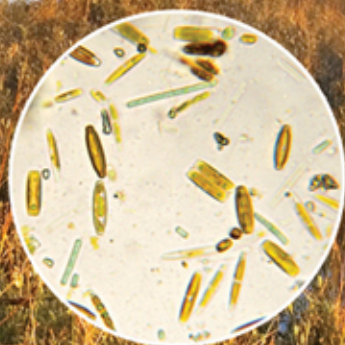


SECOND EDITION

Estuarine Ecology



EDITED BY

John W. Day

Byron C. Crump

W. Michael Kemp

Alejandro Yáñez-Arancibia

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- All figures from the textbook as Power Point slides for downloading
- Supplementary text material for Chapter 17
- Chapters 1, 10, and 20



ESTUARINE ECOLOGY

Second Edition

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This book is dedicated to our students and to all others around the world who are interested in understanding, using, managing, and protecting estuarine ecosystems in a sustainable manner for future generations.

In memory of Dr. Scott W. Nixon for his important contributions to the field of estuarine ecology.

CONTENTS

Preface, ix		
Acknowledgments, xi		
Contributors, xiii		
CHAPTER ONE		
Introduction to Estuarine Ecology	1	
<i>John W. Day Jr., Alejandro Yáñez-Arancibia, W. Michael Kemp, and Byron C. Crump</i>		
CHAPTER TWO		
Estuarine Geomorphology and Coastal Hydrology	19	
<i>Gregg A. Snedden, Jaye E. Cable, and Björn Kjerfve</i>		
CHAPTER THREE		
Estuarine Chemistry	39	
<i>Thomas S. Bianchi</i>		
CHAPTER FOUR		
Estuarine Phytoplankton	85	
<i>Hans W. Paerl and Dubravko Justić</i>		
CHAPTER FIVE		
Seagrass and Related Submersed Vascular Plants	111	
<i>Jens Borum, Renee K. Gruber, and W. Michael Kemp</i>		
CHAPTER SIX		
Coastal Marshes	129	
<i>Carles Ibáñez, James T. Morris, Irving A. Mendelssohn, and John W. Day Jr.</i>		
CHAPTER SEVEN		
Mangrove Wetlands	165	
<i>Robert R. Twilley and John W. Day Jr.</i>		
CHAPTER EIGHT		
Estuarine Benthic Algae	203	
<i>Karen J. McGlathery, Kristina Sundbäck, and Peggy Fong</i>		
CHAPTER NINE		
Estuarine Microbial Ecology	235	
<i>Linda K. Blum and Aaron L. Mills</i>		
CHAPTER TEN		
Estuarine Microbial Food Webs	263	
<i>Byron C. Crump, Hugh W. Ducklow, and John E. Hobbie</i>		
CHAPTER ELEVEN		
Estuarine Zooplankton	285	
<i>Mark C. Benfield</i>		
CHAPTER TWELVE		
Estuarine Benthos	303	
<i>James G. Wilson and John W. Fleeger</i>		
CHAPTER THIRTEEN		
Estuarine Nekton	327	
<i>James H. Cowan Jr., Alejandro Yáñez-Arancibia, Patricia Sánchez-Gil, and Linda A. Deegan</i>		

CHAPTER FOURTEEN

- The Ecology of Estuarine Wildlife 357
Russell Greenberg

CHAPTER FIFTEEN

- Ecosystem Metabolism 381
Jeremy M. Testa, W. Michael Kemp, Charles S. Hopkins Jr., and Stephen V. Smith

CHAPTER SIXTEEN

- Estuarine Food Webs 417
James D. Hagy III and W. Michael Kemp

CHAPTER SEVENTEEN

- Budget Analyses of Estuarine Ecosystems 443
Walter R. Boynton and Scott W. Nixon

CHAPTER EIGHTEEN

- Fisheries in Lagoon-Estuarine Ecosystems 465
Daniel Pauly and Alejandro Yáñez-Arancibia

CHAPTER NINETEEN

- Human Impact and Management of Coastal and Estuarine Ecosystems 483
John W. Day Jr., Alejandro Yáñez-Arancibia, and W. Michael Kemp

CHAPTER TWENTY

- Global Climate Change and Estuarine Systems 497
John M. Rybczyk, John W. Day Jr., Alejandro Yáñez-Arancibia, and James H. Cowan Jr.

CHAPTER TWENTY-ONE

- Estuarine Ecological Modeling 519
Enrique Reyes, Kenneth Rose, and Dubravko Justić

Index, 537



PREFACE

This book is a textbook for a course in estuarine ecology designed to introduce students to the function and structure of estuarine ecosystems. It is designed primarily for an introductory graduate course, but it can also serve as a general resource book for estuarine ecologists. This book is the second edition of *Estuarine Ecology*; the first edition was published in 1989. Clearly there have been enormous advances since then, and this second edition has expanded from 13 to 21 chapters to cover these advances. Some topics, such as climate change, were of relatively minor interest prior to 1989, but have since become central to estuarine ecology. And there has been a dramatic increase in information about estuarine ecosystems, growing human impacts on these systems, and their value to society. This information is documented throughout the book. Another significant change is that we moved from a book in which most of the chapters were written by a small handful of authors to an edited volume with many authors. This was necessary because of the expansion of the breadth of estuarine science and the challenge of having a few authors adequately cover the subject. Thus, we reached out to a number of well-known experts to prepare individual chapters. But we endeavored to have them use a generally consistent format to ensure a comprehensive coverage of estuarine ecology.

The chapters in the book proceed logically through the science of estuarine ecology. The first chapter introduces estuaries and estuarine ecology, and describes some of the background, definitions, theory, and issues of estuarine ecology. The next two chapters deal with physical, geological, and chemical aspects of estuaries. The nature of estuarine ecosystems is to a great extent determined by a complex and dynamic physical, geological, and chemical environment. Therefore, a basic understanding of these topics is essential for a comprehension of estuarine ecology. Then there is a group of chapters on primary producers of estuaries. Two new chapters are added compared to the first edition so that phytoplankton, seagrasses, coastal marshes, mangroves, and benthic algae are covered. After that are two chapters on microbes in estuaries covering estuarine microbial ecology and estuarine microbial food webs, the latter being a new chapter for the second edition. Four chapters follow that covering estuarine consumers including zooplankton, benthos, nekton, and wildlife. The next three chapters cover emergent, holistic properties of estuarine ecosystems including metabolism, food webs, and budgets. All of these chapters develop detailed information on taxonomy, physiology, life histories, ecological role, growth, metabolism, and interaction with abiotic factors.

The last four chapters deal with fisheries, human impact and management, the effect of climate change on estuaries, and the role of modeling in estuarine science.

Our primary motivation for preparing this book was to update the first edition that is now very much out of date. In the intervening two decades since the publication of the first edition, many very good books have been written on estuarine science. But, we believe none of them really meets the need for an introductory text on estuarine ecology. Thus, we

undertook this effort. We also hope that this book will become a “work in progress” that can be more easily updated on a regular basis because of the participation of many experts. The arduous task of preparing such a book by one or a few authors is part of the reason for the long delay in the second edition.

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Since estuarine ecology is such a dynamic science, we depended heavily on many of our colleagues in writing this book. Through discussions, suggestions and review of different chapters, many estuarine ecologists helped shape this book. Foremost among those are the authors of the different chapters. We acknowledge the intellectual stimulation of Howard and Eugene Odum. Their work, as well as that of

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CHAPTER ONE

INTRODUCTION TO ESTUARINE ECOLOGY

John W. Day Jr., Alejandro Yáñez-Arancibia, W. Michael Kemp, and Byron C. Crump

1.1 BACKGROUND, THEORY, AND ISSUES

We begin this description of estuaries and their functions by defining estuaries very broadly as that portion of the earth's coastal zone where there is interaction of ocean water, fresh water, land, and atmosphere. Large estuarine zones are most common in low relief coastal regions such as the broad coastal plains of Europe and the east coast of North America. They are much less common in uplifted coastlines such as the Pacific edge of North and South America. We begin our assessment as broadly as possible to include all portions of the earth that interact at the edge of the sea because these regions influence the smaller scale ecosystems sometimes more narrowly defined as estuaries proper.

