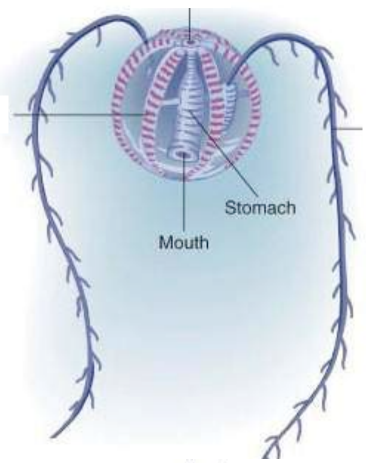
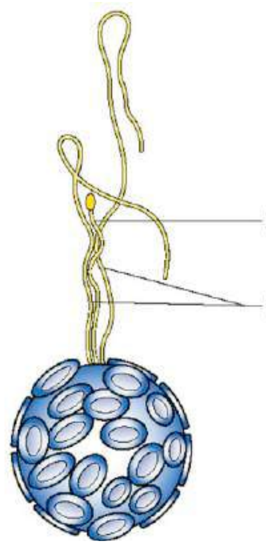
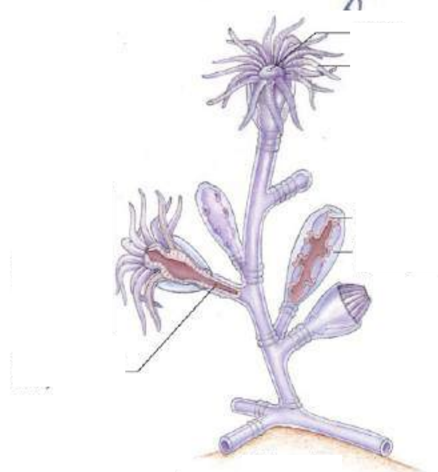
Sea│mester Programs

Introduction to Marine Biology

OCB 1001







Lecture Notes

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Version 3.6

1. Introduction: Science and Marine Biology (Karleskint Chapter 1)

1.1. Class Structure and Evaluation

Introduction to marine biology (OCB 1001) is a 3 credit class accredited through the University of South Florida. It involves a minimum of 45 contact hours that include both lectures and practical activities. This class can generally be divided in four sections.

1. Important biological and ecological concepts
2. Taxonomy of marine organisms
3. Marine ecosystems
4. Human impacts on the marine environment and management

This class is based on the following textbooks:

Karleskint, G., Turner, R. and Small, J.W. 2013. Introduction to Marine Biology, 4th edition. Thomson Brooks/Cole, Belmont CA.

Nybakken, J.W. and Bertness, M.D. 2004. Marine Biology an Ecological Approach, 6th edition. Pearson Benjamin Cummings, San Francisco CA.

Sumich, J.L. and Morrissey, J.F. 2004. Introduction to the Biology of Marine Life, 8th edition. Jones and Bartlett Publishers, Sudbury MA.

How to use these lecture notes:

This booklet is provided so you easily have access to the information that was presented in class. The class is mostly based on the book by Karleskint *et al*, but some information from that book is omitted and information from other books has been added. For each chapter in this booklet, the associated chapters from the reference books are indicated. You are responsible for everything in these lecture notes and presented in class for the exams. These notes are not a detailed explanation of all the organisms and ecosystems we cover in the class, just an outline and study guide. Some pictures are provided, but you are highly encouraged to make full use of the reference books to gain a better understanding of the topics.

Evaluation for the class will be as follows:

4 exams at 15% each	60%
2 short essays at 10% each	20%
1 field identification logbook	15%
1 identification quiz	5%

Exams are non-cumulative and cover 5-6 lectures each. Instructions and expectations for the short essays are outlined in the Marine Biology Reader provided.

1.2. Science and Marine Biology

Oceans cover 71% of the earth, and affect climate and weather patterns that in turn impact the terrestrial environments. They are very important for transportation and as a source of food, yet are largely unexplored; it is commonly said that we know more about the surface of the moon than we do about the deepest parts of the oceans!

Oceanography is the study of the oceans and their phenomena and involves sciences such as biology, chemistry, physics, geology, meteorology. Marine biology is the study of the organisms that inhabit the seas and their interactions with each other and their environment.

1.3. Brief History of Marine Biology

Marine biology is a younger science than terrestrial biology as early scientists were limited in their study of aquatic organisms by lack of technology to observe and sample them. The Greek philosopher Aristotle was one of the firsts to design a classification scheme for living organisms, which he called "the ladder of life" and in which he described 500 species, several of which were marine. He also studied fish gills and cuttlefish. The Roman naturalist Pliny the Elder published a 37-volume work called *Natural History*, which contained several marine species.

Little work on natural history was conducted during the middle ages, and it wasn't until the late 18th century and early 19th century that interest in the marine environment was renewed, fueled by explorations now made possible by better ships and improved navigation techniques. In 1831, Darwin set sail for a 5 year circumnavigation on the *HMS Beagle*, and his observations of organisms during this voyage later led to his elaboration of the theory of evolution by natural selection. Darwin also developed a hypothesis on the formation of atolls, which turned out to be correct. In the early 19th century, the English naturalist Edward Forbes suggested that no life could survive in the cold, dark ocean depths beyond 500m deep. There was little basis for this statement, and he was proven wrong when telegraph cables were retrieved from depths exceeding 1.7 km deep, with unknown life-forms growing on them. In 1877 the American Alexander Agassiz collected and catalogued marine animals as deep as 4,240 m. He studied their coloration patterns and hypothesized about the absorption of different wavelengths at depth. He also noted similarities between deep water organisms on the east and west coast of Central America and suggested that the Pacific and Caribbean were once connected.

Modern marine science is generally considered to have started with the *HMS Challenger* expedition, led by the British Admiralty between 1872 and 1876. During a circumnavigation that lasted 3.5 years, the *Challenger* sailed on the world's oceans taking samples in various locations. The information collected was enough to fill 50 volumes that took 20 years to write up. The samples taken during the Challenger expedition led to the identification of over 4,700 new species, many from great depths, and the chief scientist, Charles Wyville Thomson, collected plankton samples for the first time.

The Challenger Expedition was the start of modern marine biology and oceanography and is still to date the longest oceanography expedition ever undertaken. However modern technology has allowed us to sample organisms more easily and more effectively and to quantify things more accurately. Scuba diving and submersibles are used to directly observe and sample marine life; remote sampling can be done with nets, bottles and grabs from research vessels, and satellites are used extensively for remote sensing.

1.4. Why Study Marine Biology?

1.4.1. To dispel misunderstandings about marine life

Though many people fear sharks, in reality 80% of shark species grow to less than 1.6m and are unable to hurt humans. Only 3 species have been identified repeatedly in attacks (great white, tiger and bull sharks). There are typically only about 8-12 shark attack fatalities every year, which is far less than the number of people killed each year by elephants, bees, crocodiles or lightning.

1.4.2. To preserve our fisheries and food source

Fish supply the greatest percentage of the world's protein consumed by humans, yet about 70% of the world's fisheries are currently overfished and not harvested in a sustainable way. Fisheries biologists work to estimate a maximum sustainable yield, the theoretical maximum quantity of fish that can be continuously harvested each year from a stock under existing (average) environmental conditions, without significantly interfering with the regeneration of fishing stocks (i.e. fishing sustainably).

1.4.3. To conserve marine biodiversity

Life began in the sea (roughly 3-3.5 billion years ago), and about 80% of life on earth is found in the oceans. A mouthful of seawater may contain millions of bacterial cells, hundreds of thousands of phytoplankton and tens of thousands of zooplankton. The Great Barrier Reef alone is made of 400 species of coral and supports over 2000 species of fish and thousands of invertebrates. Each year, three times as much rubbish is dumped into the world's oceans as the weight of the fish caught. There are areas in the North Pacific where plastic pellets are 6 times more abundant than zooplankton. Plastic is not biodegradable and can kill organisms that ingest it. Many industrial chemicals biomagnify up the food chain and kill top predators. Some chemicals can bind with hormone receptors and cause sex changes or infertility in fish. Understanding these links allow us to better regulate harmful activities.

1.4.4. To conserve the terrestrial environment

Phytoplankton and algae use CO_2 dissolved in seawater in the process of photosynthesis, and together are much more important than land plants in global photosynthetic rates.

Marine photosynthesizers therefore have the ability to reduce the amount of CO_2 dissolved in the oceans and consequently in the atmosphere, which has important implications for the entire biosphere. Many marine habitats, such as coral reefs and mangroves, also serve to directly protect coastlines by acting as a buffer zone, reducing the impact of storm surges and tsunamis which may threaten human settlements.

1.4.5. For medical purposes

Because the architecture and chemistry of coral is very similar to human bone, it has been used in bone grafting, helping bones to heal quickly and cleanly. Echinoderms and many other invertebrates are used in research on regeneration. Chemicals found in sponges and many other invertebrates are used to produce several pharmaceutical products. New compounds are found regularly in marine species.

1.4.6. For human health

Several species of phytoplankton are toxic and responsible for shellfish poisoning or ciguatera. Understanding the biology of those species allows biologists to control outbreaks and reduce their impact on human health.

1.4.7. Because marine organisms are really cool

Many fish are hermaphrodites and can change sex during their lives. Others, including several deep-sea species, are simultaneous hermaphrodites and have both male and female sex organs at the same time. The blue whale is the largest animal to have ever live on earth and has a heart the size of a Volkswagen Beatle. The Indonesian mimic octopus has the ability to mimic the color and behavior of sole fish, lion fish and sea snakes, all toxic animals, which greatly reduces its likelihood of encountering predators.

1.5. How is Marine Biology studied? Using the Scientific Method

1.5.1. Science

The word *science* comes from the Latin (scientia) and means “knowledge”. Science is a systematic enterprise that builds and organizes knowledge in the form of testable explanations and predictions about the world.

1.5.2. The scientific method

The scientific method is widely used in the process of conducting science. Its general steps are to make observations, form a hypothesis to explain the patterns seen, perform experiments to test the hypothesis and then draw conclusions (Figure 1.1). Once a hypothesis has been confirmed by the scientific method in a variety of settings, in may become a scientific theory. A scientific theory is a well-substantiated explanation of some aspect of the natural world that is acquired through the scientific method, and repeatedly confirmed through observation and experimentation. For example, the theory of evolution through natural selection, first proposed in 1859, has been tested for ~150 years and has a lot of evidence to support it. By comparison, Edward Forbes ideas about how deep life can live was a hypothesis, which observations proved wrong.

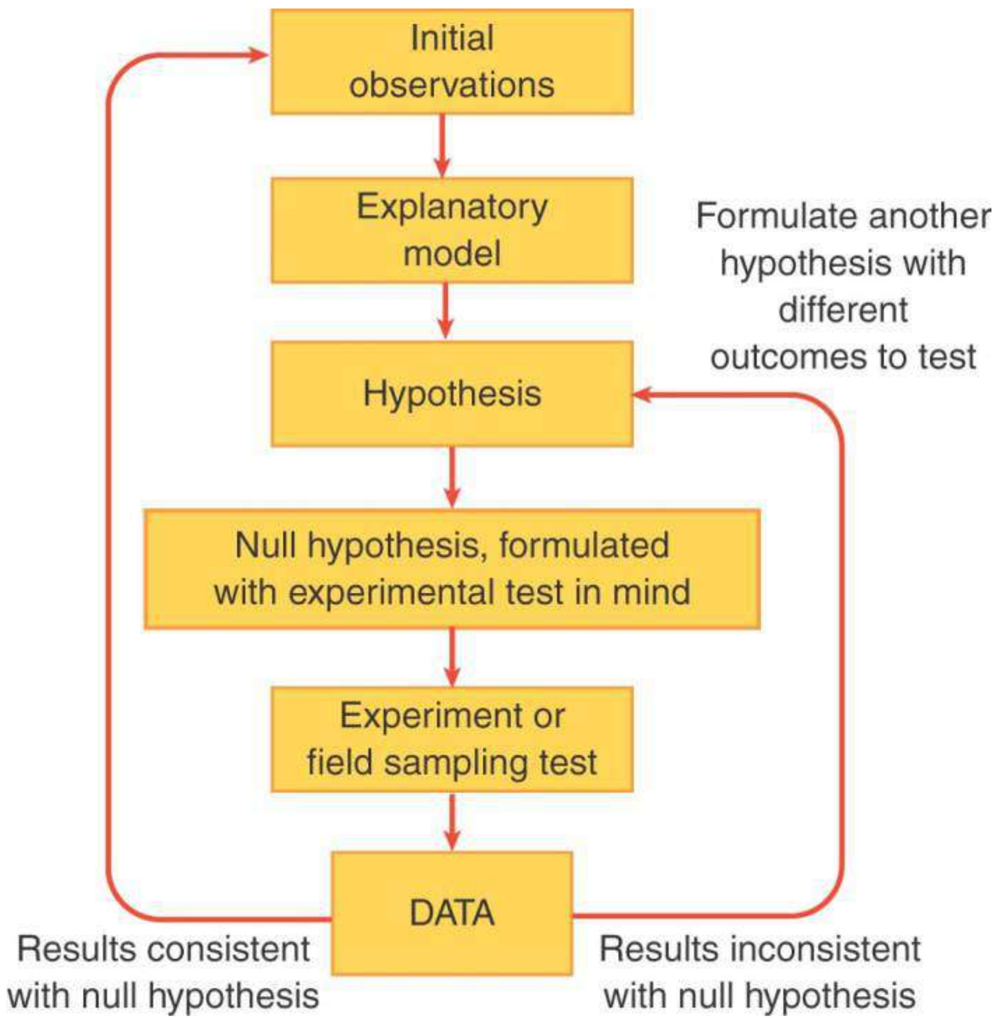


Figure 1.1. Steps of the scientific methods

1.6. Review Questions: Introduction to Marine Biology

1. What percentage of the earth is covered with oceans?

2. What was the driving force behind the initial studies into oceanography?

3. Who was the scientist on board the HMS Beagle in 1831?

4. What theories did this scientist develop?

5. In the early 19^{th} century who proposed that no life could live in the deep ocean?

6. Who was the chief scientist on board the HMS Challenger in 1872-76?

7. What theories did Alexander Agassiz develop?

8. Why study marine biology? give three reasons

9. Explain the process of the scientific method

10. Can scientific hypotheses ever be tested when controlled experiments are not possible? If so, how?

2. Fundamentals of Ecology (Karleskint Chapter 2)

2.1 Study of Ecology

Ecology (from Greek *Oikos* meaning home) is the study of interactions of organisms with each other and with their environment.

Ecosystems are composed of living organisms and their non-living environment; while the biosphere includes all of the earth's ecosystems taken together.

The **environment** is all the external factors that act on an organism:

- physical (abiotic): temperature, salinity, pH, sunlight, currents, wave action and sediment
- biological (biotic): other living organisms and their interactions e.g. competition and reproduction.

The **habitat** is the specific place in the environment where the organism lives; e.g. rocky or sandy shore, mangrove, coral reefs. Different habitats have different chemical and physical properties that dictate which organisms can live there.

Niche: what an organism does in its environment – range of environmental and biological factors that affect its ability to survive and reproduce

- physical: force of waves, temperature, salinity, moisture (intertidal)
- biological: predator/prey relationships, parasitism, competition, organisms as shelter
- behavioral: feeding time, mating, social behavior, young bearing

2.2 Environmental Factors that Affect the Distribution of Marine Organisms

2.2.1 Maintaining Homeostasis

All organisms need to maintain a stable internal environment even though their external environment may be changing constantly. Factors such as internal temperature, salinity, waste products and water content all need to be regulated within a relatively narrow range if the organism is to survive. This regulation of the internal environment by an organism is called homeostasis. The ability to maintain homeostasis limits the environments where an organism can survive and reproduce. Each species has an optimal range for each environmental factor that affects it. Outside of this optimum, zones of stress exist, where the organism can still survive but the added metabolic demands of regulating homeostasis can lead to costs such as failure to reproduce. At even more extreme environmental conditions lie zones of intolerance, where the organism cannot survive at all (Figure 2.1).

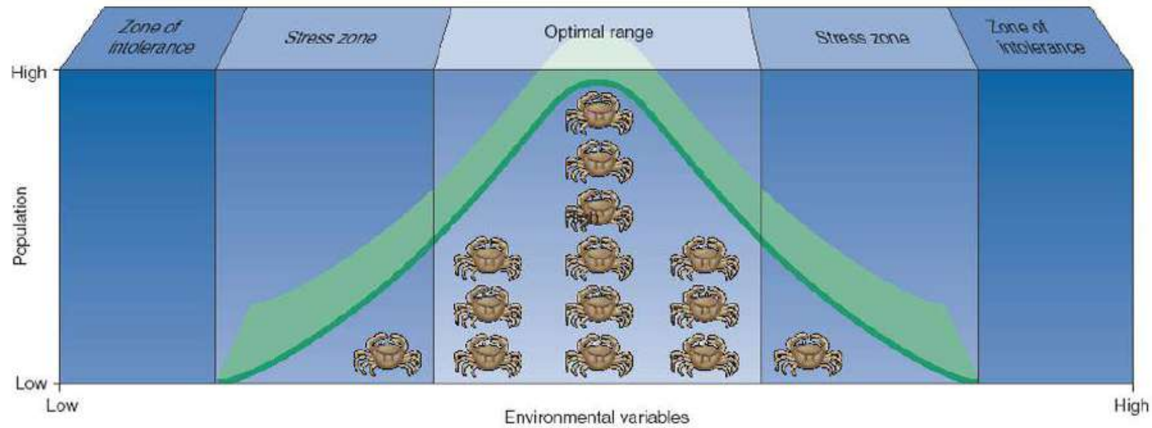


Figure 2.1. Optimal range of conditions for organisms.

2.2.2 Physical Environment

Sunlight

Sunlight plays an essential role in the marine environment. Photosynthetic organisms are the base of nearly every food web in the ocean and they are dependent upon sunlight to provide the energy needed to produce organic molecules. Light is also necessary for vision as many organisms rely on this to capture prey, avoid predation, communicate and for species recognition in reproduction. Excessive sunlight can however be detrimental to some life forms, as it may increase desiccation in intertidal areas and induce photo-inhibition through pigment damage to photosynthetic organisms in the very top of the water column.

Temperature

Most marine organisms are ectotherms (meaning that they rely on environmental heat sources) and as such are increasingly active in warmer temperatures. Marine mammals and birds on the other hand are endotherms and obtain heat from their metabolism. To keep this heat, they often have anatomical adaptations such as insulation with blubber, hair or feathers. The temperature of shallow subtidal and intertidal areas may be constantly changing and organisms living in these environments need to be able to adapt to these changes. Conversely, in the open oceans and deep-sea, temperature may remain relatively constant so organisms do not need to be as adaptable.

Salinity

Salinity is the measure of the concentration of dissolved inorganic salts in the water column and is measured in parts per thousand (‰). Organisms must maintain a proper balance of water and salts within their tissues. Semi-permeable membranes allow water but not solutes to move across in a process called osmosis (figure 2.2). If too much water is lost from body cells, organisms become dehydrated and may die. Some organisms cannot regulate their internal salt balance and have the same salinity as their external environment; these are termed osmoconformers. These organisms are most common in the open ocean, which has a relatively stable salinity. In coastal areas where the salinity may change considerably, osmoregulators are more common.

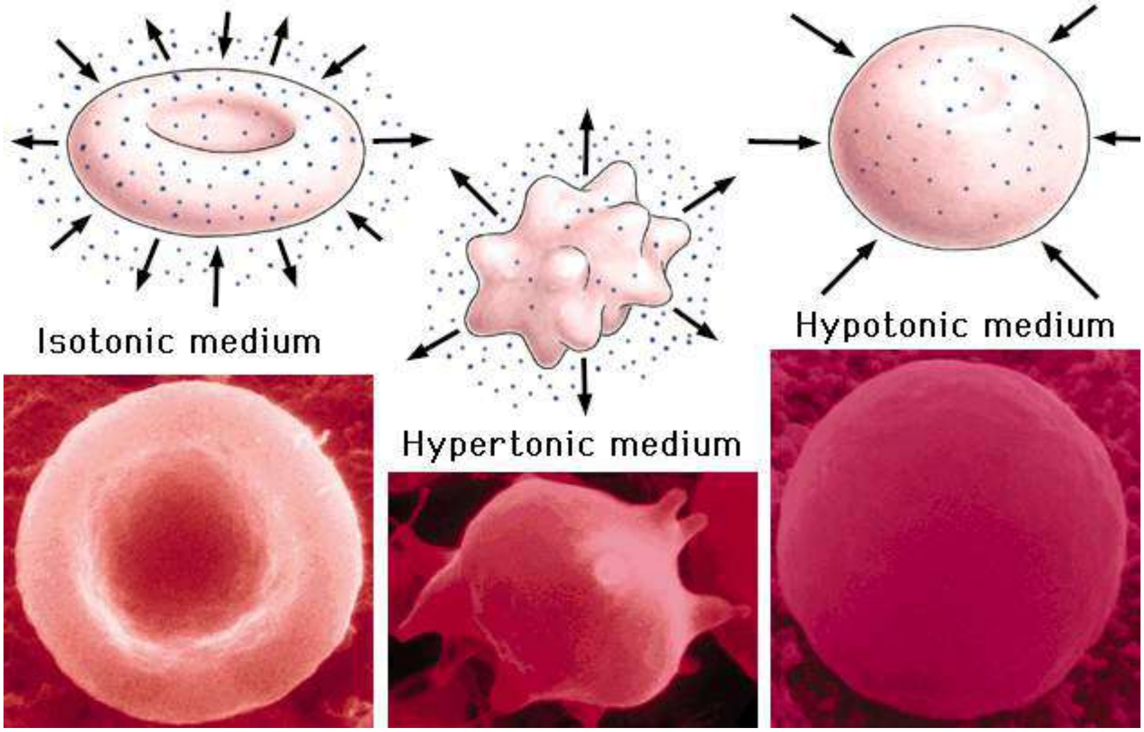


Figure 2.2. Osmosis. When a semi-permeable membrane allows water to cross but not solutes, water tends to move from to the area of higher solute concentration (in a way to even out the concentrations). When a red blood cell is in an isotonic medium (solute concentration inside the cell and in the medium are the same), it has a normal shape (left). When the same cell is places in a hypertonic solution (one that has a higher solute concentration than the cell), it loses water to the solution and shrivels (middle). When it is placed in a hypotonic solution (right), water moves inside the cell, causing it to swell and maybe even burst.

Pressure
At sea level, pressure is 1 atm. Water is much denser than air and for every 10 meters descent below sea level the pressure increases by 1 atm. Thus the pressure at 4,000 m is 401 atm and in the deepest part of the oceans at nearly 11,000 m the pressure will be about 1,101 atm. The pressure of the water affects organisms both live at these depths. Organisms found in the deep oceans require adaptations to allow them to survive at great pressures.

Metabolic Requirements
Organisms need a variety of organic and inorganic materials to metabolize, grow and reproduce. The chemical composition of salt water provides several of the nutrients required by marine organisms. Nitrogen and phosphorous are required by all photosynthesizing plants or plant-like organisms. Other minerals such as calcium are essential for the synthesis of mollusk shells and coral skeletons. Although nutrients are

essential for life, excessively high levels of nutrients in sea water can cause eutrophication. This process of nutrient enrichment can lead to vast algal blooms which eventually die and start to decompose. The decomposition may deplete the availably dissolved oxygen in the water, killing fish and other organisms.

2.3 Populations and Ecology

Population: a group of organisms of the same species that occupies a specific area and interbreed. Different populations are separated from each other by barriers that prevent organisms from breeding.

Biological community: populations of different species that occupy one habitat at the same time. The species that make up a community are linked in some way through competition, predator/prey relationships and symbiosis.

2.3.1 Population size

Since biologists can't count every single individual in a population, they must instead estimate its size by sampling. One common way to sample a population is to count all individuals within a few representative areas, and then extrapolate to the total number of individuals that are likely to be in the entire range. Of course, this method only works well if the samples are representative of the overall density of the population; if you happen to sample areas of exceptionally high density, you would overestimate population size. Another common method to estimate population size for mobile animals is the mark-recapture method. In this process, a certain number of individuals are captured and tagged, then released back and allowed to mingle with the rest of the population. After a certain period, a second sample is taken. As long as the marked individuals are dispersed well within the population and have not suffered increased mortality from the first capture, the ratio of marked:unmarked individuals in the 2nd capture should reflect the ratio of marked:unmarked individuals in the entire population (Figure 2.3). Therefore we can estimate population size with the following formula:

$$\frac{\mathbf{M}}{N} = \frac{m}{R}$$

where:

N=Population size
M=Number of animals captured and marked in first sample
R=Number of animals captured in resampling event
m=Number of "R" that were already marked

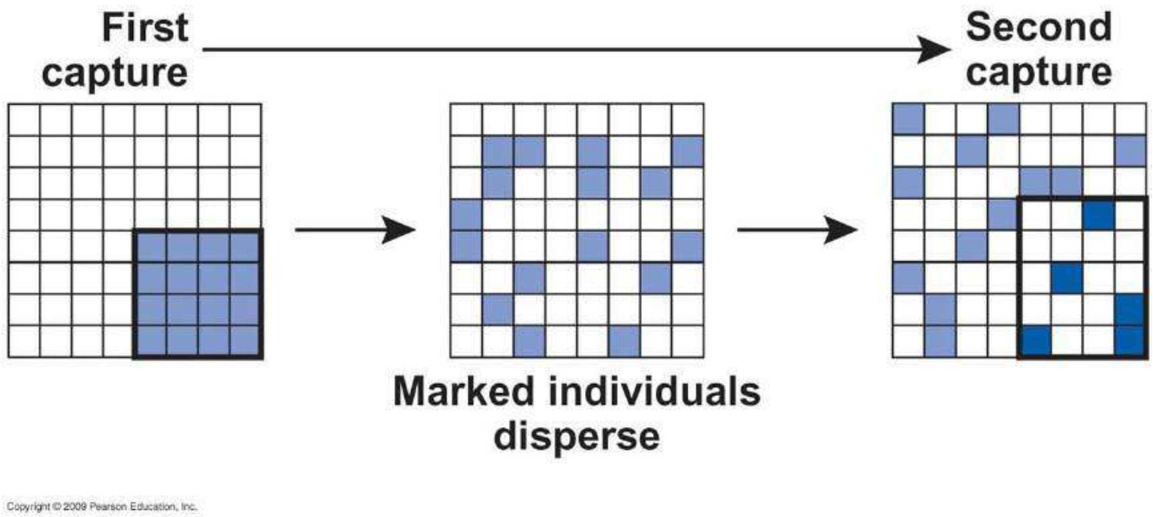


Figure 2.3. Principle of the mark-recapture method of estimating population size.

2.3.2 Distribution of organisms in a population

Population density refers to the number of individuals per unit area or volume. In many populations, individuals are not distributed evenly and the dispersion (pattern of spacing among individuals) can tell a lot about the spacing of resources and interactions between individuals. A clumped dispersion pattern may reflect variations in the physical environment, or a clumped food source; a uniform distribution (equal spacing between individuals) is often the result of strong intra-specific competition; random dispersion typically reflects weak interactions among individuals (Figure 2.4).

2.3.3 Changes in population size

Populations change in size over time. They acquire new individuals through immigration and births, and lose individuals through emigration and deaths (figure 2.5). Different species can have varying reproductive outputs, life span and generation times, all of which can affect how quickly populations of that species can grow. Collectively, these traits and others that impact births, deaths and reproduction are referred to as life history traits. On each extreme of a continuum of life history strategies are r-selected species (those that have short generation times, high reproductive potential) and K-selected species (those that have much longer generation time and are long-lived, but have low reproductive outputs and low population growth potential). The typical traits of r- and K-selected species are outlined in table 56.2.

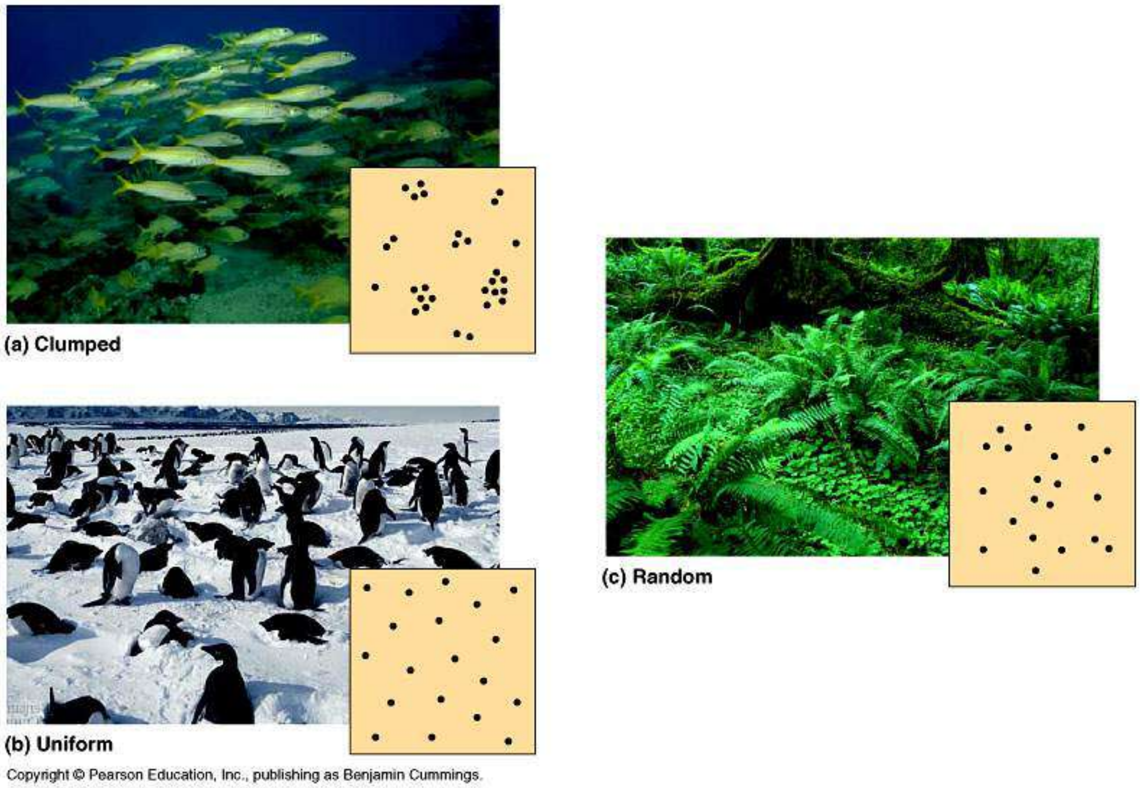


Figure 2.4. Patterns of dispersion in terrestrial organisms. Similar patterns can be recognized in the marine environment.

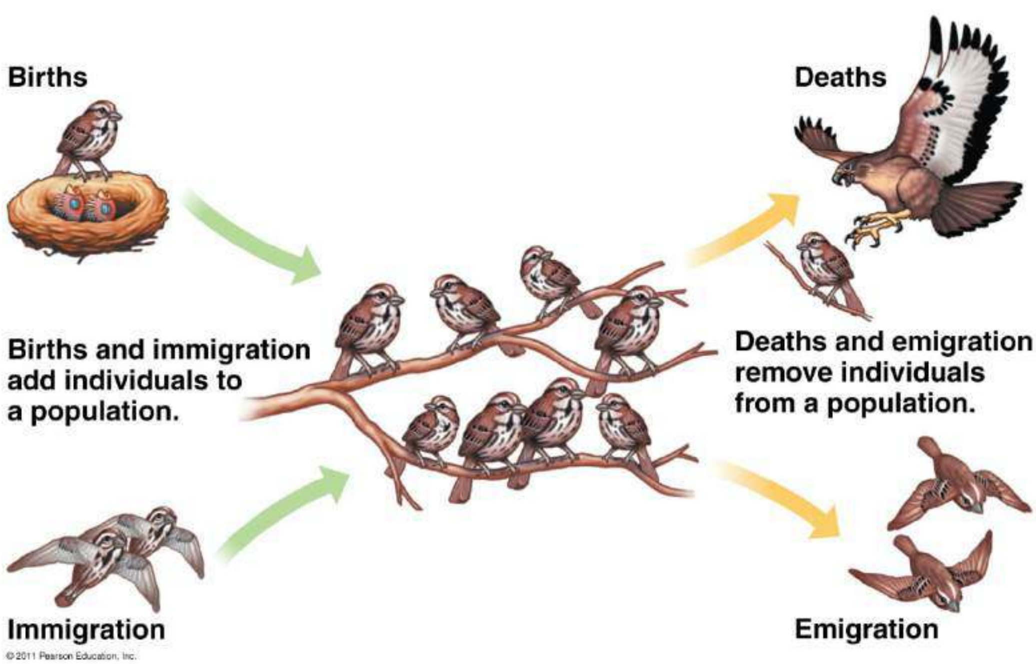


Figure 2.5. Populations change in size due to births, deaths, immigration and emigration.

Table 56.2 Characteristics of *r*- and *K*-Selected Species

Life history feature	*r*-selected species	*K*-selected species
Development	Rapid	Slow
Reproductive rate	High	Low
Reproductive age	Early	Late
Body size	Small	Large
Length of life	Short	Long
Competitive ability	Weak	Strong
Survivorship	High mortality of young	Low mortality of young
Population size	Variable	Fairly constant
Dispersal ability	Good	Poor
Habitat type	Disturbed	Not disturbed
Parental care	Low	High

2.3.4 Population growth

There are many ways in which a population can increase in size, including reproduction and immigration. When a population has sufficient food or nutrients and is not greatly affected by predation, it can grow rapidly in an exponential curve (figure 2.6). However, no population can maintain this growth forever—at some point resources become limiting and slow down population growth (either through lower birth rate or increased death rate). That population growth model is called logistic growth (figure 2.6). Here, the population levels off at size which the environment can sustain, known as the carrying capacity of the environment. The carrying capacity is a dynamic point which may fluctuate with changes in resource availability and predator behavior. Predator abundance often mirrors prey abundance with somewhat of a lag in time.

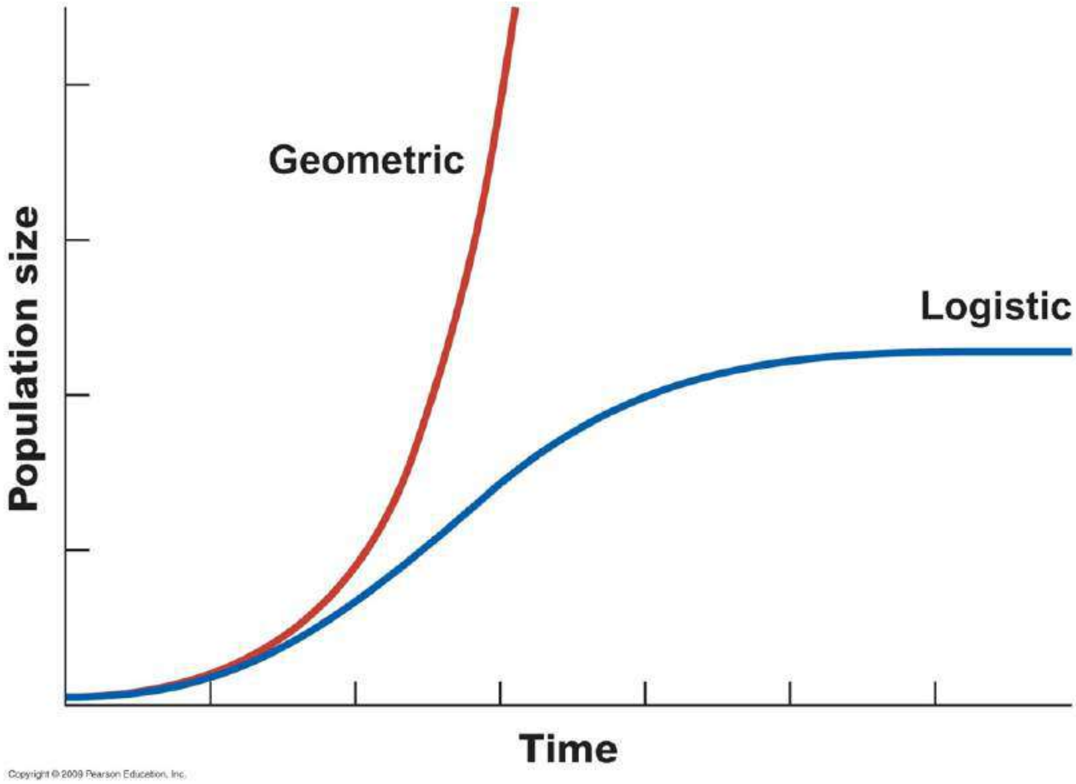


Figure 2.6. Geometric (or exponential) and logistic growth curves.

