 115–16, 226  
nitrite: requirement for reduction before biological  
assimilation, 116; in seawater, 115–16, 226  
nitrogen: in animals vs. plants, 115; anthropogenic  
flux into coastal waters, 80f, 257, 309–10, 322,  
323f, 324, 324f, 336, 340, 341; atmospheric, from  
fossil fuel combustion, 79, 80f; availability and  
fluxes of, 114, 116; biological pump and, 273,  
274; growth rate limited by, 120; intentional  
fertilization of sea with, 341; limiting primary  
producer biomass, 226, 226f; in protein, 114,  
115; seawater forms of, 115–16, 226; sediment  
organisms' processing of, 314. *See also* Haber-  
Bosch process; nutrient loading  
nitrogen cycle: changed by humans, 378; iron used  
by microbes in, 117. *See also* nitrogen  
nitrogen fixation: by cyanobacteria, 267, 355;  
industrial, 79–80, 80f; iron limitation of, 117  
no-analog ecosystems, 105. *See also* novel ecosystems  
nonallopatric speciation, 50, 51  
nonequilibrium processes: diversity and, 207; in  
ecosystems, 223–24; historical factors and, 208;  
paradox of plankton diversity and, 270–71  
nonlinear environmental forcing: fish populations  
and, 100; regime shifts and, 249  
nonlinear population dynamics, 271  
nonlinear responses to stressors: by crown-of-thorns  
starfish, 365; fish populations and, 99, 108  
nonlinear systems, 377  
nonnative species: favored by artificial structures, 105,  
344; as fouling invertebrates in harbors, 343;  
intentionally introduced, 339, 340f; novel ecosys-  
tems dominated by, 105; selection pressures  
changed by, 344; Willapa Bay reorganization by,  
339, 340f. *See also* invasions of nonnative species  
North Atlantic: cod fisheries of, 64, 65, 252;  
impoverished in coastal marine species, 40;  
low-diversity regime shifts in, 252  
novel ecosystems, 105; climate change and, 257;  
species differences in dispersal and, 164; in  
urbanized environments, 344  
NPP. *See* net primary production (NPP)  
null models, 203–4. *See also* neutral theory  
NutNet group, 345  
nutricline, 61  
nutrient availability in the ocean, 225, 226, 226f;  
phytoplankton community composition and,  
267, 267f. *See also* eutrophication; nitrogen;  
oligotrophic systems  
nutrient loading: algal blooms generated by, 258; algal  
dominance of coral reefs and, 365f; collapse of  
San Francisco Bay fish populations due to, 105;  
declining coastal ecosystems and, 346; economic  
value in reduction of, 341; managed to maintain  
foundation species, 343; phytoplankton blooms  
generated by, 316; rapid responses to, 126; seagrass  
tolerance for, 317; synergizing with other stressors,  
343; temperature interacting with, 125. *See also*  
eutrophication; nitrogen  
nutritional quality of primary producers, 115, 115f,  
116f, 131, 231  
Obama, Barack, 379  
ocean acidification, 92–95, 92f, 135–36; coral reefs  
and, 372; kelp forests and, 338; predicted effects  
of, 290, 292; seagrasses benefiting from, 319  
ocean conveyor belt, 43, 43f  
ocean currents: circumpolar, 39, 63; wind and, 40,  
41, 297  
oceanography: biological, 8–9; history of, 260–61;  
physical, and population models, 169, 170  
oceans, history of continents and, 38–40, 39f  
ocean warming, 78, 79f, 89–91; acidification enhanced  
by, 92; algae-herbivore interactions and, 125; coral  
reefs and, 371, 372f; hotspots of, 70; physiologi-  
cal effects of, 90, 90f; predicted effects of, 290–92;  
seagrass ecosystems and, 321; species differences  
in dispersal and, 164; species interactions and,  
191–92. *See also* climate warming; sea level rise  
ochre sea star. *See Pisaster ochraceus*  
Odum, Eugene P., 219, 220, 221t, 222, 253, 330  
Odum, Howard T., 219, 222, 223, 330  
oligotrophic systems: biological pump and, 237;  
carbon balance in, 274; of central ocean gyres,  
228, 261, 276; coastal macrophytes in, 317, 332;  
of coral reefs, 218, 222, 228, 351, 352, 368;  
perennial foundation species in, 110; picoplank-  
ton in, 14, 15f, 64, 132, 237, 267; supported by  
regenerated nitrogen, 228, 267. *See also* deserts  
open ocean: in Anthropocene, 289–93; controls on  
biodiversity in, 284–87, 285f; macroecology of  
ecosystem processes in, 287–88, 288f. *See also*  
pelagic ocean  
optimism: vs. pragmatism, 381; reasons for, 108–10,  
109f  
orange roughy (*Hoplostethus atlanticus*), 289, 290  
organic enrichment of benthos, 315–16, 316f

- Ostreococcus tauri*, 13  
Ostrom, Elinor, 87  
otoliths, geochemical signatures of, 164–65, 165f  
“out of the tropics” hypothesis, 60  
overfishing, 97, 98, 106; algal blooms generated by, 258; of coastal fisheries, 340; coral reef conservation and, 374, 375; coral reef disease and, 364; of coral reef fishes, 360–61, 365, 368, 369f, 373, 375; destabilizing ecosystems, 248; Jamaican coral reefs and, 363, 365; of large fishes, 338; life history and vulnerability to, 168; marine food webs altered by, 258; regime shifts triggered by, 251, 274; trophic cascades driven by, 274–76  
overfishing debt, 98  
oxycaloric coefficient, 120  