From the vantage point of an orbiting satellite, several of the most basic attributes of estuaries are observable. Plumes of sediment-laden water float seaward on the ocean surface from the largest rivers, such as the Amazon, the Ganges, and the Mississippi. Color differences among various water masses, representing waters of different histories and different biotic richness, are often apparent. Coastal waters in areas with significant riverine input and broad shelf areas generally appear more greenish brown than the

deep blue waters adjacent to many other coastlines. There are also atmospheric features of importance to estuaries obvious from space. Clouds commonly form directly over the edges of continents as one manifestation of the atmospheric "thermal engine" that maintains the freshwater cycle on which estuaries depend. At the altitude of a satellite, the dense human populations that proliferate in coastal zones are outlined at night by their lights.

The two most recent geological epochs, collectively named the Holocene, could be called *the age of the estuary*, for estuaries are abundant today, even though they are geologically tenuous. All present day estuaries are less than about 5000 years old, representing the time since sea level reached near its present level following the last ice age. Human populations flourished during this same period, in no small measure owing to exploitation of the rich estuarine resources of the coastal margin. Most "cradles of civilization" arose in deltaic and lower floodplain areas where natural biota was abundant and where flooding cycles produced the rich bottomland soils and readily available freshwater supplies on which agriculture flourished (Kennett and Kennett, 2006; Day et al., 2007). Early centers of civilization that developed in estuarine or deltaic environments include those of the Tabascan lowlands of Mexico; the valley of the Nile; Tigris-Euphrates, Yellow, and Indus

Rivers; and along the Andean coast of western South America where upwelling systems bordered estuarine systems.

Let us now continue our aerial survey of estuaries, but this time at a much lower altitude, about 1000 m, in a light airplane following the course of a coastal plain river in the temperate zone from its headwaters to the ocean. The headwater river is narrow with rapids and falls, but changes near the coast to a larger meandering form with broad marshy areas where the actual edge of the river is not always clearly evident. The color of the water changes from clear blue to yellowish brown as the river picks up silt. As the river water nears the coast tidal currents become apparent and, moving seaward, the influence of tidal currents becomes greater.

Along the banks of the estuary, fresh and brackish water marsh plants grow at the edges of embayments. These marshes are often flanked by rows of houses and yards and spanned by narrow piers to provide access to deeper water. Among these marshes, a variety of wading birds may be observed stalking their prey at the water's edge. Where the water is shallow and relatively clear, dark-colored patches indicate the presence of submersed grass beds.

As we travel seaward, the tidal influence becomes more important and the intertidal zone becomes more extensive. Larger piers and bulkheads interrupt the banks of the estuary, and brown mud flats come into view, as well as greenish gray oyster reefs fringing the banks or dotting the mud flats. Various birds such as oystercatchers feed on the reefs, along with an occasional raccoon. The mud flats are peppered with mud snails, and just beneath the surface are teeming communities of small worms and crustaceans. Various shore birds are feeding at the water's edge, and skimmers fly along in quiet areas, plowing a furrow in the water with their lower bill as they fish for silversides and other small fish. The darker colored path of a deep shipping channel maintained by dredging is evident toward the middle of the estuary and contrasts with the lighter colored shallows.

The mouth of the estuary takes the form of a broad sound that opens up behind a barrier island. The sound is shallow, and we can see porpoises herding schools of juvenile menhaden, followed by gulls trying to get in on the action. Crab pot buoys and fishing boats are much in evidence. On either side of the barrier island are narrow passes with visible eddies and strange wave patterns, indicating rapid and complex currents.

Along the ocean beach, a number of shrimp boats raise long spiraling muddy plumes of sediment as they drag their trawls along the bottom. A kilometer

or so offshore of the tidal passes the water changes color from dark brownish green to a lighter, less turbid green. Further offshore, it is a darker and bluer color.

On the landward side of most such barrier islands, there are flat intertidal areas colonized by salt marsh plants. The highest part of the island includes some oak trees. The beach may include a series of dunes, with the farthest from the ocean being covered with vegetation and the nearer dunes being less vegetated. The seaward side of the dune closest to the ocean has much less vegetation because the wave energy from storms makes it difficult for plants to survive. In parts of the beach-barrier system, vacation houses have replaced the dunes, and straight navigation channels have replaced twisting tidal channels.

In summary, from many elevations estuaries can be seen as complex, dynamic, and biotically rich environments dominated by physical forces and impacted by human activity. Their study requires a consideration and knowledge of geology, hydrology, chemistry, physics, and biology. Ideally, we can integrate knowledge gained through these specific disciplines using what we call systems science. This book is an introduction to the specifics of estuarine science and their integration into a coherent view of estuaries as ecosystems. We show how estuaries are different from one another and how they are similar, and why we need to preserve them while enhancing their value to society.

We will begin by describing a very generalized estuary, to provide the reader with an introduction to the geology, physics, chemistry, and biology of estuaries. This is done with a certain danger because, as the rest of the book shows, estuaries are characterized as much by differences as by similarities. Nevertheless, in this chapter, we attempt to describe a generalized estuary. But before we proceed further, we will define an estuary.

1.2 DEFINITIONS, TERMS, AND OBJECTIVES

1.2.1 Definitions of Estuary and of Ecology and Difficulties in Applying These Definitions to Real Estuaries

The term *estuary* comes from the Latin *aestus* meaning heat, boiling, or tide. Specifically, the adjective *asetuarium* means tidal. Thus, the *Oxford Dictionary* defines estuary as "the tidal mouth of a great river, where the tide meets the current." *Webster's Dictionary* is

more specific: “(a) a passage, as the mouth of a river or lake where the tide meets the river current; more commonly, an arm of the sea at the lower end of a river; a firth. (b) In physical geography, a drowned river mouth, caused by the sinking of land near the coast.”

Perhaps the most widely quoted definition of an estuary in the scientific literature is given by Pritchard (1967): “An estuary is a semienclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage.” Certainly, one of the most characteristic attributes of most coastal areas is the action of the tide. Pritchard’s definition makes no specific mention of tide, although the mixing of seawater and fresh water implies this. There are, however, many nontidal or minimally tidal seas, such as the Mediterranean Sea and the Black Sea, where fresh and salt water mix.

There are also estuaries in semiarid regions that may not receive any fresh water for long periods; sometimes, as in the Pacific coast of California and Mexico, Western Australia, and several parts of Africa, the estuary may become blocked by longshore sand drift, so that it is ephemerally isolated from the sea for months to even years. In other regions, the tidal limit, sometimes with a tidal bore, may reach 100 km or more above the limits of salt water intrusion. So Pritchard’s definition of estuary excludes some coastal areas where estuarine ecology is studied today.

In an attempt to address the limitations of Pritchard’s definition, Fairbridge (1980) gave a more comprehensive definition of an estuary: An estuary is an inlet of the sea reaching into a river valley as far as the upper limit of tidal rise, usually being divisible into three sectors: (i) a marine or lower estuary, in free connection with the open sea; (ii) a middle estuary subject to strong salt and fresh water mixing; and (iii) an upper or fluvial estuary, characterized by fresh water but subject to daily tidal action. The limits between these sectors are variable and subject to constant changes in the river discharge.

Fairbridge’s definition excludes some coastal geomorphic features such as lagoons, deltas, and sounds and also nontidal estuaries. The distinctions among these different terms are treated in detail in Chapter 2, but characteristic estuarine ecosystems have developed in all these coastal systems. Therefore, when the terms *estuary* and *estuarine* are used in this book, unless specifically stated otherwise, they are meant in a general ecological sense rather than any specific narrower geological

sense. Valle-Levinson (2010) provides an overview of definitions and classifications of estuaries.