2.4. Communities

A biological community comprises the various populations of different species that interact together in the same place at the same time. Organisms in a community interact with one another in a variety of ways.

2.4.1 Niche

The niche of an organism is often described as its role in the community. It refers to the environmental conditions and resources that define the requirements of an organism. The broadest niche that an organism can occupy (defined mostly by resource availability and tolerance to abiotic factors, e.g. pH, salinity) is called its fundamental niche. In reality, organisms often occupy a smaller subset of their fundamental niche because of biological interactions with other species such as competition and predation. This subset is called the realized niche (Figure 2.7).

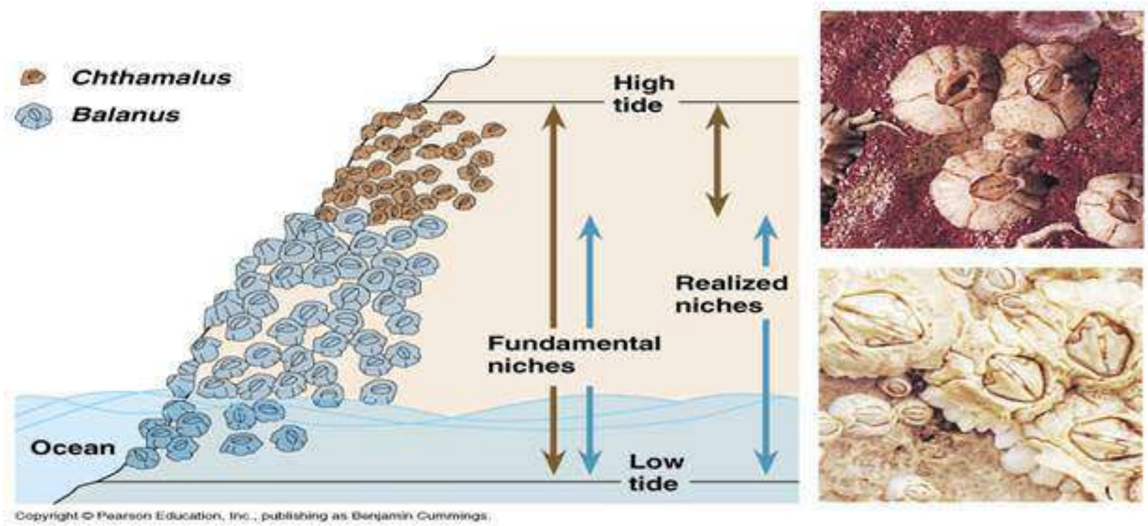


Figure 2.7. Realized vs fundamental niche in for two species of barnacles in the intertidal zone of Scotland. Temperature and moisture tolerance affect the fundamental niche of each species; e.g. the range of the intertidal zone that it can occupy. The realized niche is quite different from the fundamental niche for *Chthalamus*. While it could occupy a wide range of the intertidal zone, it is outcompeted by *Balanus* in the lower intertidal and therefore is restricted to the upper intertidal (realized niche)

2.4.2. Biological Interactions

Competition – occurs when organisms require the same limiting resources such as food, space or mates. Interspecific competition occurs between organisms of different species whereas intraspecific competition is between organisms of the same species. Interspecific competition for resources prevents different species from occupying exactly the same niche; if two species have the exact same requirements, one will outcompete the other with several possible results: local extinction (also known as competitive exclusion), displacement of the less successful competitor, or selection for traits that would lessen the competition.

To efficiently take advantage of a common resource, organisms may have unique anatomical and behavioral specializations. This is commonly seen on coral reefs. For example, fairy basslets, brown chromis and soldierfish are all plankton feeders, but they do not directly compete with each other. Fairy basslets feed close to the reef, chromis feed in the water column and soldierfish feed mainly at night. Another strategy to lessen competition is to take advantage of a resource not in demand by other species, e.g. angelfish are one of the only reef fishes that eat sponges.

Predator-Prey Relationship – may have a large influence on the abundance of different trophic levels, in either bottom-up or top-down control. In ecosystems controlled by bottom-up processes, the abundance or diversity of members of higher trophic levels is dependent upon the availability or quality of resources from lower levels. For example, if the amount of algae produced is the limiting factor that determines the amount of herbivorous fishes produced, which in turn determines the amount of piscivorous fishes the ecosystem will support. In other cases, the abundance of lower trophic levels is dependent upon the actions of consumers from higher trophic levels. This is called top-down control. For example, if a population predators becomes large and consumes many of herbivores, then the vegetation of the area may thrive. This process, where a change at one trophic level has an alternating effect at two or more trophic levels below, is known as a trophic cascade.

A **keystone species** is an organism whose effect on the biological diversity of an area is disproportionate to its abundance. For instance, the ochre sea star (*Pisaster ochraceus*) in the intertidal zone of western North America is a keystone predator and makes it possible for many other organisms to live through its predation mussels. Without the ochre sea star, the intertidal zone becomes dominated by mussels, which outcompete most other species.

Symbiosis – occurs when organisms develop close relationships to each other, to the extent that one frequently depends on the other for survival. There are three types of symbioses:

(a) Mutualism: both organisms benefit from the relationship; e.g. corals and zooxanthellae; clownfish and sea anemones
(b) Commensalism: one organism benefits while the other is not harmed but doesn't benefit; e.g. remoras and sharks
(c) Parasitism: parasites live off a host, which is harmed; e.g. worms in digestive tract of a vertebrate.

2.5 Ecosystems

Ecosystems include the biological communities and their physical environment. Examples of ecosystems include coral reefs, mangroves, rocky shore, sandy beaches, estuaries, kelp forests or the open ocean. Since different ecosystems don't exist in complete isolation from one another, important interactions between different ecosystems often exist (e.g. many coral reef fishes spend their juvenile stages in nearby mangroves).

2.5.1 Producers (autotrophs)

Most producers obtain their energy from the sun or some form of energy-rich inorganic chemicals. The vast majority of primary producers photosynthesize using a pigment called chlorophyll, which absorbs the sun's energy and convert it into an organic molecule called glucose ($C_6H_{12}O_6$; Figure 2.8). Other autotrophs may be chemosynthetic, utilizing the energy from chemical reactions to produce organic compounds. The glucose produced by autotrophs may be used by the organism for its own metabolic needs or is available for higher trophic levels.

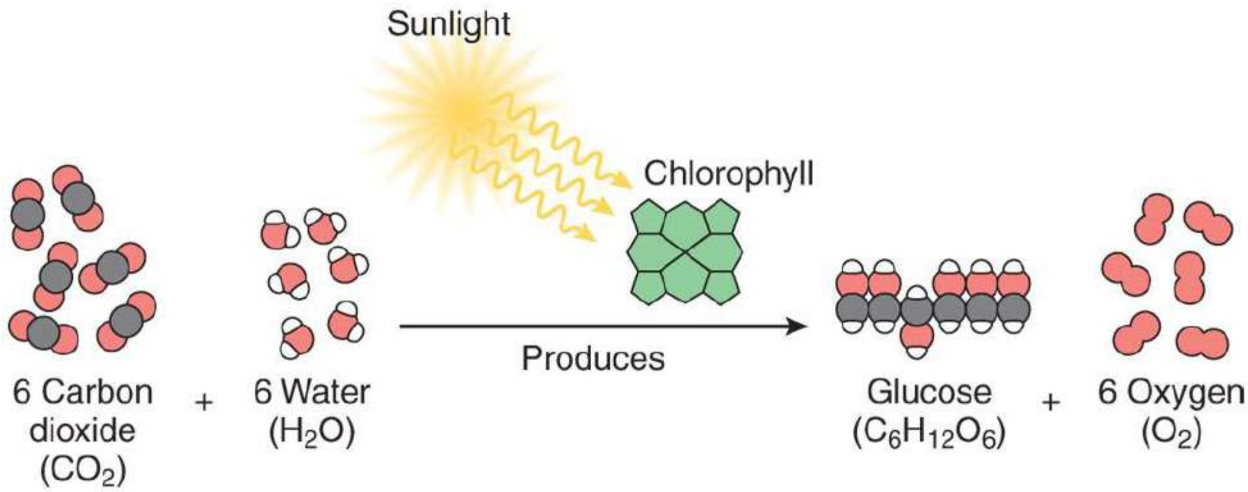


Figure 2.8. The process of photosynthesis, in which carbon dioxide and water are combined to form organic molecules and oxygen, in the presence of sunlight.

2.5.2 Consumers (heterotrophs)

Organisms that rely on other organisms for food are collectively known as heterotrophs. Primary consumers are herbivores, feeding on plants. Secondary consumers are carnivores feeding on the herbivores. Tertiary consumers then feed on the secondary consumers and so on until the top carnivores at the top of the food chain. There are also omnivores which feed on both producers and consumers and decomposers which feed on all organic matter breaking it back down to simple molecules.

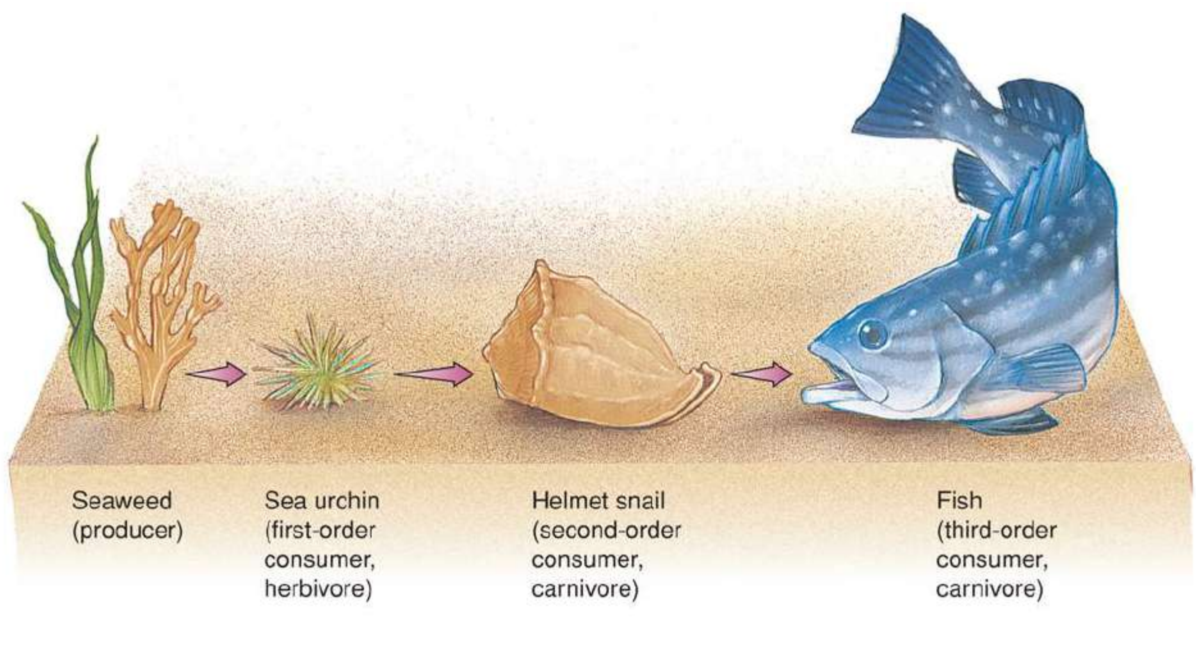


Figure 2.9. A food chain, representing a primary producer and the successive consumers.

2.5.3 Food chains and food webs

Food chains are simple, linear representations of the feeding relationships in an ecosystem. They show one organism feeding on one prey whilst being eaten by a predator (Figure 2.9). In reality these interactions may be much more complex with one organism feeding on several prey at different trophic levels whilst having several potential predators. These more complex (and more realistic) relationships are called a food web (Figure 2.10).

2.5.4 Other energy pathways

Not all energy pathways in the marine environment involve one organism feeding on another. Through several inefficient feeding and metabolic mechanisms, organic matter is released into the marine environment in the form of Dissolved Organic Matter (DOM). These energy-rich organic molecules can be incorporated by bacteria and other small plankton which in turn are eaten by larger organisms. This will be revisited in the chapter on the open ocean, where this energy pathway is an important element of food webs. In this way DOM, which would otherwise be lost to the environment, is funneled back into the food web. Detritus from feces and decaying plants and animals is also an extremely important food source for organisms in the marine environment. Detritivores feed on this detritus returning energy back into the food chains.

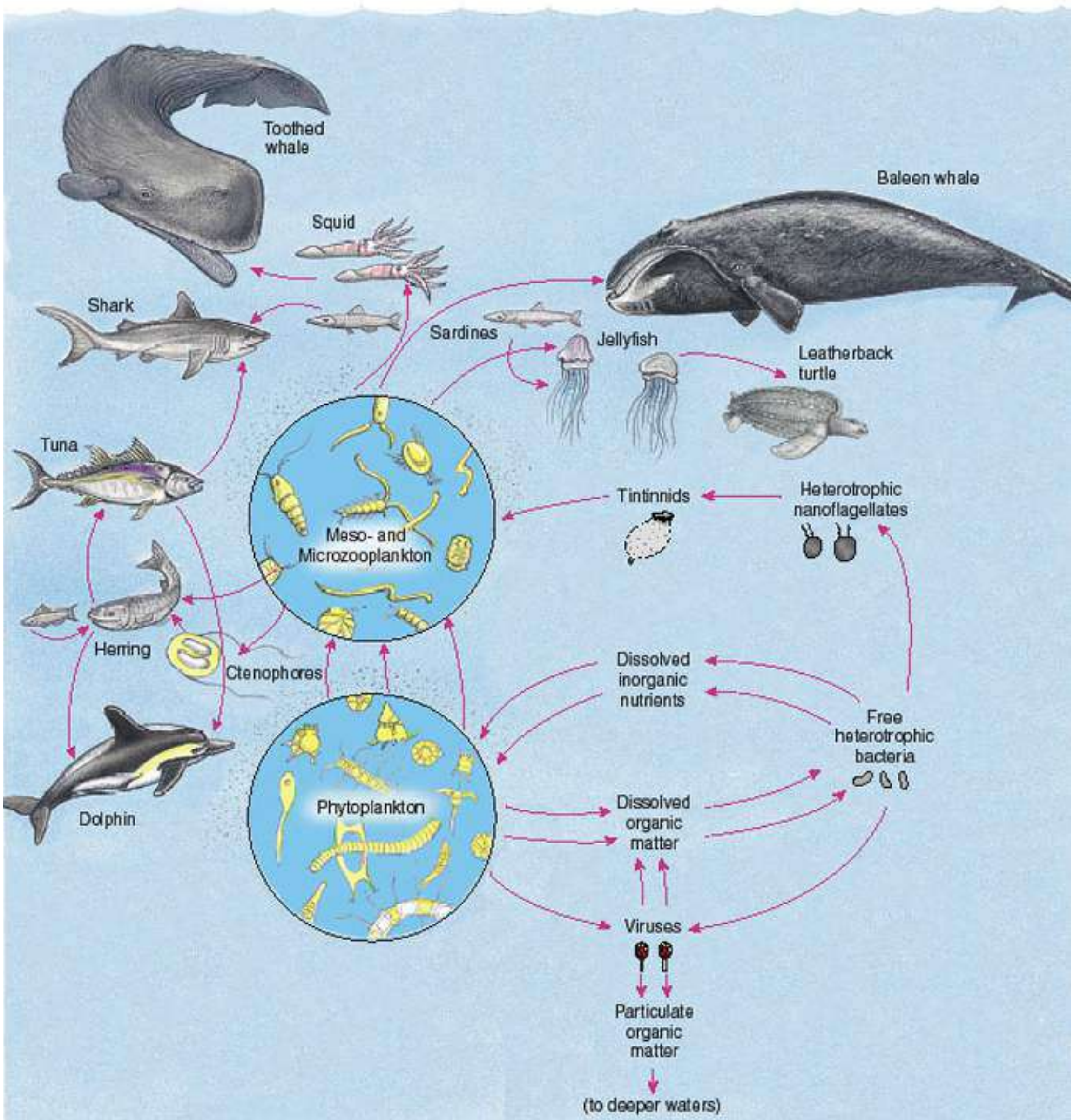


Figure 2.10. A food web is a more realistic representation of trophic interactions in ecosystems. Many organisms have multiple food sources which may be at different trophic levels. This highly simplified food web also shows dissolved organic matter being taken up by bacteria and re-channeled back into the food web.

2.5.5 Trophic levels

Energy flows from the sun through producers to higher orders of consumers. Energy received from photosynthesis, or from food, is temporarily stored as organic matter until the organism is eaten or dies and is decomposed. Thus energy storage in an organism can be portrayed as a trophic level. Primary producers represent the first trophic level; primary consumers the 2nd, secondary consumer the 3rd, and so on. Energy transfer between trophic levels is inefficient; primary producers capture and store less than 1% of the sun's energy. From there an average of only 10% of the energy is passed on to successive higher trophic levels while the rest is used for movement, feeding, metabolism, reproduction, etc. (Figure 2.11).

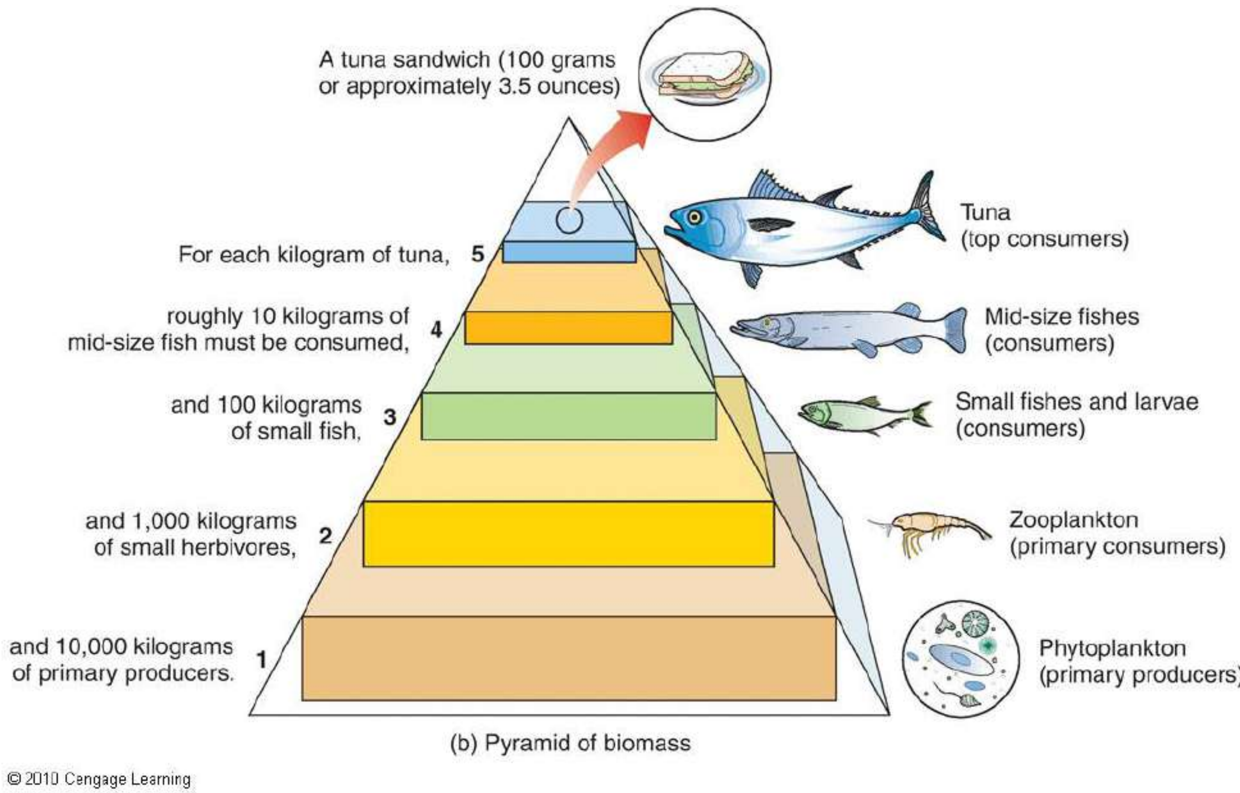


Figure 2.11. An energy pyramid, representing the amount of energy or biomass at each trophic level.

2.6. The Biosphere

2.6.1. Distribution of Marine Communities

Marine communities and ecosystems can be designated by the regions of the oceans which they inhabit (Figure 2.12) and in the 2nd part of this class we will review these various ecosystems. In the water column, known as the pelagic zone, the area of water overlying the continental shelf is known as the neritic zone whereas the area above deep ocean basins is known as the oceanic zone. The organisms that inhabit the pelagic division exhibit one of two different lifestyles. Plankton drift with the currents whereas nekton are active swimmers that can move against the currents. The benthic realm can be broadly divided into the intertidal area, the continental shelf and the deep. Organisms in the benthic division are either epifauna, organisms that live on the sediment or infauna, organisms that live within the sediment.

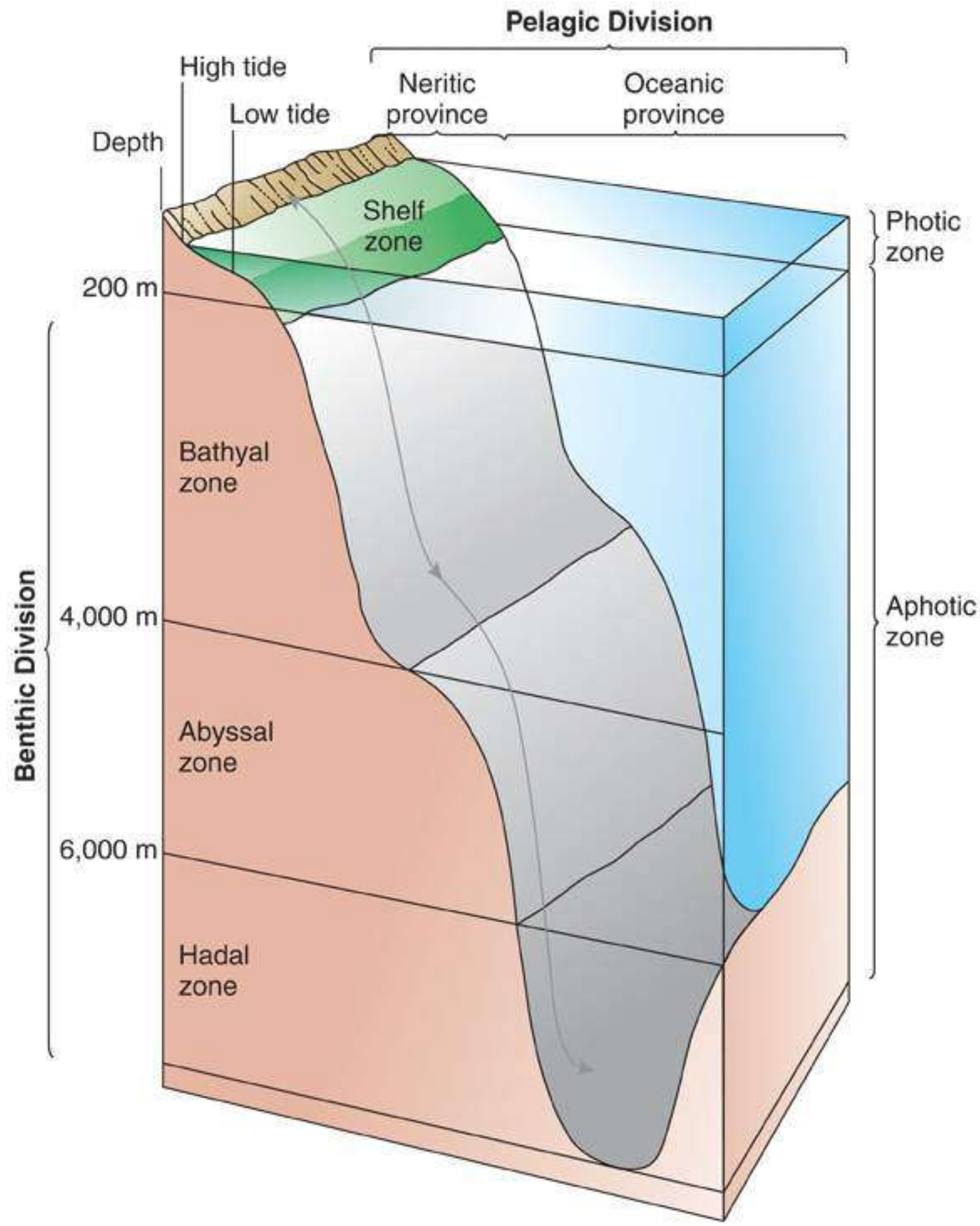


Figure 2.12. Various regions of the ocean.

2.6. Review Questions: Fundamentals of Ecology

1. Define the term ecology.
2. Define the term ecosystems.
3. Give an example of abiotic factors affecting marine organisms.
4. Give an example of biotic factors affecting marine organisms.
5. Define the term habitat.
6. Define the term niche.
7. Define the term homeostasis.
8. What is an ectotherm/poikilotherm?
9. What is an endotherm/homeotherm?
10. What is the difference between interspecific and intraspecific competition?
11. What is resource partitioning? Give an example on a coral reef?
12. Define a keystone predator and give an example of one?
13. Name and describe the three types of symbiotic relationships.
14. What is osmosis?
15. What are osmoconformers?
16. In which type of symbiotic relationship does one organism benefit and the other is not harmed in any way but does not benefit?
17. Define the term population?
18. What is the carrying capacity of a population?
19. What does the term neritic refer to?
20. What is plankton?
21. What does benthic refer to?
22. What does pelagic refer to?

23. What is the difference between epifauna and infauna?

24. What is an autotroph?

25. What is the equation for photosynthesis?

26. What is the primary energy source for autotrophs?

27. What inorganic nutrients do photosynthetic organisms require?

28. How do chemosynthetic organisms generate energy?

29. What do detritivores feed on?

30. What is the average percent of energy passed from one trophic level to another in a food chain? What is the rest used for?

31. What is a realized niche and how does it compare to the fundamental niche of an organism?

32. What is an r-selected species? Give an example of an r-selected marine animal.

33. Explain how marine fishes maintain an internal salinity that is lower than their environment.

3. Biological Concepts (Karleskint Chapter 5)

All living organisms are composed of cells, which are the basic units of life. Cells contain all the chemical compounds necessary to support life and to pass on their genetic information. The activities of all organisms are ultimately geared towards their survival and reproduction. Those that are best at surviving will pass the most copies of their genetic information onto the next generation.

3.1 Building blocks of life: macromolecules

Living organisms are composed of chemical compounds which make up their cells. To understand the basis behind the biology of living cells one must understand these macromolecules.

3.1.1 Carbohydrates (Carbon water – C, H, O)

Carbohydrates have two major uses in organisms. Firstly they can be used as energy (mono- and disaccharides), for example glucose, sucrose and starch, which are the basic fuel molecules for living cells. Their second function, performed by polysaccharides, is that of structure within cells. These long-chained structural carbohydrates may be found in plant cell walls (e.g. cellulose) or the exterior structures of some marine animals, such as crabs & lobsters (e.g. chitin).

3.1.2 Lipids

Fat, oils and waxes are all examples of lipids. Marine organisms use lipids to store energy, to cushion vital organs and to increase buoyancy. Phospholipids are a major component of cell membranes. Some homeothermic animals may also use lipids as insulation to trap heat in cold climates. Lipids also play a role in controlling reproduction, through chemical messengers called steroids, such as testosterone.

3.1.3 Proteins

Chains of amino acids assemble to form proteins. The complex structure of protein molecules allow them to serve several functions. They form the primary structural components of muscles and connective tissue in animals. They can also form enzymes, which are biological catalysts that speed up the rate of chemical reactions and are vital for life.

3.1.4 Nucleic acids

Nucleic acids assemble to form large molecules that function as genetic material (DNA) and in protein synthesis (RNA). DNA (deoxyribonucleic acid) forms a two strand double-helix shape which contains all the genetic material, or genes, of an organism, and is capable of replicating itself and passing these genes onto the next generation. RNA (ribonucleic acid) is made mostly of the same nucleic acids as DNA yet is composed of only a single strand. RNA functions in protein synthesis by copying the genes in DNA to produce new cell parts and enzymes.

3.2 Cells

All living organisms are composed of basic units, called cells, which are capable of all the basic processes of life: metabolism, growth and reproduction. Each cell is surrounded by a simple cell membrane, which separates the cytoplasm (cytosol (fluid) and organelles) from the external environment. Some cells, such as those of plants, fungi and bacteria, also have a cell wall which may give then protection and support.

3.2.1 Types of Cells

There are two major types of cells in nature; prokaryotic and eukaryotic. Prokaryotic cells lack a nucleus and do not have membrane-bound organelles. Organisms with prokaryotic cells are known as prokaryotes, and are always unicellular. Marine prokaryotes include marine bacteria and archaeons. Eukaryotic cells possess a well-defined nucleus and many membrane-bound organelles. Organisms made of eukaryotic cells are known as eukaryotes and can be either unicellular or multicellular. Marine eukaryotes include protists (e.g. algae & protozoans), plants, animals and fungi.

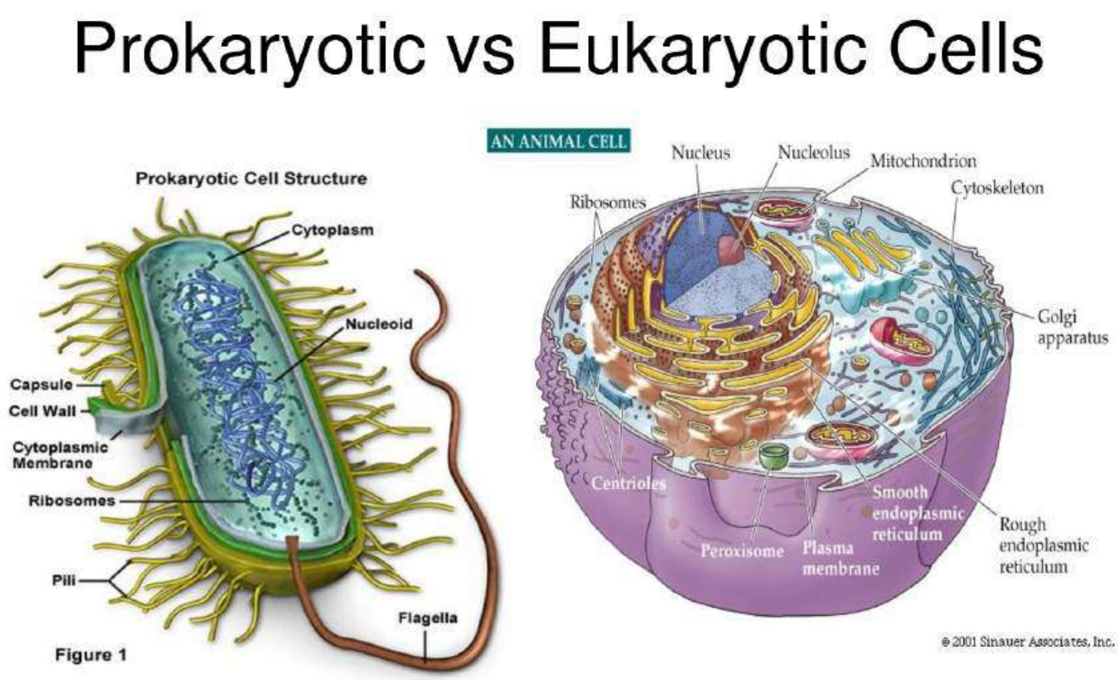


Figure 3.1. A prokaryotic cell is small and has no membrane-bound organelles. The genetic material is found in the nucleoid region, which is not separate from the rest of the cytosol. In contrast, a eukaryotic cell has multiple sub-cellular structures that are bound by membranes, such as the nucleus, mitochondria and (in photosynthetic organisms) chloroplasts. There is strong evidence that eukaryotic organelles originated from prokaryotic cells.

3.2.2 Organelles

Every organelle within a eukaryotic cell has a specific function within that cell. Examples of membrane-bound organelles include the nucleus, chloroplasts and mitochondria. The nucleus contains all the DNA and ribosomes within the cell and functions in protein synthesis. The chloroplasts and mitochondria both function in energy conversion. In photosynthetic organisms, chloroplasts are the site of photosynthesis, where energy from the sun is used to fix carbon in the following reaction:

$$6H_2O + 6CO_2 \longleftrightarrow C_6H_{12}O_6 + 6O_2$$

Photosynthesis occurs only during the daytime when there is sufficient light and releases oxygen (O_2) as a byproduct. Respiration occurs in the mitochondria where food molecules are broken down to release energy. Respiration, the reverse of the above equation, releases carbon dioxide (CO_2) as a byproduct and occurs both throughout the day and night.

Organelles that function in movement include flagella and cilia. Flagella are long, hair-like structures, of which a cell typically has 1, 2 or 3, and they are used in propulsion. Cilia are short hair-like structures, which can be numerous and cover large areas of the cell. Cilia can function in locomotion in unicellular organisms or to move things along the cell's surface in multicellular organisms.

3.2.3. Cellular division

Cells reproduce by cell division. In unicellular organisms, cellular division leads to population growth. In multicellular organisms, cellular division may lead to growth or reproduction.

Cell division in prokaryotes in relatively simple and is known as binary fission. In this process, the single circular chromosome replicates itself, then the cell divides so that each daughter cell receives one copy of the genetic information.

In eukaryotic cells, the nucleus divides through mitosis prior to cell division. In this process, all chromosomes are replicated and then separated, so that each daughter cell receives a completed set of chromosome.

3.2.4. Levels of organization

In multicellular organisms, cells of one type assemble together in a tissue; multiple tissues form organs, which work together in organ systems (Figure 3.2).

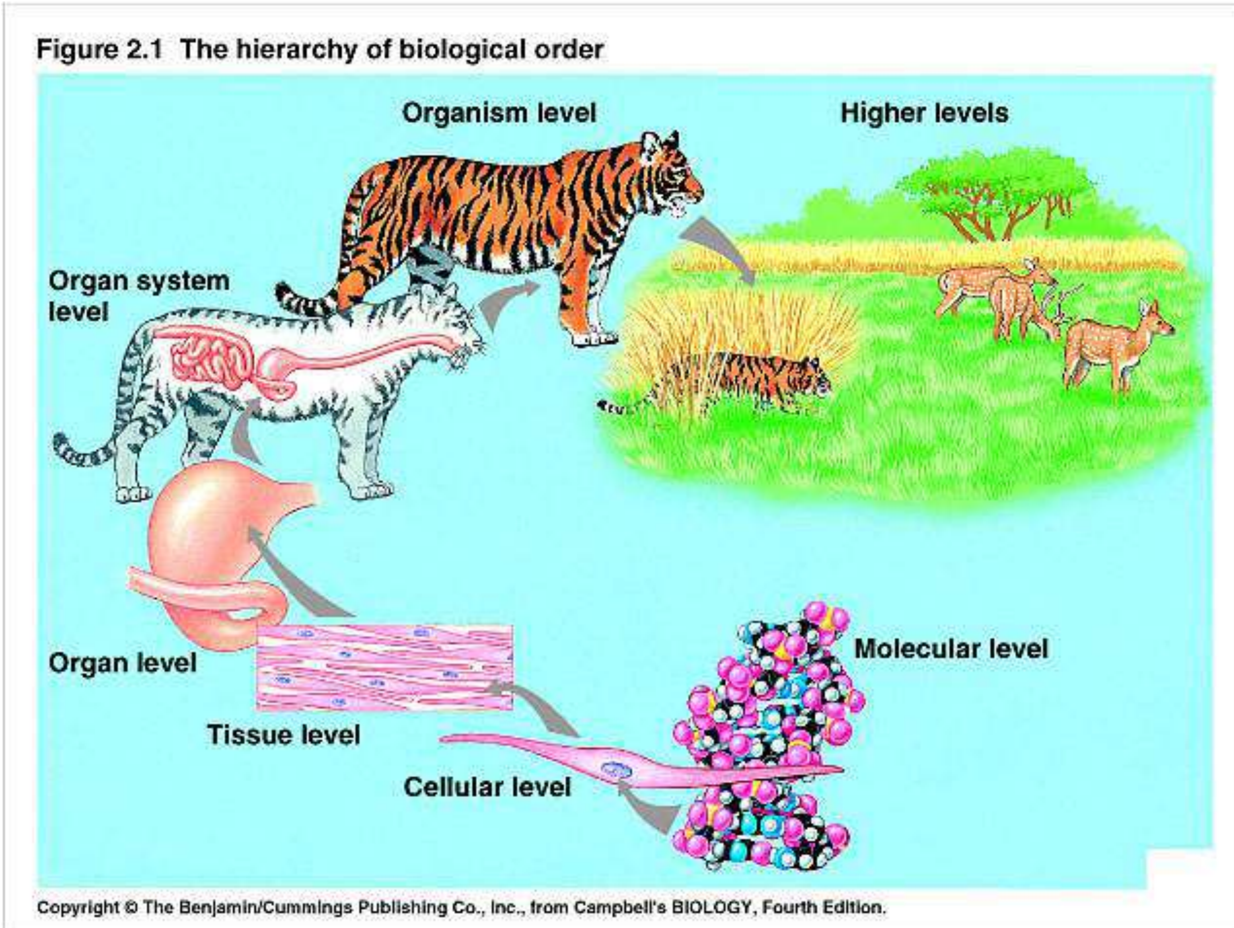


Figure 3.2. Levels of biological organization.