oxygen: declining in warmer water, 215, 291, 341; depleted in polluted sediments, 316, 316f; minimum in upper mesopelagic, 264, 291; predicted seawater decrease by 2100, 290; released by photosynthesis, 118  
oxygen consumption, 120; in sediments, 314; temperature and, 121  
oyster reefs, 300f, 314–15; estuarine habitats dominated by, 299, 338; nearly wiped out, 338, 339; predatory crabs on, 336; restoration projects for, 109f, 345  
oysters: aquaculture of, 339; as foundation species, 301; human exploitation of, 314, 315f; intentionally introduced, 339, 340f; introduced along with disease-causing organisms, 339  
  
Pacific Ocean: active continental margins of, 297; separated from Atlantic 2.8 Mya, 39; species richness in, 52  
Paine, Robert, 175, 304  
paleontology, 197, 209; stasis observed in, 156  
Pangaea, 38, 39f  
paradox of hyperdiverse tropical forests, 204  
paradox of the plankton, 130, 198, 207; proposed solutions to, 269–71; reef fish diversity and, 359  
parallel communities, 48  
parapatric speciation, 50  
paraphyletic group, 18f, 20  
parasites, 184–85; heterotrophic protists as, 26–27; in microbial loop, 272; scaling of abundance with body size of, 240, 241f; selectively grazing on phytoplankton, 270  
parrotfishes (Scaridae), 179, 355, 356f, 359, 360, 373  
parsimony, in phylogenetic reconstruction, 21  
particulate organic carbon (POC): declining flux with ocean warming, 291; from mesopelagic microbes and zooplankton, 273, 273f; seasonality of flux to deep seabed, 278  
passive continental margins, 297; salt marshes on, 327; sediment plains of, 310  
path dependency, of ecosystems, 224, 249  
pathogens, as type of predator, 184. *See also* disease in marine organisms  
pelagic armourhead (*Pseudopentaceros wheeleri*), 289  
pelagic-benthic coupling: deep-sea, 278–79, 279f; sediment in shallow water and, 315  
pelagic communities, 269–71  
pelagic ecosystems: biological oceanography of, 8–9; defined, 21; functioning of, 272–76; physical forcing of, 261–66; representative organisms of, 23f; top-down control in, 274–76  
pelagic food webs, 272–73, 272f  
pelagic functional diversity, 21–28; body size and, 22–24, 24f; nutrition and metabolism, 23, 24f, 25–28, 27t  
pelagic ocean: biogeographic provinces of, 61, 61f, 63; four main biomes of, 61–62. *See also* open ocean  
perennial algae, 133, 258, 302, 307, 308, 310  
periwinkle (*Littorina saxatilis*), 51, 51f  
*Perkinsus* spp., 339  
Petersen, C. G. J., 186  
*Phaeocystis*: in blooms, 266; climate warming and, 26; defensive colony formation of, 268; *P. globosa*, chemical sense of, 179  
phages, 24–25  
phase shifts: in complex adaptive systems, 249; between coral- and algal-dominated reefs, 365, 365f, 366f, 373; mediated by herbivores, 70. *See also* alternative stable states; regime shifts  
phenological mismatch: climate warming and, 90–91; species interactions and, 192  
phenology: climate warming and, 68, 69, 292; defined, 68  
phenotype, 126, 127, 127f  
phenotypic plasticity, 128  
phosphorus, 114, 115, 119; intentional fertilization of sea with, 341; limited availability in the ocean, 226, 226f  
photosynthesis, 118; on coral reefs, 367–68; fossil fuel built by, 86; herbivore feeding on plankton and, 125, 125f; iron required for, 117; origin of, 1; pigments used in, 25–26, 118, 119, 119f; primary production by, 118, 225–26; by zooxanthellae, 351–52, 371  
photosynthetically active radiation (PAR), 118, 119, 211, 225  
phototrophs, unicellular, 22, 23, 24f, 25–26, 27t. *See also* phytoplankton  
phyla: of marine animals, 12–13, 13t, 14f; of marine autotrophs, 13; of recently discovered invertebrates, 11, 12f; of terrestrial animals, 12, 13t  
phylogenetic classification, 14, 18–21  
phylogenetic conservatism of traits, 18; in benthic macrophytes, 32, 34f, 133; community structure and, 214; in functional form models, 133; of marine primary producers, 25; of suites of interrelated functional traits, 131  
phylogenetic reconstruction, 18, 20–21  
phylogenetic structure of communities, 214  
phylogenetic systematics, 18  
phylogenetic trees, 18f, 20  
phylogeny, 18  
physical oceanography, and population models, 169, 170  
phytoplankton, 25–26; bacterial associations with, 25; biogeographic patterns in functional traits of, 64; carbon fixed by, 273; cell size as fundamental trait of, 132–33, 132f, 267; in coastal regions, 300–301; compared to land plants, 230; diverse taxa of, 267, 267f; diversity of, 285, 285f; diversity of photosynthetic pigments in, 118, 119, 119f; ecosystem model based on, 255, 256f; equatorial upwelling and, 42; eukaryotic, 25–26; evolving in response to climate change, 158; functional groups of, 131–33, 132f; functional types of, 266–68, 268f; global and regional patterns of, 9, 9f, 261–62, 294; grazing on, 268, 269; herbivore interactions with, 125–26, 125f; Hutchinson’s paradox of, 198 (*see also* paradox of the plankton); induced defenses of, 179; iron requirements of, 117, 266; large-scale patterns of biomass in, 226; net primary production by, 225; niche differentiation in, 130, 130f; nitrogen assimilated by, 116; nutrient limitation in the world ocean and, 226, 226f; ocean acidification and, 136; ocean warming and biomass of, 291; resource use efficiency and biodiversity of, 244; retained in epipelagic zone, 263; in sediment bottom food webs, 311, 312; species composition of, 237, 285; traits of higher plants compared to, 5; variance in nutrient requirements of, 237; viral influence on dynamics of, 25. *See also* cell size of phytoplankton; plankton picoplankton, 22, 22t, 25, 267. *See also* *Prochlorococcus* pigments, photosynthetic, 25–26, 118, 119, 119f  