All of the definitions of estuaries given above reflect, for the most part, physical and geological characteristics of estuaries. But why is this so? The people who first defined and classified estuaries were geologists and physical oceanographers, because in many respects the most salient features of estuaries are physical and geomorphic. And the ecosystems that exist in estuaries are often physically dominated. We can illustrate this point by comparing an estuarine ecosystem with a tropical forest ecosystem. A visitor to a rain forest is immediately struck by the richness of the vegetation. If the visitor stays in the forest for some time, he or she will notice that it rains a lot and the temperature is warm. If the visitor is a careful observer, he or she will perhaps learn about the soils of the forest. But the most striking characteristic is the vegetation. Rain forests are biologically dominated systems and have been described primarily by their biological characteristics.

In contrast, a visitor to an estuary cannot escape noticing the impact of abiotic characteristics. These include the rise and fall of the tide, complex water movements, high turbidity levels, and different salt concentrations. The nature of land-forms such as beaches, barrier islands, mud flats, and deltas and the geometry of the basin are also very noticeable. There are, of course, outstanding biotic characteristics of estuaries such as salt marshes, mangrove swamps, submersed grass beds, and oyster reefs. But, in general, one has to look carefully to obtain even an idea of the biological structure of estuaries.

The visibility of the abiotic attributes of estuaries reflects the fact that estuaries are, to a large degree, physically dominated ecosystems. To begin to understand estuarine ecosystems and how they function, an estuarine ecologist must have a good understanding of the geology, physical oceanography, and chemistry of estuaries. Thus, one of the basic goals of Chapters 2 and 3 is to provide physical and chemical bases that will lead to an understanding of the biotic processes.

Before we go further, it is necessary to define ecology, since this book is about estuarine ecology. Usually ecology is defined as the study of the relation of organisms or groups of organisms to each other and to their environment. Margalef (1968) gives a definition of ecology that is, perhaps, more appropriate to the way we approach estuarine ecology. He stated that “ecology is the study of systems at the level in which individuals or whole organisms can be considered as elements of interaction, either among

themselves, or with a loosely organized environmental matrix. Systems at this level are called *ecosystems*, and ecology is the biology of ecosystems.” Thus, in this book, we will consider the environmental matrix of estuaries, the interactions among specific organisms and the environment, and the structure and functioning of whole estuarine ecosystems.

1.3 FIVE VIEWS OF A GENERALIZED ESTUARY

We now discuss estuaries in a more systematic and scientific manner, and we do this through five views of a generalized estuary, emphasizing common characteristics among these divergent systems.

1.3.1 Top View

The first view of a generalized estuary is from above (Fig. 1.1). At one end there is a river entering a large bay and at the other end a barrier island separating the bay from the ocean. Wave energy along the barrier island is high and there is a wide sandy beach. On the beach, there is little immediate evidence of life other than a few birds. Studies have shown, however, that abundant and diverse communities of tiny organisms live among the sand grains on beaches. Wave energy is very important to these organisms because the waves pump water containing oxygen and food constantly through the sand while carrying away waste products. The beach is an area of very high physical energy and the sediments

are completely oxidized. This is an example of the importance of physical processes in determining the biotic characteristics of the estuarine environment.

In the tidal pass, the water is still clear and the salinity high. Wave activity is somewhat reduced but currents are still strong. At the entrance to the pass, the sediments are still sandy and completely oxidized, but are beyond the influence of strong currents, anoxic conditions occur a few tens of centimeters below the sediment surface. The biota is abundant and diverse in the pass, including epifauna, in contrast to the barren surface of the beach. The pass is often the deepest part of the estuary.

As we move through the estuary, there are distinct changes in depth, physical energy levels (current and turbulence), water clarity, salinity, biota, chemical concentrations, oxidizing and anoxic conditions in the sediments, and so on. In intertidal and subtidal areas with significant currents, there are often worm flats or mollusk beds. These filter-feeding organisms depend on currents to transport oxygen and food and to carry away wastes.

In the shallow subtidal waters of somewhat reduced currents where light reaches the bottom, marine meadows of submersed aquatic vegetation or seagrass beds often occur. Water clarity is high and sediments are finer, partially as a result of the grass's ability to trap sediments. The reduced zone of the sediments extends to within a centimeter or less of the surface. In high salinity tropical waters, these submersed grass beds are often dominated by turtle grass, *Thalassia testudinum* and in the temperate zone by eel grass, *Zostera marina*. In lower salinity waters

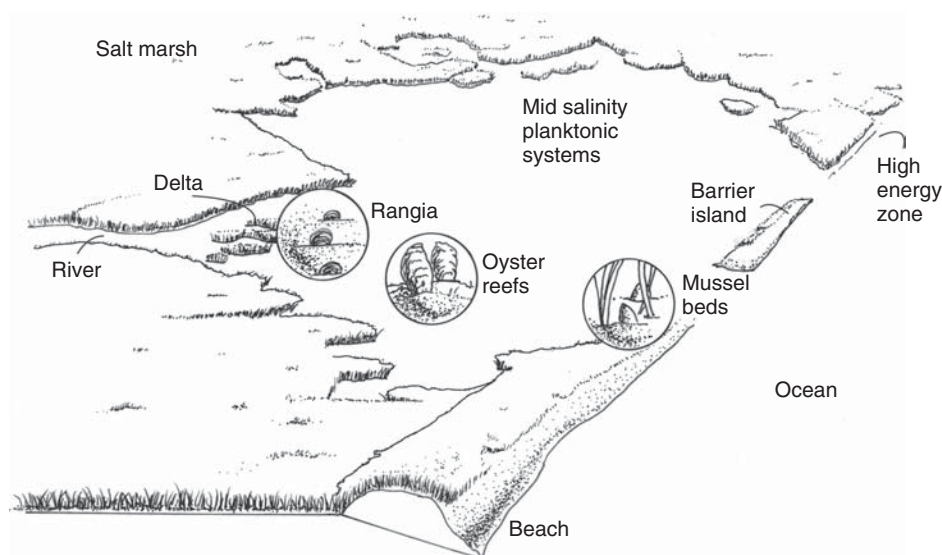


FIGURE 1.1 Idealized oblique aerial view of a typical estuarine system showing some of the major subsystems.

(<5 ppt) genera such as *Ruppia*, *Potamogeton*, and *Valisneria* are common.

In this typical estuary, salinity decreases steadily from the ocean to the river. The high salinity area of the estuary (30–35 ppt), is called *polyhaline*, middle salinities around 15 ppt constitute the *mesohaline*, and the low salinity region (0–5 ppt) is called the *oligohaline zone*.

Bordering the estuary in areas of mild to sluggish currents are intertidal wetlands where salt marshes occur in the temperate zone and mangrove swamps occur in the tropics. These are areas of turbid waters and highly reducing and very fine sediments. The vegetation has very high growth rates and the animals tend to be deposit feeders.

1.3.2 Cross-Section View

A cross-section view of the estuary (Fig. 1.2) illustrates a number of vertical as well as horizontal attributes of estuarine ecosystems. Vertical gradients are important in determining the nature of these ecosystems. Perhaps the most obvious is the intertidal zone that is alternately flooded and exposed. In the intertidal zone, there may be salt marsh or mangrove wetlands, algal beds, sand or mud flats, or reefs of oysters, mussels, or clams. Most organisms that live in the intertidal zone have developed special adaptations, which are discussed in numerous places in this book and specifically in chapters 6, 7, and 12.

A second important vertical gradient is that of light. The lighted zone in an aquatic system is called the *euphotic zone*, while the zone with no light is the *aphotic zone*. Obviously, photosynthesis occurs only in the euphotic zone. Where light reaches the bottom, plants can live attached to the bottom. Estuarine

water clarity tends to be much greater near the ocean, so both rooted plants and plankton can generally photosynthesize at greater depths than in lower salinity regions. Animals that live in the aphotic zone are dependent on food being transported from other parts of the estuary.