3.3. Evolution and natural selection

3.3.1 Darwin and the Theory of Evolution.

In 1831 Charles Darwin sailed aboard the *HMS Beagle* for a 5 year voyage around the world. He was already familiar with the process of artificial selection, selection being forced by human hands, for instance through practiced farmers breeding animals for a certain desired trait. Darwin suggested that a similar process may be happening in the wild through natural selection. Darwin receives most of the historical credit for formulating this theory, but another naturalist, Alfred Wallace, had independently formulated similar ideas around the same time. Darwin and Wallace's views were presented together in 1858 at the Linnaean society. A year later Darwin published his full ideas in his book "On the origin of species by means natural selection". In it, he postulated that those individuals which were best suited for their environment would have a higher survival and reproduction rate, therefore passing on more of their genes to the next generation.

Darwin's theory of evolution contains four premises:

i) All organisms produce more offspring than can survive to reproduce

ii) There is a great deal of variation in traits amongst individuals in natural populations and many of these traits are inherited.

iii) The amount of resources necessary for survival (e.g. food, light, living space) are limited and organisms must compete with each other for these resources.

iv) Those organisms that inherit traits that make them better adapted to their environment are more successful in the competition for resources. They are more likely to survive and produce more offspring. The offspring inherit their parent's traits, and they continue to reproduce, increasing the number of individuals in a population with the adaptations necessary for survival

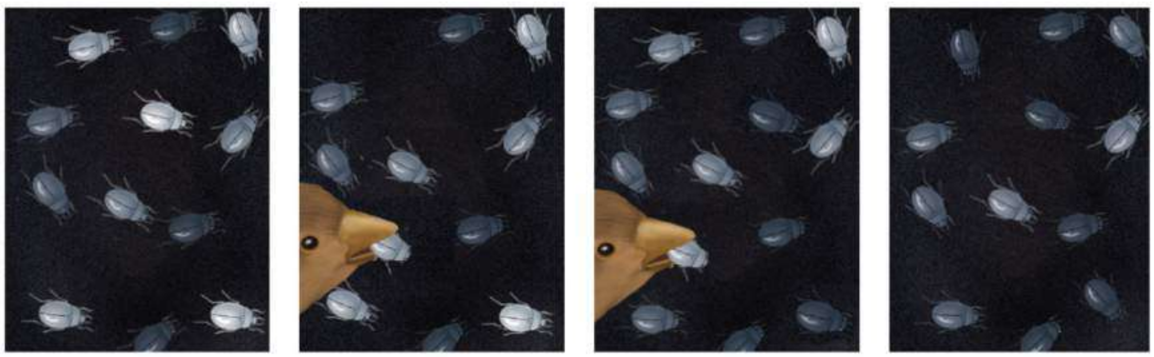


Figure 3.3. An example of natural selection. A population of beetles has natural variation in color. The lightest individuals are easier to see against the dark background and therefore caught at a higher rate by predators; dark individuals have a higher survival rate and higher reproduction rate than light individuals. After several generations, there is a greater proportion of dark individuals.

3.4. Genes and Natural Selection

Darwin's ideas were proposed before any of the basics of cell division and genes, that we understand today, had been discovered. The discovery of DNA has revolutionized biology and the development of molecular biology has expanded our understanding of the evolutionary process. Much of Darwin's initial hypotheses still hold true today but have been refined by the modern knowledge of genetics.

3.4.1. Modern evolutionary Theory

It is now known that the gene is the basic unit of hereditary information producing such traits as eye color or size of limbs in offspring. Genes are a sequence of DNA that code for a particular trait. They can be present in different forms, known as alleles. An individual has two alleles for each gene, one coming from each parent. There will be different combinations of alleles within a population which is shown as variations in that trait.

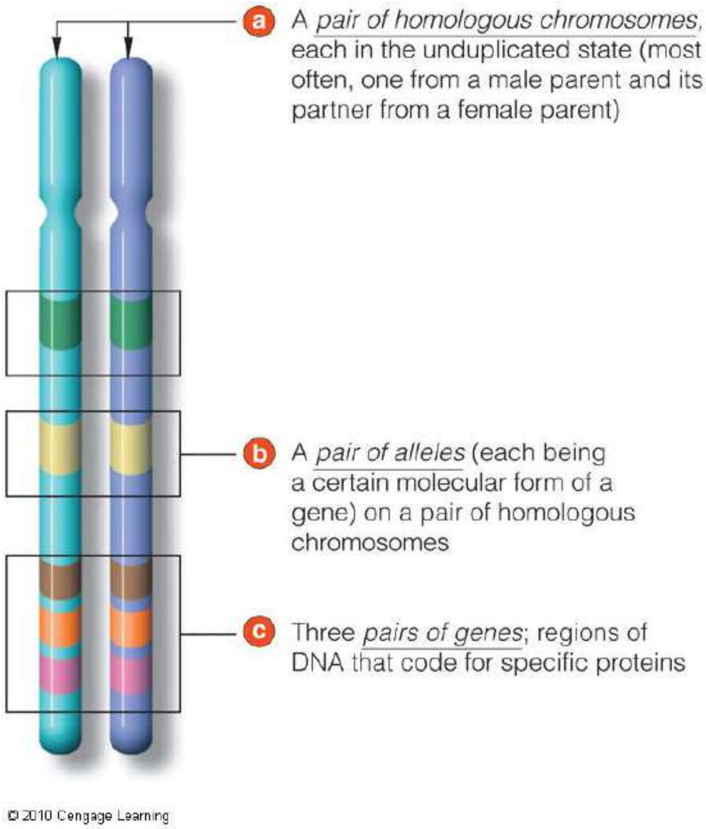


Figure 3.4. Genes are a segment of DNA that code for a particular proteins and therefore traits. Diploid organisms have two sets of genetic material on homologous chromosomes.

3.4.2. Role of Reproduction

Genes are transferred from one generation to the next when DNA is passed from parent to offspring through reproduction. Reproduction may be either asexual (one parent) or sexual (two parents). In asexual reproduction the offspring is identical to the parent; in effect a clone. There is no genetic variation within the population, except through chance mutations. Asexual may be common in organisms that live in stable environments where rapid reproduction is advantageous; asexual reproduction doesn't require finding a mate and every member of the population can reproduce. In sexual reproduction on the other hand, chromosomes from two parents are combined when gametes unite. This recombination of genes forms a genetically unique individual and therefore sexual reproduction leads to greater genetic variation than asexual reproduction. This genetic variation is an important factor allowing for natural selection.

3.4.3. Population Genetics

Environmental factors are constantly changing. Organisms which have the combination of traits that make them well-adapted to their environment are more likely to survive and reproduce, passing on their genetic material to their offspring. The biological success of an organism, called fitness, is a measure of the number of their genes present in the next generation.

3.5. Evolution of new species

3.5.1. Typological definition of species

The definition of a species has changed over time with our understanding of evolution and molecular biology. In the past a species has been defined by its morphology. This definition comes with difficulties however, because individuals of one species can look very different (e.g. through sexual dimorphism, or in species with a high level plastic variation) and conversely, in some cases two different species may appear to look identical.

3.5.2. Modern species definition and reproductive isolation

A species is now defined as "one or more populations of potentially interbreeding organisms that are reproductively isolated from other such groups". Some scientists also specify that individuals of one species can potentially interbreed *to produce viable and fertile offspring*. That is, groups of organisms that can mate but whose offspring dies before reproduction or is infertile are considered distinct species (e.g. horses and donkeys can mate to produce mules, which are themselves infertile. Horses and donkeys are therefore distinct species). Since the biological definition that relies on mating compatibility can be difficult to apply in practice (e.g. when organisms wouldn't normally encounter each other to mate, or in the case of asexual organisms), species are also often classified based on the degree of genetic differentiation between groups of organisms.

For a new species to arise from a previous species, a population must become reproductively isolated from other populations of the species. If enough time elapses and the selective pressures on various populations are different, they may each evolve independently to the point where the populations are so different that can no longer interbreed, and therefore are now distinct species. There are several different mechanisms by which reproductive isolation (and potentially new species) may arise. Habitat isolation occurs when different populations are found in different locations, thereby limiting gene flow. Anatomical isolation refers to differences in size or anatomy which prevents successful mating. Behavioral isolation includes differences in courtship behaviors which would prevent individuals from recognizing each other as potential mates. Temporal isolation occurs when members of different populations are active at different times of the day or year, and therefore reproduce at different times. In some cases, closely related species may succeed in mating but their gametes are incompatible (biochemical isolation), or they can have hybrid offspring which are infertile or weak. All these mechanisms are reproductive isolation contribute to the formation of new species and the maintenance of distinct species.

3.5.3. Process of speciation

Speciation refers to the formation of new species from previously existing ones. A common way in which new species arise is through habitat isolation, when two or more populations of the species become geographically isolated, perhaps through migration or geological change. There will be different selection pressures on these isolated groups of organisms and without gene flow between them, in time they may diverge enough to become distinct species. Sympatric speciation refers to the formation of new species without geographic isolation; it may happen through anatomical, behavioral, temporal or biochemical isolation between organisms.

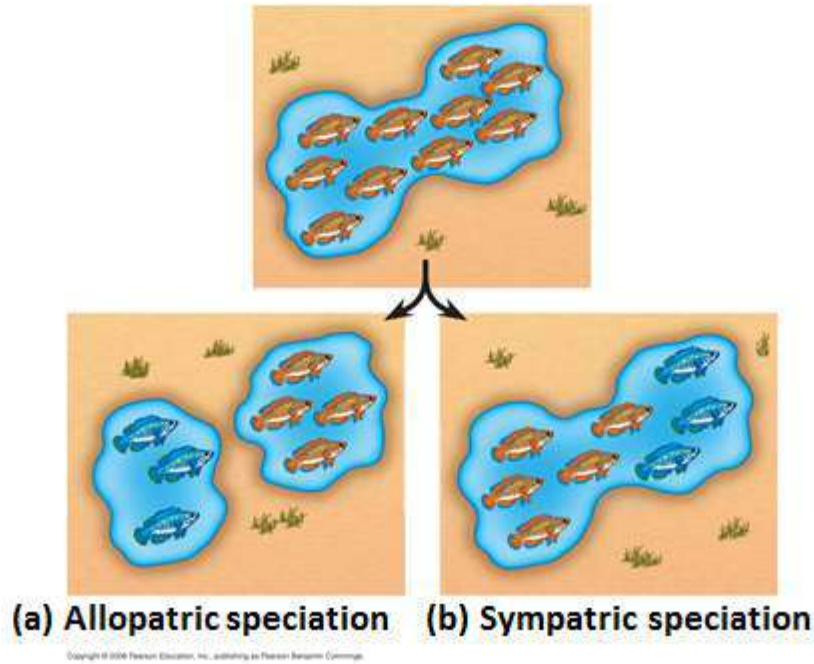


Figure 3.5. Speciation may occur with geographic isolation (allopatric speciation) or without (sympatric speciation).

3.6. Biological Classification

Taxonomy is the science that describes, classifies and names organisms based on evolutionary links between them. Scientists use a universal system of naming organisms which enables scientists all over the world to exchange information.

3.6.1. Binomial System of Naming

The basic system that modern biologists use for taxonomy is binomial nomenclature, and it was first introduced by Karl von Linné, (who later changed his name to Carolus Linnaeus), a Swedish botanist, in the mid-1700s. Linnaeus categorized organisms with two words, based on morphological characteristics. The first part identifies those that shared certain similar traits, which he grouped within the same genus. For instance, all butterfly fish belong to the same genus: *Chaetodon*. The second part of the name identifies those of a certain species for instance the long-nosed butterfly fish is called *Chaetodon longirostris*. Note that the first letter of the genus is always capitalized and both genus and species names are italicized. Linnaeus then categorized organisms into higher groups of orders and classes. Today, we use a very similar system of taxonomy except that classification relies strongly on molecular and genetic evidence as opposed to simple morphology.

3.6.2. Modern Taxonomic categories

The taxonomic categories used today include eight different major divisions. Listed from most inclusive to least inclusive these are Domain, Kingdom, Phylum, Class, Order, Family, Genus and Species.

Taxonomic group	Gray wolf found in	Number of species
Domain	Eukarya	~4–10 million
Supergroup	Opisthokonta	>1 million
Kingdom	Animalia	>1 million
Phylum	Chordata	~50,000
Class	Mammalia	~5,000
Order	Carnivora	~270
Family	Canidae	34
Genus	*Canis*	7
Species	*lupus*	1

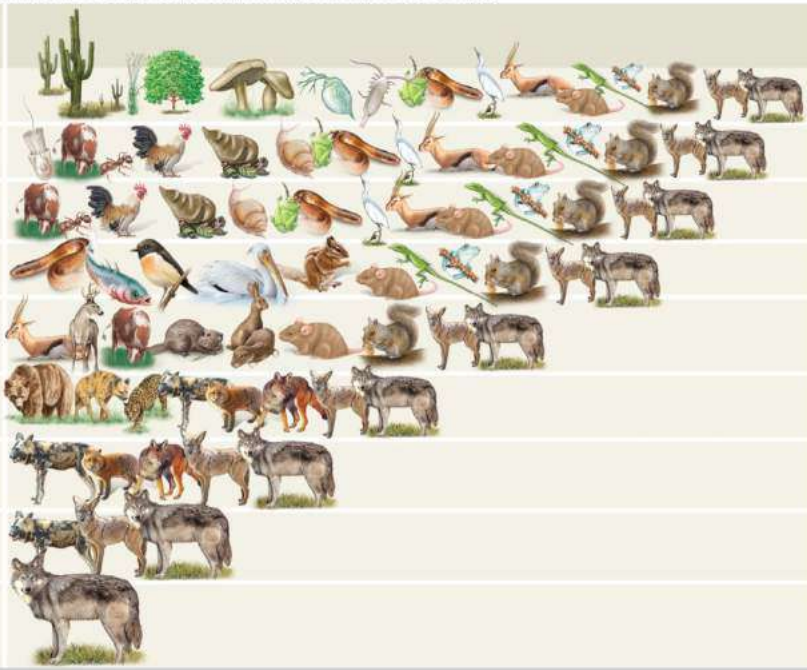


Figure 3.6. The taxonomic hierarchy for the grey wolf, *Canis lupus*, showing other species that are also included at various levels of classification.

There are three Domains: Archaea, Bacteria and Eukarya. Archaea and Bacteria both contain single-celled prokaryotic organisms but differ in many ways at the biochemical level; Eukarya include all eukaryotic organisms (Figure 3.7).

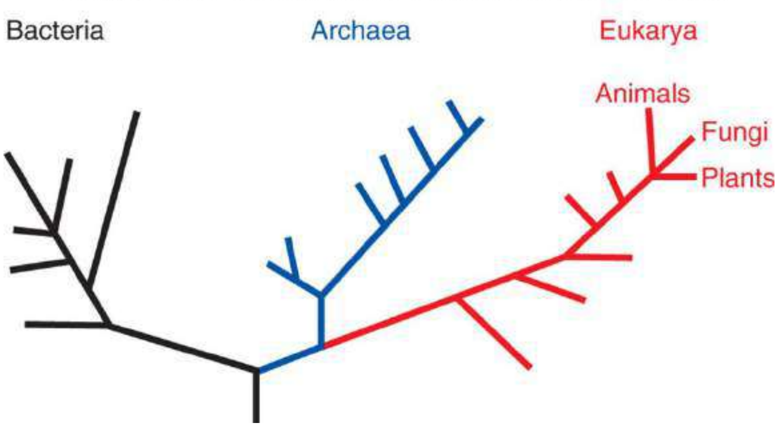


Figure 3.7. The three domains of life: Bacteria, Archaea and Eukarya.

The Eukarya may be broken down into four kingdoms. Three of them are well-defined and clearly related by common ancestry: Fungi, Plants, and Animals. The fourth kingdom, the Protists, includes various phyla that do not fit the definition of plants, animals or fungi (Figure 3.8).

i) Fungi are heterotrophic eukaryotic organisms that are not capable of photosynthesis. Their cell wall contains chitin and they can either be unicellular or multicellular. They are primarily decomposers but some may be parasites living off hosts.
ii) Plants (Plantae) are multicellular organisms capable of photosynthesis, which generally have specialized vessels that carry water and nutrients, and give structural support (xylem and phloem). Their cell walls typically contain cellulose.
iii) Animals (Animalia) are multicellular heterotrophs with cells that lack cell walls.
iv) Protists are eukaryotic organisms that don’t fit the definition of animal, plant or fungus. They include algae, protozoans and slime molds. They are are mostly unicellular but can also be multicellular (e.g. seaweeds). They can be autotrophs, heterotrophs, decomposers, or a combination of all.

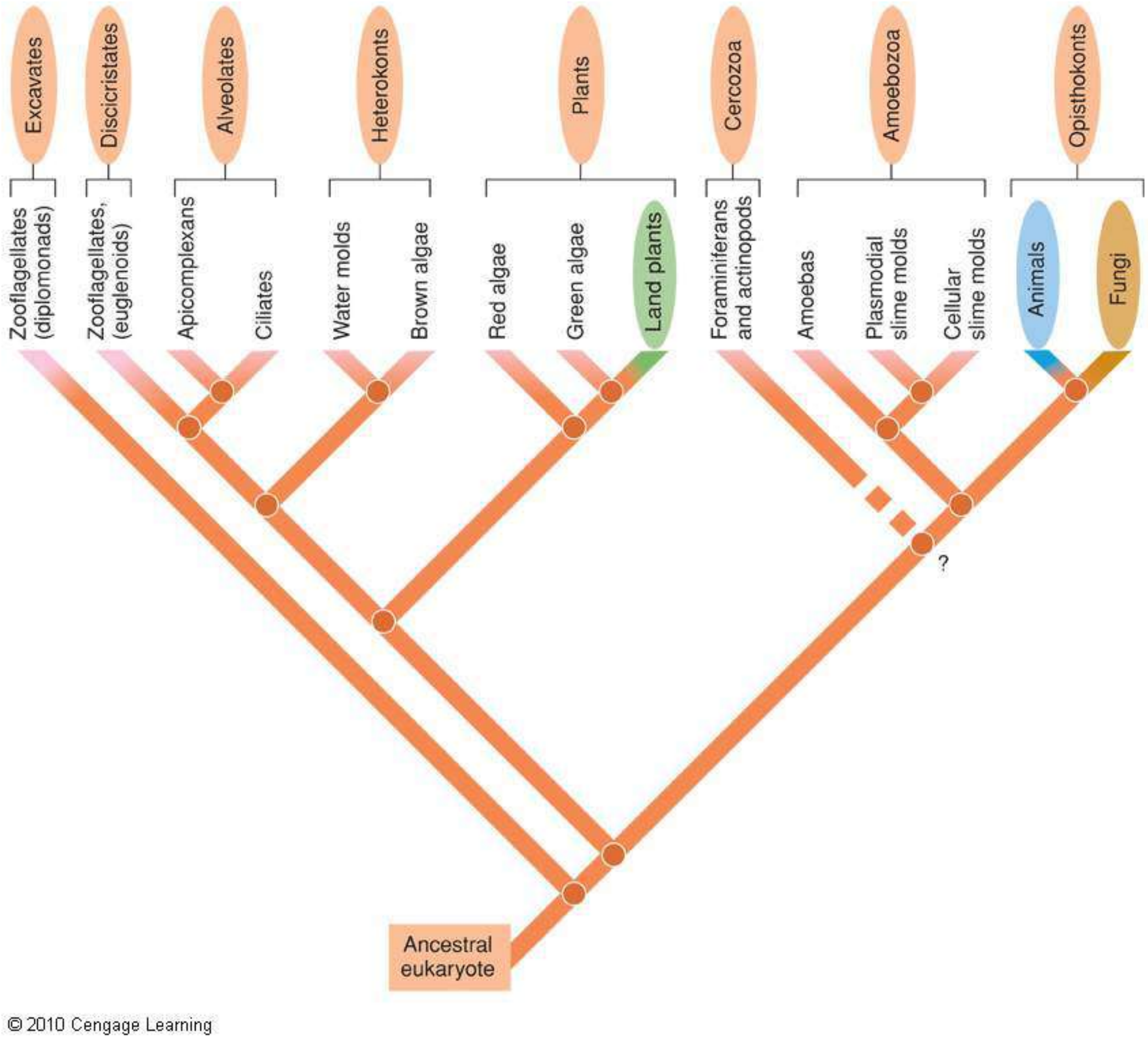


Figure 3.8. Classification of eukaryotes. All groups that are not in the circles right above the lines (land plants, animals, fungi) that define the three clear eukaryotic kingdom are considered protists. Many taxonomists also use a "supergroup" classification in the domain Eukarya, indicated by the circles above the brackets.

3.6.3. Tracing relationships

The evolutionary history of a species (or group of species) is its phylogeny. Taxonomists (biologists who study biological classification) often use phylogenetic trees to represent the hypothesized relationships between species or groups (figure 3.8). Species relationships have traditionally been evaluated based on morphological similarities but rely increasingly on molecular data: two species that are more closely related to one another share more of their genetic code.

In the most modern approach to phylogeny, biologists use cladistics to classify organisms. In this method, one pays attention to the order of evolution of traits; the order of branch points in a cladogram (phylogenetic tree derived from cladistics) relates to the appearance of new traits (termed derived characteristics). The branch point on a cladogram represents the splitting of two or more groups from their common ancestors (Figure 3.9). Note that traits used in cladistics can be morphological (as shown in Figure 3.9) or molecular (e.g. the appearance of a new DNA sequence).

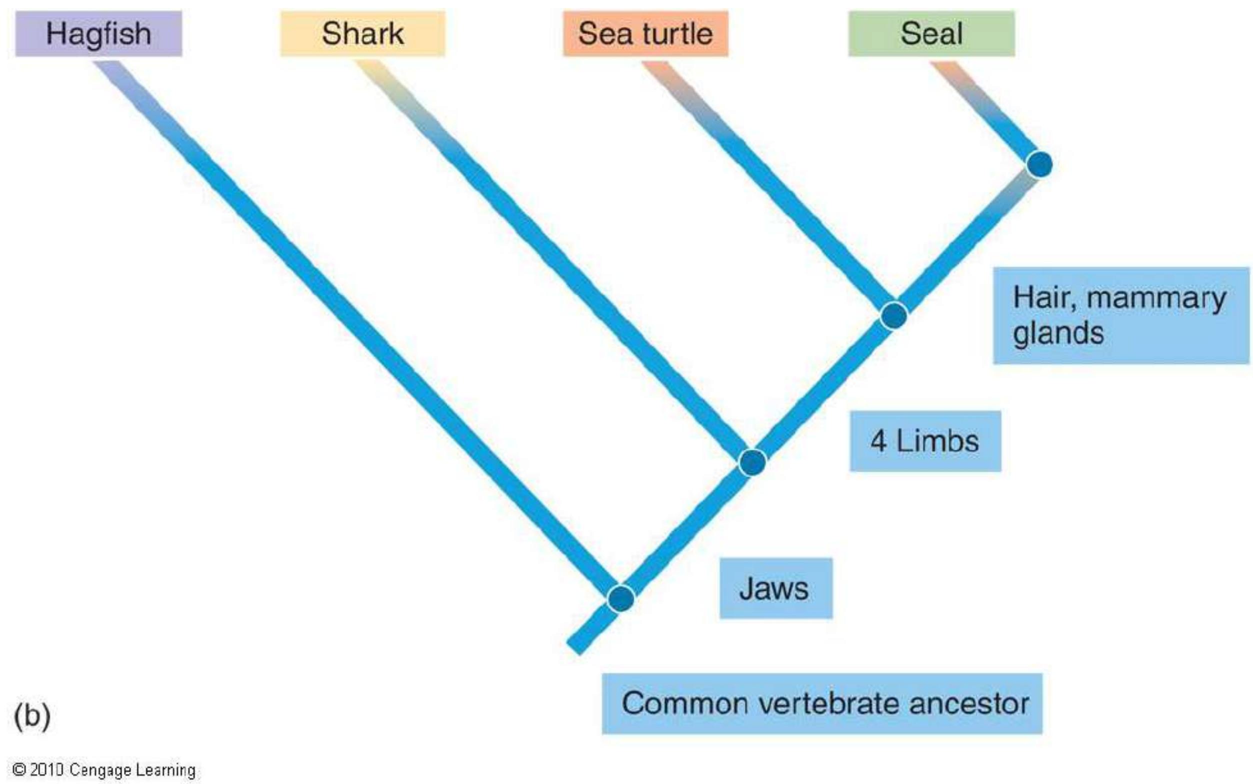


Figure 3.9. A cladogram, showing the appearance of particular traits between the various branch points.

3.7. Review Questions: Basics of Life

1. Which polysaccharide is used for structure in the cell wall of plants?

2. Which polysaccharide is used for the hard exterior of crabs and lobsters?

3. What are the two major roles of carbohydrates in living organisms?

4. Give three roles of lipids in marine organisms?

5. Which macromolecule is an enzyme an example of?

6. What are the two types of nucleic acids?

7. What is the major role of nucleic acids in living organisms/

8. What is the difference between prokaryotic & eukaryotic cells?

9. How do prokaryotic cells divide?

10. How do eukaryotic cells divide/

11. Which organelle is the site for photosynthesis in eukaryotic cells?

12. What organelle is a long hair-like structure used in propulsion?

13. Who independently formulated similar ideas to Darwin on the theory of evolution by natural selection?

14. Explain the process of evolution by natural selection.

15. What is a gene?

16. What is fitness in evolutionary terms/

17. What is the modern definition of a species?

18. Which 2 words are use to describe a species in the binomial nomenclature system?

19. List 4 possible isolating mechanisms that lead to sympatric speciation?

20. What term describes the mechanism by which new species arise due to geographical isolation?

21. Which comes first, the genus or species name when describing an organism using the binomial system?

22. Which is capitalized, the genus or species name when describing an organism using the binomial system?

23. Are protists prokaryotic or eukaryotic organisms?

24. Compare sexual and asexual reproduction

25. What is the difference between a cladogram and a traditional phylogenetic tree?

26. What are the various levels of taxonomic classification, from most to least inclusive?

4. Marine Micro-organisms (Karleskint Chapter 6)

Micro-organisms are the most abundant organisms in the oceans. They include viruses, prokaryotes, protists and some fungi. Even though they are not visible to the naked eye they have very important ecological roles. They are the basis of the food chains and play an important role in decomposition and recycling of nutrients.

4.1. Marine Viruses

Marine viruses are extremely abundant in the oceans and play an important ecological role. Marine viruses are 10 times more abundant than marine prokaryotes, and can be found in densities of up to 10^{10} virions/liter in surface water and up to 10^{13} virions/liter in sediment. Viruses are generally not considered to be alive because they have no metabolism, and can only reproduce by injecting their DNA into a host, which is called viral replication. Viruses can use both prokaryotic and eukaryotic organisms as hosts. They are sub-cellular particles that are between 10 and 400 nanometers in length. Outside their host they are called virions, and consist of a nucleic acid core surrounded by a protein coat (Figure 4.1)

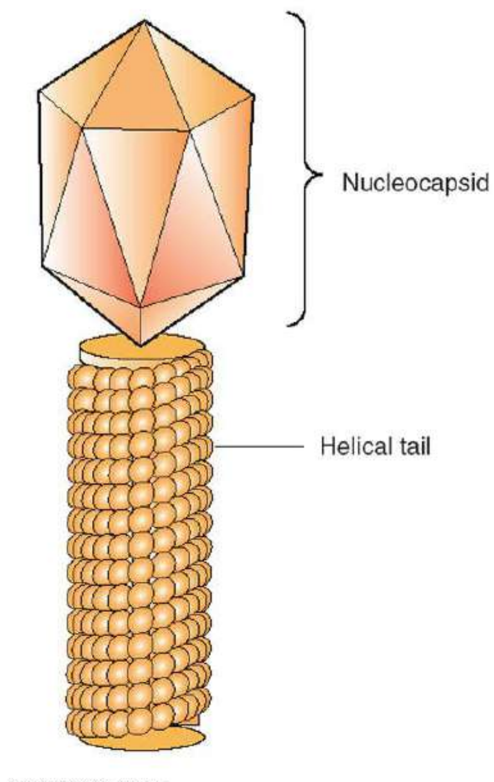


Figure 4.1. Typical structure of a marine virus. The exact structure varies with virus strain. The capsid is a protein coat that envelopes the genetic material; the helical tail, when present, helps attach to the host.

Viral replication often leads to cell lysis and the death of the cell (Figure 4.2). Through cell lysis, viruses can reduce the populations of bacteria and other micro-organisms and in the process release nutrients back in the water column.

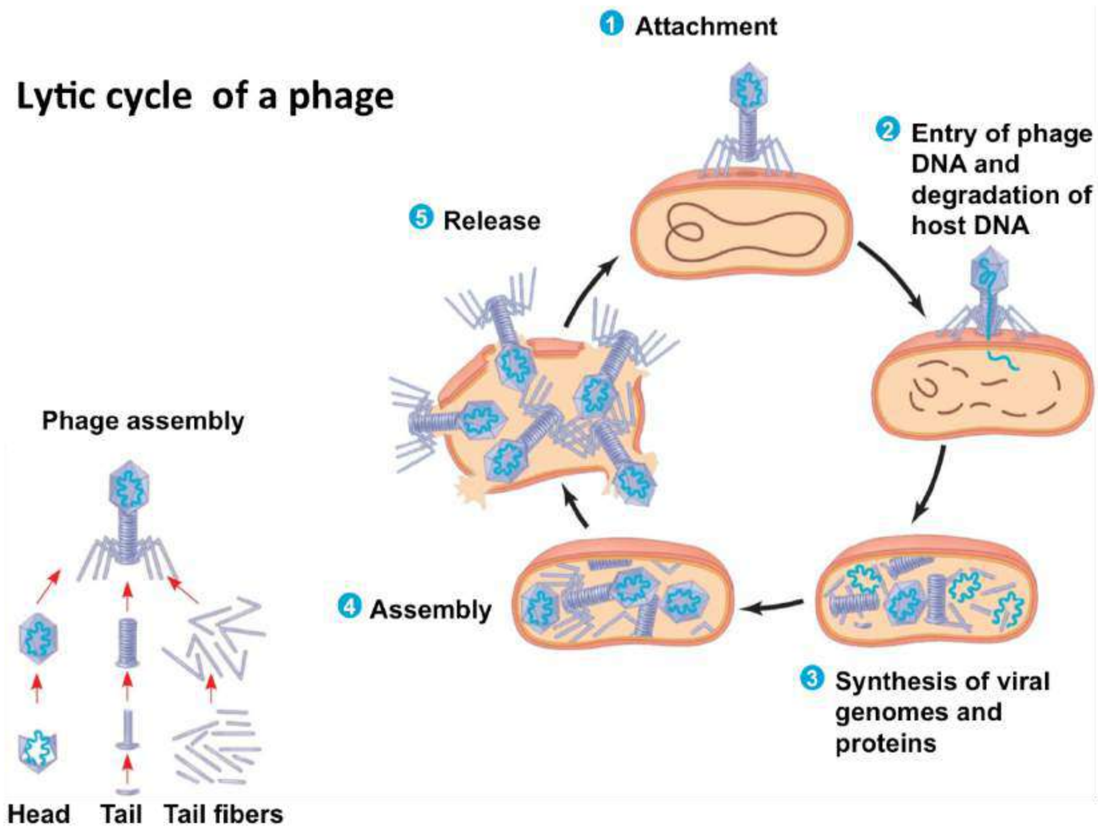


Figure 4.2. This phage (virus that infects bacteria) causes lysis (disintegration) and death of the cell after it has replicated itself.

4.2. Marine Bacteria

Bacteria have a simple prokaryotic organization, and like the Archaea (See section 4.3), they lack nuclei and membrane-bound organelles. Most marine bacteria are rod-shaped (bacillus) or spherical (coccus) (Figure 4.3) and are small, between 200 nanometers to 750 micrometers in length.

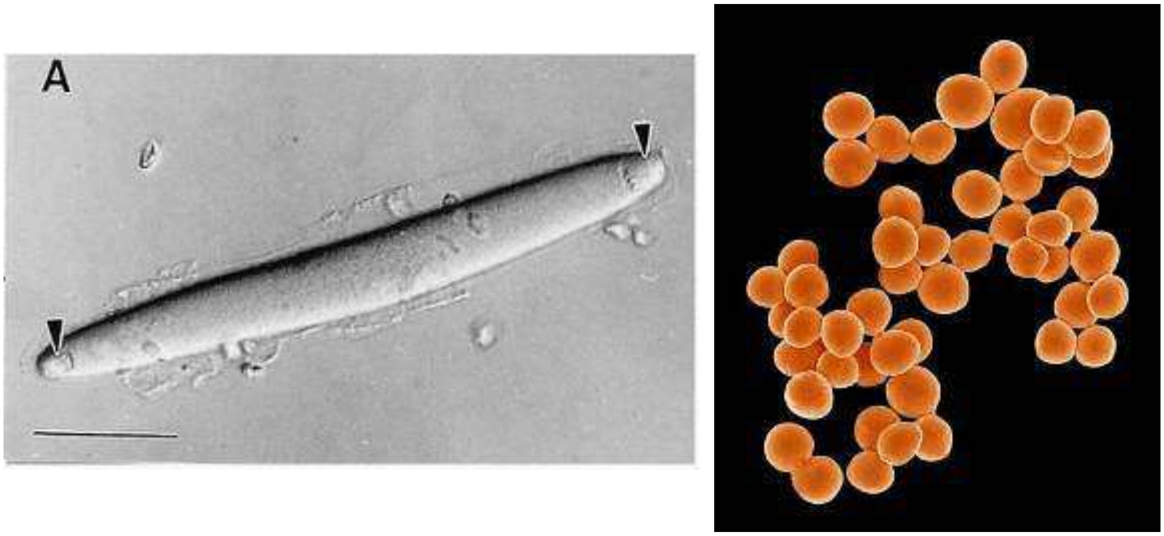


Figure 4.3. Typical shapes of marine bacteria: bacillus (left) and coccus (right)

4.2.1. Nutritional Types of Marine Bacteria

Cyanobacteria are also known blue-green algae (Figure 4.4). They are the **only photosynthetic prokaryotes** and in fact photosynthesis has evolved only once, in this group. All other photosynthetic organisms have acquired their plastids (photosynthetic organelles) at some point by endosymbiosis with cyanobacteria. Many species of cyanobacteria can use N_2 as a source of nitrogen—allowing them to thrive where low levels of nitrogen nutrients (nitrates (NO_3^- and nitrites NO_2^-) limit the photosynthesis and growth of most other photosynthetic organisms. They possess unique accessory pigments, which capture different wavelengths of light, enable chromatic adaptation with depth, and protect the cell from damaging wavelengths of light. The cyanobacteria *Prochlorococcus* sp., which thrives in nutrient-poor tropical waters, is believed to be most abundant life form throughout the oceans. Blooms of cyanobacteria can form dense mats that may discolor the water. Other cyanobacteria form mats that trap sediment and precipitate chemicals forming structures known as stromatolites, now only seen in the Bahamas and Australia (Figure 4.4).