Pinker, Steven, 379  
*Pisaster ochraceus* (ochre sea star): as keystone predator, 12, 14f, 68, 91, 173, 175, 304, 306–7; temperature-mediated effect on predation by, 191; viral infection of, 307  
planetary atmospheres, 2t  
plankton: consumer size scaling with prey size in, 182, 183f; four biomes affecting productivity of, 61–62; less genetically structured than benthic organisms, 55; oceanographic research on communities of, 8–9; size classes of, 22, 22t. *See also* phytoplankton; zooplankton  
planktonic larvae, warming-related life history changes in, 192  
planktotrophic larvae, less common in cold regions, 64, 66f  
planktotrophy, 140–42  
plant communities, biomass and NPP of, 301t  
plant-herbivore interactions, 176–79; climate change and, 91; phylogenetically conserved traits and, 214. *See also* chemical defenses  
plants: in ecosystem energy pathways, 113f; global database of terrestrial species, 136–37; referring to all primary producers, 225; stoichiometry of, 115, 115f. *See also* flowering plants  
plastic pollution, 289, 364  
plastids, 25, 26  
pneumatophores, 331f, 332  
POC. *See* particulate organic carbon (POC)  
poikilothermic vertebrates, interaction strengths of, 193  
polar biome, 62  
polar regions, higher productivity in, 261  
politics, 84–85, 106, 108  
pollution by human activities, 337; declining in prosperous societies, 380; plastic in, 289, 364; of sediment communities, 315–16, 316f; in urbanized estuaries, 344; water pollution and coastal restoration, 322, 323f  
polychaetes, 33–34, 35f; on sediment bottoms, 312, 312f, 314  
polygenic traits, 127  
polynyas, 43  
polyphyletic group, 18f, 20  
population genetic structure, and connectivity, 162, 164  
population growth, human, 75, 76f; driven by technological innovation, 83, 84; impact on earth system and, 84; industrial nitrogen fertilization and, 79–80; trend since 1972 predictions, 81f, 82, 379  
population growth, quantitative theory of, 144–49

- population growth rate: discrete ( $\lambda$ ), 146, 148, 152t; elasticity of, 148, 152, 152t, 154f; intrinsic ( $r$ ), 146, 153f, 165–66
- populations: in the Anthropocene, 168; defined, 138; macroecology of, 165–68; smaller at higher temperatures, 215
- portfolio effect, 246, 247
- pragmatism, 381
- predation: artificial structures and, 344; climate warming and, 191–92; diversity of communities affected by, 175, 185; by keystone species *Pisaster ochraceus*, 12, 14f, 68, 91, 175; larval dispersal as protection from, 142–43; mass spawning of coral species and, 143–44; mesograzers protected from, 179, 181f, 186; more intense at low latitudes, 66–68, 67f; ocean acidification and, 94, 136; phenological mismatch and, 192; in sediment communities, 313; in vent communities, 283
- predator-prey systems, regime shifts in, 251–52
- predators: declining on coral reefs, 356; diversity affecting trophic cascade and, 242, 244f; generalist or specialist, 184; nonconsumptive effects of, 182–84; ocean acidification and, 372; pathogens as, 184; in salt marshes, 329, 330; in seagrass meadows, 319, 320f; traits of, 184; trophic skew caused by decline of, 193. *See also* top-down control
- press perturbations, 365, 376
- prey: diversity of, and predator impact, 246, 248f, 308; traits of, 182–84, 183f
- primary producer biomass: of different plant communities, 301, 301t; global distribution of, 294; satellite imagery of, 9, 9f, 98, 261–62; virus-induced reduction of, 25. *See also* primary productivity
- primary producers: of coastal ocean, 296; consumers' profound effect on, 224; on coral reefs, 222, 354–55, 354f; diversity of, 13, 15f; extinctions during most of earth history and, 58–59; major types in aquatic systems, 27t; marine vs. terrestrial, 13, 15f; nutrient influence on competition and dominance in, 194; nutritional quality of different types of, 115, 115f, 116f, 131, 231; pelagic vs. benthic, 5; stoichiometry of, 115, 115f; as vascular plants and algae, 225. *See also* algae; flowering plants; macrophytes
- primary production, 118, 225–26; acidification experiments and, 93; appropriated by marine fisheries, 98; in coastal and estuarine ecosystems, 300–301, 302–3, 303f; on coral reefs, 222; fates for different types of producers, 116f; limited by inorganic nutrients, 225, 226, 226f; limited by trace nutrients, 117; of mangrove trees, 334; supported in seagrass habitats, 321. *See also* gross primary production; net primary production (NPP)