Another extremely important gradient for biological and chemical processes in estuaries is that from oxidizing (where oxygen is present) to reducing (where oxygen is absent) conditions. An oxidizing environment is also called *aerobic* or *oxic* and a reducing one *anaerobic* or *anoxic*. The estuarine water column is normally aerobic, but estuarine sediments usually are anaerobic a short distance below the sediment surface. The amount of oxygen in the sediments is related both to the rate at which oxygen moves into the sediments and the rate at which it is consumed by the metabolic activity of microbes. In areas with high physical energies, such as waves or strong currents, there are well-sorted coarse sediments that are oxidized. The physical energy serves both to replenish the oxygen to the sediments and to wash out finer materials that, for several reasons, support microbial communities that consume oxygen rapidly. The opposite condition exists in areas of fine sediments. There the currents are too weak to sort the sediments or replenish oxygen rapidly, and in some cases (such as highly reduced marsh soils), anaerobic conditions extend up to the sediment surface. Since most estuaries are underlain with fine sediments, the reduced zone is widespread.

The activities of the biota, including the construction of burrows by organisms such as worms and fiddler crabs, facilitate the movement of water and oxygen through sediments. Many plants that grow in

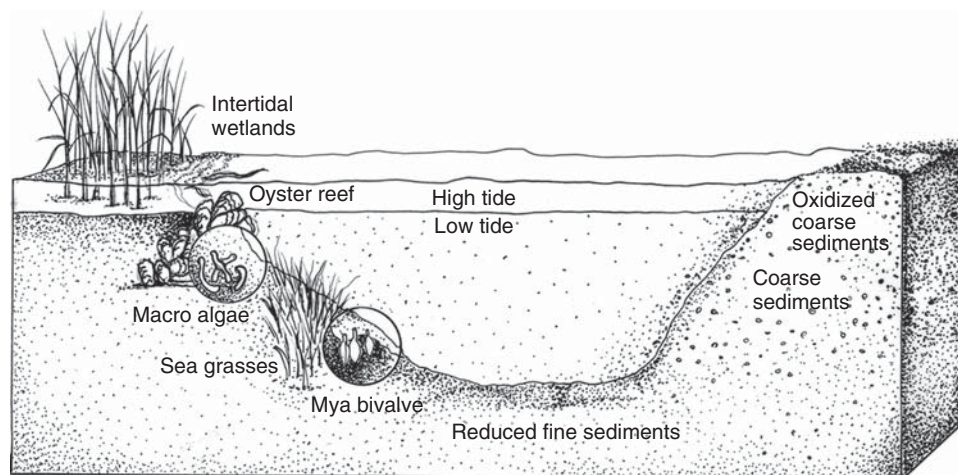


FIGURE 1.2 Idealized cross section through a typical estuary showing vertical distribution of several important elements; note that organism sizes and vertical scale are exaggerated.

reduced conditions, including species of the genera *Spartina*, actively pump oxygen into the soil and create a thin oxidized zone around their roots and support an aerobic root-associated microbial community.

1.3.3 Longitudinal Section

The longitudinal section (Fig. 1.3) demonstrates some of the attributes that result from the mixing of fresh water and seawater. Salinity gradually increases along the length of estuaries, and the isohalines (lines of equal salinity) show that salinity generally increases with depth. This salinity distribution results from the density difference between salt and fresh water. Fresh water from the river tends to flow on top of the salt water because it is less dense. As the fresh water flows to the sea, deeper salt water mixes with it, making it saltier. This outward flow of fresher water causes more salt water to move into the estuary and results in a net outflow of fresh water to the sea at the surface and a net inflow of salt water on the bottom. This circulation pattern, and the resulting salinity distribution, is a general feature of many estuaries that have significant river input and is discussed in more detail in Chapter 2.

We again see the euphotic and aphotic zones in the longitudinal section, but the depth of the euphotic zone decreases toward fresh water because of increasing turbidity. The most turbid water occurs at salinities from 1 to 5 ppt, and this “turbidity maximum” is a result of several physical and chemical changes that occur as river water and sea water mix. These changes are addressed in Chapter 3.

Because this transect is through the deepest part of the estuary, there are fine sediments and reducing conditions below the sediment surface along the

entire transect. At the mouth of the river, the “platform” of riverine sediments that have settled out of the water where the river enters the estuarine bay is to be noted.

Organisms that occur in the water column include bacteria, phytoplankton, zooplankton, and nekton (freely swimming organisms such as fishes). The sizes of these organisms range from bacteria that are $<1\ \mu\text{m}$ to large animals such as seals and dolphins. Benthic animals include infauna that live in the sediments such as polychaete worms, amphipods, and the very small meiofauna. Of special note is the dense bed of the clam *Rangia cuneata* in the oligohaline region. The diversity of benthic organisms along this transect is discussed in more detail later in this chapter as well as in Chapter 12 on estuarine benthos.

1.3.4 A Typical Estuarine Food Web

Thus far our observations of the typical estuary have been of the structure and, as such, have been rather static. We now discuss more dynamic aspects of the estuary by considering a typical estuarine food web (Fig. 1.4). This allows for a more detailed consideration of some of the organisms that live in estuaries. For illustrative purposes, we compare estuarine and marine systems.

We begin by listing several terms with definitions derived from E.P. Odum 1971. The transfer of food energy from the source in plants (or more appropriately, primary producers) through a series of organisms eating one another is referred to as a *food chain* or, more properly, *food web*, for food chains interconnect with one another. The word *trophic* is used interchangeably with food, and trophic dynamics refers to the pattern of food production and consumption as it occurs and changes over time.

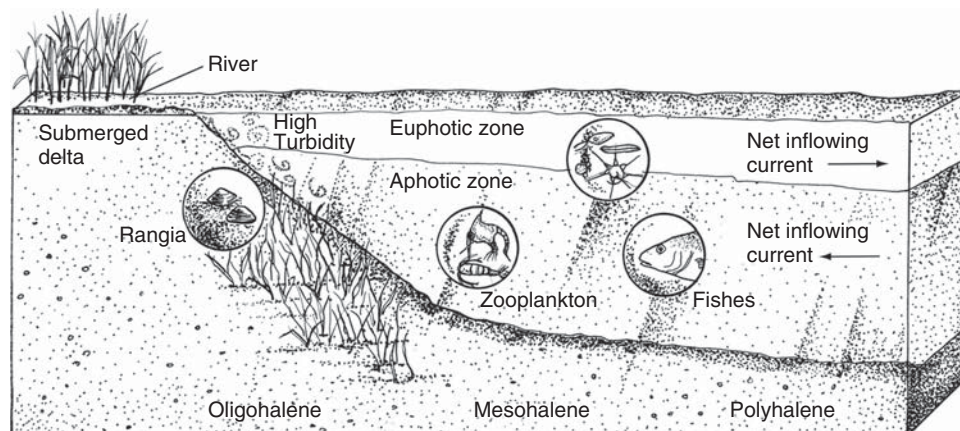


FIGURE 1.3 Idealized longitudinal section through a typical estuary from river to the sea. The vertical scale is exaggerated, and the darker area near the sediment surface indicates an oxidized zone.

The trophic dynamics of estuaries tend to be complex. Figure 1.4 illustrates a number of important characteristics of estuarine trophic dynamics. First, there are almost always several different types of primary producers in estuaries, including phytoplankton, salt marsh plants, mangroves, submersed sea grasses, and benthic algae. In contrast, the open ocean has only phytoplankton. There are other important distinctions between the open sea and estuaries. For example, in the sea, practically all phytoplankton are consumed alive. A food web that begins with consumption of live plants is called a *grazing food web*. In estuaries, many important plants are not heavily grazed, but die and begin to decompose before being consumed. This decomposing material is called *organic detritus* and the food web it supports is called a *detrital food web*. Organic detritus is an important food in estuaries, and an important area of research over the past four decades concerns detrital dynamics. Detritus is considered in a number of chapters, especially Chapters 9 and 16 on microbial ecology and trophic webs.

Nevertheless, the part of the estuarine food web that is the most readily recognizable to students is the grazing web based on phytoplankton. These small primary producers are eaten by zooplankton, which are then eaten by small planktivorous fish. In this example, they are herring, but in other estuaries, these fish may be anchovies or sardines. Zooplankton are also eaten by larvae of larger fish. At the top of the food web are larger carnivores such as bluefish. We now know that phytoplankton and the organisms

that consume them form an extremely complex set of interactions called the *microbial food web*. This is covered in Chapters 10 and 11.