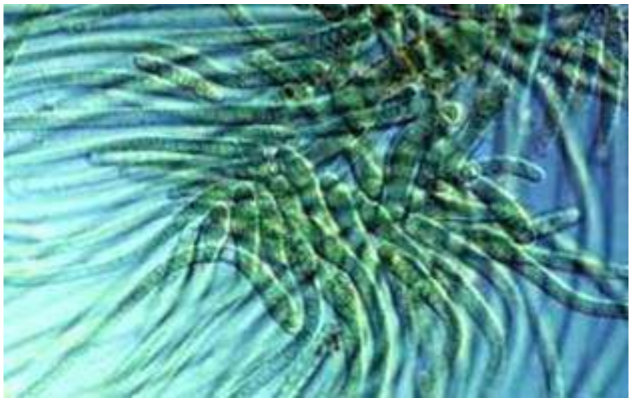



Figure 4.4. Cyanobacteria (left), can form structures called stromatolites (right)

While cyanobacteria are the only photosynthetic prokaryotes, many other bacteria are autotrophs through chemosynthesis. Chemosynthetic bacteria are found in areas that are rich in compounds that can be oxidized to release energy, such as hydrothermal vents (where they use hydrogen sulphide, H_2S) and cold seeps (use methane, CH_4). They may be free-living or occur in symbiosis with other organisms. Chemosynthetic bacteria are often anaerobic (don't need oxygen) and do not need sunlight.

Heterotrophic bacteria are decomposers that break down available organic matter to obtain their energy. As a result, they release inorganic chemicals back into the water which can then be used again by primary producers. Heterotrophic bacteria are therefore very important in nutrient cycling. Many heterotrophic bacteria release exoenzymes that can digest cellulose, chitin, keratin and other molecules largely resistant to decay.

4.2.2. Nitrogen fixation and nitrification

Nitrogen fixation is the process by which molecular nitrogen (N_2) dissolved in seawater is converted to ammonium (NH_4^+). Some cyanobacteria and a few archaeons (see section 4.5) are capable of fixing nitrogen, allowing them to thrive in low nutrient conditions. Nitrification is the bacterial conversion of ammonium (NH_4^+) to nitrite (NO_2^-) and nitrate (NO_3^-), forms usable by most plants and algae (Figure 4.5).

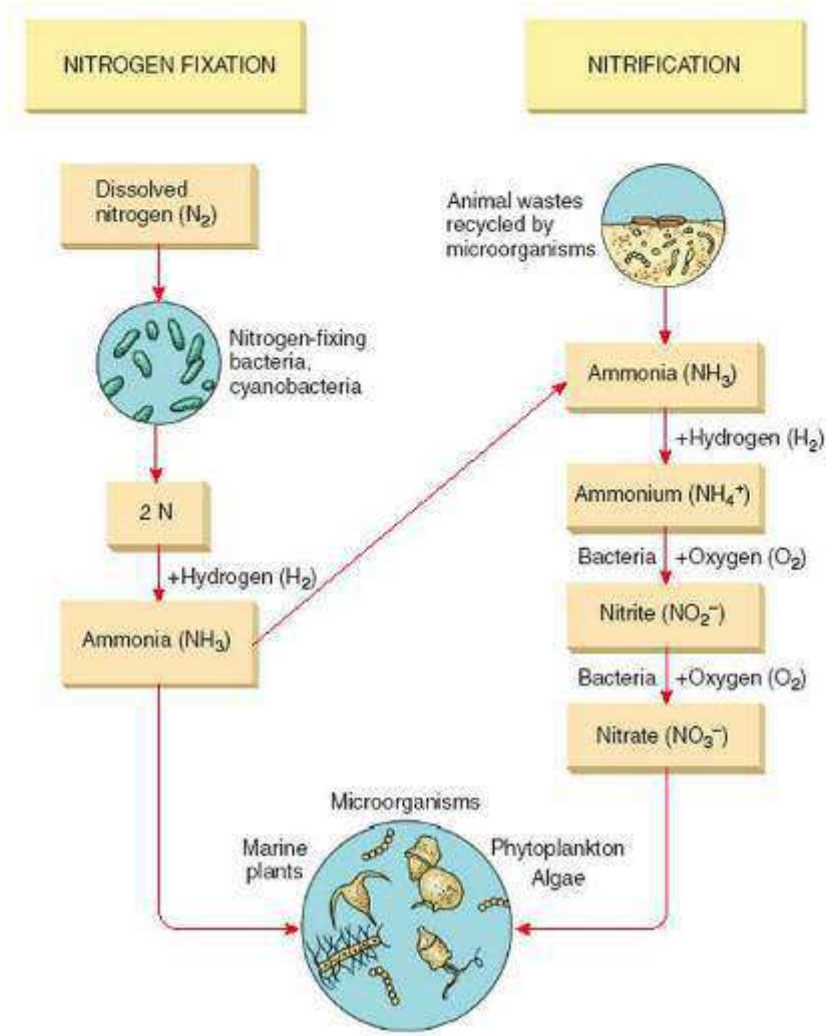


Figure 4.5. Processes of nitrogen fixation and nitrification.

4.2.3. Symbiotic bacteria

Symbiosis is the phenomenon in which two different organisms live in very close association. Many marine bacteria have evolved symbiotic relationships with a variety of organisms. For example, mitochondria and chloroplasts found in modern eukaryotic cells originated from prokaryotic organisms that started living inside another cell (endosymbiosis; Figure 4.6); at hydrothermal vents, many bacteria live within tissues of worms and clams supplying their hosts with organic food molecules through chemosynthesis; the bioluminescence of deep-sea fish or squid is often the result of a symbiosis with light-producing bacteria.

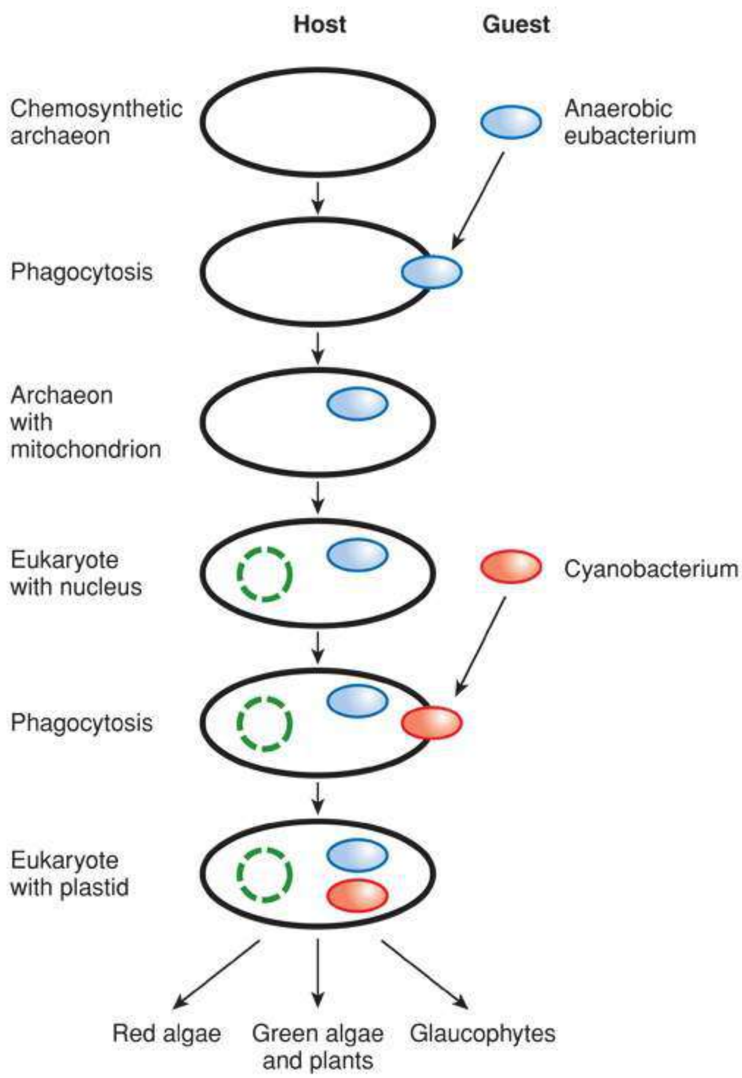


Figure 4.6. Mitochondria and plastids (photosynthetic organelles such as chloroplasts) in eukaryotic cells are now understood to be the result of endosymbiosis, where an ancient archaeal cell acquired a bacterium through phagocytosis, but did not digest it and instead the bacterium became a part of the archaeon's metabolism. Photosynthesis has evolved only once in the earth's history (in cyanobacteria), and all photosynthetic organisms acquired their plastids through endosymbiosis of cyanobacteria (primary endosymbiosis, shown here) or through endosymbiosis with a eukaryote which itself acquired plastids from cyanobacteria (secondary endosymbiosis).

4.3. Archaea

The Archaea are also prokaryotes, but they differ from the Bacteria in a few important ways. Probably most important is the biochemistry of their cell walls, which in Archaea is more resistant to heat and other extreme environments. For this reason, many archeons inhabit extreme habitats: high or low temperatures, high salinities, low pH or high pressure. Hyperthermophiles are archaeons which can tolerate temperatures of over 100°C and many hyperthermophiles inhabit hydrothermal vents.

Archaeons are generally smaller than bacteria, measuring 0.1 to 15 micrometers in length. They may be either autotrophs or heterotrophs, though none are photosynthetic. Some archaeons are methanogens: anaerobic organisms that live in environments rich in organic matter, releasing methane as a waste product of metabolism.

4.4. Domain Eukarya

The domain Eukarya includes all organisms with eukaryotic cells, such as plants, animals, fungi and protists. There is an incredible diversity of micro-organisms in the domain Eukarya in the ocean, and this chapter only covers some of the most important groups.

4.4.1. Marine fungi

Fungi are eukaryotes with cell walls made of chitin (the same compound used in the exoskeleton of crustaceans). They are heterotrophs and use exoenzymes to digest organic matter. A large proportion of fungi are decomposers important in recycling organic matter. Fungi are strict aerobes; anaerobic decomposition is carried out by bacteria. Marine fungi are not very abundant (less than 1% of fungi are marine), and they are mostly microscopic.

Marine fungi can be classified on the basis of where they live. By far the most diverse group of marine fungi can be found on decomposing wood of terrestrial origin although others types may inhabit coastal salt marshes, mangroves, sand or the planktonic communities of the open ocean. Fungi are also important as disease agents, for example aspergillosis, a disease found in Caribbean sea fans, is caused by the fungus *Aspergillus sydowii*.

Lichens are mutualistic associations of fungus and algae. The fungus provides the attachment, general structure, minerals, and moisture, while the alga produces organic matter through photosynthesis. This association allows lichens to inhabit inhospitable environments, for example high up in the intertidal zone.

4.4.2. Stramenopiles

The stramenopiles are a diverse group of protists with two flagella of unequal length. They are named for one of their flagella which has hair-like filaments (stramen=straw; pilos=hair; Figure 4.7). Some stramenopiles are photosynthetic, others are not. Those that photosynthesize have acquired their plastids (photosynthetic organelles) through secondary endosymbiosis. This means that stramenopiles acquired through endosymbiosis a photosynthetic eukaryotic organism which itself had acquired its plastics from endosymbiosis with cyanobacteria (Figure 4.6). The stramenopiles are a varied group which includes the brown algae, diatoms, ochrophytes and labyrinthomorphs. Brown algae, which are multicellular and macroscopic, are discussed in the next chapter. Of the microscopic stramenopiles, only diatoms will be discussed in this course.

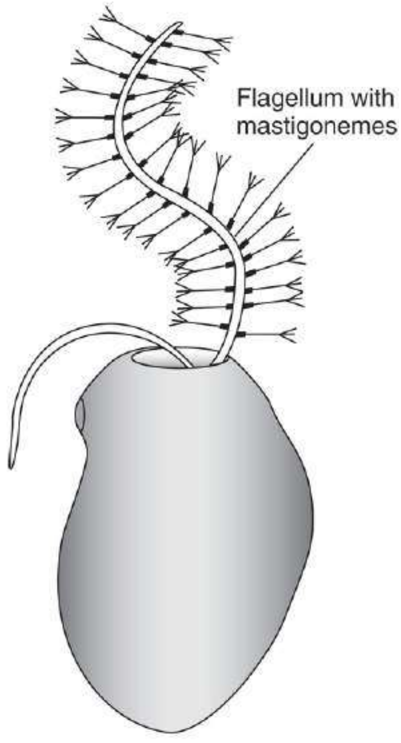


Figure 4.7. A typical Stramenopile, showing one of the flagellum having mastinogemes, or flagellar hair.

Diatoms are important members of both planktonic and benthic communities. They are photosynthetic primary producers and have a cell wall made of silicon dioxide (also known as silica, SiO_2; a major constituent of glass). This cell wall, called a frustule, is composed of two halves, or valves, with one fitting over the other like a shoe box. They exhibit either radial symmetry (centric), usually seen in planktonic species, or bilateral symmetry (pinnate), more typical in benthic diatoms (Figure 4.8). They are most abundant at high latitudes and in areas of upwelling where nutrient levels are relatively high, as they are large phytoplankton and require large amounts of nutrients (nitrates and phosphates, and in their case also silica) in order to thrive. Some diatoms can produce a toxin called domoic acid, which when present in high concentrations can kill some organisms that ingest them.

Diatoms reproduce both asexually and sexually. They reproduce asexually by fission, in which the valves separate and each valve secretes a new valve inside the old valve. This asexual reproduction leads to progressively smaller individuals (Figure 4.9), and when a diatom has reached 50% of its original size, it reproduces sexually through the formation of an auxospore. Under poor environmental conditions, diatoms can form resting spores which sink to the bottom and stay dormant until favorable conditions return.

Because silica is insoluble and does not decompose, when diatoms die their frustules sink to the benthos and accumulate in the sediment, creating siliceous oozes abundant at high latitudes. When brought to the surface, diatomaceous earth can be used as commercial filters (used in swimming pools, and beer and champagne production) or abrasives (used in silver polish and toothpaste).

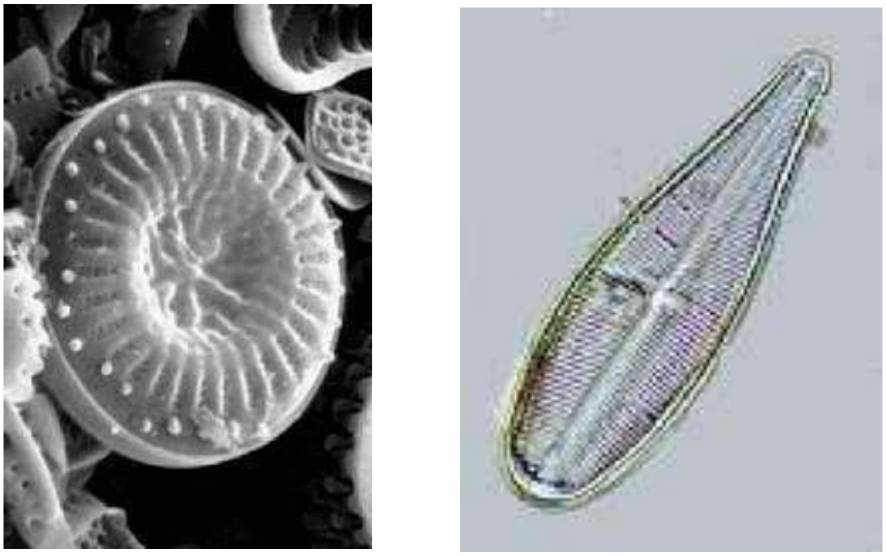


Figure 4.8. Diatoms may have radial symmetry (centric) (left), or bilateral symmetry (pinnate) (right).

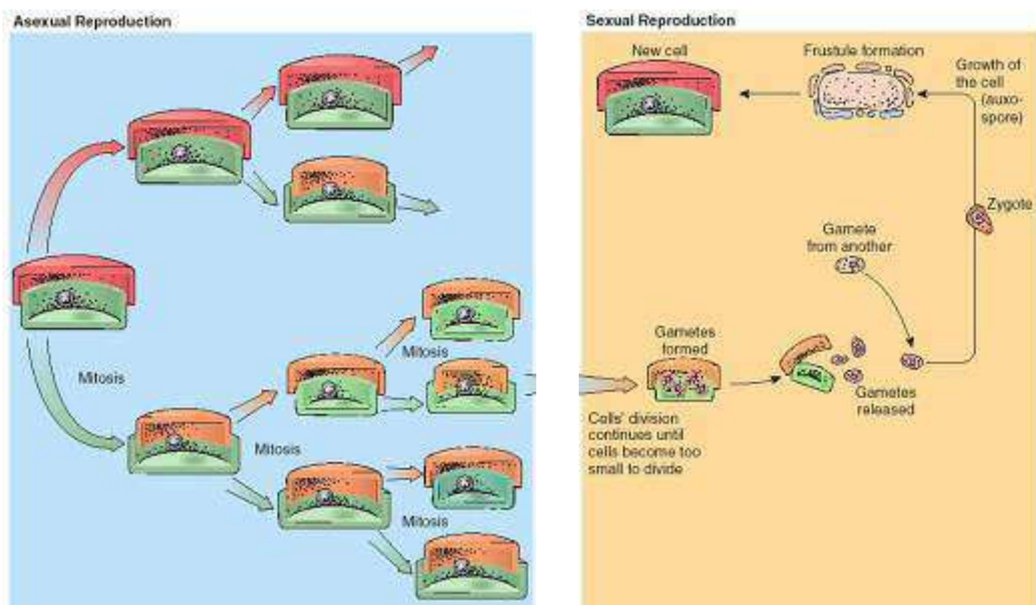


Figure 4.9. Reproduction cycle in diatoms.

4.4.3. Haptophytes

The haptophytes are a group of mostly photosynthetic organisms that are closely related to the stramenopiles but have to simple flagella (without hair) and a unique structure called the haptonema. The haptonema is used to capture food in heterotrophic

haptophytes but is also present (yet usually shorter) in photosynthetic ones. The largest group of haptophytes are the coccolithophores.
Coccolithophores are exclusively marine and photosynthetic. They have a calcium carbonate shell made of coccolith plates (Figure 4.10), which may account for up to 40% of modern carbonate production in the oceans, and form sediment known as calcareous oozes. In some areas these sediments have been uplifted and form chalk cliffs, e.g. the White Cliffs of Dover.

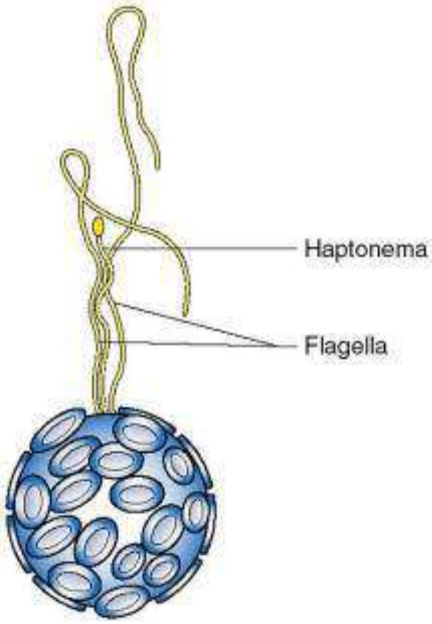


Figure 4.10. Coccolithophores showing flagella, haptonema and coccolith plates.

4.4.4. Alveolates

Alveolates have membranous sacs under their cell membranes. They include several closely-related groups; by far the most important in the marine environment are the dinoflagellates, which is the only group of Alveolates discussed here.

Dinoflagellates are globular, single-celled organisms which have two flagella that lie in grooves on the cell's surface. One of the flagella creates forward propulsion while the other makes the dinoflagellate spin (Figure 4.11). Armored dinoflagellates are covered in cellulose plates which give protection and aid in species identification (Figure 4.12).

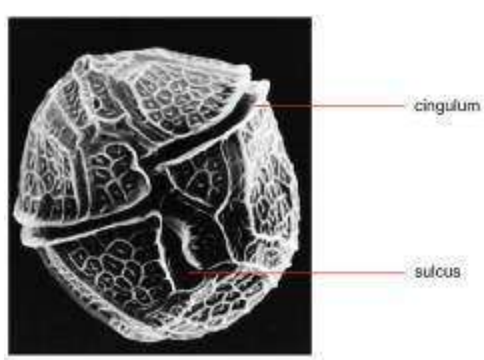


Figure 4.11. Dinoflagellate showing the grooves where the flagella lie.

Dinoflagellates mostly reproduce asexually by fission, yet many species may also reproduce sexually. Dinoflagellates also occasionally produce dormant cysts which are resistant to decay and environmental stress, and can mature when environmental conditions are favorable.

Dinoflagellates, unlike diatoms, do not require silica as a nutrient. Moreover, they can be autotrophic, hetetrophic, or mixotrophic (capable of both autotrophy and heterotrophy). These characteristics allow dinoflagellates to be more abundant than diatoms in nutrient-poor tropical waters. Some dinoflagellates are parasitic, while others occur in mutualistic symbioses such as the zooxanthellae that live in the tissues of corals and other cnidarians. Some dinoflagellates are bioluminescent (e.g. *Noctiluca*) and light up when they are disturbed, e.g. in the wake of boats and breaking waves.

Dinoflagellates are one of the most important groups responsible for harmful algal blooms, also known as red tides. Some species produce toxins that may be concentrated by filter feeders and are harmful to humans and other organisms that consume them.

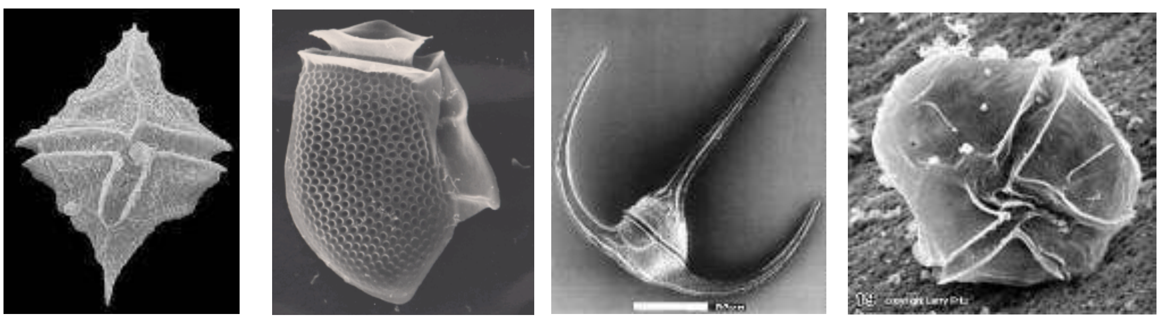


Figure 4.12. Various species of armored dinoflagellates.

4.4.5. Choanoflagellates

Choanoflagellates are the protists most closely related to the animal kingdom. They occur as single cells or in colonies, and their cells closely resemble the feeding cells of sponges (Figure 4.13).

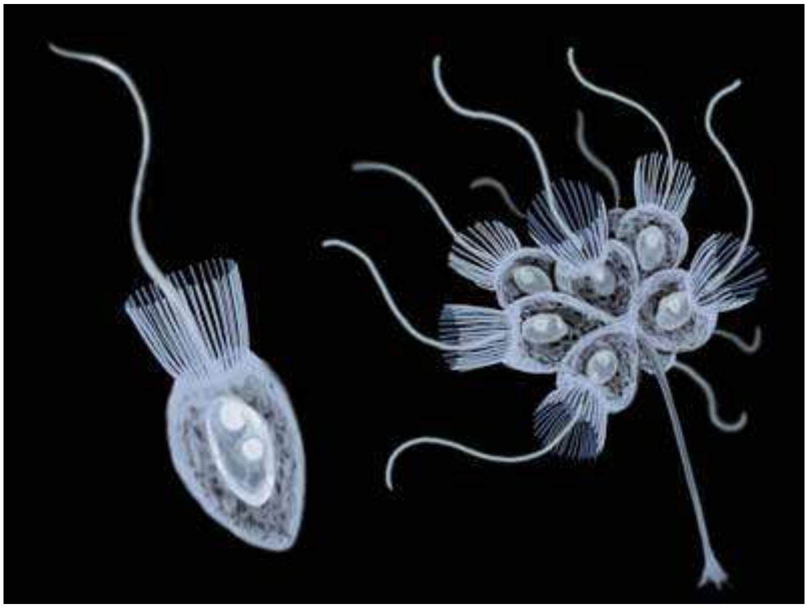


Figure 4.13. Choanoflagellates, which can occur as single cells or colonies. The beating of their single flagellum creates a current over their collar of tentacle-like projections, where food particles gets trapped.

4.4.6. Amoeboid protozoans

Foraminiferans and radiolarians are heterotrophic protists grouped together as amoeboid protozoans. They have organelles called pseudopods which are extensions of the cell surface that can change shape and are used for propulsion or to catch prey. Amoeboid protozoans are heterotrophs and consume bacteria and other small organisms by phagocytosis. Most have a shell or test which form a thick ooze over vast areas of the deep sea floor.

Foraminiferans have branched pseudopods that form netlike structures used to catch prey, reduce sinking rate or crawl on the benthos (Figure 4.14). They produce a multi-chambered calcium carbonate test (Figure 4.14) and are a major constituent of deep-sea calcareous sediment, in areas shallower than 5000m. Foraminiferans also contribute to the pink sands of many Caribbean islands.

Figure 4.14. Foraminifera showing pseupdopods (left) and $CaCO_3$ test (right).

Radiolarians have an external organic membrane called a capsule, which bears pores that allow pseudopods to pass through (Figure 4.15). They also secrete an internal shell of silica (Figure 4.15), which doesn't decompose and accumulates as a siliceous ooze at low latitudes.

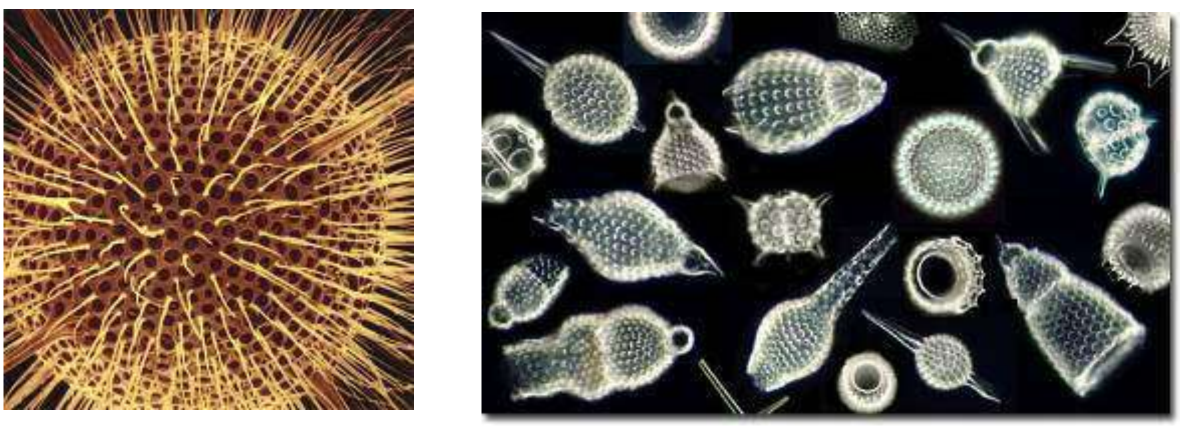


Figure 4.15. Radiolarian showing pseudopods (left) and several silica shells of radiolarians (right)

4.5. Review Questions: Marine Micro-organisms

1. Why is a virus not considered to be alive?

2. How do viruses replicate?

3. Which bacteria can photosynthesize?

4. Symbiosis with which organisms gave rise to eukaryotic cells?

5. What are two roles of accessory pigments in photosynthetic organisms?

6. What are stromatolites? Where are they found?

7. What is the source of energy for chemosynthetic bacteria?

8. In what ecosystem do you find chemosynthetic bacteria?

9. Some cyanobacteria can fix nitrogen, what does this mean?

10. Why are nitrogen fixation and nitrification important?

11. Give an example of symbiotic bacteria?

12. Which domain includes the single-celled prokaryotes that are similar to bacteria but very well adapted to extreme conditions?

13. Can diatoms photosynthesize?

14. What group of macroalgae are diatoms closely related to?

15. What is impregnated in the cell wall of diatoms?

16. When does a diatom switch from asexual to sexual reproduction?

17. How does diatomaceous earth form, and what are three of its uses?

18. What is the name of the feeding structure in coccolithophores?

19. What are the coccoliths of coccolithophores made of?

20. Can dinoflagellates photosynthesize?

21. Give an example of an important dinoflagellate on coral reefs?

22. What organism is typically responsible for red tides?

23. What compound forms the multi-chambered test in formaniniferans?

24. What organism is responsible for the pink sands on beaches in Tonga & the Bahamas?

25. What are the two major shapes of marine bacteria?

26. Explain the major ecological role that viruses play in the world's oceans.

27. Explain the major ecological roles that bacteria play in the world's oceans.

28. What is a decomposer?

29. What is a lichen, and where are lichens found in the marine environment?

30. What are the cell walls of fungi made of?

31. What are the major ecological roles of marine fungi?

32. Are protists prokaryotic or eukaryotic?

5. Multicellular Primary Producers (Karleskint Chapter 7)

Most of the primary production in the oceans is carried out by phytoplankton (diverse species of photosynthetic micro-organism that live in the water column), which are small yet extremely abundant. Multicellular primary producers (seaweeds and flowering plants) need to be attached to the benthos and for that reason are limited to shallow coastal areas. In these ecosystems, they provide a significant portion of the primary production, contribute to detrital food chains and provide habitat for many organisms. Further, the roots of flowering plants are important in trapping and stabilizing sediment.

5.1. Multicellular Algae: Kingdom Protista

There are three groups of multicellular macroalgae (seaweeds): the red algae, the green algae, and the brown algae. These three groups represent distinct evolutionary lines, with green algae being most closely related to land plants of the Kingdom Plantae. Red algae are also included in the same eukaryotic supergroup as land plants and green algae; while brown algae are in the distinct lineage of the Stramenopiles and closely related to diatoms (Figure 5.1).

5.1.1. Distribution of Seaweeds

Almost all species of macroalgae are benthic, and attach to hard substrates. Like microalgae, they must live in areas where they receive enough light to conduct photosynthesis. At very high light levels (at the very surface), rates of photosynthesis are often reduced through photoinhibition, but generally speaking, the rate of photosynthesis decreases with decreasing light level and thus with increasing depth. All plants must also respire, and in the process they use some of the products of photosynthesis for their own metabolic needs. Respiration rate is constant with depth. The depth at which the rate of photosynthesis is equal to the rate of respiration is called the compensation depth (Figure 5.2). Seaweeds (just like phytoplankton) cannot live below the compensation depth for any extended period of time.

The distribution of seaweeds is therefore greatly influenced by light availability, which changes with depth, latitude and seasons. Different seaweeds have different accessory pigments, and these may play a role in the depth that a seaweed can tolerate. Red algae, which have pigments that can absorb blue light (which penetrates the deepest in coastal waters), typically are found deepest. Green algae, which have pigments that absorb red wavelengths (which are absorbed quickly), are found at the shallowest depths. Brown algae are usually found at intermediate depths. This pattern is found in many environments though seaweeds do not always show this zonation based on their pigments (called chromatic adaptation), as many other factors influence distribution, including herbivory, competition, and ability to alter growth form.

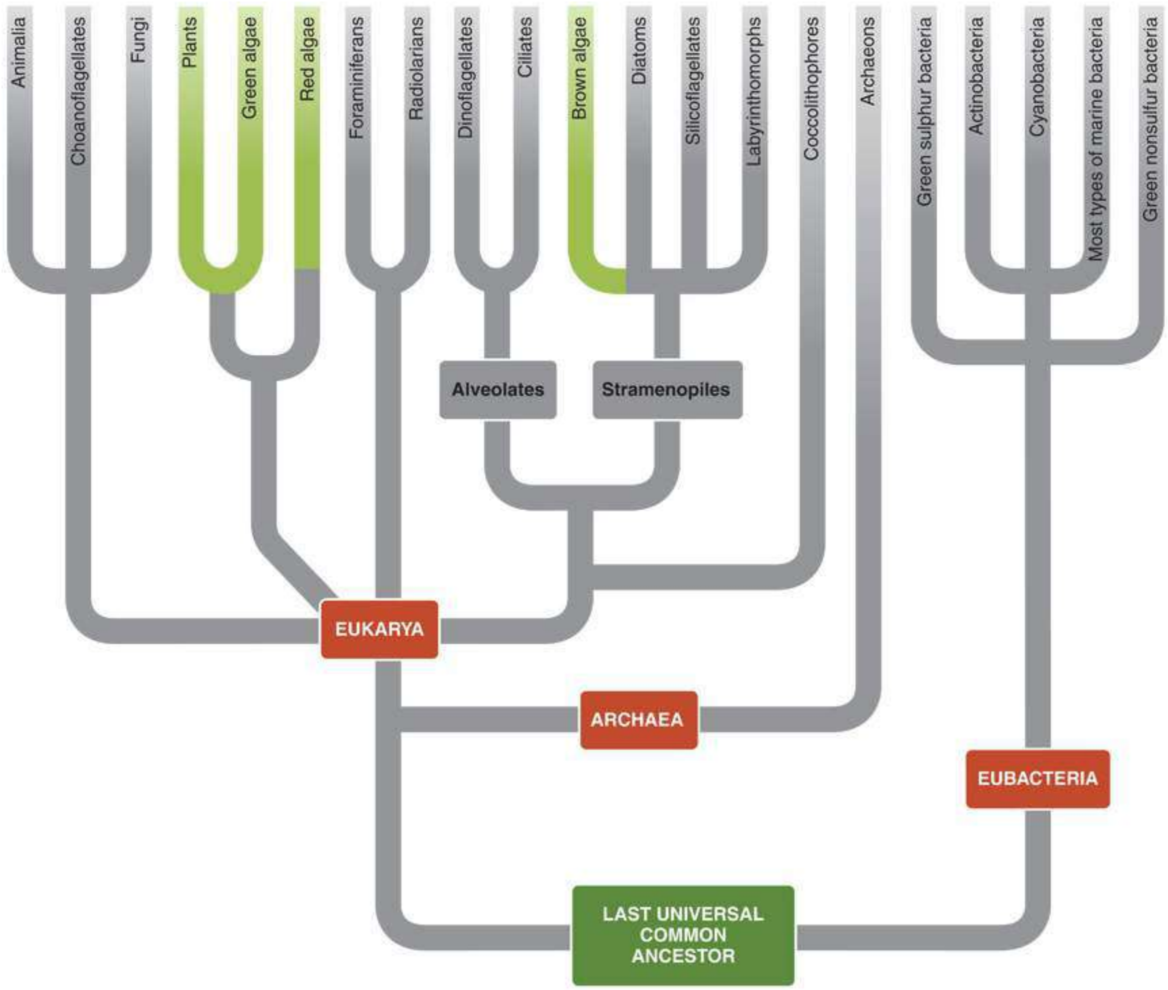


Figure 5.1 Phylogenetic tree of living organisms, with multicellular primary producers highlighted in green.

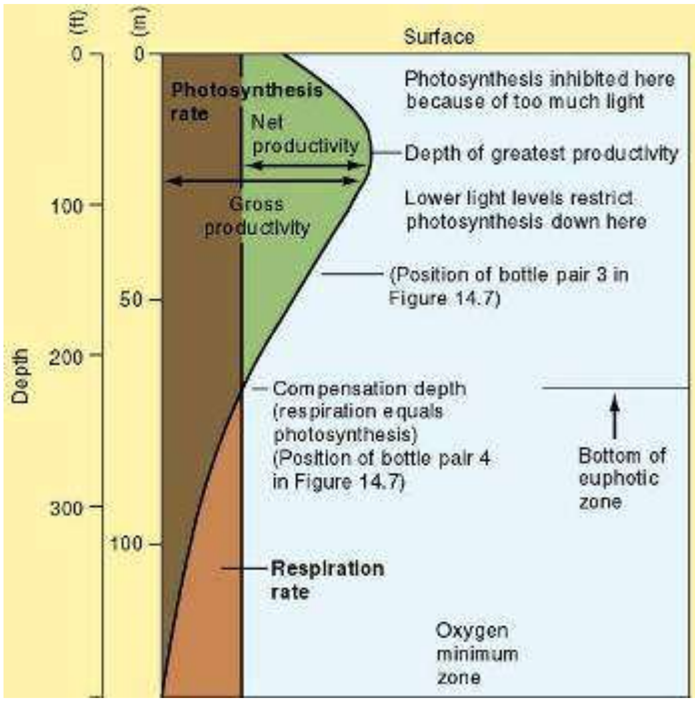


Figure 5.2. The compensation depth, where the rate of photosynthesis equals respiration for plants.