- primary productivity: defined, 118; in four main biomes, 61–62; in salt marshes, 326, 330. *See also* primary producer biomass; productivity
- Prochlorococcus*, 14, 15f, 22, 25, 132, 237, 267; ecotypes of, 256f, 270; model reproducing distributions of, 255, 256f
- productivity: of coastal and estuarine fisheries, 302, 303f, 304, 326, 326f; of coastal vs. oceanic waters, 301; control of biomass distribution and, 228–36; of coral reef ecosystems, 367; decreasing in warmer ocean, 290, 291; in estuaries, 299; global distribution of, 261–62; in harvested fish populations, 157. *See also* primary productivity; secondary (animal) production
- protein: metabolism of, 120; nitrogen in, 114, 115
- protists: heterotrophic, 26–27; multicellular, 30; phylogenetic relationships and, 20; size classes of, 22t; traditional kingdom of, 20
- Protozoa, as paraphyletic group, 20
- pycnocline, 42, 43, 262, 263f; at coastal regions, 44
- pyramid of numbers, 238, 239f
- quantum yield of photosynthesis, 118
- rabbitfishes (Siganidae), 355, 359, 360
- range size: body size and, 167, 167f; climate-mediated expansion of, 103; extinction risk and, 59; macroecology of, 167–68; speciation and, 52
- Rapoport's rule, 287
- reaction norm, 128
- realized niche, 129, 130, 199, 199f
- recalcitrant carbon reservoir, 273
- red algae, 26
- Redfield, Alfred, 115
- red-listing of ecosystems, 257
- red seaweed *Hypnea*, facilitated by *Sargassum*, 185–86, 186f
- red tides, 266, 267f
- reef communities: ancient earth history of, 348; nutrient inputs shifting dominant organisms of, 352; of other than stony corals, 354. *See also* coral reefs; oyster reefs; temperate reefs
- reef fishes: biomass increasing with species diversity of, 245f; coexistence of ecologically equivalent species, 202, 205; coral gobies, 51, 51f; dispersal mode affecting genetic structure in, 54–55, 55f, 161; diversity of, 358–59, 358f, 366–67, 369; East Indies as center of origin for, 60; ecological selection in, 359; feeding in seagrasses or mangroves, 335–36, 367; fisheries of, 253, 368–69, 369f, 373; geographic range size of, 167–68; geological history affecting distributions of, 57; grazing on algal turfs, 355; herbivorous, 179, 248, 355–56, 356f, 365, 368–69, 373, 375; hydrodynamic simulations of larval dispersal in, 161; larval sensory biology and, 163, 163f; microhabitats of, 359; proximity to nursery habitat of, 336; slow life histories of, 368; topographic complexity and, 351. *See also* fishes, herbivorous
- ReefLife Survey program, 345
- regenerated production, 116, 226, 228
- regime shifts, 249; empirical evidence for, 250–51, 250f, 380; mechanisms of, 251–52; trophic cascades and, 274, 275, 276, 293. *See also* alternative stable states; phase shifts
- regional enrichment, 209–10, 209f, 212–13, 212f
- regional richness, 199, 209–10
- regional species pool, 198–99, 200, 201; species density of coral reefs and, 357
- Remane, Adolf, 299
- reproductive value, 146, 148
- rescue effect, 201
- resource availability, and biodiversity, 284–86, 285f
- resource partitioning: deep-sea biodiversity and, 280; by phytoplankton, 270. *See also* niche partitioning
- respiration, 120, 120f, on coral reefs, 367–68; herbivore interactions with plankton and, 125, 125f; pelagic profile of, 264
- respiration rates, rising with temperature, 214–15
- response traits, 21, 215–16
- Riftia pachyptila*, 281f, 283
- Riley, Gordon, 265
- risk assessment of ecosystems, 257
- river deltas, 298. *See also* estuaries
- rivers, high productivity around mouths of, 261
- rockfish. *See* *Sebastes*, limiting similarity in
- rock wall invertebrate communities, regional enrichment of, 212f, 213
- rockweed (*Fucus*), 51, 51f; as invasive species, 310; trophic cascades on shores dominated by, 302, 325
- rocky intertidal communities, 304–10; in the Anthropocene, 309–10; community organization of, 2, 9, 306–8, 308f, 309f; competitive exclusion in, 174–75, 174f, 176; deterministic control of, 206; differing on opposite sides of Atlantic, 197; facilitation in, 307; interaction networks in, 189; interaction strengths in, 190, 190f; neutral theory tested in, 204–6; organisms of, 305–6; persistent coexistence of Chilean barnacles in, 205; processes affecting structure of, 198; species interactions in, 173, 174–75, 174f; water flow and energy in, 308, 309f; zonation of, 195, 196f, 304. *See also* rocky shores
- rocky shores: as dominant coastal habitat in many places, 309; dominant macrophytes of, 181, 301; geomorphology and environment of, 305, 306f; nonconsumptive effects of predators in communities on, 183; surfgrasses on, 317; wave energy on, 305, 306f, 309. *See also* rocky intertidal communities; rocky subtidal habitats
- rocky subtidal habitats, 304; alternative ecosystem states on, 181; environmental drivers on, 305; kelps and coralline algal crusts on, 181; productive macroalgae on, 309. *See also* rocky shores
- Romer, Paul, 381
- Ross Sea protected area, 110
- salmon: diversity in Alaskan fishery of, 247, 247f; farmed, 104, 105, 158; ocean fertilization experiment and, 107
- salps, 22, 23f; biological pump and, 237, 274; as grazers on picoplankton, 268