An extremely important characteristic of estuarine food webs is the importance of the bottom of estuaries. First, a variety of plants grow on the bottom in shallow waters (e.g., marsh grasses, sea grasses, and benthic algae). Second, there is significant flow of food and inorganic nutrients from the water column to the bottom as well as in the opposite direction. Benthic animals such as oysters, clams, and mussels are filter feeders; that is, they remain in one place and concentrate food that flows past them in the water currents. There are other benthic organisms that live in areas of weak currents. They move over and through the sediments and take food from the sediment itself. These are called *deposit feeders* and include worms, amphipods, and a host of other small organisms. There are also a large number of non-bottom-dwelling organisms that feed on the bottom. These include a variety of invertebrates, fish, and birds. In fact, the majority of fish species found in estuaries have adaptations for bottom feeding.

All of this flow of food energy from phytoplankton, detritus, and through the bottom converges on a group of top carnivores that are generalist feeders on a wide variety of organisms. These top carnivores include many species of fish, including sea trout, striped bass, and flounder, birds such as sea gulls, and mammals such as seals and dolphins.

In summary, estuarine trophic dynamics are characterized by a variety of primary producers; grazing

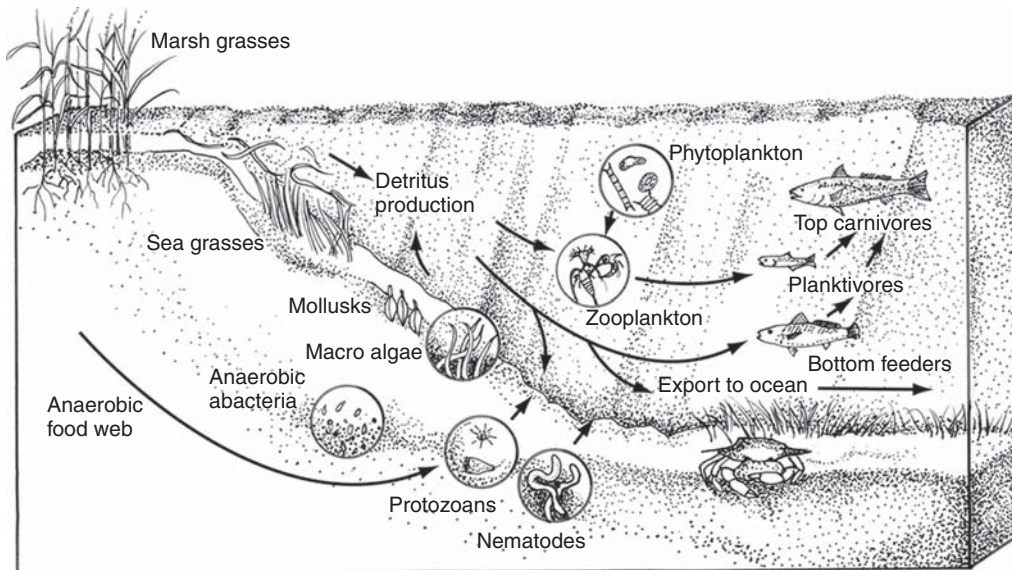


FIGURE 1.4 Food web diagram for a typical estuarine ecosystem showing some feeding links among some of the major trophic groupings. Black lines and arrows indicate flow of food from source to consumer.

and detrital food chains; a high degree of interaction between the water column and bottom; a complex, highly interconnected food web; and a large number of generalist feeders. More details on food webs is found throughout the book and especially in Chapter 16.

1.3.5 An Estuarine Energy-Flow Diagram

Thus far, we have discussed visible aspects of estuarine ecosystems. We can see an oyster reef and a salt marsh and a sample taken from the bottom. We can watch a trout eat an anchovy and, if we have a microscope, we can even observe a zooplankter ingesting a phytoplankton cell. But important processes go on which are not visible. We cannot see sunlight interacting with chemicals during photosynthesis. Nor can we watch phosphorus flowing out of bottom sediments and being moved into surface

waters by currents. It is very difficult to measure organic detritus flowing out of a marsh, much less visibly observe it being degraded and consumed by bacteria. Nevertheless, an understanding of these and other processes is essential if we are to begin to comprehend how estuaries work. Thus, in this section, we use an energy-flow diagram (Fig. 1.5), both to present systematically some of the concepts we have discussed and to conceptualize some of these invisible processes. To do this, we use the symbols developed by H.T. Odum (1971, 1983).

The diagram illustrates the grazing and detrital food webs we discussed in the previous section. It shows the importance of tidal currents in transporting detritus out of the marsh and in moving phytoplankton to benthic filter feeders. The dynamics of nutrient cycling are important and complex in estuaries. Our diagram shows input of nutrients and

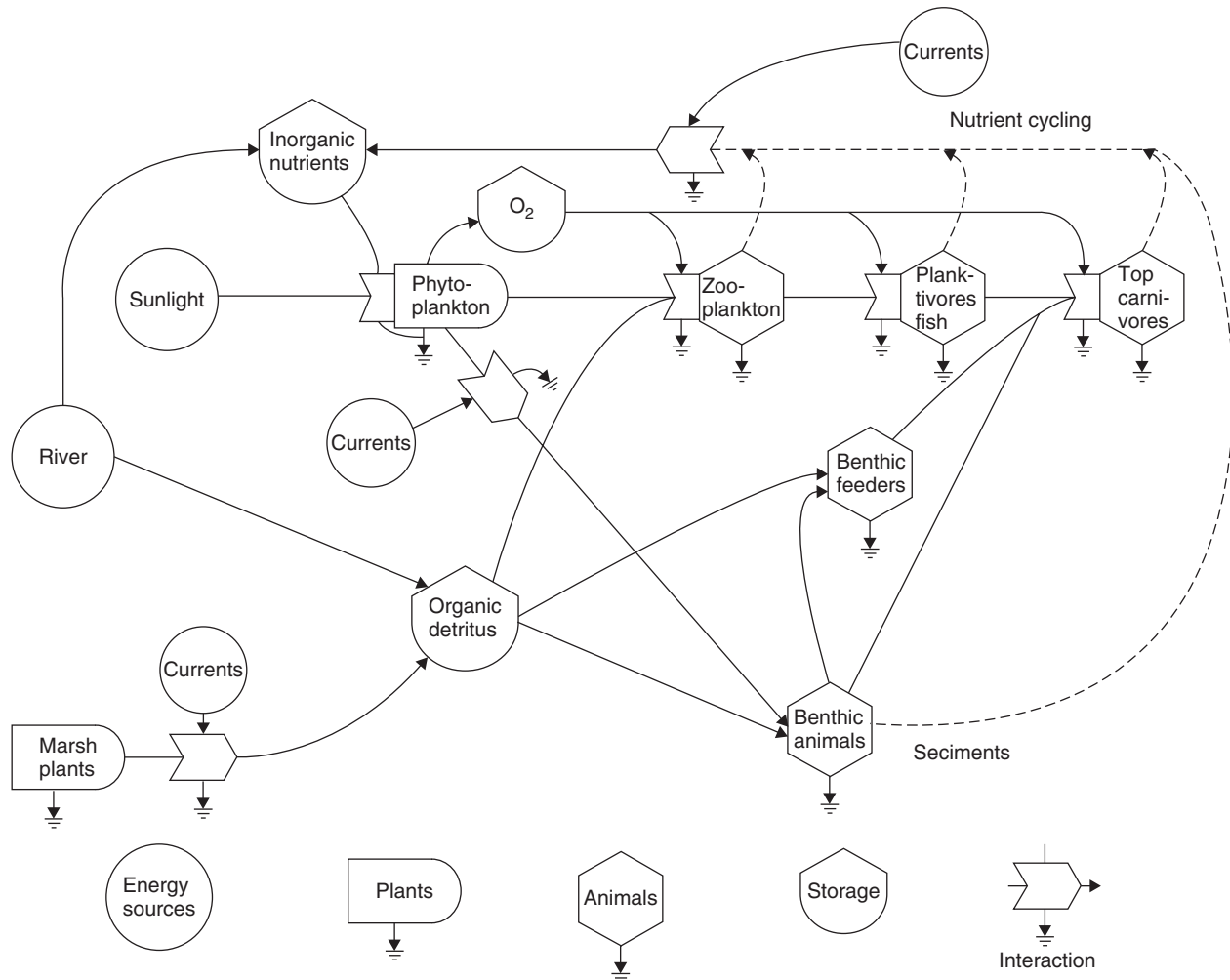


FIGURE 1.5 An energy-flow diagram illustrating some major structural and functional attributes of estuarine ecosystems. Note that the five types (shapes) of symbols used are defined along the bottom of the figure.

organic matter from the river as well as recycling from both sediment and water-column organisms. Again, the importance of currents in transporting nutrients is illustrated. Finally, the diagram shows that there is an interaction of sunlight and inorganic nutrients during primary production by phytoplankton and that plankton produce oxygen that is subsequently used by animals. There are, of course, many interactions and details left out of this energy diagram as well as the preceding views of estuaries. Throughout this book, the concepts we have introduced here are developed in much more detail to provide a fuller general understanding of estuaries. At this point, however, the reader should have a good foundation to begin a more in-depth study of estuaries. In the following section, we discuss a classification of estuarine ecosystems.