Temperature also affects the distribution of seaweeds. The greatest diversity of seaweeds is found in the tropics, although the biomass of seaweeds in the tropics is low. There is a much greater biomass in temperate zones, where many species (e.g. kelps) are perennials and live more than two years. Many cold water algae are reduced in the winter when light is limited and turbulence increases, and initiate new growth in the spring. Other abiotic factors such as duration of exposure and desiccation, wave action and surge, salinity, availability of mineral nutrients also affect the distribution of seaweeds.

5.1.2. Structure of Seaweeds

Seaweeds have no roots, stems, or leaves, as they lack the vascular tissue that flowering plants have. All their cells are photosynthetic. The thallus is the seaweed body, and the blade (or frond) is the flattened part of the thallus. The holdfast attaches the thallus to the hard bottom. The stipe is the stem-like region between the holdfast and the blade. Some seaweeds have air bladders which hold the blade closer to the surface and therefore allow for increased rates of photosynthesis (Figure 5.3).

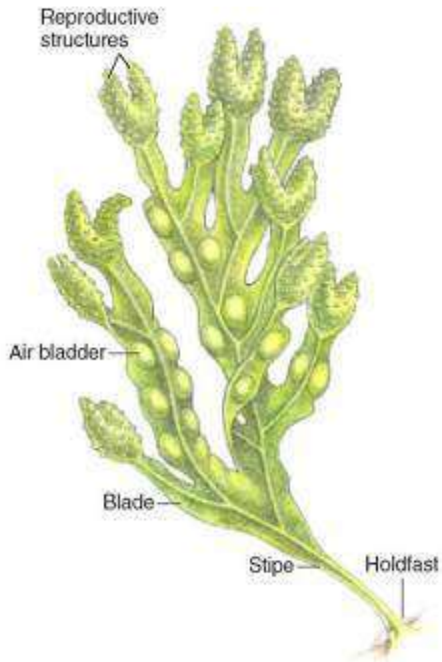


Figure 5.3. Structure of a seaweed.

5.1.3. Biochemistry of Seaweeds

The color of the thallus is due to the wavelengths that are not absorbed by pigments in the seaweed. All seaweeds have chlorophyll a, and some have chlorophyll b (green algae), c (brown algae) or d (red algae). The chlorophyll pigments are responsible for photosynthesis. Seaweeds also have accessory pigments such as carotenes, xanthophylls and phycobilins, which absorb different wavelengths of light and pass energy to the chlorophyll for photosynthesis. Accessory pigments allow seaweeds to photosynthesize in different light levels, and some protect from light damage at high light levels.

The cell wall of seaweeds is primarily composed of cellulose, but some species also have calcium carbonate (calcareous seaweeds). Many species produce slimy gelatinous mucilage that holds water and may slow down desiccation of exposed seaweeds in intertidal areas. The mucilage can also be sloughed off if epiphyte loads become too great.

5.1.4. Reproduction in Seaweeds

Seaweeds can reproduce sexually and asexually. Many species reproduce asexually by fragmentation, e.g. the thallus breaks into several pieces and each piece can reattach to form a new individual. Most species of seaweeds also show sexual reproduction, usually with an alternation of generations: the organism alternates between a haploid stage and a diploid stage (Figure 5.4).

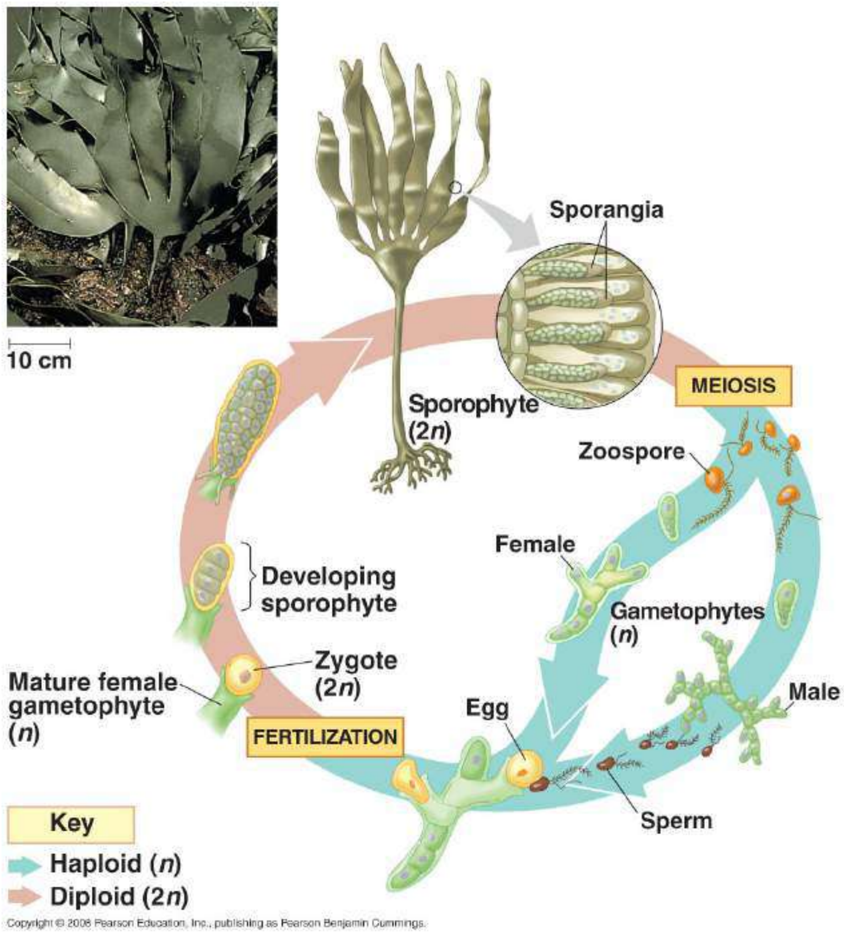


Figure 5.4. Many seaweeds exhibit a sporic life cycle, or alternation of generations, in which both the haploid and diploid phase develop into a multicellular structure (by contrast, in the gametic life cycle of animals, haploid gametes do not undergo cell division until they are fertilized. Only then does the diploid zygote undergo mitosis). In this and other species of kelp, only the diploid sporophyte grows into a large seaweed. The haploid gametophyte remains much smaller. In some other species (e.g. the green alga *Ulva lactuca*), both the diploid sporophyte and haploid gametophyte develop into a full-grown seaweed. The life cycle in red algae is even more complex, with 2 separate diploid multicellular stages.

5.1.5. Medicinal uses of Seaweeds

There are many interesting medicinal uses for seaweeds, some dating back as early as 300BC when the iodine concentrated in seaweeds was used to treat goiter. The slimy mucilage produced by seaweeds was used in Roman times to relieve discomfort and prevent infection on burns and rashes. Red algae were eaten directly as a good source of vitamin C to prevent scurvy, being more readily available than citrus fruit. Still today there are many uses for seaweeds, for example agar and carrageenan are used to treat stomach ulcers as they slowly dissolve and are not digested, therefore coat the stomach. Similarly, a polysaccharide from red algae is used to coat pills and produce time-release capsules.

5.1.6. Green Algae: Phylum Chlorophyta

Green algae have the same pigments as vascular plants: chlorophyll a, b, and carotenoids. Most species of green algae are found in freshwater and most of those in the marine environment are microscopic. Some macroscopic green algae in the tropics are coenocytic, meaning they are composed of a single giant cell or a few large cells with multiple nuclei. For example, *Valonia* (sea pearl) is coenocytic and has a saclike thallus and elaborate multi-layered cellulose cell wall (Figure 5.5). Many green algae produce deterrents to herbivory like calcium carbonate or toxins, others avoid problems of predation by growing extremely fast or occupying small unreachable crevices. For example, the calcareous green alga *Halimeda* sp, which is an important source of calcium carbonate sand in the Caribbean (Figure 5.5).

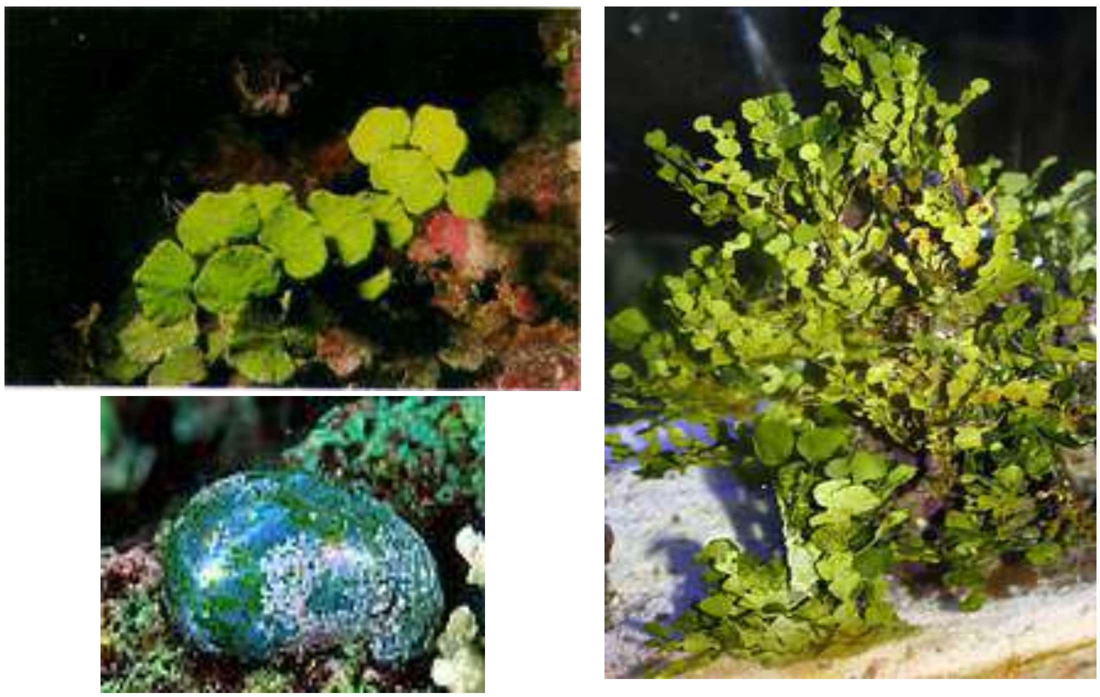


Figure 5.5. *Halimeda* sp., a calcareous green alga (top left and right), and *Valonia*, a coenocytic green algae (bottom left)

5.1.7. Red Algae: Phylum Rhodophyta

The red algae are primarily marine and are most diverse in the tropics. Their pigments include chlorophyll a, d, phycoerythrins (which gives the red color) and phycocyanins. They are almost all multicellular, but are seldom larger than 1m. Red algae are mostly benthic, and exhibit many types of growth forms, including blade-like, leafy, branching, encrusting, calcareous or turf. Many red algae deter herbivores by incorporating calcium carbonate into their cell wall, making the thallus difficult to eat and digest. A group of such algae, the coralline red algae, are important in reef consolidation in the tropics (Figure 5.6).

Figure 5.6. Crustose coralline alga.

Red algae are harvested commercially for many uses. They are harvested for agar and carrageenan which are used for their gel-forming capacity in pharmaceuticals and foods (e.g. laboratory gels, ice creams, cosmetics, salad dressings). Many species, such as Irish moss, Dulse and Nori (used in sushi), are harvested to be used as food. Others are harvested to be used as animal feed or fertilizers.

5.1.8. Brown Algae: Phylum Phaeophyta

The species in this phylum are almost exclusively marine, and include rockweeds, kelp and sargassum (Figure 5.7). The brown algae are the largest seaweeds, and have been known to attain lengths of 100m. They contain chlorophyll a and c, and their olive-brown color is caused by the accessory pigment fucoxanthin, which is also found in diatoms.

Figure 5.7. Kelps found in temperate zones.

Brown algae are most diverse and abundant at temperate latitudes, which is where large kelp forests form (Figure 5.7). Many are perennials, and they are an important source of food and habitat for many other species. Although they are not vascular plants, larger kelps have specialized cells, called trumpet cells, to conduct photosynthetic products to the deepest part of the thallus. *Sargassum* spp. (Figure 5.8) is one of only genus of seaweed that does not grow attached to the benthos. It is found in the tropics. The blades of *Sargassum* spp. have gas-filled bladders that allow the seaweed to remain at the surface.

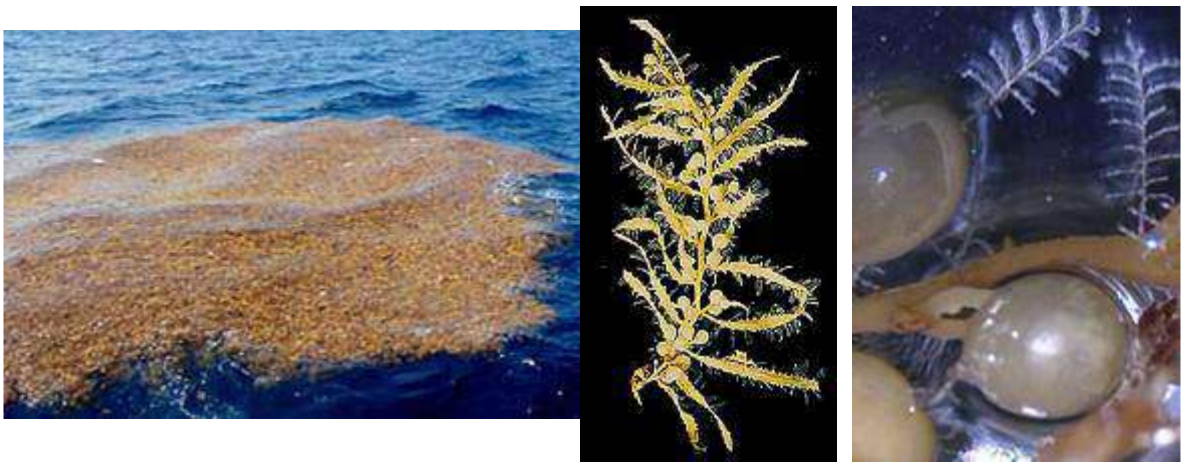


Figure 5.8. *Sargassum* sp. free-floating brown seaweed.

Kelp forests are very productive ecosystems and they are home to many species of plants and animals. Similarly, free-floating *Sargassum* spp. weeds form a three-dimensional habitat in the middle of the Atlantic, and clumps of *Sargassum* spp. at the surface are home to many species.

5.2. Marine Flowering Plants

The kingdom Plantae includes several major groups including mosses, ferns, conifers and flowering plants, which all have adaptations for life on land. All of these groups except mosses are included in the vascular plants, which are characterized by the presence of xylem and phloem, structures that provide structure and carry water and nutrients, respectively. Unlike seaweeds, vascular plants have well differentiated roots, stems and leaves. Advanced vascular plants reproduce through seeds, which are held in cones (conifers) or fruit (flowering plants). Conifers are exclusively terrestrial, but a few species of flowering plants, called halophytes, live in the marine environment.

5.2.1. Adaptations of Marine Flowering Plants

Marine flowering plants evolved from land plants and because of that, they have lost many adaptations for the marine environment found in seaweeds, such as the reliance on the buoyant effect of water, the presence of flagellated sperm for dispersal in water, the ability to absorb nutrients through their entire body, and the ability to photosynthesize at low light levels. Marine flowering plants therefore live in shallower water than seaweeds, and absorb nutrients only through their roots. Their cell walls contain large amounts of cellulose and lignin, therefore they are not easily digested by herbivores.

5.2.2. Seagrasses

Seagrasses are hydrophytes, as they live beneath the water (Figure 5.9); they are the group of flowering plants that is best adapted to the marine environment. Seagrasses are found in both temperate and tropical waters.

Figure 5.9. Seagrass meadow

Structure
Seagrasses exhibit vegetative growth much like many lawn grasses. Rhizomes (horizontal stems) generally lie in the sand or mud, and vertical stems arise from them. Stems of seagrasses are bamboo-like, with cylindrical sections (internodes) separated by rings (nodes). Roots arise from the nodes of the rhizomes, and anchor the seagrass in the sediment. As seagrasses depend on their roots for nutrient absorption, they don't benefit from an increase in nutrients in the water column. The ribbon-like leaves arise from vertical stems and have a lower protective sheath that has no chlorophyll and an upper blade that carries out photosynthesis (Figure 5.10). Leaves also control salt balance, and have an aerenchyme, a gas-filled tissue that aids in oxygen transport (Figure 5.11).

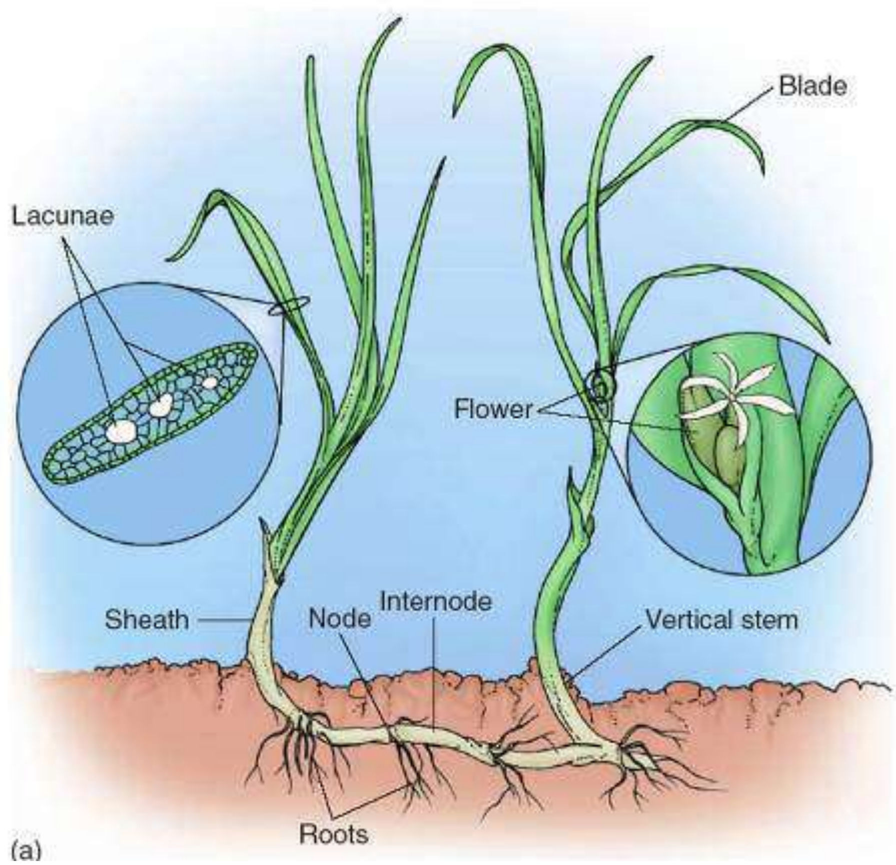


Figure 5.10. Structure of a seagrass.

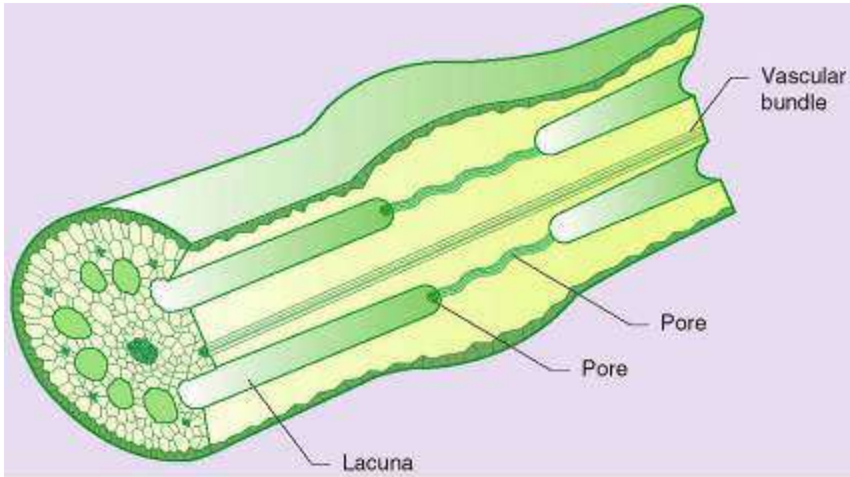


Figure 5.11. Aerenchyme of a seagrass.

Reproduction
Many seagrasses have lost their flowers in the process of evolution, and reproduce asexually by fragmentation and re-rooting. In the flowering species, the flowers are small and inconspicuous. Submerged flowering seagreasses rely primarily on hydrophilous pollination for fertilization, where the sperm-bearing pollen is carried by currents to the female pollen receptor.

Ecological roles
Seagrass meadows have a high rate of primary production. This is due to the ability of seagrasses to extract nutrients from the sediment, the presence of symbiotic nitrogen-fixing bacteria in the roots, and the epiphytes growing on the seagrasses. However, unlike seaweeds, seagrasses are not fed upon directly by most marine herbivores as they are too tough to digest. Only a limited number of herbivores, including waterfowl, manatees, green sea turtles, dugongs, certain parrotfish and some urchins, are adapted to eat seagrasses. Therefore seagrasses makes only a small direct contribution (i.e. through herbivory) to higher levels of the food chain. However their fragmentation and loss of leaves contributes to the detrital and microbial food chains where they form a substantial food base for bacteria, brittle stars, sea cucumbers and deposit feeding worms.

Seagrasses play an important role in aiding deposition and stabilizing sediments. Their blades reduce water velocity, which in turn increases the deposition of particles in suspension. Moreover the decay of seagrasses adds detritus to the sediment. Their rhizomes and roots stabilize the bottom and prevent currents from re-suspending sediments, which in turn reduces water turbidity.

Seagrasses are also an important habitat for many species. Their blades create a three-dimensional habitat and shelter for many species of animals, and the complexity of the sand increases with the rhizomes. They are a habitat for the juveniles of many species of fish and invertebrates. At high tide many eels, flounder and fish come in to seagrass meadows to feed. Many snails (e.g. conch, whelks and tulip snails) thrive in seagrass meadows. Seagrass blades provide an attachment site for many epiphytes and epifauna, e.g. hydrozoans, tubeworms, bryozoans and tunicates. These organisms are responsible for a large portion of the primary production in seagrass meadows, however they can become detrimental if the load becomes too great and blocks radiant energy from reaching the leaves.

5.2.3. Salt Marsh Plants

Salt marsh plants, as opposed to seagrasses, must have some exposure to air to flourish and therefore they inhabit only the intertidal zone. They are found in temperate zones, along the gentle slopes of river deltas and bays. Salt marsh plants are halophytes, which means that they can grow in soil with a high salt content. When the surrounding salinity is high, they tend to lose water through osmosis, and for that reason have several adaptations to retain water. Their leaves are covered by a thick cuticle; some species have salt glands to excrete excess salt, and many have water-retaining succulent (enlarged) parts. Salt marshes tend to be species poor due to the difficult conditions of varying salinities and anoxic conditions.

Ecological Roles of Salt Marsh Plants

Like seagrasses, few herbivores can consume salt marsh plants and therefore they contribute little directly to higher trophic levels, but contribute substantially to detrital food chains. Herbivores that can consume salt marsh plants are mostly terrestrial, e.g. grasshoppers, beetles, crabs and geese. Salt marsh roots and rhizomes stabilize sediments and prevent erosion, and they may remove some excess nutrients and toxic organic pollutants from land runoff. They also serve as a buffer to storm damage and prevent erosion.

5.2.4. Mangroves

Mangroves replace salt marshes in the tropics. They are found in the intertidal zone, and only their roots are submerged by the tides. They are the tropical equivalent of salt marshes and inhabit tropical shores with low wave action, high rates of sedimentation, and a gradual slope. There are 54 species of mangroves worldwide, but the most important are the red and black mangroves. Both have specialized roots that rise out of the sediment.

Structure

Mangroves are trees with simple leaves and complex root systems. Their roots grow in loose, anoxic sediment and many species have aerial roots (above water) that have an aerenchyme. The aerenchyme is linked to the atmosphere through the lenticels, and supplies oxygen to the root system. The stilt roots of red mangroves (Figure 5.12) branch above ground and extend the root system far out away from the tree, increasing its stability. Smaller nutritive roots emerge from larger anchor roots. Black mangroves, on the other hand, have a root system below ground called cable roots (Figure 5.13). Anchor roots grow down from the cable root to anchor the tree, while aerial roots (pneumatophores) grow out of the sediment and into water or air, and have an aerenchyme and lenticels for gas exchange. Nutritive roots emerge from the aerial roots.

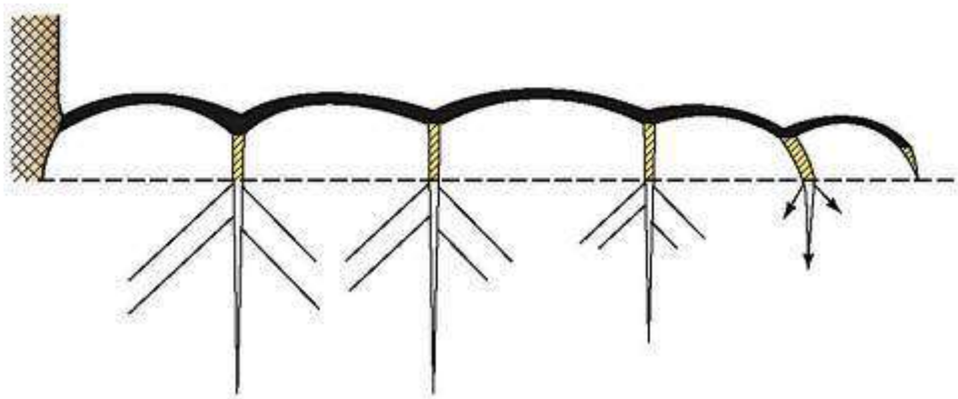


Figure 5.12. Stilt roots of red mangroves.

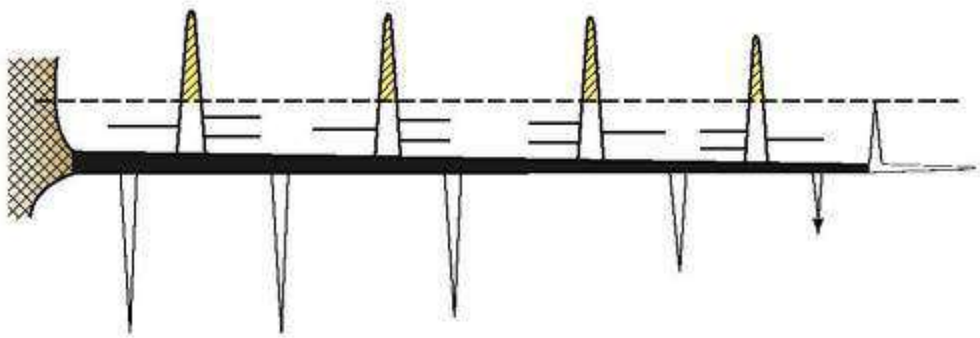


Figure 5.13. Cable roots of black mangroves.

The leaves of mangroves are simple, oval, leathery, thick and succulent, much like salt marsh plants. However the leaves of mangroves are never submerged. The epidermis is covered by a thick cuticle to reduce water loss, and the stomata (openings for gas exchange) are usually located on the underside to reduce water loss through evaporation. Some species of mangroves can eliminate excess salts through salt glands or by concentrating it in old leaves (sacrifical leaves), which are then shed from the tree.

Reproduction

Mangroves have simple flowers that are pollinated by wind or insects. Some mangroves in the high intertidal zone produce small buoyant seeds that drift with currents (e.g. black mangroves), others in the mid to low intertidal show viviparity (e.g. red mangroves), where the embryo grows on the parent plant before detaching to reattach elsewhere.

Ecological roles of mangroves

The ecological roles of mangroves are similar to that of seagrasses and salt marsh plants. Their roots stabilize sediments, and aerial roots increase deposition accumulating sediments and producing new coastal land. They offer a variety of habitats, for example, their roots provide a substrate for epiphytes, the canopy of mangroves is home to a diversity of insects and birds, and their root system is a nursery ground for many reef fish. They have low levels of herbivory due to their high salt content and abundant cellulose and lignin, but contribute to the detritus and thus to the microbial food chains.

They act as a buffer protecting the shore from erosion and as biochemical filters of terrestrial runoff

5.3. Review Questions: Multi-cellular Primary Producers

1. What is chromatic adaptation?

2. How do seaweeds differ from marine flowering plants?

3. How do seaweeds anchor to the substrate?

4. Why are air bladders important in seaweeds?

5. What are 2 of the roles of the slimy gelatinous mucilage of seaweeds?

6. What are three medicinal uses of seaweed?

7. Which of the following seaweeds would you expect to inhabit the deepest water; green algae, red algae, brown algae?

8. Give an example of a member of the phylum Chlorophyta?

9. Give an example of a member of the phylum Rhodophyta?

10. What is carrageenan used for?

11. Give an example of a member of the phylum Phaeophyta?

12. How do large kelp conduct the products of photosynthesis to the deepest part of the plant?

13. Where would you find *Sargassum* spp.? Why does it accumulate in that area?

14. What are three examples of marine flowering plants?

15. What are the horizontal underground stems of seagrasses called?

16. Name three organisms that feed on seagrasses directly?

17. Do a lot of marine herbivores feed on seagrasses

18. What are three ecological roles of seagrasses?

19. Must salt marsh plants always be submerged?

20. Would you expect to find marsh plants in the tropics or temperate regions?

21. Give 3 ecological roles of salt marsh plants?

22. Where would you expect to find mangroves?

23. Describe the roots of the red mangrove?

24. Describe the roots of the black mangrove?

25. Describe 3 adaptations of mangrove leafs to prevent water loss and salt accumulation?

26. How do red and black mangroves reproduce?

27. Give 3 ecological roles of mangroves?

28. Point out two ecological similarities between salt marsh plants, mangroves and seagrasses.

29. How do mangroves get rid of excess salt?

30. What kind of wave action are mangroves well adapted for?

31. What kind of multicellular primary producer can be used to treat goiter?

32. Where is kelp most abundant?

33. Which seaweed phylum has the greatest diversity?

34. Which seaweed phylum includes the largest seaweeds?

35. What is a coenocytic thallus? Which seaweed phylum includes many species that display one?

36. Describe the alternation of generation that is common in seaweed reproduction.

37. What is a stipe?

38. What is the compensation depth?

6. Sponges, Cnidarians and Comb Jellies (Karleskint Chapter 8)

6.1. Animals

Animals are organisms that are multicellular, eukaryotic and that lack rigid cell walls. They are heterotrophs: cannot produce their own food and need to consume other organisms. Except for adult sponges, animals can actively move, even those that have a sessile lifestyle. Animals that don't have a backbone are called invertebrates; they represent the vast majority of animal species. Animals with a backbone are called vertebrates.

6.2. Sponges: Phylum Porifera

Sponges are the simplest of multicellular animals. They have no tissues, organs or nervous system and their cells show little differentiation and specialization. They are asymmetric and sessile, and show a variety of growth forms and colors.

6.2.1. Structure of Sponges

Sponges are filter feeders, and constantly circulate water through their bodies. They have many small incurrent holes called ostia, and one or few excurrent holes called the osculum (Figure 6.1). The cavity inside the sponge is called the spongocoel.

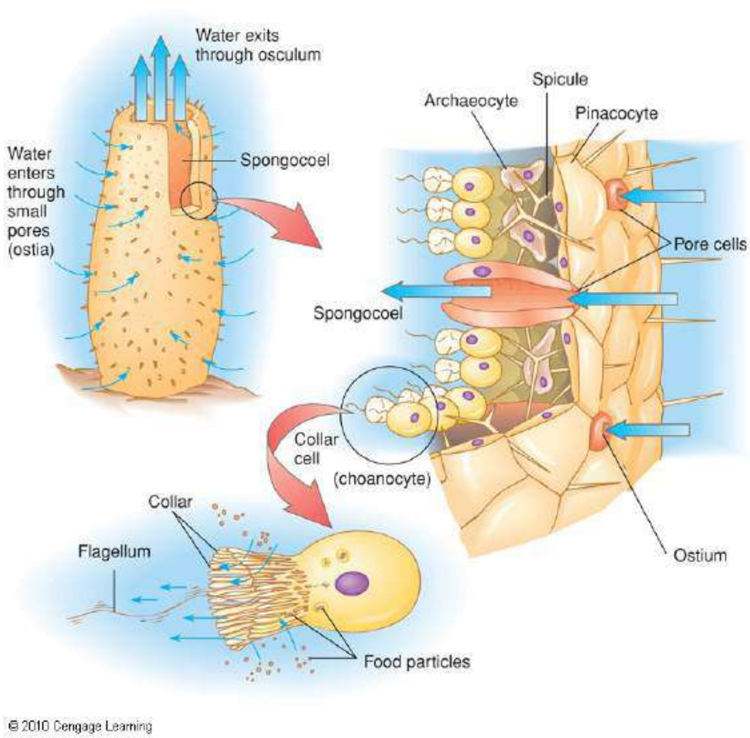


Figure 6.1. Parts of a typical sponge, with main types of cells.

Sponges lack specialized tissues, but they do have several cell types that are specialized to perform a function. Choanocytes (collar cells) line the spongocoel and use a flagellum to move water through. They also trap suspended food particles. Archaeocytes are amoeba-like cells that move throughout the body to transport food and aid in repair and regeneration. Pinacocytes are flattened cells on the outside of the sponge that play a structural role.

Sponges have spicules, skeletal elements made of calcium carbonate, silica or spongin that provide structural support. Spongin is a protein that forms a flexible fiber found in sponges of the class Desmospongia, the sponges that are harvested commercially.

6.2.2. Size and Body Form of Sponges

The size of a sponge is limited by its ability to circulate water through its body, which in turn is limited by its body form. The simplest of sponges are small and tubular. Increasing folding of the body wall in more complex sponges allows for an increased surface area for choanocytes and allows those sponges to grow to a bigger size (Figure 6.2).

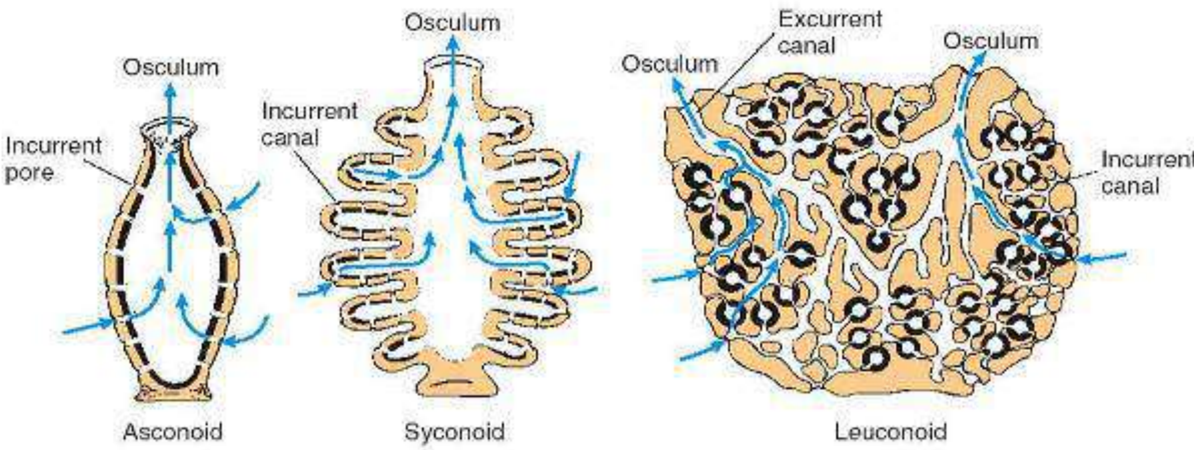


Figure 6.2. Main growth forms in sponges. More complex folding (e.g. leuconoid) allows increased surface area for collar cells and a bigger size.