- salt marshes, 325–31; in the Anthropocene, 330–31; basic features of, 325–26; community organization in, 328–29; cordgrass in trophic cascade of, 234f; detritus-based food web and, 235; drought stress leading to herbivore outbreak in, 302; ecosystem services of, 330; expanded by European colonization of Americas, 330; geomorphology and environment of, 326–27, 327f; global distribution of, 317f; mangroves expanding into, 335; metabolic scaling of grazing snails in, 194; nontrophic interactions in, 189; organisms and traits in, 327–28; overgrazing caused by fishing and, 338; plants growing better under salt stress and, 192; plant species characteristic of, 325; restoration of, 345; species interactions in, 328, 329, 330; Teal's early ecosystem study of, 222–23; top-down vs. bottom up control in, 328–29, 330; trophic cascades in, 329; zonation of, 327, 327f, 328. *See also* marsh grasses
- sampling phenomenon: diverse prey community and, 246; productivity of diverse species and, 242
- Sanders, Howard, 279–80
- San Francisco Bay estuary: Asian clam invasion in, 342–43, 342f; as most invaded estuary, 339; as novel ecosystem, 105

- SAR. *See* species-area relation
- Sargassum*, 23f; facilitation of seaweed *Hypnea* via associational defense with, 185–86, 186f; temperature effect on herbivory in, 125
- satellite imaging: of global primary producer biomass, 9, 9f, 98, 261–62; oceanographic data derived from, 61; of phytoplankton biomass in warmer ocean, 291
- scaling relationships. *See* metabolic scaling
- Scotian Shelf, regime shift in, 276
- sea bass. *See* *Sebastes*, limiting similarity in
- seagrasses, 15f, 30, 31–32, 36; biological traits of, 318–19; conservation of, 231; detritus-based food web and, 235; epiphytic algae on, 319, 324; estuarine habitats dominated by, 299, 300; as foundation species, 102–3; genetic and species diversity of, 325; global distribution of, 317, 317f; low nutritional quality of, 115, 131, 231; regime shifts involving sediment conditions and, 251; of sediment shores, 301; spatially escaping from herbivores, 177; submerged, as coastal primary producers, 296. *See also* eelgrass (*Zostera marina*); eelgrass, Japanese (*Zostera japonica*)
- seagrass meadows, 300f, 317–25; African, nontrophic interactions in, 189; ancient reef-like escarpments of, 318, 318f; in the Anthropocene, 322–23, 325; community organization in, 319–21, 320f; diverse herbivores supported by, 319; ecosystem processes and services in, 321–22; epiphytic algae with productivity superior to, 319; geomorphology and environment of, 317–18; large vertebrates historically grazing on, 373; overgrazing caused by fishing and, 338; protected from nitrogen loading by marshes, 336; providing corridors for predatory crabs, 336; reducing disease prevalence in corals and humans, 336; restoration of, 323, 323f, 325; in shallow soft sediment environments, 300; supporting diversity and productivity, 317
- seagrass wasting disease, 175, 321, 322–23, 341
- sea level rise, 78, 79f, 91–92; coastal impact of, 337–38; coastal vegetation protecting against, 303; mangroves threatened by, 335; marshes threatened by, 330
- sea otters, 179, 180f, 181, 232, 249, 324
- sea slugs: as mesograzers on chemically defended algae, 181f, 186; *Phyllaphysia smaragda*, 101
- sea squirts, favored in biotic homogenization, 104
- sea star wasting syndrome, 307, 341
- sea surface temperature: geographic distribution of anomalies in, 80f; rise in, 78, 79f
- sea turtles, 89, 102, 102f; Caribbean decline in, 323, 373; as coastal herbivores, 302, 319, 321; conservation of, 151–52, 153; grazing on coral reefs, 355; overharvesting of, 338
- sea urchins, 12; on Caribbean reefs, killed by epidemic, 175; grazing on coral reefs, 355, 360, 361f; grazing on seagrass meadows, 319, 321; ocean acidification and, 135–36; in trophic cascade, 179, 180f, 181, 232, 249. *See also* *Diadema antillarum*
- seaweeds, 15f, 30, 32; calcium carbonate in tissues of, 178; canopy-forming, as foundation species, 344; canopy-forming, multiple stressors on, 343; chemically defended, mesograzers on, 181f, 186; as coastal primary producers, 296; facilitation between sparid fishes and, 185–86; *Halimeda* defenses against herbivores, 178; reefs dominated by, 365; on rocky shores, 304, 305. *See also* fleshy seaweeds; kelps; macroalgae
- Sebastes*, limiting similarity in, 187–89, 188f
- secondary metabolites, 178
- secondary (animal) production: acidification experiments and, 93; in estuaries and coastal ecosystems, 299, 302–3, 303f; in salt marshes, 326, 328, 330; supported in seagrass habitats, 321. *See also* productivity
- sedimentary shores: macrophytes on, 301; non-native species on artificial structures of, 344; wave energy on, 306f
- sediment bottoms, 310–17; in the Anthropocene, 315–17, 316f; community organization in, 313–14; ecosystem processes and services in, 314–15; environmental drivers of, 310–11; human impacts on, 314–15; organic enrichment changing community structure of, 315–16, 316f; organisms of (*see* sediment-dwelling organisms); parallel communities and, 48; pollution of, 315–16, 316f; properties of sediments in, 310–11, 311f; regime shifts of plants rooted in, 251, 252; seagrasses rooting in, 317, 321; water depth and, 311