1.4 ESTUARINE HABITAT TYPES

The previous two sections demonstrated the high diversity of habitat types within estuarine systems. This diversity is caused by two things. First, from an abiotic point of view, estuaries include a great number of physical habitats, including beaches, passes, intertidal and shallow subtidal flats, deeper areas, and deltas. Second, adapted assemblages of organisms can fully exploit each of these different habitats and, in many cases, can dramatically alter those habitats, further expanding the total habitat diversity of estuaries. For example, in the intertidal zone, there may be salt marshes, tide pools, algal flats, mud flats, oyster reefs, and mussel beds. Oyster reefs and mussel beds, in turn, create new types of habitat by changing the physical environment. Subtidal areas can include seagrass beds, sandy shoals, soft muddy bottoms, or mollusk beds. Some of the more important biotic habitats are described in Table 1.1.

1.4.1 Characterization of the Ecosystem

We defined estuary and ecology, but because these definitions are so broad, it is difficult to define “estuarine ecosystems,” except as those ecosystems that have developed and persist in estuaries. We can easily describe, however, the abiotic factors that are most important in determining the specific nature of estuarine ecosystems as well as the salient ecological characteristics of these ecosystems.

The physical environment (climate, geomorphology, presence or absence of water, salt, etc.) is the primary determinant of the type of ecosystem that will develop in a particular location. The constancy and

regularity, or the lack thereof, of the physical environment is an important attribute of physical conditions that influence the biota. That is, the biota is more determined by the degree of change over various time intervals (e.g., diel, tidal, and seasonal), than by the absolute level of such factors as microclimate, water movement, chemical cycling, and physical structure. Both abiotic factors and the biota itself can reduce the degree of these fluctuations. Tropical rain forests and coral reefs are examples of ecosystems where the ambient physical environment is greatly modified by the biota. In contrast, alpine lichen herb and sandy beach ecosystems are strongly affected by physical inputs and are relatively unaffected by the biota. Estuarine ecosystems are intermediate between these extremes but are still strongly physically dominated.

The following abiotic features are important in determining the specific nature of estuaries:

1. The degree to which they are protected from and hence buffered against direct oceanic forces.
2. The quantity of fresh water input along with the amount of associated dissolved and suspended materials.
3. The water circulation patterns as determined by riverine and tidal currents, winds, and geomorphology. Tides are particularly important because they exert a profound influence on estuarine circulation and biological processes.
4. The depth of the estuary. Where estuaries are shallow there is a stronger interaction between the water column and the bottom. This allows, for example, nutrients released from the bottom to be used by phytoplankton in the surface waters.
5. The sharpness and pattern of the gradient in salinity from the sea to fresh water. This salinity variation has a pronounced impact on water circulation as well as on many biological processes and organisms.
6. The rate of geomorphological change is rapid compared to that in many terrestrial systems. Sand banks and mud flats form, degrade, and migrate within estuaries. Wetlands form at the mouths of rivers as sediments are deposited. Biogenic processes, such as reef formation, contribute to the geomorphology of estuaries.

Most estuarine ecosystems are open, variable systems dominated and subsidized by physical processes, resulting in large exchanges of biotic and nonbiotic materials, including water, salt, nutrients, sediments, and organisms, with neighboring systems. The exchange of organisms over millions of years has

TABLE 1.1 Key physical and biological characteristics of eight common estuarine habitats

Habitat	Physical Characteristics	Biological Characteristics
High physical energy	Tidal passes and beaches; strong currents and or waves; often clean water; coarse sediments such as sand; well-oxidized water column and sediments; generally high salinities	Benthos dominated by filter feeders; high diversity and biomass; high rates of metabolism supported by current transport of food; heterotrophic; motile organisms mostly transient
Mid-estuarine systems: middle-salinity plankton-nekton system	Strong to moderate turbulence (waves and currents); salinity 10–25 ppt; oxygenated water column; bottom deeper than euphotic zone; medium water clarity	Grazing food chain of phytoplankton, zooplankton, fishes; diatoms, dinoflagellates, and nanoplankton; common phytoplankters; copepods and meroplankton important zooplankters; relatively high rates of primary production with strong seasonal pulse in temperate zone disappearing in the tropical, balanced community metabolism; intermediate diversity
Mid-estuarine systems: deep benthos	Sluggish currents; fine sediments; no light on bottom; reducing conditions just below sediment surface; water column normally oxygenated	Deposit feeders dominate (worms and amphipods); low density and biomass; heterotrophic with relatively low metabolic rate; low diversity
Shallow littoral areas: submerged grass beds	Moderate to strong currents; bottom within euphotic zone; oxygenated water column; sediment reduced just below surface; sediments range from sandy to fine	High salinity grass beds dominated by eel grass (<i>Zostera</i>) in temperate zone and by turtle grass (<i>Thalassia</i>) in tropics; high rates of gross primary productivity, community net productive; detrital food chain important; direct grazing increases in tropics; both deposit feeders and filter feeders important in benthos; high biomass, low diversity; complex chemical cycling; important nursery and feeding area for migratory species; high epiphytic community
Shallow littoral areas: algal mats	Shallow, clear, often hypersaline water; sediments sandy to fine silts: highly reduced below mat; large oxygen changes due to metabolic activity	Blue-green algal mats; extremely productive, P/R close to one; low consumer diversity
Wetlands	Sluggish currents; intertidal wetlands act as sediment traps, sediments generally very soft often with peats; strong reducing conditions in sediments sometimes to sediment surface; often low oxygen in water column; complex chemical cycling; wetlands occur from fresh to marine salinities and from the arctic to the tropics	Saline wetlands characterized by marshes (<i>Spartina</i>) in temperate zones and mangrove swamps (<i>Rhizophora</i>) in tropics; freshwater wetlands swamp or marsh; freshwater areas have high producer diversity; high rates of gross primary production; detrital food chain important; high biomass of both producers and consumers; low diversity; deposit feeders most common; important nursery and feeding area for migratory species
Reefs, worm, and clam flats	More or less constant currents—moderate to strong; intertidal or subtidal; oxygenated water column; reduced sediments; reef structure often amplifies currents; intermediate salinities for oysters; sediments for mollusks flats normally oxygenated; oyster reefs normally in fine, soft sediments, others in firmer sediments of sand or shell	High biomass; low diversity; relatively high food supplies in water column; filter feeders predominate; high rates of metabolism; heterotrophic; often exploited commercially; <i>Crassostrea</i> and <i>Ostrea</i> common genera of oysters; oysters epifaunal, flats populated by infauna organisms
Oligohaline	Located at river mouth–estuary boundary; highly variable salinity; water contains high levels of suspended solids and nutrients; high sedimentation rates, high turbidity, “nutrient trap”	Low species diversity; very high biomass; high rates of metabolism; heterotrophic; filter feeders dominate; <i>Rangia cuneata</i> and <i>Mya arenaria</i> very common in south and north temperate, respectively; heavily used by migratory fishes

resulted in a rich genetic heritage, and the biota is derived from marine, freshwater, and terrestrial sources. Over time periods of hundreds to thousands of years, deltas grow and erode and barrier islands shift. On shorter timescales, salinity changes with tide and river flow, and water levels fluctuate so that the intertidal region is subjected to wetting and drying and extremes of temperature. But estuarine organisms have developed physiological and behavioral patterns to deal with this dynamic environment, and many are able to directly modify the physical environment. Many organisms use the intense and variable physical energies as subsidies, as, for example, in the case of an oyster reef “using” the flow of tides to exploit phytoplankton produced elsewhere. Nevertheless, such an ever-changing world imposes considerable potential stress on estuarine organisms because large changes in salinity, temperature, and so on, can be deleterious, even lethal, for estuarine organisms. The relative importance of physical forces as subsidies or stresses forms the basis for the estuarine classification discussed in the following section.