6.2.3. Nutrition and Digestion in Sponges

Sponges are suspension feeders (or filter feeders), and create a current of water through their body by the beating of the flagella in the choanocytes. In this way they capture small particles in the water including bacteria, plankton and detritus. Food particles get trapped in the collar cells (choanocytes) and are transported through the sponge by the archaeocytes which also function in food storage. Undigested materials and waste products exit the sponge through the osculum.

6.2.4. Reproduction in Sponges

Sponges can reproduce asexually by budding, where a group of cells on the outer surface of the sponge develop and grow into a new sponge. When these are developed, the new sponges drop off and settle nearby. Another method of asexual reproduction is fragmentation, in which pieces broken off by waves and storms develop into new individuals.

Sponges also reproduce sexually. Most species are hermaphrodites and produce both male and female gametes, although not usually at the same time. Sperm is released in the water column and captured by another sponge. The sperm is engulfed by a choanocyte and transported to an egg. The fertilized eggs are released in the water column, where the larvae develop until they are ready to settle on the benthos (Figure 6.3).

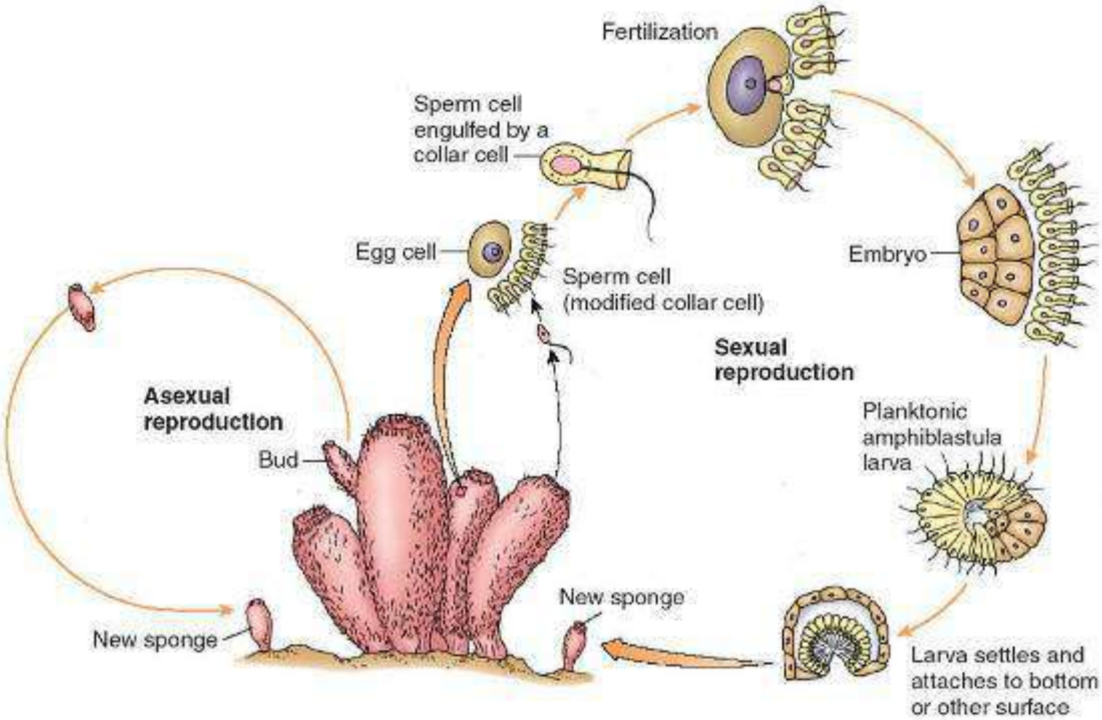


Figure 6.3. Reproduction in sponges.

6.2.5. Ecological Roles of Sponges

Sponges are important inhabitants of shallow water ecosystems and compete for space with other sessile animals like corals and bryozoans. Many produce chemicals (toxins) to kill or inhibit their competitors. Other sponges create their own habitat, such as boring sponges that burrow into coral, thereby playing an important role in calcium recycling. The spicules and toxins of sponges deter most predators, though hawksbill sea turtles and angelfish have evolved adaptation to withstand them. Sponges form symbiotic relationships with a variety of other organisms. Many bacteria and some dinoflagellates live within their tissues, and the spongocoel offers shelter for a variety of organisms.

Chemicals have been isolated from Caribbean sponges that block DNA synthesis in tumor cells and there is the prospect of utilizing these compounds in cancer treatment. The antibacterial properties of sponges are also being studied.

6.3. Cnidarians

6.3.1. Structure of Cnidarians

Cnidarians have radial symmetry, with their body organized around a central mouth. This type of symmetry is common in organisms that are sessile or do not live an active lifestyle, and allows them to respond to stimuli equally from all sides. Cnidarians have two main body plans, a benthic polyp and a pelagic medusa (Figure 6.4). Many groups of cnidarians alternate between the two body plans, while others have lost one or the other.

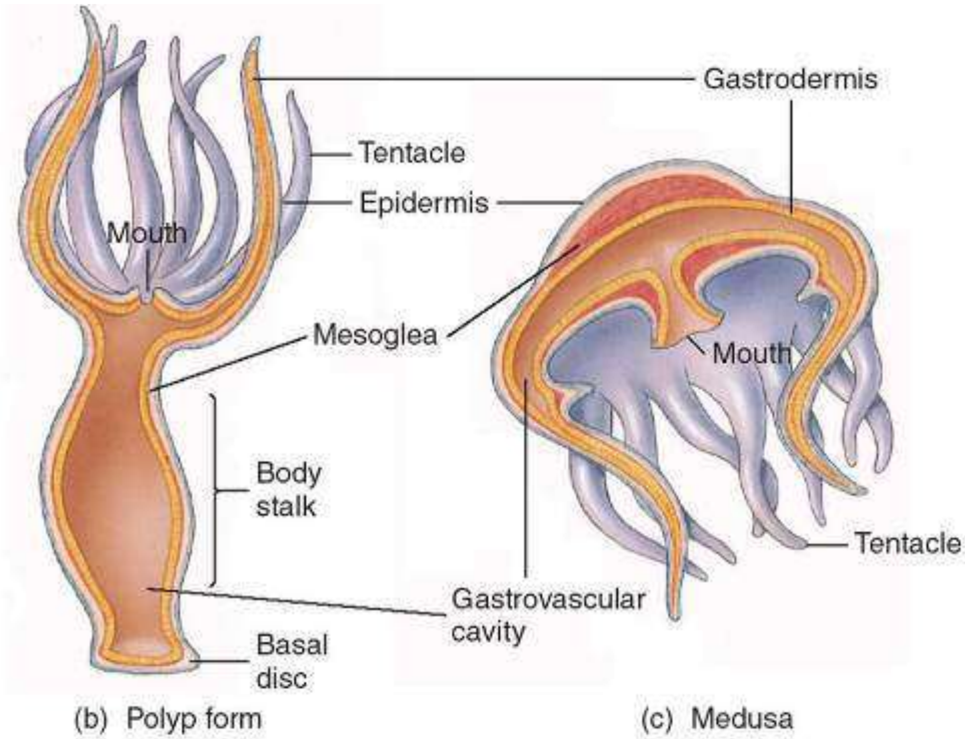


Figure 6.4. Typical polyp and medusa stages of cnidarians

The phylum Cnidaria is characterized by stinging cells called cnidocytes, which contain a stinging organelle called a cnida. The spearing type of cnida, called nematocysts, can be triggered by touch or chemical stimulus. They are found mostly in the tentacles but also in the outer body walls and gastrodermis. They are used both in catching prey and in defense. The sting of some species, including the Portuguese man-o-war and box jellyfish, is so powerful that it can be deadly to humans. However most species have a much milder sting and some animals (e.g. anemone fish) are immune to cnidarian stings.

6.3.2. Cnidarian classes

There are four classes in the phylum Cnidaria, each showing different life histories. The hydrozoans (class Hydrozoa) have an alternation of polyp and medusa stages, both of which are small. The polyps are mostly colonial. The colony includes feeding polyps and reproductive polyps (Figure 6.5). Fire coral (Figure 6.6) is a type of hydrozoan that secretes a calcium carbonate skeleton and contributes to reef building, and because of that is often confused with true corals (class Anthozoa). The Portuguese man-o-war is another type of hydrozoan in which the polyp colony, rather than being benthic, is attached to a float (Figure 6.6).

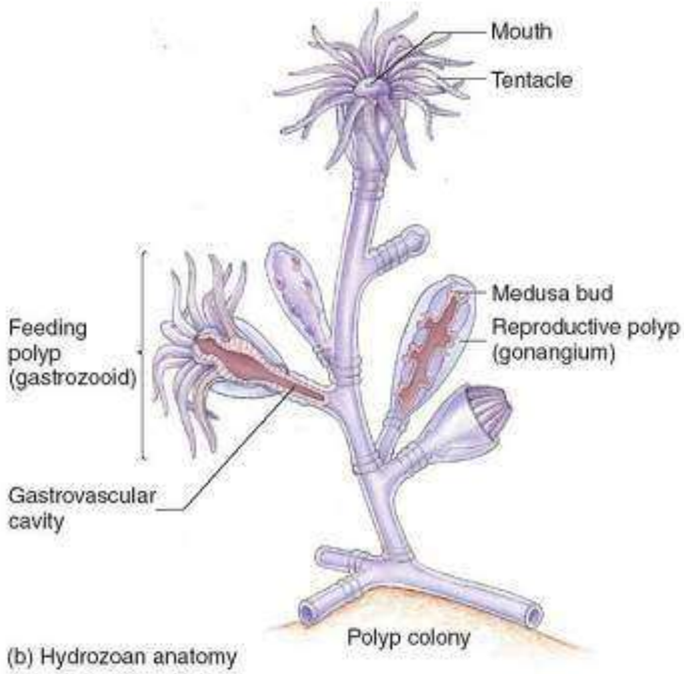


Figure 6.5. Typical polyp stage of a hydrozoan. The reproductive polyps release medusae through asexual reproduction.

Figure 6.6. Hydroids (class Hydrozoa); Fire coral (left) and Portuguese Man-o-war (right)

The true jellyfish (class Scyphozoa) have a dominant medusa stage, with a reduced or absent polyp stage (Figure 6.7). Scyphozoan medusae are larger than hydrozoan medusae, and they can swim better. They swim by pulsating their bodies, but are still considered part of the plankton because they cannot swim against a current. Jellyfish, as all cnidarians, have a very simple nervous system without a brain or eyes, but some species have photoreceptors that allow them to tell light from dark. Several species avoid sunlight and come to the surface on cloudy days and at twilight.

Box jellies (class Cubozoa) are closely related to scyphozoans. They are voracious predators and feed primarily on fish (Figure 6.7).

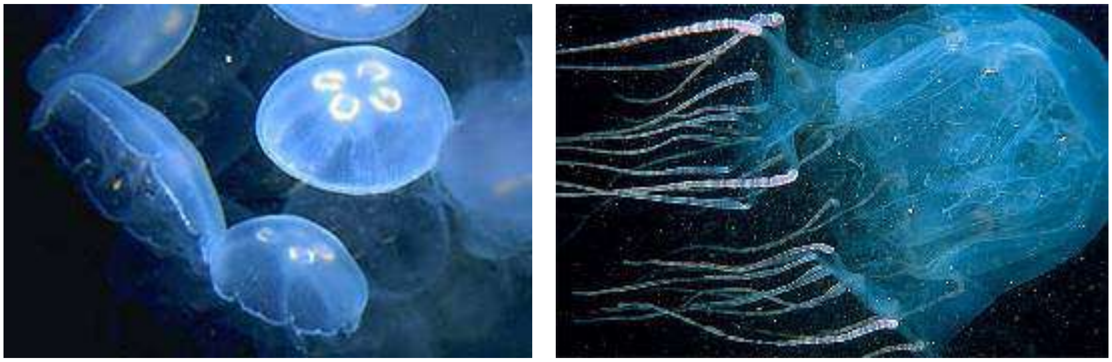


Figure 6.7. Typical Scyphozoan (left) and Cubozoan (right)

The Anthozoans (class Anthozoa) are benthic cnidarians with a polyp stage only, and all adults are sessile. This class includes corals, gorgonians and sea anemones (Figure 6.8). In sea anemones, the polyps are larger and more complex than hydrozoan polyps. They are typically solitary and attached to the substrate. Sea anemones catch prey with their tentacles, which they can move and withdraw into the gastrovascular cavity. Hard corals (subclass Hexacoralia) are polyps that secrete a hard skeleton, most often of calcium carbonate. Most hard corals are large colonies made of smaller polyps, where all polyps are interconnected. Some others are solitary. Polyps of hard corals exhibit a six-part radial symmetry. Hard corals form the extensive calcium carbonate reefs found in many tropical regions (see Chapter 14). Soft corals (subclass Octocoralia) have an eight-part radial symmetry and produce a flexible skeleton. They include gorgonians (sea fans and sea whips) as well as sea pansies and sea pens.

Figure 6.8. Representative anthozoans: hard coral (left), sea anemone (center) and gorgonian (right).

6.3.3. Nutrition and Digestion in Cnidarians

Many hydrozoans and anthozoans are suspension feeders. Scyphozoans, cubozoans and sea anemones are mainly carnivorous and feed on fish and invertebrates, although many also feed on plankton. Cnidarians trap food on their tentacles with their nematocysts and bring it to their central mouth by movement of cilia on the tentacles. Cnidarians do not have a complete digestive tract with an anus; they digest their prey in the central gastrovascular cavity, and then expel their waste back through their mouth (Figure 6.9).

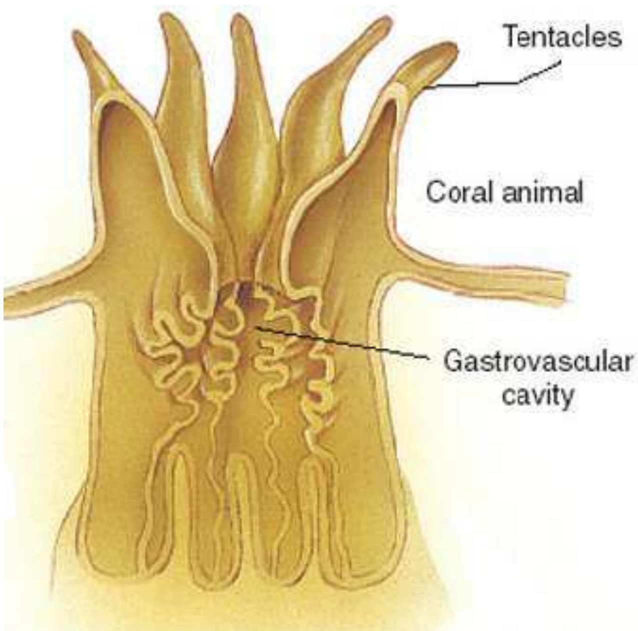


Figure 6.9. Cross-section of a coral polyp showing the gastrovascular cavity and the central mouth.

Many cnidarians have symbiotic algae within their tissues. The upside-down jellyfish has algae in its tentacles and swims upside down to expose the algae to higher light levels. Corals obtain most of their nutrition from their symbiotic zooxanthellae (a type of dinoflagellate), and also feed on plankton.

6.3.4. Reproduction in Cnidarians

Cnidarians can reproduce both sexually and asexually. Asexual reproduction usually occurs in the polyp stage through budding, fission, fragmentation, or the production of medusae.

Sexual reproduction occurs in different ways for the different groups of cnidarians. Hydrozoans have both an asexual polyp stage and a sexual medusa stage, and sexual reproduction happens in the medusa stage, which release gametes in the water column to be fertilize and develop into a new polyp stage (Figure 6.10). Scyphozoans have a similar reproduction to hydrozoans, but the polyp stage is much reduced or completely absent.

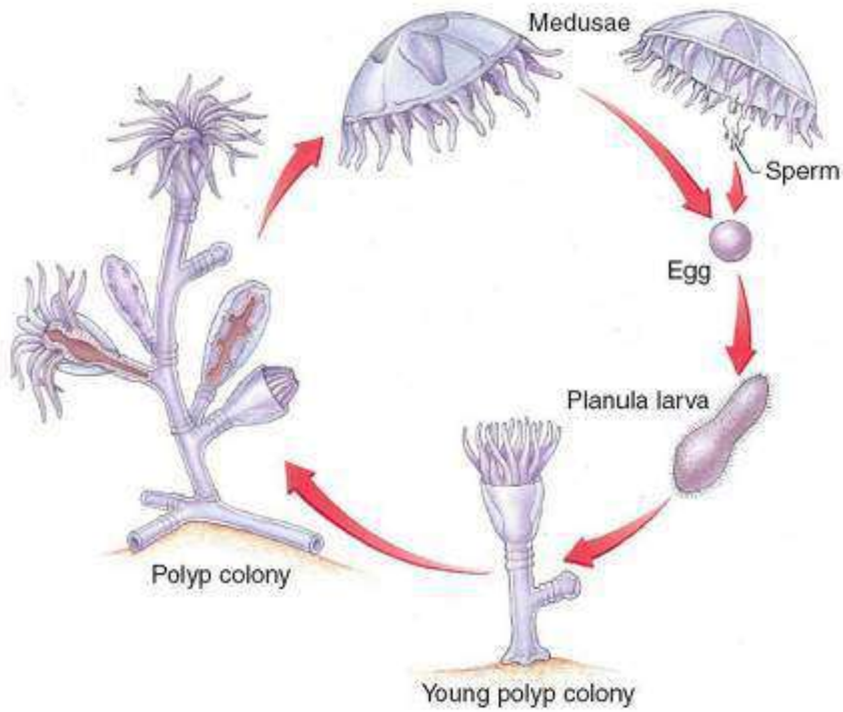


Figure 6.10. Reproduction in *Obelia*, a typical hydrozoan showing the medusa and polyp phases. The benthic polyp reproduces asexually to produce medusae, which reproduce sexually.

Anthozoans have a well-developed polyp stage and a reduced or absent medusa stage. Asexual reproduction is common for most anthozoans, and fragmentation is an important mode of reproduction in some tropical corals. Moreover, large coral colonies are created by the asexual reproduction of polyps through budding. As there is no medusa stage, sexual reproduction is conducted by the benthic polyps which release their gametes in the water column. This is often timed with lunar cycles and other environmental cues to form mass spawning that may include several different species (e.g. in tropical corals). Mass spawning of several species has the advantage of overwhelming predators with a large amount of eggs at the same time, thereby reducing the mortality of eggs and larvae.

6.3.5. Ecological Roles of Cnidarians

Many cnidarians are important predators and catch prey with their tentacles and stinging cells, therefore they have few predators themselves. However some species are adapted to eat jellyfish, including several sea turtles and some fishes, and the crown-of-thorns starfish is an important predator of corals in the Indo-Pacific.

Reef-building corals create the largest living structure on the planet, which is a three-dimensional habitat for many other species and offers a solid substrate for attachment of benthic organisms. Tropical coral reefs are one of the environments with the highest species diversity on earth. Moreover, they are important wave buffers and protect the coast from storm damage.

Cnidarians form symbiotic relationships with many other organisms. The most obvious is probably the zooxanthellae that live in the tissues of hard corals and provide them with food and oxygen while receiving shelter, carbon dioxide and nutrients. Sea anemones are often found with anemone fish (clown fish) or cleaner shrimps. These organisms are immune to the sting of the anemone and find shelter in its tentacles. Many sea anemones and hydrozoans are found on the shell of hermit crabs. As they move around with the crab they are exposed to more sources of food than they would by remaining in the same location.

6.4. Phylum Ctenophora: Comb Jellies

Ctenophores are planktonic, nearly transparent and exhibit radial symmetry (Figure 6.10). At first glance they look similar to jellyfish, but they lack stinging cells and have eight rows of comb plates (ctenes). Ctenes are composed of large cilia that propel the animal with their beating. Ctenophores do not have rings of tentacles that surround their mouth like jellyfish, although some have two long tentacles that are lined with adhesive cells and used in catching prey. Many ctenophores are iridescent during the day and luminescent at night, and their bioluminescence is thought to be used to attract mates or scare predators.

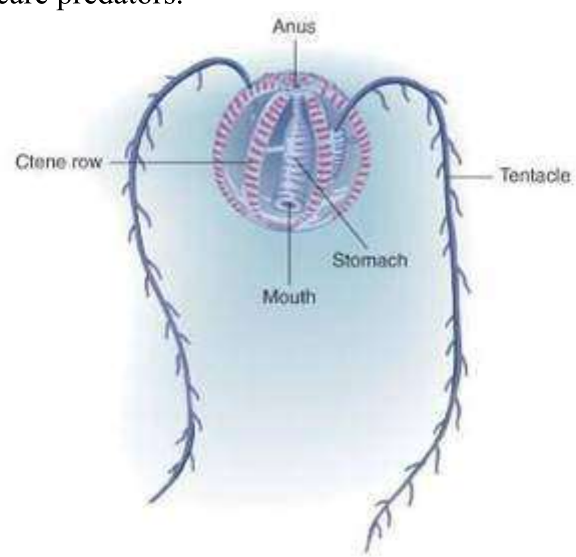


Figure 6.10. A ctenophore showing rows of ctenes and tentacles lined with sticky cells.

Ctenophores are carnivorous and are important predators of smaller plankton. Ctenophores catch prey with the adhesive cells on their tentacles and carry them to their mouth. Ctenophores have the beginnings of a complete digestive tract but although they have anal pores, most expel undigested food back through their mouth like cnidarians. Some ctenophores prey on jellyfish, and can incorporate the cnida of their prey and use them to capture subsequent prey.

Almost all ctenophores are hermaphrodites. Most release their gametes in the water column, where fertilization occurs. Some brood the eggs in their bodies.

6.5. Review Questions: Sponges, Cnidarians and Ctenophores

1. What are 4 distinctive characteristics of animals?

2. What is the phylum that contains sponges?

3. What is the name of the incurrent and excurrent pores in sponge?

4. Are the cells in sponges organized into tissues and organs?

5. What are choanocytes (collar cells)?

6. What is the role of spicules?

7. What are spicules made of?

8. What is spongin?

9. How do sponges reproduce asexually?

10. How do sponges eat? Where does digestion occur?

11. How do sponges prevent predation?

12. Give an example of commensalism involving sponges?

13. Which organisms are members of the phylum Cnidaria?

14. What is the benefit of radial symmetry in the cnidarians?

15. What are the two types of cnidarian body plans?

16. What is an example of a spearing type of stinging organelle?

17. What triggers the stinging cells in cnidaria?

18. Give an example of a member of the class Hydrozoa?

19. What is the skeleton of fire coral made of?

20. Is the Portuguese Man-Of-War an example of a solitary or colonial hydrozoan?

21. Give an example of a member of the class Scyphozoan?

22. Is jellyfish part of the plankton?

23. Give an example of a member of the class Anthozoan?

24. What is the skeleton of hard coral made from?

25. Do cnidarians have an anus?

26. How does the upside-down jellyfish obtain its food?

27. How do hard corals feed?

28. What are the advantages of mass spawning in hard corals?

34. How do corals reproduce asexually?

35. Give an example of a serious coral predator in the Pacific?

36. Give an example of a mutualistic symbiotic relationship involving Cnidaria?

37. Can a ctenophore sting you?

38. Describe the life cycle of a typical hydrozoan

39. How do corals reproduce?

40. How many tentacles would you expect on the polyp of a soft coral?

41. Explain three differences between scyphozoans and ctenophores.

7. Worms, Bryozoans and Mollusks (Karleskint Chapters 8 & 9)

7.1. Bilateral symmetry

Animals covered in the previous section show no symmetry (sponges) or radial symmetry (Cnidarians and Ctenophores), where any plane that runs through the center of the animal separates two identical halves. The majority of animals, however, exhibit bilateral symmetry, in which the animal has identical parts on either side of an imaginary plane running from its anterior end to its posterior end (Figure 7.1). This body plan allows a more streamlined body than organisms with radial symmetry, and concentrates sense organs at one end (the head), a process known as cephalization. Bilateral symmetry is usually advantageous for animals with an active lifestyle.

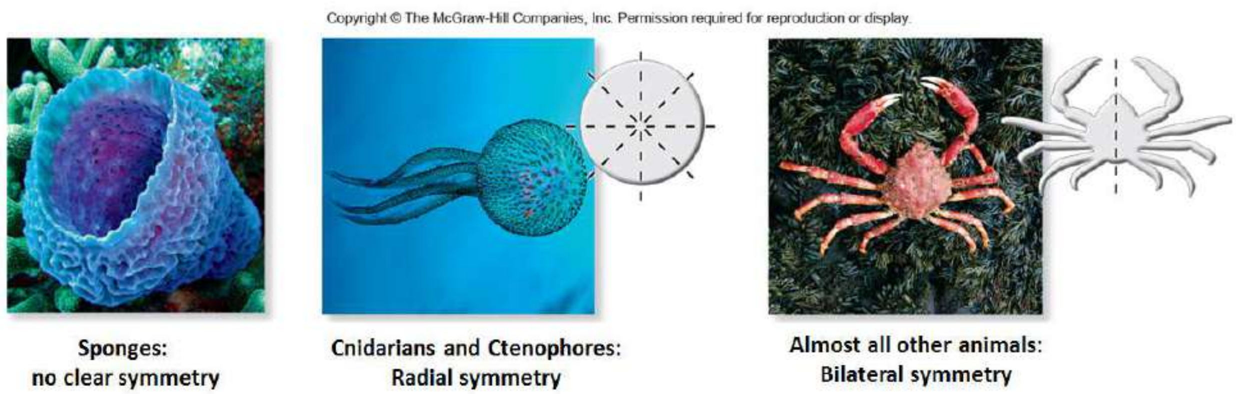


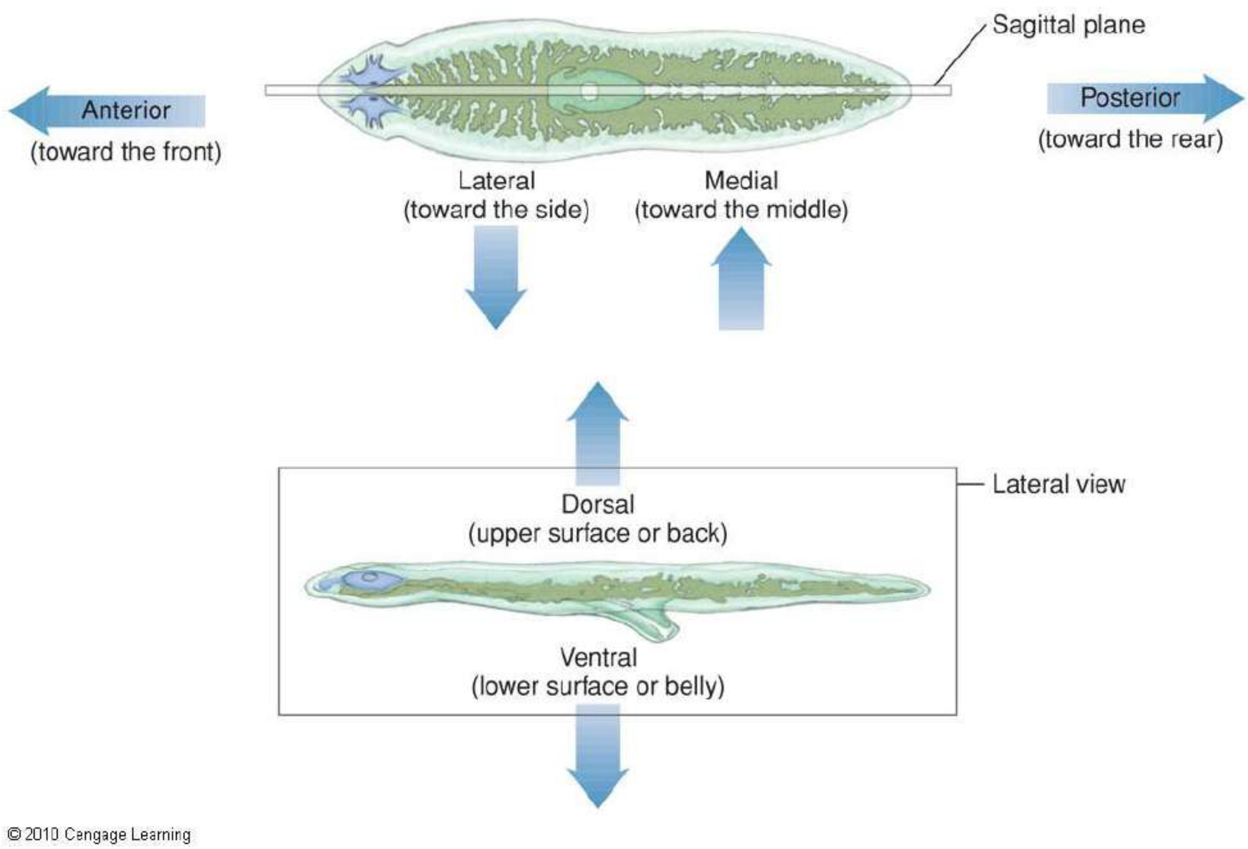
Figure 7.1. Types of symmetry found in various groups of animals

7.2. Marine Worms

Marine worms have elongated bodies and lack any external skeleton. They gain support for their body from fluid contained in body compartments, known as a hydrostatic skeleton. Marine worms are a very large group comprising many different phyla. This chapter will cover only a few of the important groups of worms.

7.2.1. Platyhelminthes (Flatworms)

Structure and description
Flatworms, as their name suggests, have a flattened body. They show bilateral symmetry, with a head and a posterior end (Figure 7.2). They have eye spots that allow them to sense differences in light intensity (for example, the shadow of a predator above). Flatworms have a blind gut, and like cnidarians, their waste products are expelled back through their mouth. Some flatworms are free-living while others are parasitic. Free-living flatworms move by gliding on their ventral side through the action of cilia.



7.2. Typical platyhelminthe, showing bilateral symmetry and cephalization.

Groups of Platyhelmintes

Turbellarians are a group of free-living flatworms, which measure from a few millimeters to 50 cm long. Most are benthic, and they are often found in the meiofauna, occupying interstitial spaces between sediment grains. They are common in the Arctic and Antarctic waters, where they feed on sea ice diatoms. There are also several colorful species of Turbellarians that are regularly seen on tropical coral reefs.

Flukes are parasitic worms with a complex life cycle, frequently involving several hosts. Tapeworms are parasites that live in the digestive tract of their host. They can get quite large, and may attain 30m long in whales (Figure 7.3).

Figure 7.3. Representatives of the Phylum Platyhelminthes: turbellarian (left), fluke (middle) and tapeworm with fish host (right).

Nutrition and Digestion
Most free-living flatworms are carnivorous and feed on small invertebrates. They have chemoreceptors to help locate their prey. Flatworms have various strategies to catch and eat their prey; some entangle their prey in mucus to suffocate it, others stab their prey with a sharp penis (stylet) that comes out of their mouths. The food is digested externally or in the gastrovascular cavity. Wastes from digestion are ejected through the mouth.

Reproduction
Flatworms can reproduce both asexually or sexually. Asexual reproduction enables regeneration of missing body parts. Flatworms are typically hermaphrodites and sexual reproduction involves reciprocal copulation and internal fertilization. In many species, sperm is inserted through the skin of the mate with the sharp stylet in a process called traumatic insemination.

7.2.2. Nematodes (Round Worms)
Nematodes are the most numerous animals on earth, and can be found in densities of up to 4,400,000 individuals/m^2 in some sediments. Their body is cylindrical and elongated, tapered at both ends (Figure 7.4). Most of them are small (less than 5cm) but some can reach lengths of over 1m. Nematodes may be scavengers, parasites, predators, or eat algae and bacteria. They have a complete digestive tract with separate mouth and anus. Most are hermaphrodites.

Figure 7.4. Nematode worms.

7.2.3. Annelids (Segmented Worms)
The bodies of segmented worms are divided internally and externally into repeated segments (Figure 7.5), which allows them to have increased mobility with a more efficient hydrostatic skeleton. Their body wall has longitudinal and circular muscles for movement: crawling, swimming and burrowing. Their skin often has bristles (setae) that can be used for locomotion, digging, or protection. Annelids have a complete digestive

tract with a mouth and an anus. The most common marine annelids are polychaetes, which live in various habitats: sand, mud, under rocks, in crevices, or in tubes they create. Many are mobile, or errant, others are sedentary.

Figure 7.5. Annelid worm showing repeated segments. This bearded fireworm (*Hermodice* sp.) has calcareous setae which break off and release a poison for defense.

Feeding and Digestion

Errant polychaetes tend to be predators or deposit feeders. Many are active predators feed on small invertebrates, dead animals and algae. Many have jaws or teeth to catch their prey. Non-selective deposit feeders (e.g. lugworms, *Arenicola*) ingest sediment and digest the organic matter in it, releasing the non-digestible mineral particles in their feces as mounds of sediments called fecal casts (Figure 7.6). Selective deposit feeders (e.g. spaghetti worm, *Eupolymnia crassicornis*) separate organic materials from minerals and ingest the organic matter (Figure 7.6).

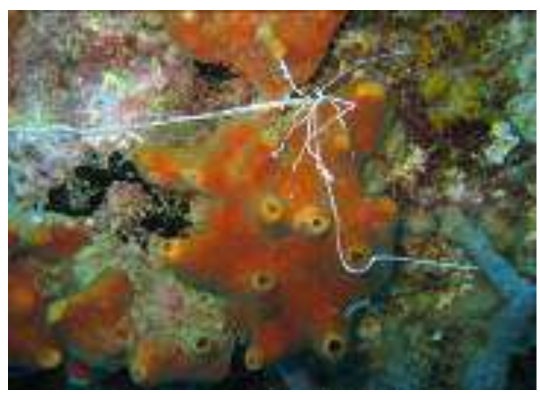


Figure 7.6. Faecal casts produced by the lugworm, a nonselective deposit feeder (left) and a spaghetti worm, a selective deposit feeder (right)

Sedentary polychaetes are either burrowers that live in sediments, or tube dwellers that construct a tube. Sedentary polychaetes are usually suspension feeders, and their head is usually modified with special feeding structures to collect detritus and plankton from the water (Figure 7.7). Food particles are then passed to the mouth.

Figure 7.7. Sedentary polychaetes showing modified head appendage used in feeding.

Reproduction
Some polychaetes can reproduce asexually, through the process of budding or division of the body into fragments. They therefore have a high ability to regenerate lost body parts, such as tentacles, the head, even nearly their entire body. However, most species only reproduce sexually and they are gonochoristic (single sexes). The gametes accumulate within the body cavity and are released through ducts or the rupture of the body cavity, in which case the adult subsequently then dies.

7.2.4. Ecological Roles of Marine Worms

Nutrient cycling
Burrowing worms can be important in recycling nutrients. Most decomposition occurs on the benthos, and through their burrowing, worms bring nutrients back to the surface where they can be used by other organisms.

Predator-prey relationship
Many small worms consume organic matter that is too small for bigger organisms and they are therefore an important link in the food chain. For example, marine nematodes, which are the most abundant meiofauna, feed on micro-organisms and detritus in the sediment and are an important source of food for fish, birds and marine invertebrates.

Symbiotic relationships
Some tube-dwelling or burrowing polychaetes provide a home for other organisms such as small crabs, bivalves or scale worms, in a commensal symbiotic relationship.

7.3. Bryozoans (Phylum Bryozoa)

Bryozoans are part of a group called the lophophorates. Lophophorates have bilateral symmetry, but lack a distinct head. They possess a feeding and gas exchange appendage called a lophophore, composed of ciliated tentacles that surround the mouth. They have a completed digestive tract shaped like a U, which means that they excrete their wastes close to their mouths (Figure 7.8). There are 3 phyla of lophophorates, but here we will only consider the most important, the bryozoans.

Bryozoans are sessile and live in a variety of habitats, including on seaweeds and are very abundant, especially in shallow water. They form colonies of small animals called zooids that live in box-like chambers. They are filter feeders and are important fouling organisms.