- sediment-dwelling organisms, 311–13, 312f; body sizes of, 30, 32f; of deep sea, 48; microbes, 31f, 32; sediment grain size diversity and, 280; similar in distant regions, 48. *See also* infauna; meiofauna
- sediments, 30; biogeography of predators digging in, 64; classification of grain size in, 310–11; deep-sea, 136, 244; layering of, 30, 31f; microbial mats on, 311; primary production stored in, 231; ungrazed seagrass buried in, 317; vertical geochemical zonation in, 311, 311f, 335
- self-organization: fisheries management and, 108; of humans to behave sustainably, 87
- semistable states, 249, 251
- sensitive dependence on initial conditions, 224, 271. *See also* chaos
- sensory physiology: acidification and, 93, 136; body size and, 124; larval choice of habitat and, 163, 163f. *See also* chemical cues
- Sepkoski, John, 54
- sexual selection: stabilizing selection and, 155, 156f; sympatric speciation and, 50, 51
- shallow regions, 44
- shared derived characters, 20–21
- sharks: banned fishing of, 110; on coral reefs, 356; direct development in, 140; inverted biomass pyramid for, 240; migration patterns of white sharks, 160; slow life history of, 102
- shelf-break front, 44, 297; coastal biome and, 62
- shifting baseline phenomenon, 87, 89, 258, 379
- shrimps: aquaculture of, 77f, 334, 340; host specialization of snapping shrimps, 357, 359; reef-dwelling mantis shrimps, 57
- silicon, 271. *See also* diatoms
- silversides (*Menidia menidia*), 157
- sirenians, 302, 319, 321
- sixth mass extinction, 59, 72, 101
- size spectra, 237–40, 238f
- Smetacek, Victor, 268
- snapping shrimps (Alpheidae), host specialization of, 357, 359
- snowball earth, 1
- social-ecological systems, 106; fisheries as, 108; general approach to challenges in, 110; poorest people depending on Anthropocene ocean and, 293
- sociality of humans, 84, 378
- social policy, 381–82
- sociocultural niche construction, 85
- socioeconomic status, and energy use, 84, 85f
- soft corals (Alcyonaceae), 354
- soft substrata. *See* sediments
- solar energy: latitudinal gradient of, 40, 41; species richness and, 54
- Sommer, Ulrich, 129, 130
- source-sink dynamics for community dispersal, 201
- southeast Asia, as evolutionary hothouse, 44
- sparid fishes, facilitation between seaweeds and, 185–86
- Spartina* cordgrasses, 325, 327–28, 327f; facilitative interactions of, 329; salt marsh zonation and, 328
- Spartina alterniflora*, 66–67, 325, 327, 327f; in anoxic environments, 328; facilitation by, 186, 329; invaded from East to West Coast of USA, 339, 340f; salt marsh zonation and, 328; supporting snail and crab populations, 329; trophic cascade in salt marshes and, 234f
- Spartina patens*, 328
- specialization: coexistence of species and, 270; diversity of snapping shrimps and, 357, 359; extinction risk and, 59; speciation and, 55. *See also* niche differentiation
- speciation, 44–45, 45f, 49–56; allopatric, 49, 50; body size and, 54; coastal geography and, 44; community dynamics and, 209; composition of communities and, 198; dispersal ability and, 54–55, 55f, 57; ecological, 50, 51; ecological opportunity and, 55–56, 56f; ecological specialization and, 55; extinction rates and, 59; habitat age and, 52, 52f; habitat area and, 50, 52; island biogeography and, 58; latitudinal diversity gradient and, 60; in mixed patterns of biodiversity, 60; parapatric, 50; summary of factors leading to, 56; sympatric, 50, 51; temperature and, 53–54, 53f, 124
- species, total number on Earth, 11
- species-area relation (SAR), 45–46, 46f; extinction due to habitat loss and, 59, 72; extinctions before human population stabilizes and, 379; latitudinal diversity gradient and, 50, 52, 211
- species density. *See* species richness
- species distribution models, 69–70, 69f
- species-energy hypotheses, 54, 210–11; deep-sea animals and, 285–86
- species interactions: in the Anthropocene, 191–93; on artificial structures, 105; biogeography of, 64, 66–68; climate change and, 191–92; community organization and, 2, 9; between competitors, 175–76; ecosystem stability and, 248; functional traits in models of global change and, 106; general considerations about, 171–75; graphical webs of, 171, 172f; latitudinal diversity gradient and, 53; in mangroves, 333; metagenomics of, 17, 17f; between plants and herbivores, 176–79, 181f; between prey and predators, 182–85; realized niche and, 199, 199f; in rocky intertidal communities, 307; in salt marshes, 328, 329; temperature and, 121, 124; three general types of, 171; warming-related interactions and, 91. *See also* interaction strengths; networks, ecological
- species pool, 38, 49
- species richness: body size and, 210; centers of origin and, 60; climate change affecting, 103; on coral reefs, 357; defined, 44; dispersal and, 209–10, 209f; equilibrium of factors determining, 58; estuarine, 299, 299f; foundation species in community and, 189; functional diversity and,