1.4.2 Functional Classifications of Estuarine Ecosystems

Chapter 2 presents several estuarine classification schemes based on physical and geomorphic characteristics. These definitions help us understand the origin and physical nature of estuaries and can be used as the beginnings of an estuarine classification system. From the standpoint of estuarine ecology, however, we need a classification system that leads to a better understanding of estuaries as ecosystems. We discuss here an approach to conceptualize estuaries based on energy inputs and landscape features.

Odum and Copeland (1972) proposed a “functional” system for understanding and classifying coastal ecosystems based on an analysis of energetics. We like their approach because it is a true ecosystem classification addressing both biotic and abiotic properties and it recognizes the importance of energy. Their idea is that the status of an ecosystem is a balance between energies that build structure and order and stresses that cause a loss of structure and order. The former are called *energy sources* or *ordering energies* and the latter *energy stresses* or *disordering energies*. This idea is shown diagrammatically in Figure 1.6a.

We want to emphasize that energy sources and stresses are not always mutually exclusive categories of energies, but rather that a particular energetic force affects organisms relative to the ecosystem (or part of an ecosystem) in question. A few examples illustrate this point. Moving water can be either an energy

source or stress in estuarine ecosystems. Moderate currents are a source of energy for seagrass beds because they transport organic matter and nutrients to the beds and wastes away. If the currents become very strong with high waves, however, the grass bed may be eroded. In the latter case, the hydraulic energy is a stress. But the same strong waves are an energy source for tiny animals living among the sand grains on a beach because the waves pump oxygen and food through the sand. Likewise, heat from the sun is an energy source for a marsh because it increases the rate of metabolism. But the intense heat of a fire will destroy a marsh.

The distinction between energy source and energy stress is the central concept in this classification system. Whether an energy input is ordering or disordering depends on the particular system or subsystem in consideration, and it is the balance between the two that is important. If energy sources are greater than stresses, the system will build structure and maintain order. However, if stresses are greater, there will be a loss of structure and order.

There are three general categories of energy sources for estuarine ecosystems: (i) the mechanical energy of moving water, (ii) sunlight, and (iii) organic and inorganic fuels imported into estuaries (Fig. 1.6b). Moving water does work, such as by connecting trophic components in the bottom and surface waters, bringing food to filter feeders, recycling nutrients, and removing wastes. Organisms in effect “conserve” their own energy by using the water current energy instead. The energy of sunlight drives photosynthesis of plants, which in turn supports estuarine food chains. Sun energy also supplies heat and thus produces thermal gradients in estuarine ecosystems. Supplementary organic and inorganic fuels are imported into estuaries via rivers, terrestrial runoff, and the sea. The organic matter is an added food to that produced in estuaries and the inorganic compounds such as nitrogen can increase photosynthesis by providing needed materials.

There are three general categories of stress energies for estuarine ecosystems: (i) stress due to energy diverted from the system, (ii) stress due to microscale random disordering, and (iii) stress due to forced losses within the system (Fig. 1.6c). Stress caused by energy diverted refers to energy that could be a source but is, for some reason, lost. For example, turbidity caused by natural conditions or human activities lowers the amount of light energy that enters the water column and thus the photosynthesis of deeper submersed plants. For another, when a marsh is impounded, the energy of tidal currents is

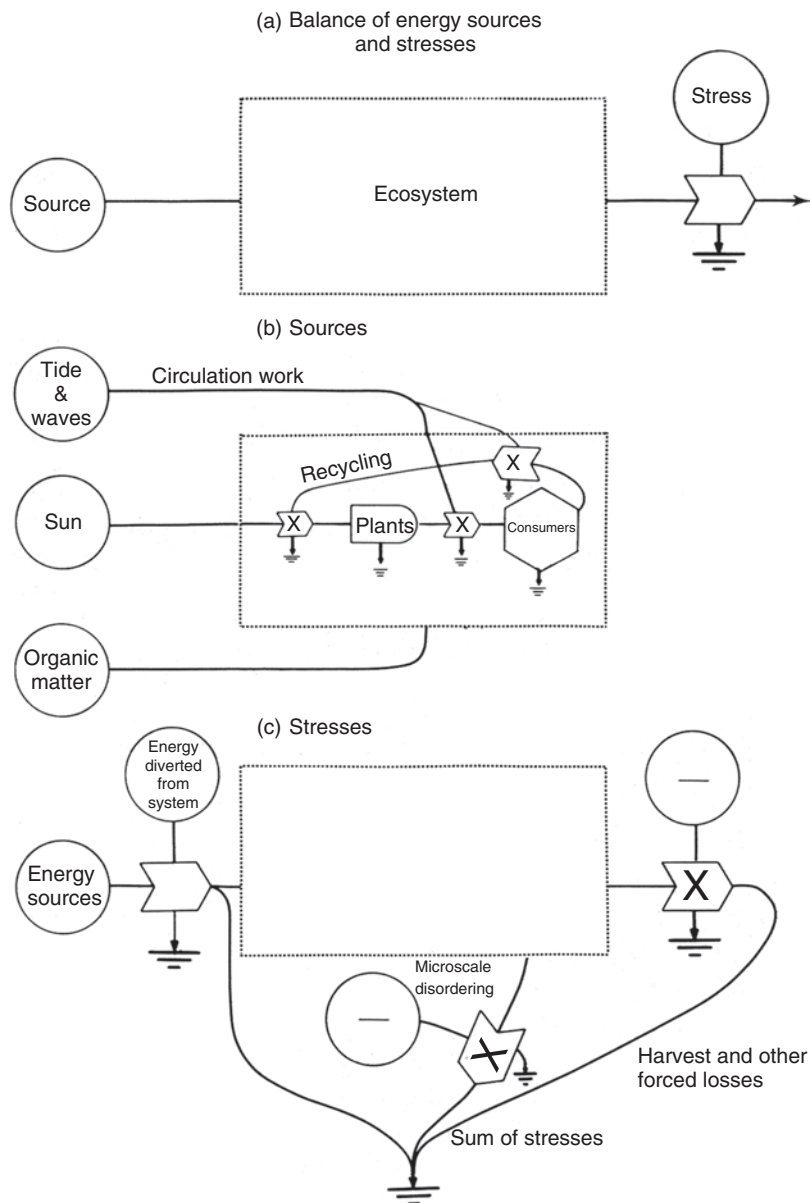


FIGURE 1.6 An energy-flow diagram illustrating how ordering and disordering energies are related in estuarine ecosystems. The status of an ecosystem results from a balance between energy sources, which build structure and order, and energy stresses, which cause a loss of structure and order (a). For estuaries, there are three main kinds of energy sources: sunlight, water movement (due to gravity, tides, and waves), and inputs of organic or inorganic nutrients (b). Three general kinds of energy stresses are (i) energy diverted from the system, (ii) microscale or entropic disordering, and (iii) harvest and other forced losses (c). See text for further discussion. *Source:* Figures from Odum and Copeland, 1972, used by permission.

eliminated and marsh productivity normally is lowered. A dam or river also can reduce the input of water and organic and inorganic matter entering an estuary. When the Aswan Dam was constructed in Egypt, the amount of river-borne material entering the estuary was drastically reduced, resulting in the collapse of the eastern Mediterranean sardine fishery that depended on the material.