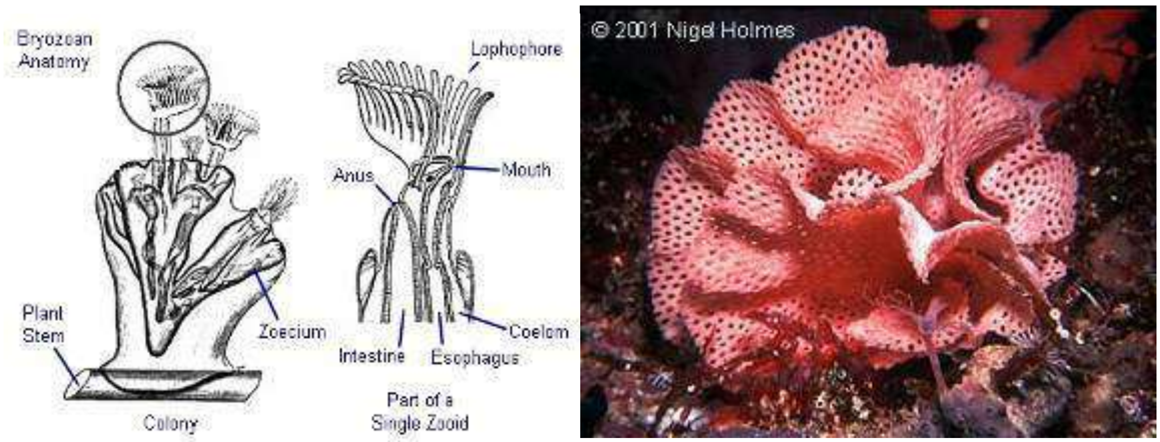


Figure 7.8. Bryozoan anatomy and bryozoan colony, phylum Ectoprocta.

7.3. Mollusks

Mollusks are a large and varied group of animals that have a soft body and are most often covered with a calcium carbonate shell. Their body is divided into two major parts (Figure 7.9). The head-foot region includes the head, mouth, sensory organs and the foot, which is usually used for locomotion. The visceral mass includes all the other organ systems. The mantle of mollusks covers the visceral mass and hangs from the sides of the body. The mantle produces the shell (when present) and in some groups is used in locomotion or gas exchange. All mollusks except bivalves have a radula (Figure 7.10), a ribbon of tissue that contains teeth, used for scraping, tearing, piercing and cutting.

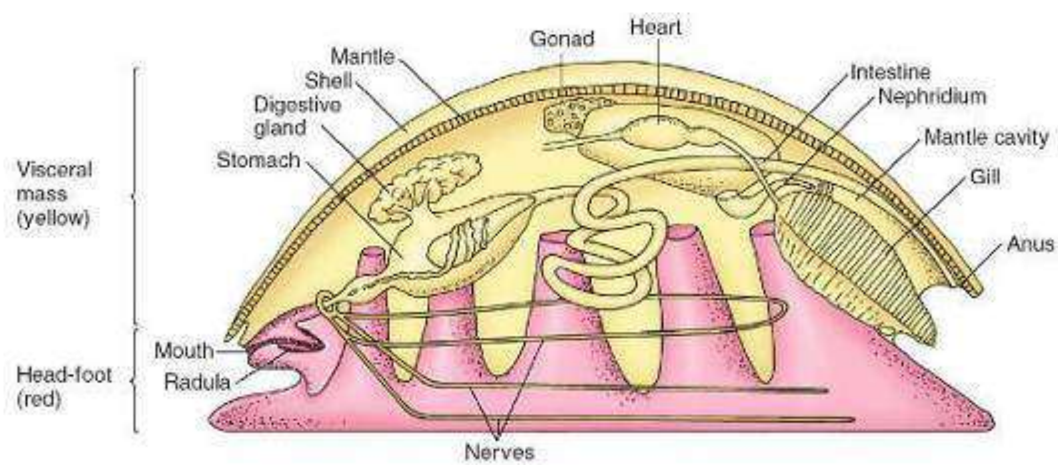


Figure 7.9. Hypothetical mollusk showing the head-foot region, visceral mass and mantle.

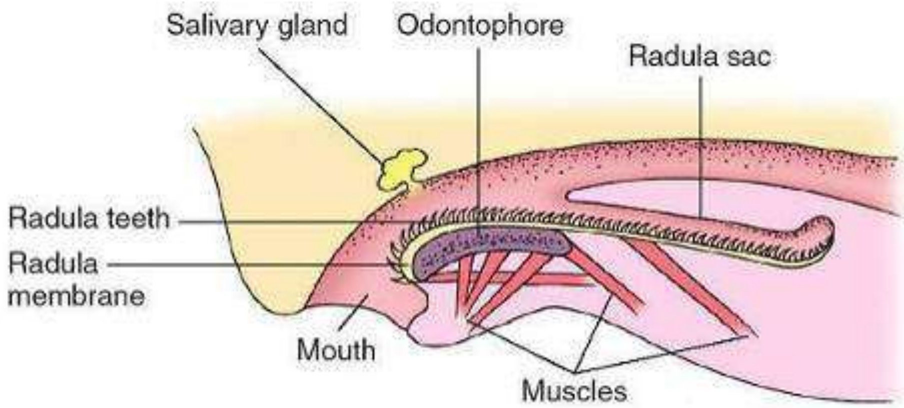


Figure 7.10. Radula of mollusks.

7.3.1. Chitons (Class Polyplacophora)

Chitons have a flattened body covered by eight calcareous plates held together by a girdle (Figure 7.11). Chitons are common in the intertidal zone, where they attach to rocks and scrape off algae and other organisms with their radula.



Figure 7.11. Chiton (left) and microscopic details of radula (right).

7.3.2. Gastropods (Class Gastropoda)

Gastropods move by sliding along the bottom on their foot. Most gastropods have a shell, which may be coiled (e.g. snails) or not (e.g. limpets) (Figure 7.10). Others, the nudibranchs, lack a shell. Many snails can retreat in their shell and close the aperture with the operculum (Figure 7.12), which can be used as defense or to reduce water loss in the intertidal zone. The shape of the shell reflects the environment a snail is adapted to live in, for example; snails that live in exposed intertidal zones often have low, broad shells that reduce drag and allow them to cling to rocks.

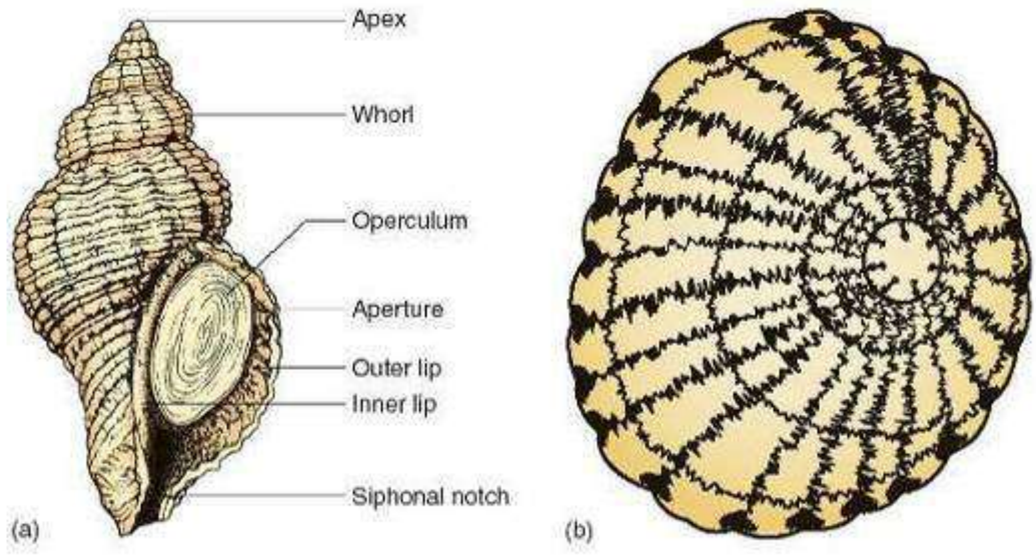


Figure 7.12. Gastropods: snail (left) and limpet (right).

Feeding and Nutrition
Gastropods have wide range of feeding strategies. Herbivores usually eat small algae that they scrape off rocks with their radula. Some can eat seaweeds, such as kelp. Carnivorous gastropods locate their prey with chemical cues, and eat a variety of prey including cnidarians, echinoderms and bivalves. Cone snails have a modified harpoon-like radula which is coated with a toxin and allows them to kill their prey. Other gastropods are scavengers, deposit feeders (e.g. conch) or filter feeders (e.g. sea butterfly, Figure 7.13).

Figure 7.13. The sea butterfly, a planktonic gastropod mollusk. Not the lack of shell, which is advantageous for staying afloat in the water column.

Nudibranchs
Nudibranchs are marine gastropods that lack a shell (Figure 7.14). They are often bright in color, which may be an indication of toxicity. Many have cerata on their back,

extensions of the mantle that increase the surface area of the mantle available for gas exchange. Some nudibranchs will feed on cnidaria and retain their nematocysts as protection for themselves.

Figure 7.14. Nudibranchs showing cerrata.

7.3.3. Bivalves (Class Bivalvia)

The body of bivalves is compressed laterally, and they have two valves (shells) attached dorsally by ligaments. The valves are closed by adductor muscles and opened as the muscles relax and the weight of the valves pulls it apart. Bivalves have no head or radula, and their foot is located ventrally and functions in burrowing and locomotion. Their mantle forms inhalant and exhalent openings and cilia on the gills move water, exchange gases, and filter food particles that are then brought to the mouth (Figure 7.15)

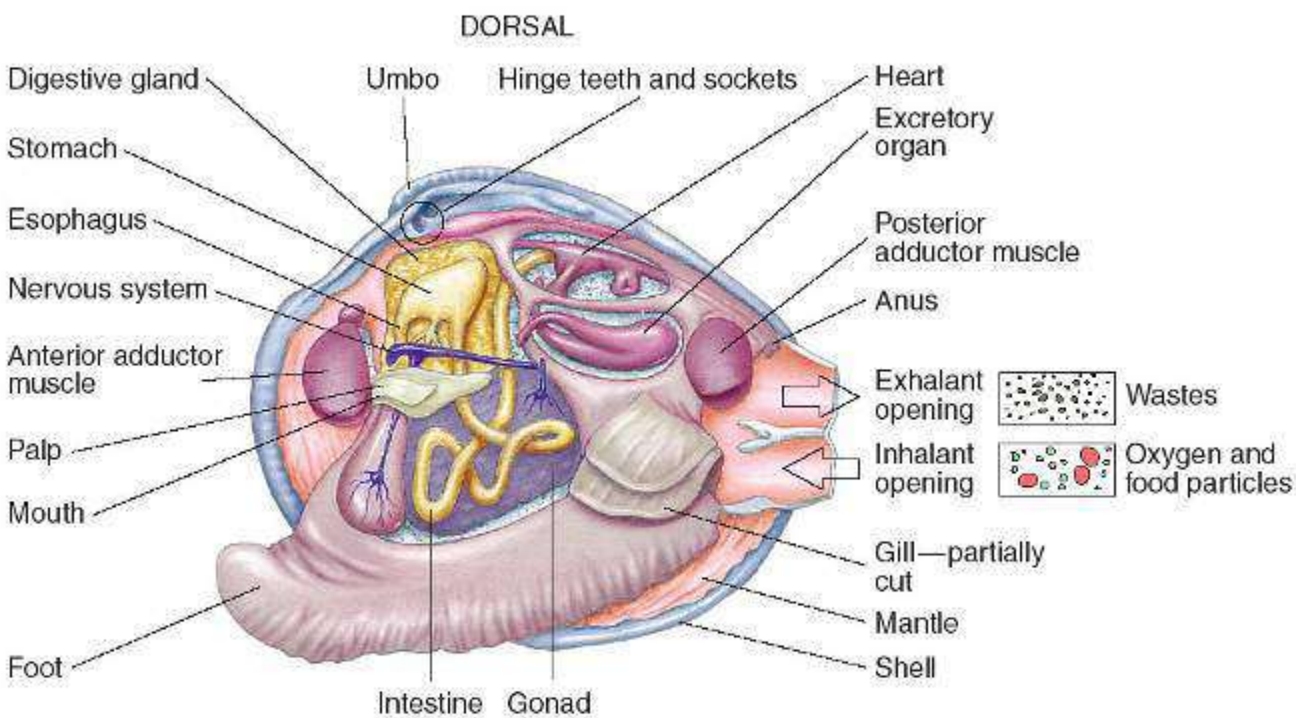


Figure 7.15. Longitudinal section of a bivalve.

Bivalves have evolved adaptations to live in a variety of different habitats. Those that burrow in soft bottoms (infauna), such as clams, often have their mantle fused around their inhalant and exhalant openings, creating a siphon that can draw water in from above the sediment. Others live attached to the surface of hard substrates (epifauna), and may attach by cementing one valve to the substrate (e.g. oysters), or by byssus threads, made from a tough protein (e.g. mussels). Unattached surface dwellers such as scallops and file clams can swim by jet propulsion as they open and close their valves rapidly. Boring bivalves include some boring clams which live in soft rocks, and shipworms, which burrow into wood by swallowing and digesting the wood, with the help of enzymes from their symbiotic bacteria.

7.3.4. Cephalopods (Class Cephalopoda)

The foot of cephalopods is modified into a head-like structure, and they have a ring of tentacles that projects from the anterior end of the head. The tentacles are used to capture prey, for defense, reproduction and locomotion. With the exception of the Nautilus, cephalopods lack a shell or have a small internal shell. Most cephalopods can move by jet propulsion, where water is taken into the mantle, then channeled through a small funnel and expelled. The funnel directs the flow of water and therefore the direction of movement. Some, like octopus, can also crawl on the benthos.

Nautiloid Cephalopods

These cephalopods have a large, coiled shell with multiple chambers filled with gas which can be used to regulate buoyancy. The animal itself lives in the last chamber. Nautiloids have 60 to 90 tentacles, many of which have chemosensory and tactile functions, while others bring food to the mouth. They commonly come to the surface at night, although they feed on the bottom during the day.

Figure 7.16. Nautilus, live (left) and section of shell (right).

Coleoid Cephalopods

Coleoid cephalopods include squids, octopus and cuttlefish. These cephalopods have the most complex nervous system of all invertebrates, and have highly developed eyes and well-developed tactile senses. They release a cloud of ink when disturbed to distract predators. Squids have a large cylindrical body with a pair of fins derived from the mantle. Squids have an internal shell remnant called a pen which is made of flexible, hard protein. Cuttlefish are similar to squids but have a wider body and their shell remnant, the cuttlebone, is larger than the squid's pen and made of calcium carbonate. Both squids and cuttlefish have 10 appendages: eight short arms and two long tentacles. Octopuses have eight arms and no tentacles. Their bodies are sac-like and lack fins, and since they have no shell at all they are very flexible and can fit into very small openings.

Figure 7.17. Coleoid cephalopds: octopus (left) and cuttlefish (right).

Color and Shape in Cephalopods
Cephalopods have an impressive ability to change color, pattern and texture, which is used in communication and camouflage. They can achieve this by modifying the distribution of pigments in specialized cells in their skin called chromatophores.

Feeding and Nutrition in Cephalopods
Most cephalopods are carnivores. They locate their prey visually and capture it with their arms and tentacles. Cephalopods have a radula, but they mostly use their large beak to bite their prey; the salivary gland in octopus and cuttlefish produces a poison. The actual diet depends on the species and its habitat.

Reproduction in Cephalopods
Sexes are usually separate, and mating involves a courtship display. Many species reproduce only once and then die.

7.3.5. Ecological Roles of Mollusks
Mollusks are an important source of food for many marine animals as well as for humans. Sperm whales consume high numbers of squids. Gastropod shells and cuttlebones can be an important source of calcium for some seabirds. Shipworm can damage wooden boat and wood pilings.

7.4. Review Questions: Marine Worms, Bryozoans and Mollusks

1. Why is bilateral symmetry favored in platyhelminthes (flatworms)?

2. What is cephalization?

3. Some flatworms reproduce sexually by reciprocal copulation. What does this mean?

4. What phylum do round worms belong to?

5. Give an example of an annelid with toxins in its setae?

6. What are characteristic features of annelids?

7. How does a typical errant polychaete move?

8. How does a typical round worm move?

9. What are the most common annelids in the marine environment?

10. What type of feeding is characteristic of sedentary polychaetes?

11. Give an example of a sedentary polychaete worm?

12. What part of the mollusk produces the shell?

13. What is the radula of a mollusk?

14. What phylum and class contains chitons?

15. Do all members of the class Gastropoda have a shell?

16. What is the operculum?

17. Are all gastropods herbivores?

18. Which phylum contains Bivalves?

19. What is the role of byssus threads in mussels?

20. Describe the shell of the Nautilus?

21. What are chromatophores?

22. What is the name of the individual animals that make up a colony of Bryozoans?

23. What is the name of the crown of tentacles on the head of a bryozoan?

24. How many appendages do coleoid cephalopods have?

25. Which class of mollusk has a complex eye similar to vertebrates?

26. Which phylum includes the segmented worms?

27. Are any polychaetes detritivores?

28. Do flat worms have an anus?

29. Which class of mollusks has the most complex brain?

30. Which class of mollusks has 2 valves?

31. What is the name given to pelagic gastropods with reduced shells?

32. Do annelids have a complete digestive tract?

33. True or false. All nematodes are parasites.

34. True or false. Some flatworms are parasites.

8. Arthropods, Echinoderms and Invertebrate Chordates
(Karleskint Chapter 9)

8.1. Arthropods (Phylum Arthropoda)

Arthropods are an extremely diverse group; they include terrestrial insects and represent 75% of all animal species. Arthropods have an exoskeleton made of chitin, which provides protection and a point of attachment for muscles. However this exoskeleton does not grow with the animal, and arthropods have to molt periodically in order to grow.

The body of arthropods is divided into segments, and each usually has a pair of appendages that can be sensory, or used in locomotion or feeding. They have a highly developed nervous system with sophisticated sense organs.

Marine arthropods can be divided into two major groups: the chelicerates and the mandibulates. The subphylum Crustacean makes up the vast majority of mandibulates. The taxonomy of arthropods is still debated by scientists and the exact grouping of the various taxa changes from textbook to textbook. Table 1 shows the classification used in this class for the organisms that will be covered.

Table 1. Taxonomic classification of some important groups of marine arthropods.

Subphylum	**Class**	**Order**	**Common name**
Chelicerata	Merostomata	Xiphosura	Horseshoe crab
Crustacea	Malacostraca	Decapoda	Lobsters, crabs, shrimps
		Euphausiacea	Krill
		Amphipoda	Amphipods
		Stomatopoda	Mantis shrimps
	Copepoda	Various	Copepods
	Cirripedia	Various	Barnacles

8.1.1. Chelicerates (subphylum Chelicerata)

Chelicerates are a primitive group of arthropods that includes spiders, ticks and scorpions. Marine chelicerates have bodies composed of 3 parts; this group includes horseshoe crabs and sea spiders. Chelicerates have 6 pairs of appendages, one of which, the chelicerae, is an oral appendage modified for feeding. They lack mouthparts for chewing and predigest their food externally before sucking it up in a semi-liquid form.

Horseshoe crabs are chelicerates and therefore more closely related to spiders than to true crabs. They live in shallow coastal waters and their body has three regions: the cephalothorax, which contains most appendages, the abdomen, which contains the gills and the telson, which is a long spike used in steering and for defense (Figure 8.1). Horseshoe crabs are mostly scavengers and feed on dead invertebrates, small fish and algae.

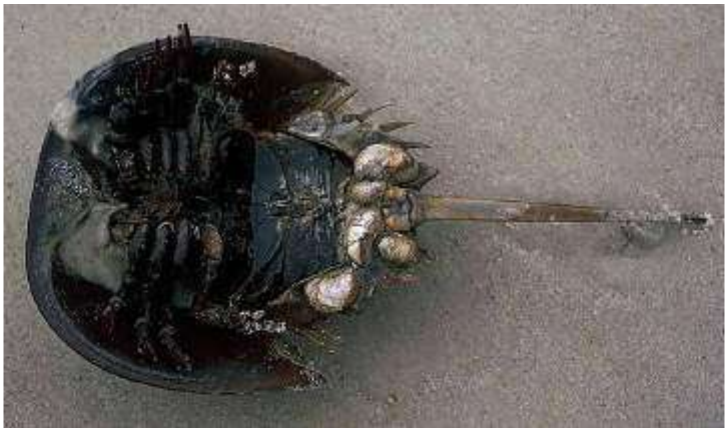


Figure 8.1. A horseshoe crab, subphylum Chelicerata.

8.1.2. Mandibulates

In mandibulates, the feeding appendages are called mandibles and they are used to crush and chew food before it is ingested. Marine mandibulates belong to the subphylum Crustacea.

The body of crustaceans is segmented and can be divided into the head, thorax and abdomen. In some species (e.g. lobsters), the head and thorax are fused together to form the cephalothorax (Figure 8.2). Each segment has a pair of appendages that have a specific function. All crustaceans have 2 pairs of sensory antennae, and depending on the species they may also have walking legs, swimmerets (for swimming) and chelipeds (for defense).

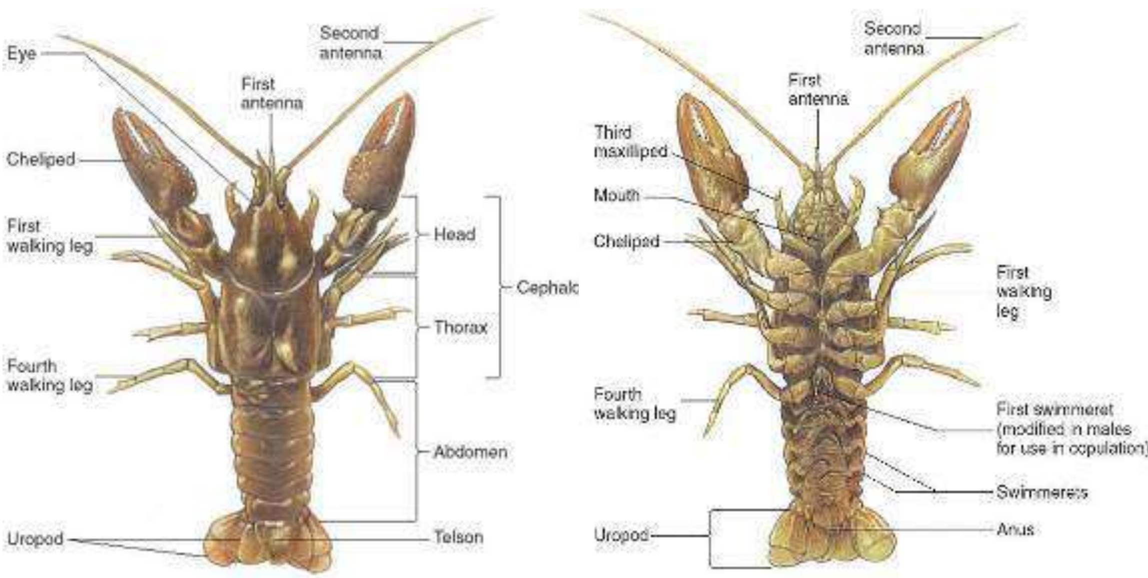


Figure 8.2. Anatomy of a lobster, subphylum Crustacea.

Crustaceans, like all arthropods, have to molt as they grow. Molting is controlled by hormones and is often initiated by changes in environmental conditions. The frequency of molting decreases with age. Crustaceans are much more vulnerable immediately after molting, and often seek a hiding place until their new exoskeleton hardens.

Decapods

Decapods are a group of crustaceans with five pairs of walking legs. The first pair is often modified into chelipeds (pincers) used in catching prey and in defense. Decapods include lobsters, crabs and true shrimps (Figure 8.3).

Figure 8.3. Lobster and shrimp, Order Decapoda.

Many decapods exhibit specialized behaviors. Hermit crabs live in the discarded shells of gastropods, and must find larger shells as they molt and grow. Decorator crabs attach other organisms to their shells for camouflage. The last pair of legs of blue crabs has been modified into paddles, allowing them to be very powerful and agile swimmers.

Many decapods are predators, and can use their chelipeds to catch prey. Others are scavengers, deposit feeders or filter feeders. Food is ground using the mandibles and plates in the stomach.

Mantis Shrimp

Mantis shrimps are highly specialized predators that range in size from 5 cm to 36 cm. Their second pair of thoracic appendages is enlarged and they have a movable finger that can be extended very rapidly to spear and smash prey and in defense. They can even smash aquarium glass (Figure 8.4).

Figure 8.4. Mantis shrimp

Krill

Krill are pelagic, shrimp-like crustaceans that measure 3-6 cm in length (Figure 8.5). They are filter feeders and eat phytoplankton and other zooplankton. They occur in large swarms and one species, *Euphausia superba*, is extremely abundant in Antarctica and is the main food source for many species of marine mammals, birds and fish. One species of krill can molt so quickly it literally jumps out if its skin—this is used as a technique to avoid predation

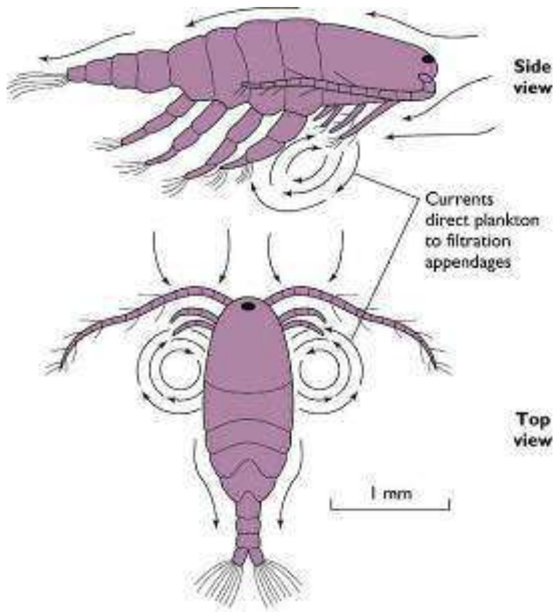
Figure 8.5. Krill

Amphipods

Amphipods resemble shrimps and are small and laterally compressed (Figure 8.6). Their posterior three appendages are directed backwards and are modified for jumping, burrowing or swimming. Many are burrowers and tube dwellers, and they can be abundant in the intertidal zone on beaches. They are commonly known as beach fleas.

Figure 8.6. Amphipods

Copepods
Copepods are the largest group of small crustaceans (Figure 8.7). They are the dominant zooplankton throughout the world's oceans. Many exhibit daily vertical migrations to feed in the photic zone at night and descend to the aphotic zone during the day (see chapter 16). They are mostly herbivorous suspension feeders.



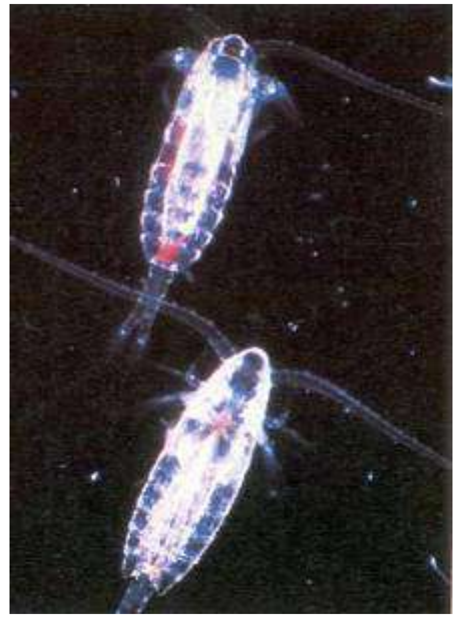


Figure 8.7. Copepods, class Copepoda.

Barnacles
Barnacles are the only sessile crustaceans (Figure 8.8). They are found on rocks, shells, hulls of boats, dock pilings and even on marine mammals. They secrete a shell made of calcium carbonate and many superficially resemble bivalves. However their taxonomic relationship to other crustaceans is clear in their larvae and internal anatomy. Upon reaching a suitable settlement site, larvae attach to the substrate by their antennae which contain adhesive glands. They then extend their cirripeds (legs) into the water to feed and exchange gas. Many are adapted to live in the intertidal zone and can close their shells at low tide to keep water in. Like many other crustaceans, barnacles reproduce sexually through internal fertilization. However because they are sessile, they have evolved the longest penis relative to body size in the entire animal kingdom, which increases the rate of successful reproduction.

Figure 8.8. Barnacles

8.1.3. Ecological Roles of Arthropods

Decapods such as crabs, lobsters and shrimps are an important source of food for humans. Copepods and krill are an important link in pelagic food chains, feeding on small phytoplankton and in turn being food for larger organisms (such as baleen whales and penguins). Many, such as cleaning shrimps, act in symbioses with other organisms by removing their parasites. Other arthropods are themselves parasites on fish (e.g. salmon lice, a type of copepod). Barnacles are important fouling organisms that can create problems for boats, sometimes reducing a ships speed by 30%.

8.2. Echinoderms (Phylum Echinodermata)

Echinodermata means "spiny skin". This phylum is a strictly marine group that includes animals such as urchins, sea stars and sea cucumbers. They have a complete digestive tract, and though their larvae show bilateral symmetry, adults exhibit modified radial symmetry (usually five part radial symmetry) which allows these slow moving organisms to respond to stimuli from all directions. They are common in shallow ecosystems and in the deep sea. Echinoderms have great powers of regeneration, giving them the ability to grow a new body part when it is lost. Some can even reproduce asexually in this way; for example a sea star cut in half will grow back into two individuals, as long as each half has a portion of the central disk. Echinoderms can also reproduce sexually through external fertilization and they release their gametes into the water column.

8.2.1. Structure of Echinoderms

Echinoderms have an endoskeleton made of calcareous ossicles (plates) held together by connective tissue. The ossicles may be fused together to form a hard test (e.g. urchins) or far apart forming a softer covering (e.g. sea cucumbers). Spines may project outward from the ossicles. Echinoderms have a unique water vascular system which is used in locomotion (through the tube feet), feeding and gas exchange (Figure 8.10). Water enters the water vascular system through the madreporite, and is pumped into the tube feet from the ampullae when it contracts, causing the feet to project. Then when the muscles in the tube feet contract water is forced back into the ampullae, and the feet shorten.

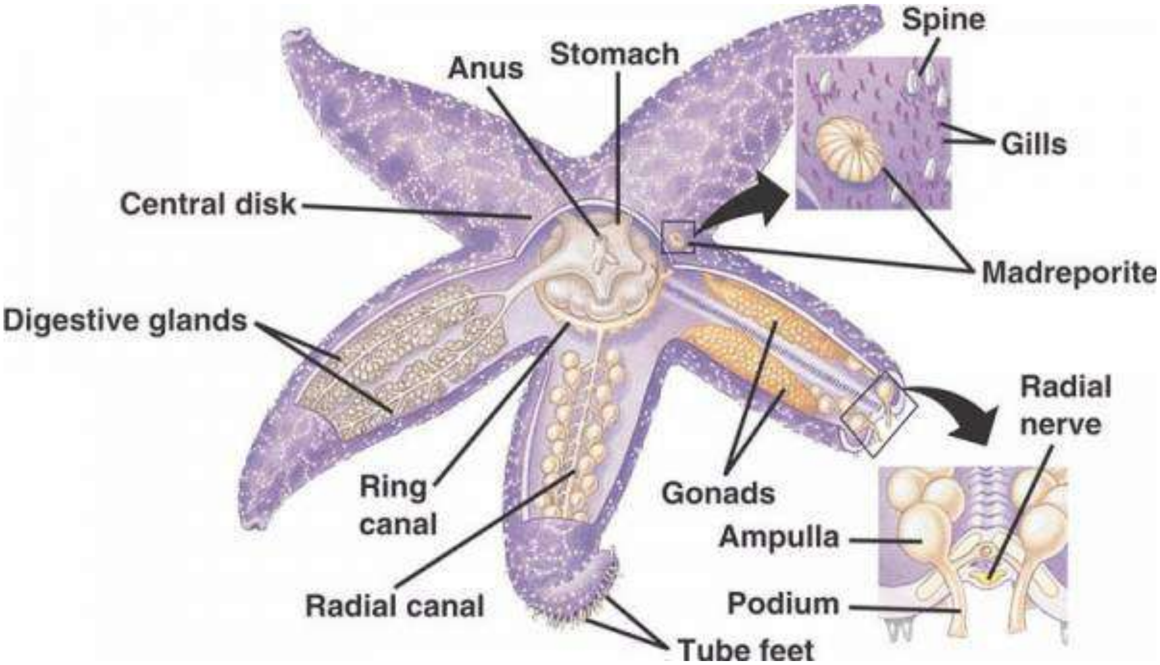


Figure 8.10. Detailed structure of a sea star, phylum Echinodermata. The water vascular system includes the madreporite, ring canal, radial canal, ampullae and tube feet.

8.2.2. Sea Stars (Class Asteroidea)

Sea stars typically have a central disk and five arms that radiate from it. Their mouth is on their underside, along with the tube feet used in locomotion, which are found in the ambulacral grooves. The top surface is often rough or spiny. Most sea stars are carnivores or scavengers, and they can evert their stomach to digest prey outside their body (Figure 8.11). Sea stars, like most echinoderms, have great power of regeneration, and can regenerate lost arms (Figure 8.11); extra arms are often produced in the process. If the lost arm includes a portion of the central disk it can also regenerate a new individual. Some species reproduce this way through division of the central disk, and each half recreates an entire individual.


Figure 8.11. Sea star eating a mussel (left) and in the process or regenerating 3 arms (right).

8.2.3. Brittle Stars (Class Ophiuroidea)
Brittle stars also have five arms, but they are more slender than those of sea stars, and are quite distinct from the central disk (Figure 8.12). They have no suckers on their tube feet, and can move their arms for locomotion. They tend to hide in crevices in the day and come out at night to feed. Brittle stars have a variety of feeding strategies, and can be carnivores, scavengers, deposit feeders or suspension feeders. For example, some species string mucous between the spines on adjacent arms to form a net.

Brittle stars can reproduce asexually through division of the central disk, like sea stars. If caught by predators, they can autotomize and cast off an arm, which undulates wildly to distract the predator. The brittle star can later regenerate the lost arm.

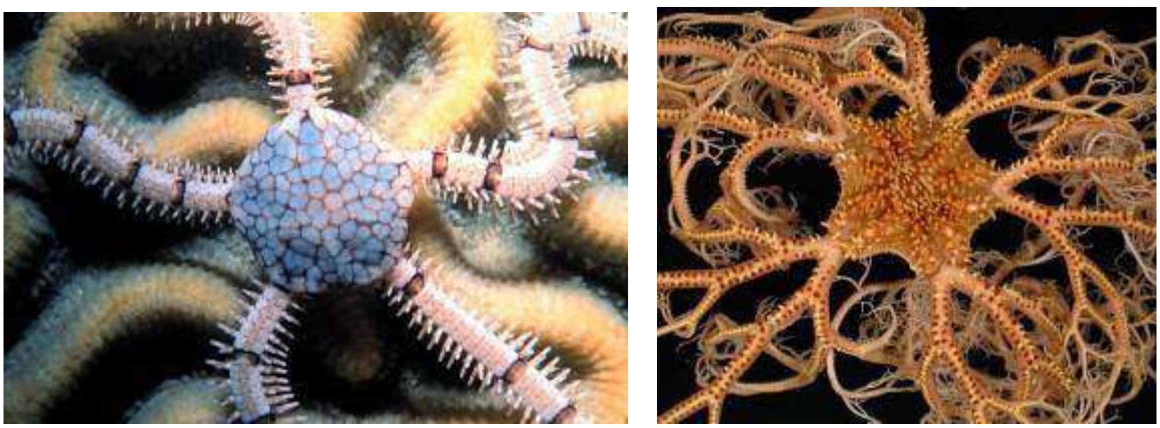


Figure 8.12. Brittle stars

8.2.4. Sea Urchins and their Relatives
The body of echinoids is enclosed by a calcareous test. Spines project from the test and function in defense, containing venom in some species (e.g. *Diadema* sp.). Spines also dissipate the energy of waves for urchins living in the intertidal zone

In regular echinoids (sea urchins), the body is roughly spherical and armed with moveable spines (Figure 8.13). The mouth is on the underside and the anus on top. They typically live on hard substrates and graze on algae with their five-part mouth parts called the Aristotle's lantern (Figure 8.14). Urchins are important herbivores in many ecosystems, including coral reefs.

Irregular echinoids (heart urchins and sand dollars) have adapted for burrowing in the sand. They are flattened and their test is covered in very small spines which function in locomotion and keeping sediment off their body (Figure 8.14). They are selective deposit feeders and consume organic material from the sediments.