- 241–42; habitat area and, 211; of plankton, 285; of rocky shore prey communities, 308; species-energy hypothesis and, 54; temperature and, 54, 210; temperature-related trends in life history and, 64, 66f; theory of island biogeography and, 57–58, 57f; in unified neutral theory of biodiversity, 204. *See also* biodiversity; diversity in communities
- specific production (P/B), 151
- sperm whale, 264
- spinner dolphin (*Stenella longirostris*), 51, 51f
- spiny lobsters (*Panulirus argus*): larval dispersal as protection for, 142–43, 143f; seagrass as larval settlement habitat for, 336
- sponges (Porifera), 12–13, 14f; on degraded Caribbean reefs, 354; on overfished Caribbean reefs, 360–61
- spreading centers, 282
- spring bloom, 265–66, 278, 279
- squids, 28
- squirrelfishes (*Sargocentron*), 359
- stabilizing mechanisms, and coexistence, 176
- stabilizing selection, 155–56, 156f
- stable age distribution, 148
- stage-structured populations, 148–49, 149f, 152t; choice of habitats to protect and, 154; vulnerability of populations and, 168
- staghorn coral (*Acropora cervicornis*): beginning to revive, 381; threatened status of, 102; white-band disease of, 185, 362–63, 370, 375
- starfish. *See* brittle stars; crown-of-thorns starfish; *Pisaster ochraceus* (ochre sea star); sun star
- Stebbins, G. Ledyard, 49
- Steller's sea cow, 101, 302, 309
- stenothermal species, 121
- Stern, Nicholas, 86
- stoichiometry, 113–15, 114f; defined, 114; ecological, 115, 115f, 116f; ecosystem processes and, 237; food choice influenced by, 182; of phytoplankton in warming ocean, 292
- Stommel, Henry, 261, 262f
- storage, 116f, 118; in sediments of coastal systems, 131, 303, 330, 334
- stressful environments: facilitation and, 192, 302, 307, 308f, 329, 333; low diversity in, 307; water flow and, 308
- stressors, multiple: coastal, 341, 343; on coral reefs, 363, 364, 370–71, 375
- stromatolites, 311, 348, 348f
- substrata, 30; epifauna on, 34. *See also* sediments
- succession of a community, 196–97, 219–20
- sun star (*Heliaster kubiniji*), 307
- surfgrasses (*Phyllospadix* spp.), 317
- surgeonfishes (Acanthuridae), 355, 356f, 359
- survivorship, 145, 147
- suspension-feeders, 312, 312f, 313, 314, 315; increased by nutrient enrichment, 341, 352; macroinfauna as, 33–34; in salt marshes, 328
- sustainable systems of resource use, 87
- Sutherland, John, 307, 308f
- Sverdrup, Harald, 265–66
- sympatric speciation, 50, 51
- synapomorphies, 20–21
- Syndiniales, 27
- syngameons, 21
- systems approach in ecology, 222, 223
- tagging of marine animals, 159–60, 160f
- Tansley, Arthur, 219
- Teal, John, 222–23
- technological innovation, 75, 76, 76f; fossil fuel use and, 78; Haber-Bosch process and, 79; human population growth and, 83, 84
- tectonic events: long-term legacies of, 209. *See also* volcanism
- tectonic plates: hydrothermal vents and, 282; Indo-Pacific coral species and, 39–40, 57
- temperate reefs: ocean-warming shift to coral dominance of, 70, 71f; rocky, alternative ecosystem states on, 181
- temperature: balance between photosynthesis and respiration and, 287; greenhouse effect and, 78, 78f; interaction strengths and, 193–94; latitudinal patterns in interactions and, 67–68, 67f; life history and, 64, 66f, 166; metabolic scaling as function of, 122f, 123–24, 123f, 166; metabolism of heterotrophs vs. autotrophs and, 191; of open ocean vs. land, 297; organism's normal range of, 120–21; oxygen consumption and, 121; of sea surface, 78, 79f, 80f; speciation and, 53–54, 53f; species interactions and, 121, 125; species richness and, 210. *See also* climate warming; ocean warming
- terrestrial ecosystems, 12, 13t; connections to marine ecosystems, 293
- Tethys Sea, 38, 39, 39f, 348
- thermal niche models, 291–92
- thermocline, 263f, 264
- thermohaline circulation, 43, 43f
- Thorson, Gunnar, 48, 64
- Thorson's rule, 64
- tides, 297
- tippling points, 249, 343, 363, 365, 380
- top-down control, 113f, 231–32, 232f; in coastal ecosystems, 302; in pelagic ecosystems, 274–76; in salt marsh ecosystems, 328–29, 330
- top predators: abundant on coral reefs, 355–56; cascading effects of decline of, 180–81, 215, 232, 233; extinctions of, 193; feeding at convergent fronts, 42; food webs destabilized by loss of, 190, 232; homeothermic, 28; human role in ocean as, 87, 292; intensely harvested, 95; nekton as, 28; strongly reduced in modern times, 102, 258; targeted human pressure on, 233; trophic skew caused by loss of, 338
- trace elements: limiting primary production, 117; population structure and, 164–65, 165f. *See also* iron
- trade. *See* commerce
- trades biome, 61
- trade winds, 40; monsoon and, 61
- tragedy of the commons, 86–87; catch-share programs and, 101
- trait-based approaches, 131, 136–37
- traits: ecosystem functioning and, 224–25; extinction vulnerability and, 59; taxonomic group effects and, 73. *See also* functional traits; phylogenetic conservatism of traits