The second kind of stress on estuarine ecosystems and their inhabitants is that due to microscale random disordering of the kind described by the second law of thermodynamics. This stress is the inevitable tendency of order and complexity to degrade into disorder and is characteristic of all living organisms. If an animal does not eat for a relatively short period of time, it dies because food is the potential energy

source it uses to maintain its internal order against this constant tendency toward disorder. The struggle against random disorder is a problem for all living creatures, and particularly for estuarine organisms, because much of the ordering energy available for estuarine organisms must be used to compensate for the large environmental variability. Human activity can aggravate the problem for estuarine organisms, for example, by the introduction of toxins, which tend to increase physiological “disorder” and thus make it even more difficult for an organism to cope with natural variability.

The last type of stress is forced loss. This means that potential energy within the system is removed before it can be used to do work. For example, the constant seaward flow of rivers and the action of tides flush material out of estuaries. Thus, water movement can be a stress as well as an energy source, and, most often, it is both. Human activities such as fishing and wetland destruction are also ways in which potential energy can be lost from an ecosystem.

Many estuarine organisms have evolved various behavioral and physiological adaptations to cope with stresses that would kill most other aquatic organisms (Vernberg and Vernberg, 1972, 1976). In doing so they are better able to exploit the available energy sources. These adaptations also allow organisms to use energies that would be stressful to most other organisms. For example, the small animals that live among the sand grains on a beach would be destroyed by the full force of the waves if they were not adapted to them, and meanwhile they use the oxygen and food that the waves pump through the sand. The *Rangia* clam of the oligohaline zone is adapted to high

siltation rates, periodic low oxygen, and extremely variable salinity and thus is able to live where it can use the large input of organic matter from the river without much predation or competition from other filter feeders. Many other examples of this type of adaptation are discussed throughout the book.

Because different estuarine systems and subsystems have characteristic energy stresses and sources, the biota of these various areas have adapted to these energies in different ways. These different energies and adaptations serve as the basis for the functional classification system of Odum and Copeland (Fig. 1.7). For most estuarine ecosystems, stress energies are moderate and similar so that the latitudinal variations in temperature and sunlight regime are the most important factors determining the distinguishing characteristics of these systems. Tropical, temperate, and polar estuarine ecosystems are conveniently distinguished. Solar energy input is highest and most regular in the tropics, but because of higher temperatures, there is more thermal disordering to overcome, so that tropical organisms have higher energy requirements. Seasonal changes are more distinct in temperate latitudes and the productivity of estuaries is concentrated into shorter periods of time; hence, seasonal “programming” of activities and migratory species becomes more important. At polar latitudes, ice and extreme cold are important stress energies.

When stress energies become large, either naturally or because of human activity, the associated biotic adaptations are, in a sense, similar over a wide latitudinal range. Thus, in these circumstances, the estuarine ecosystem can be classified according to the

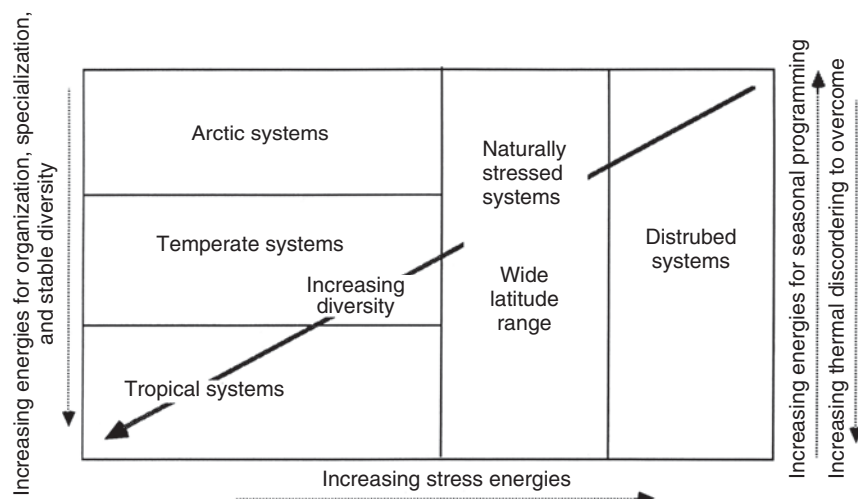


FIGURE 1.7 A functional classification of coastal ecosystems based on important energy sources and stresses. *Source:* From Odum and Copeland, used by permission.

characteristic stress. Sedimentary deltas, hypersaline lagoons, and beaches are natural examples of these types. Disturbed systems also develop due to human induced stresses and include eutrophied planktonic systems, organisms affected by toxins, and systems stressed by hydrologic changes (such as impounded marshes).

The energy input to coastal ecosystems is not constant but occurs in pulses. Pulsing is considered essential for most ecosystem functioning and has been called *nature's pulsing paradigm* (Odum et al., 1995). For example, understanding river ecosystems can be described in terms of the flood pulse (Junk and Bayley, 2008; Schram and Eggleton, 2006) and dynamic habitat interactions (Stanford et al., 2005). The functioning of coastal systems is affected by energetic forcings that serve to enhance productivity, increase material fluxes, and affect the morphology and evolution of these systems. This type of pulsing applies to many natural systems, but it is especially important for coastal ecosystems (Blum, 1995).

Eugene Odum (1980) recognized the importance of pulsing when he described estuaries as “tidally subsidized, fluctuating water-level ecosystems.” But the tide is not the only energy subsidy to coastal systems. Energetic forcings occur over a hierarchy of different spatial and temporal scales (Day et al., 1995, 1997, 2000). These energetic events range from waves and daily tides to switching of river channels in deltas that occur on the order of every 1000 years and include frontal passages and other frequent storms, normal river floods, strong storms, and great river floods (Table 1.2). The primary importance of infrequent events such as channel switching, great river floods, and very strong storms such as hurricanes is in sediment delivery and in major spatial changes in geomorphology such as changes in river channels in deltas. More frequent events such as annual river floods, seasonal storms, and tidal exchange are also important in maintaining salinity gradients, delivering nutrients, and regulating biological processes. Throughout this book, the importance of these forcings is discussed for a variety of biotic communities and organisms and important processes.

1.5 ESTUARIES AND ESTUARINE ECOSYSTEMS IN A GEOLOGICAL CONTEXT

It is interesting to note that all of the estuaries discussed in this book did not exist 10,000–15,000 years

TABLE 1.2 A hierarchy of forcing or pulsing events affecting the formation and sustainability of deltas

Event	Timescale	Impact
Major changes in river channels	500–1000 yr	New delta lobe formation, Major deposition
Major river floods	50–100 yr	Channel switching Major deposition
Major storms	5–20 yr	Major deposition
Average river floods	Annually	Enhanced production Enhanced deposition Freshening (lower salinity) Nutrient Input Enhanced 1° and 2° production
Normal storm events (frontal passage)	Weekly	Enhanced deposition Organism transport Net transport
Tides	Daily	Drainage/marsh production Low net transport

Source: From Day et al., 1997, 2000.

ago and that they will cease to exist in the near geological future. The world's present estuaries were formed when sea level rose after the last glaciation. Since that time, they have been progressively infilled and will continue to be. Thus, present estuaries will, for the most part, cease to exist because they will fill up with sediment or because sea level will change again. However, estuaries will continue to exist at the edge of the sea, wherever it exists. At times like the present, when sea level is high enough to flood the edge of the continents, estuaries are widespread. When sea level was low enough so that the edge of the sea was on the continental slopes, as during the height of the glaciers, total estuarine area was small. The situation we see along the western coast of the Americas is the rule when sea level is low.

Of course the species and the types of biological communities that presently exist in estuaries have certainly existed for much longer than the estuaries themselves. Rivers have always flowed to the sea, whether it was higher or lower than at present. Estuarine ecosystems, with their characteristic species composition and adaptations, have moved back and forth with the edge of the sea. Therefore, even though particular estuaries are relatively short lived, estuarine organisms and estuarine ecosystems are very old.