- transport structures, fractal network of, 122–23, 124
- trawling damage to seabed, 292, 295, 315, 316–17, 337
- tree of life, 18–21, 19f
- Trichodesmium*, 267, 274
- trophic amensalism, 313
- trophic cascades, 173, 173f, 179, 180–81, 180f, 232–33; in Black Sea, 251, 274, 275, 276; in coastal ecosystems, 234f, 302; in coral reef communities, 361–62; foundation species depending on, 302; green world hypothesis and, 229; human impact on large animals and, 258; increasing with predator diversity, 242, 244f; nonconsumptive effects in, 183–84; overfishing and, 274–76; pelagic, 293; in salt marshes, 329, 331; stronger in marine than in terrestrial systems, 230; uncommon in open ocean, 274, 276
- trophic-dynamic approach of Lindeman, 219, 220f, 222, 330
- trophic efficiency, 237–38
- trophic levels, 130; alternating between bottom-up and top-down control, 233, 234f; biomass distributions among, 135, 135f; correlated with body size of individual fish, 144, 144f, 184; diversity-biomass relationship and, 242–43, 245f; ecosystem concept and, 219; energetic equivalence rule and, 240, 241f; functional groups and, 213; green world hypothesis and, 228–29, 229f; interaction strengths and, 189, 190, 190f. *See also* bottom-up control; top-down control
- trophic skew, 193, 193f, 215, 233, 258, 338
- tropicalization, 68, 70, 71f; of seagrass-associated fish communities, 322
- tube worms, 281, 281f, 283, 284
- turbulence: composition of phytoplankton and, 267, 267f, 292; recruitment of coral larvae and, 365; sediment grain size and, 311
- turf algae. *See* filamentous (turf) algae
- turnover. *See* beta diversity ( $\beta$ )
- turtle excluder devices, 153
- turtles. *See* sea turtles
- ultrasocial behavior, human, 84, 378
- unicellular chemoautotrophs, 23, 24f, 26, 27t, 225
- unicellular eukaryotic heterotrophs, 23, 24f, 26–27
- unicellular phototrophs, 22, 23, 24f, 25–26, 27t
- unicornfish (*Naso*), 360
- unified neutral theory of biodiversity. *See* neutral theory of biodiversity and biogeography
- upwelling: around reef islands, 367; climate warming and, 90, 91; coastal, 44, 62, 261, 297, 298f, 299, 305; equatorial, 42, 261–62; nitrate coming from, 116, 117, 226, 228; *Pisaster ochraceus* feeding on mussels and, 91
- urbanized estuaries, 337, 343–44
- urea: ocean fertilization proposal and, 107; in seawater, 115, 116, 226
- values, 107–8, 110
- vascular plants. *See* flowering plants
- velvet worms (Onychophora), 12
- vents. *See* hydrothermal vents; volcanic vents
- Vermeij, Geerat, 58–59
- vertebrates: grazing on seagrass meadows, 373; interaction strengths of, 193
- vertical migration, diel, 261, 264; carbon export to deep ocean and, 273; between complementary habitats, 335
- vicariance biogeography, 56, 57
- viruses, 23, 24–25, 24f; in microbial loop, 272, 272f; phytoplankton defenses against, 268
- visually foraging poikilotherms, 23, 24f, 28
- volcanic vents: acidified ocean waters at, 94, 135–36, 372; low coral diversity at, 372
- volcanism, and end-Permian mass extinction, 58
- Wallace, Alfred Russel, 358
- wall of mouths, 142

- water-column stratification, 262–65, 263f; four pelagic biomes and, 61; gyre circulation and, 41, 42; ocean warming and, 291, 292; phytoplankton cell size and, 132–33, 285; phytoplankton diversity and composition related to, 285; spring bloom and, 265–66
- water flow: community interactions on rocky shores and, 308, 309f. *See also* wave energy
- water pollution. *See* pollution by human activities
- water quality: coral reefs and, 363, 364; oyster reefs and, 338
- wave energy: on rocky shores, 305, 306f, 309; sediment grain size and, 311. *See also* water flow
- weakfish (*Cynoscion regalis*), geochemical signatures in, 164–65, 165f
- web of life, 21
- weedy species: favored in biotic homogenization, 103–4; replacing foundation species, 36, 103, 338
- westerlies biome, 61–62
- western boundary currents, 41
- wetlands. *See* coastal ecosystems
- whales, 28–30, 29f; blue whale, 23f, 28, 264f; evolved to exploit deep-water prey, 264; fishing impacts on, 292; gray whale, 29, 29f, 159–60; invertebrates feeding on carcasses of, 278f, 279, 280; as keystone species, 102; sperm whale, 264; threatened species of, 102, 102f
- white-band disease of *Acropora*, 185, 362–63, 370, 375
- Williamson, Oliver, 87
- Wilson, Edward, 57
- wind: coastal upwelling and, 298f, 299; mixed layer and, 263; ocean currents and, 40, 41, 297; thermohaline circulation and, 43
- Wootton, Tim, 205, 206
- World3 computer model, 80, 82
- worms: meiofaunal nematodes, 33, 35f, 313; nematodes of deep-sea benthos, 287; on sediment bottoms, 312, 312f, 313–14
- xenophyophores, 280
- zooplankton: biogeographic patterns in functional traits of, 64; biological pump and, 273–74, 273f; crustacean, top-down control of diatoms by, 233; ctenophores in top-down control of, 233, 234f, 275, 275f; fecal pellets of, 235, 237, 273, 278; grazing by microzooplankton, 268, 269, 272–73, 293; ocean warming and, 215, 291–92; selective grazing by, 270. *See also* plankton
- zooxanthellae, 222, 301, 351–52, 351f, 354, 367, 368, 371, 375–76