Figure 8.13. Regular (left) and irregular (right) echinoids.

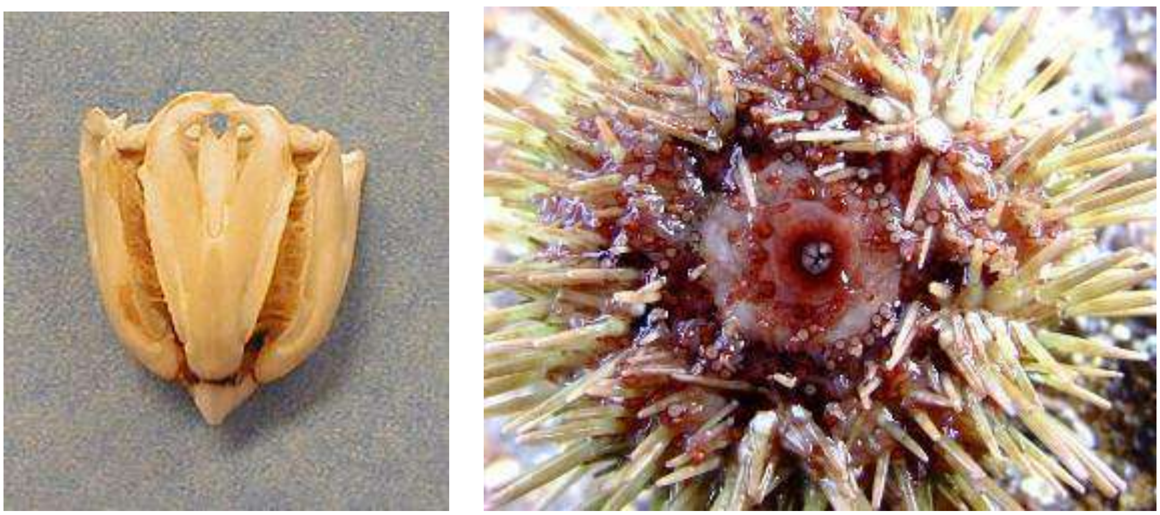


Figure 8.14. Aristotle's lantern, used in feeding in regular urchins.

8.2.5. Sea Cucumbers (Holothurians)

Sea cucumbers have an elongated body and lie on their side. Superficially they may resemble worms but the five-part radial symmetry characteristic of echinoderms is still evident, even if only internally in some species (but see also the rows of tube feet in figure 8.15). Their body wall is leathery as they have few ossicles. Like sea stars, they move with their tube feet, which are only present on their underside. Gas exchange occurs through the respiratory tree located in their anus. Sea cucumbers are deposit feeders or suspension feeders and their oral tentacles used in catching food are modified tube feet coated in mucous. Sea cucumbers are slow moving and do not have spines or an external test, therefore they have evolved interesting adaptations to avoid predation. Some species release sticky Cuvierian tubules from their anus which can immobilize crustaceans and are distasteful to fish. Others can eviscerate (release their internal organs) through their anus or mouth. Both tactics can distract the predator while the animal escapes. The sea cucumber can regenerate the Cuvierian tubules or its internal organs later on.

Figure 8.15. Sea cucumber

8.2.6. Crinoids

Crinoids are the most primitive of echinoderms. The majority of present-day crinoids are feather stars, which cling to the bottom with their grasping cirri and extend their arms into the water at night to feed. They are able to swim by undulating their arms, as an escape response. They are suspension feeders and like most echinoderms have high powers of regeneration.

8.2.7. Ecological Roles of Echinoderms

Because of their spines, echinoderms do not have many predators, but some sea otters, mollusks, crabs and fish eat sea stars and sea urchins. In some parts of the world humans eat the gonads of urchins and sea cucumbers, believed to be an aphrodisiac.

Many echinoderms are important herbivores or predators, and sometimes play a disproportionately important role in ecosystems. The crown-of-thorn sea star is a major predator of corals in the Indo-Pacific, and its population explosions, which may be caused by overfishing of their predators, threaten many Pacific reefs. The sea urchin *Diadema antillarum* is an important herbivore on Caribbean reefs, and when its population suffered from a mass mortality in the early 1980s, the resulting overgrowth of macroalgae on reefs resulted in a massive decline in coral cover (Figure 8.16). Sea urchins in temperate zones can also be very important in shaping the ecosystem; in the Northwest Atlantic the decline in sea otters allowed for an increase in the population of urchins (*Strongylocentrotus* sp.) and consequently a decline in kelps. Some sea cucumbers produce a poison that can be used to poison tide pools and suppress growth of tumours, due to its effects on nerves & muscles.

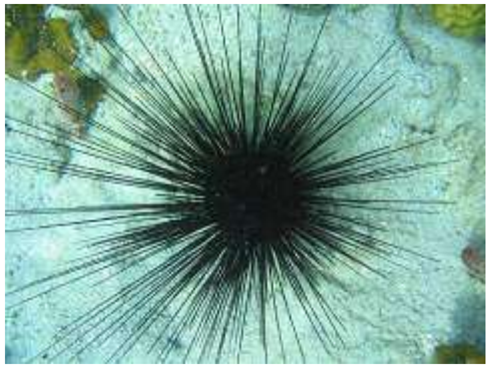


Figure 8.16. The long-spined sea urchin, *Diadema antillarum*

8.3. Tunicates (Phylum Chordata, Subphylum Urochordata)

Tunicates are mostly sessile animals named after their body covering of tunic, largely similar to cellulose. Tunicates are part of the phylum Chordata, which also includes all vertebrates. Their larvae share many features with vertebrates, including a notochord and gill clefts. However they lose those features as adults.

Sea squirts are sessile tunicates, with a round or cylindrical body (Figure 8.17). They are filter feeders with an incurrent and excurrent siphon, and food gets trapped in a mucus net in the pharynx. Sea squirts can be solitary or colonial.

Salps and larvaceans are pelagic tunicates often found in the open ocean. Their incurrent and excurrent siphons are located at opposite ends of the body. Larvaceans produce a mucous net to trap food particles, which is frequently shed every few hours when clogged. This mucus net sinks, becoming marine snow, and carries a substantial portion of the upper ocean's productivity to the deep seabed as a source of food for deep sea animals.

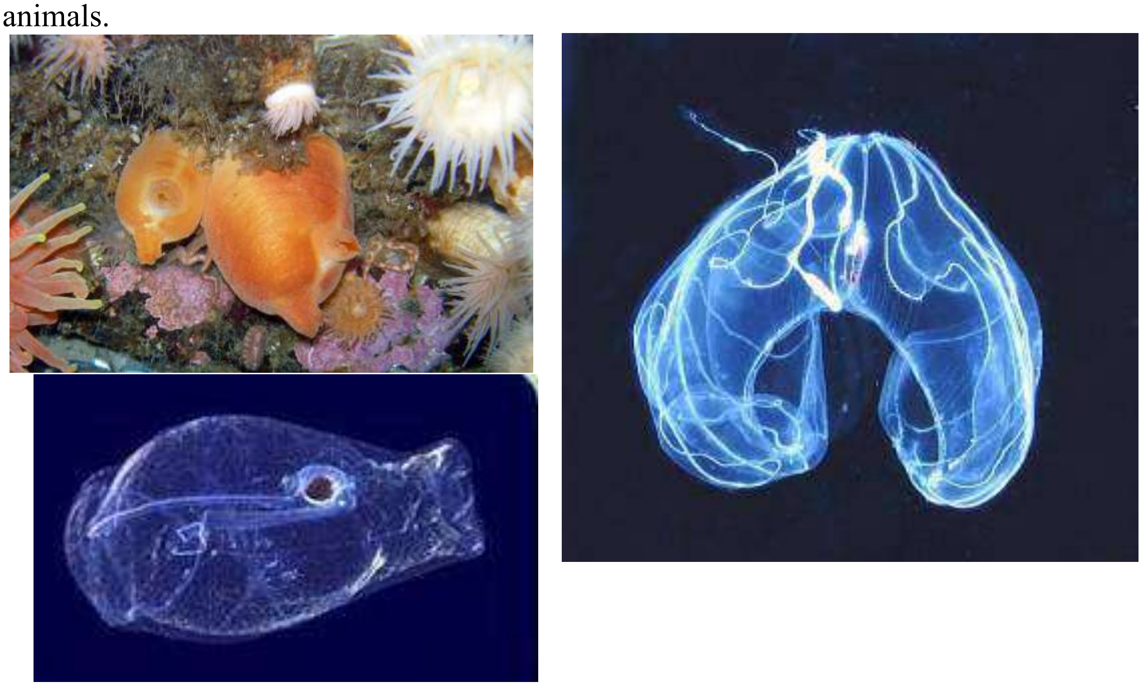


Figure 8.17. Solitary sea squirts (top left), pelagic tunicates; larvacean (right) and salps (bottom left)

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8.4. Review Questions: Arthropods, Echinoderms and Invertebrate Chordates

1. What is the exoskeleton of an organism in the Phylum Arthropoda composed of?

2. Is a horseshoe crab more closely related to a king crab or a spider?

3. Which phylum contains organisms which need to molt their exoskeleton?

4. Which subphylum of Arthropods lacks mouthparts for chewing food, and must suck up its food in a semi-liquid form?

5. Which phylum contains Crustaceans?

6. Give an example of an organism in the order Decapoda?

7. Give two examples of important crustacean zooplankton in pelagic food chains.

8. Which phylum and class do barnacles belong to?

9. What does the term echinoderm mean?

10. What is the advantage of radial symmetry shown by members of the Phylum Echinodermata?

11. What is the system unique to echinoderms that is used in locomotion, feeding and gas exchange?

12. Give an example of a member of the Phylum Echinodermata that has venom in its spines?

13. What is the name of the 5 toothed feeding structure in sea urchins?

14. Give an example of a method of defense in sea cucumbers?

15. Give an example of a pelagic Tunicate?

16. What group of crustaceans often fouls ships' bottoms?

17. Which group of small, laterally-compressed crustaceans is common on sandy beaches?

18. Why are tunicates members of the Phylum Chordata?

19. T/F: Crustaceans are all benthic.

20. What is the advantage of cephalization in Arthropods?

21. What are the defining features of Chelicerates?

22. Which group of Arthropods have 2 pairs of antennae?

23. What are mandibles? Name two species that have them.

24. What body part is used for filter feeding in barnacles?

25. What class and phylum do barnacles belong to?

26. How do barnacles reproduce?

27. What are the two main ways in which mantis shrimp catch their prey?

28. Echinoderm larvae have ________________ symmetry.

29. What is the water vascular system of echinoderms used for?

30. What are tube feet used for in echinoderms?

31. What are pedicellariae used for in echinoderms?

32. Compare and contrast sea stars and brittle stars in their morphology and ecological roles.

33. T/F: Echinoids are all herbivores.

34. What are the four features that all chordates display at some point in their lives?

9. Marine fishes (Karleskint Chapter 10)

All fishes are vertebrates and have a series of bone or cartilage that supports their spinal cord and provides attachment sites for muscles. Marine fishes can be found from the surface waters to the deepest trenches; from the highly diverse coral reef communities to the almost barren open oceans. There are more marine fish species than all other vertebrate species in the ocean combined, and they display an amazing array of adaptations enabling them to thrive in almost every ecological niche available. Fishes are a valuable resource to humans, being commercially harvested as food for humans and animals, fertilizers and many other products.

Like many other taxonomic groups, classification of fishes has been shifting as more molecular data become available. Our current understanding of fish phylogeny recognizes five main groups (Figure 9.1). The two most primitive groups, the hagfishes and lampreys, lack jaws and paired fins. The cartilaginous fishes have a skeleton made of cartilage and include sharks, rays and relatives. The ray-finned fishes have a bony skeleton and are by far the most diverse group of fishes. The lobe-finned fishes (Actinistia and Dipnoi) have a bony skeleton, with skeletal extensions into some of their fins. They share a common ancestor with land vertebrates.

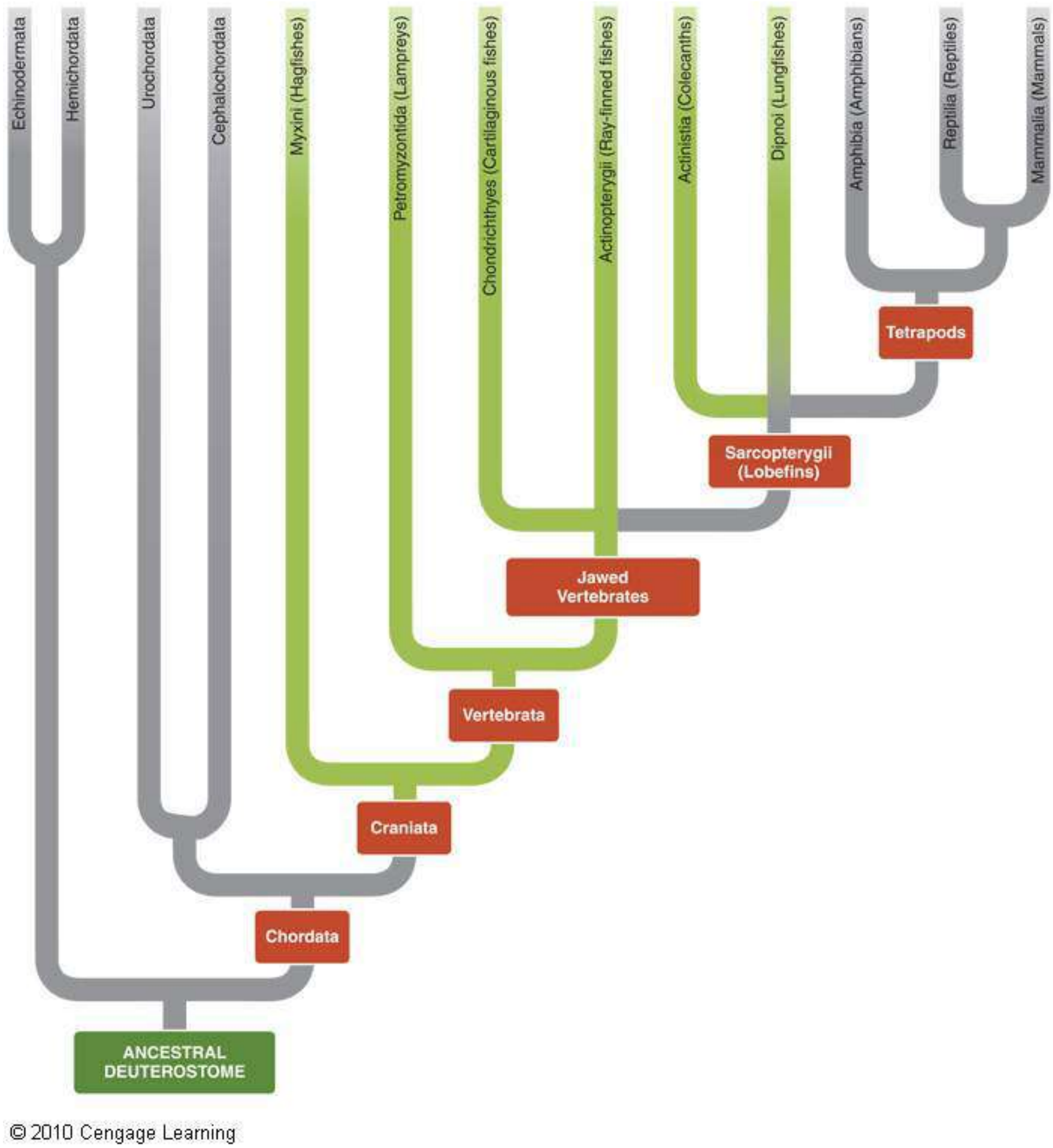

Figure 9.1. Phylogenetic tree showing relationships between groups of fishes, highlighted in green.

9.1 Jawless fish

The earlies fishes lacked both paired fins and jaws, and probably spent their time scavenging for food in the bottom sediments of the early seas. Modern jawless fish include the hagfish and lampreys which both still lack jaws and paired appendages. Their skeletons are entirely composed of cartilage and their bodies lack scales. Although superficially similar, hagfish and lampreys are morphologically and ecologically very different.

9.1.1 Hagfish – also known as slime eels.

Hagfish are deep-sea bottom dwelling fishes found throughout the world. They inhabit depths of more than 600 m, often in the tropics, although they are sometimes found in the shallower seas. Hagfish feed using two dental plates, containing horny cups, with which grab their prey and draw it into their mouth. They feed primarily on small invertebrates but may also be scavengers on larger carcasses found on the sea floor. Hagfish can produce large amounts of milky gelatinous slime when disturbed. This slime is thought to be used for protection as it coats the gills of predatory fish, either suffocating them or at least discouraging them. To remove the copious amount of slime that can build up on its body, they have the ability to tie themselves in a knot, then move the knot along their bodies and scrape off excess slime (Figure 9.2). This property is also used to gain leverage to tear flesh from large carcasses, such as whales.

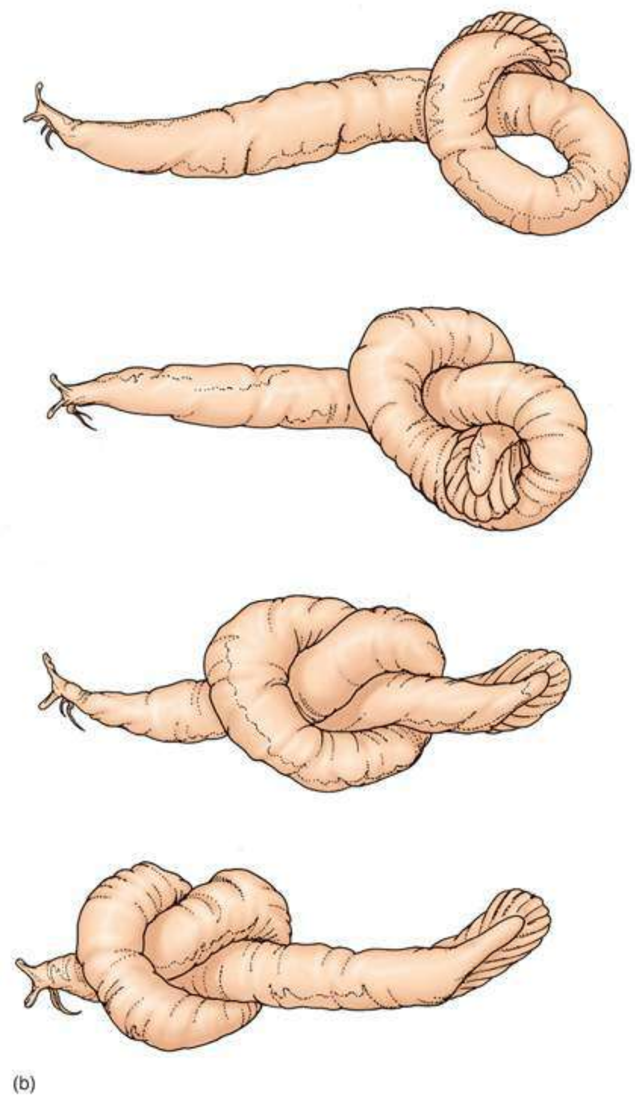

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Figure 9.2. Hagfish removing slime from its body

9.1.2 Lampreys

Lampreys can inhabit both salt and freshwater. They have a rudimentary vertebral column. Their mouthparts consist of an oral disk and rasping tongue covered with tooth-like plates of keratin (Figure 9.3). Several species use these plates to grasp prey, rasp a hole in the victim and suck out the tissue and fluids. Marine lamprey species spend their adult life in the open oceans but have been found to migrate to freshwater to spawn, where they die shortly afterwards. They have very large nerves, making them a great subject for neurobiological research.

Figure 9.3. A lamprey, showing oral disk.

9.2 Cartilaginous Fishes

Modern cartilaginous fishes include sharks, skates, rays and chimaeras, which possess both jaws and paired fins. Their skeletons are composed entirely of cartilage, although this is often strengthened by calcium salts. The bodies of cartilaginous fishes are covered in placoid scales (dermal teeth; Figure 9.4). They have several rows of teeth on their jaws. There are two major groups of cartilaginous fishes; the elasmobranchs (sharks, skates and rays) and the holocephalans (chimaeras and ratfish).

9.2.1 Sharks

Sharks typically have streamlined bodies and are excellent swimmers, using their strong body in a sideways sweeping motion. Their caudal fin is heterocercal in shape, meaning the dorsal (upper) lobe is longer than the ventral (lower) one, which gives the shark lift as it swims (Figure 9.4). The paired pelvic fins of males are modified into claspers which transfer sperm to the females when mating (Figure 9.5). Sharks do not possess swim-bladders, and so will sink if they stop swimming. To counteract this buoyancy problem, their livers contain large quantities of an oily substance called squalene, which helps to offset the shark's high density. Their heterocercal caudal fin and enlarged pectoral fins also help maintain position in the water column.

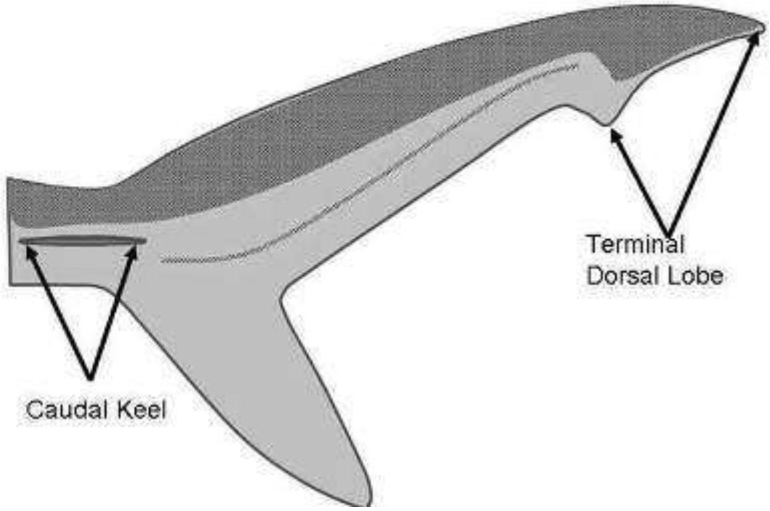


Figure 9.4. The heterocercal caudal fin of sharks

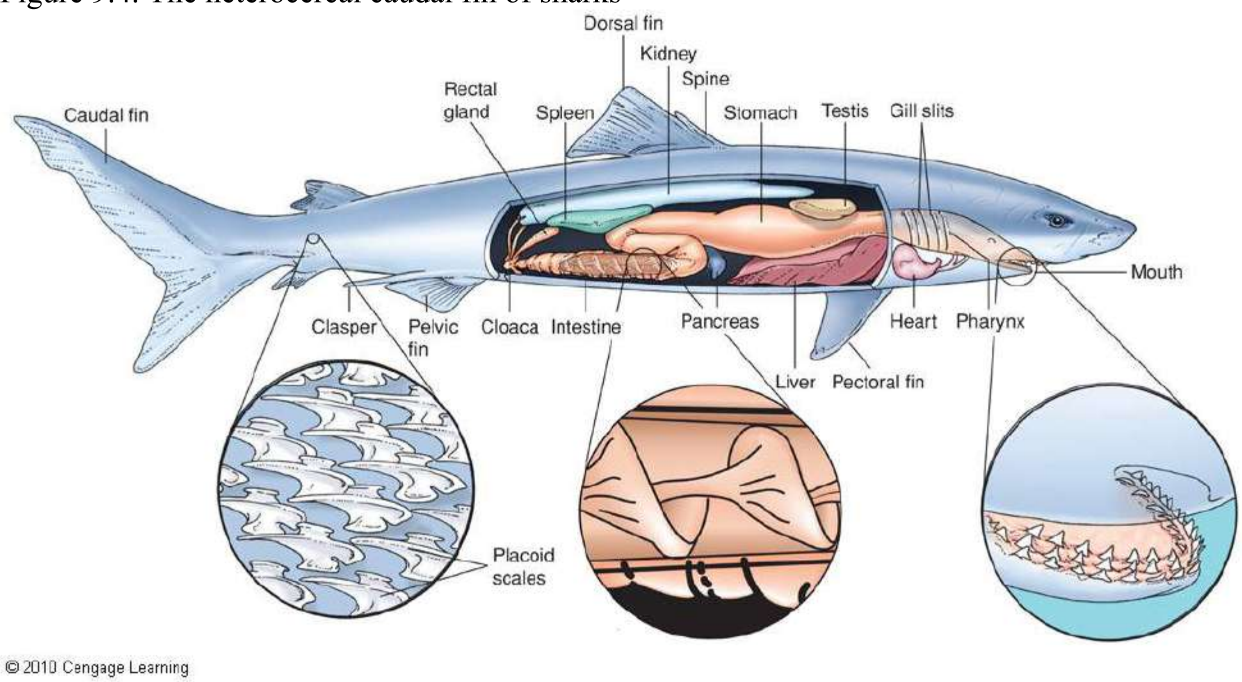


Figure 9.5. The anatomy of sharks

9.2.2 Skates and Rays

Skates and rays differ from sharks by having flattened bodies with greatly enlarged pectoral fins, reduced dorsal and caudal fins and no anal fins. Their eyes and spiracles (openings for the passage of water) are located on the top of their heads while their gill slits are on the ventral side, allowing debris-free water to enter through the spiracles and be passed out over the gills (Figure 9.6). Most skates and rays are adapted to live a benthic lifestyle where they feed on invertebrates (e.g. crustaceans and mollusks) using their specialized crushing teeth. However a few species, including manta rays (*Manta birostris*) and eagle rays glide through the water column. Eagle rays feed primarily on benthic invertebrates like most rays, while manta rays are filter feeders, collecting plankton on the tissue between gill arches, then passing it to the digestive tract (Figure 9.7).

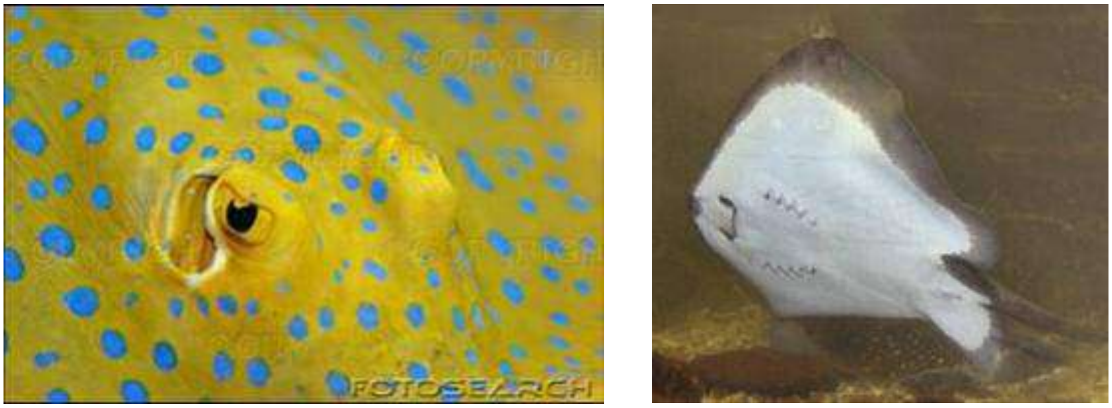


Figure 9.6. Most skates and rays have adapted to a benthic lifestyle with eyes and spiracles on their upper surface and mouth and gill slits on their lower surface.

Figure 9.7. Manta rays are pelagic and feed on plankton.

Although they may be visually very similar, skates and rays have very different morphology and behavior. Skates swim by creating sinusoidal ripples which travel along their pectoral fins as opposed to rays which move their fins up and down. They reproduce by oviparity, producing egg cases sometimes known as mermaid's purses. Skates also have small fins on their tail. These tail fins are not present in rays, though rays may have venomous barbs instead. Rays often grow larger than skates (Manta rays can be up to 7m wide) and reproduce in an ovoviviparous manner, meaning that the fertilized egg is retained for development within the female reproductive tract.

Skates and rays have evolved various defensive mechanisms to protect themselves from predators. Electric rays can deliver up to 220 volts from organs in their heads which may also help them navigate and stun prey. Stingrays utilize hollow barbs on the base of their tails which may be lined with venom. Sawfishes and guitarfishes (types of rays) have a series of barbs running along their pointed rostrums which can be used to inflict damage on either predator or potential prey as they shake their head.

9.2.3 Chimaeras

Chimaeras are generally bottom dwellers found in a variety of habitats from the shallows to deep waters (Figure 9.8). They include species such as the ratfish, rabbitfish and spookfish, named because of their pointed heads and long slender tails. Unlike other cartilaginous fishes, their gills are covered with an operculum and water is taken in through the nostrils before being expelled over the gills. Chimeras are oviparous, producing large eggs in leathery cases. They feed on a variety of prey, including crustaceans, mollusks and fish, crushing them between oral plates (instead of teeth).

Figure 9.8. Chimera

9.3 Bony Fish

There are approximately 25,000 species of modern bony fish, with most being characterized by the presence of a swim bladder, bony skeleton, bony scales, and rays constituting part of their fins. They can be divided into two major lineages; the lobefins and ray-finned fishes.

9.3.1 Lobefin fish

Coelacanths (Figure 9.9) are living fossils, in that they have changed very little in the last 300 million years. Biologists knew of the coelacanth first from the fossil record. They were thought to be extinct until a living specimen was discovered in 1938. Several other coelocanths have been seen and caught since then. Their skeletons consist of both bone and cartilage. Their skeleton is reduced and light and they have a fat-filled swim bladder which allows them to remain neutrally buoyant. Coelacanths, like sharks, maintain high concentrations of urea within their body fluids to remain relatively isotonic to the surrounding environment. Coelocanths, along with lungfishes, are known as lobefins because of rod-shaped bones that extend into their pelvic and pectoral fins. Lobefin fishes represent the evolutionary line that gave rise to the tetrapods.

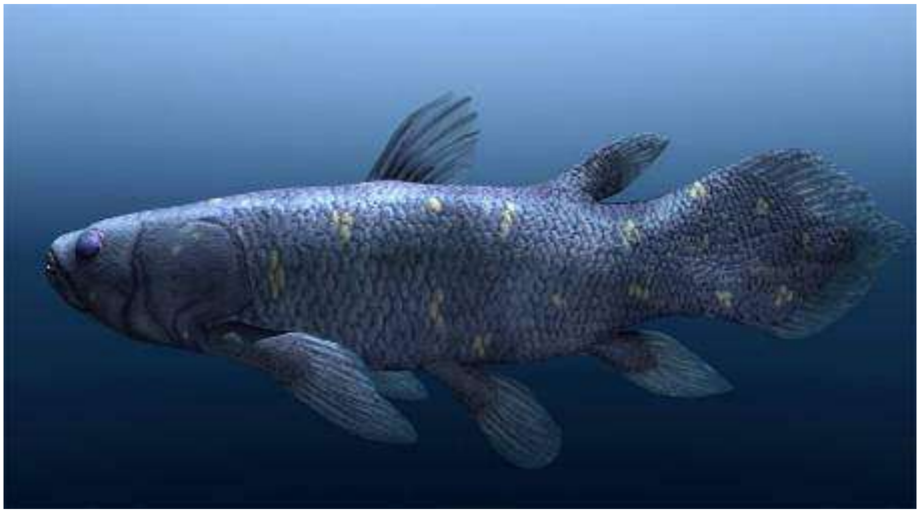


Figure 9.9. Coelacanth, a type of lobefin, the evolutionary line giving rise to tetrapods.

9.3.2 Ray-finned fishes

The ray-finned fish are the most numerous group of vertebrates in the ocean. They are typically covered in scales and their fins are attached to their bodies by fin rays. They have a homocercal caudal fin, where the dorsal and ventral lobes are relatively similar. The caudal fin is typically used for propulsion. They maneuver with paired pectoral and pelvic fins which give increased stability (Figure 9.10). In some fish the pectoral fins have been modified for flying (e.g. flying fish) or walking (e.g. mudskipper). Wrasse and parrotfish use their pectoral fins as their main force for propulsion.

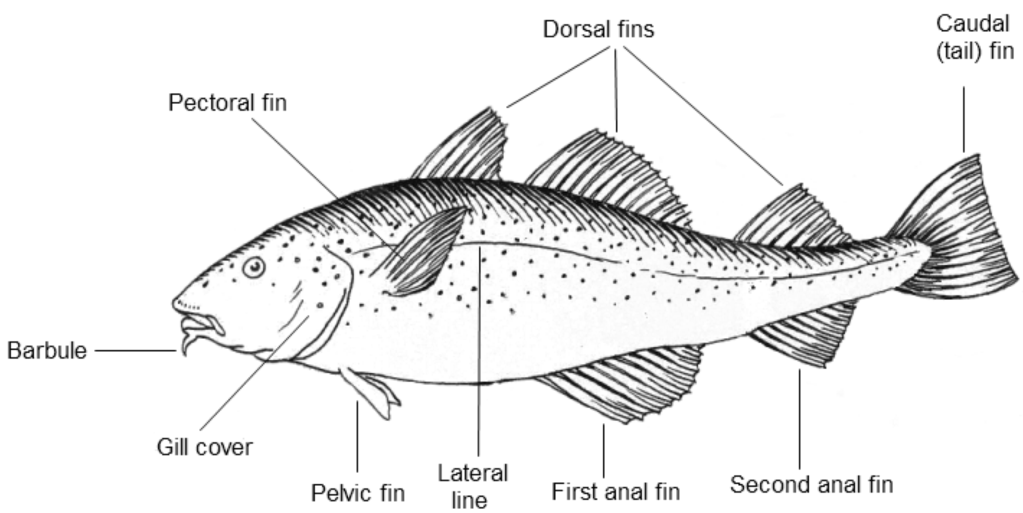


Figure 9.10. The anatomy of a ray-finned fish

Ray-finned fishes are represented by many different body shapes, which are correlated with the lifestyle and characteristics of their habitats (Figure 9.11). Fish that are active swimmers, such as tuna and marlin, have a very streamlined shape tapered at both ends, known as fusiform, which allows the fish to move through the water with great efficiency. Fish that live in seagrass meadows or coral reefs, such as butterflyfish

(*Chaetodon* spp.) or angel fish (*Pomacanthus* spp), typically have laterally-compressed bodies for increased maneuverability in these complex habitats. Some bottom-dwellers, such as flounders, have dorso-ventrally depressed bodies adapted to their benthic lifestyle whereas others, such as scorpionfish (*Scorpaena*) or anglerfish (*Antennarius*) have evolved globular bodies, ideal for a sedentary lifestyle. Others, which may burrow or hide in tight crevices, such as moray eels (*Gymnothorax*) have long, thin snake-like (attenuated) bodies with reduced pelvic and pectoral fins.

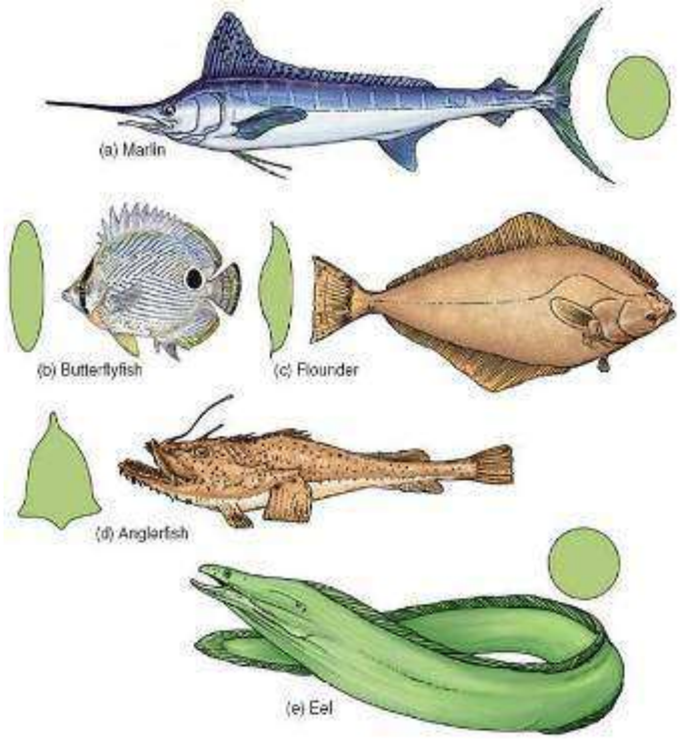


Figure 9.11. The shape of bony fishes is determined by behavior and habitat

The shape of the caudal fin (Figure 9.12) also varies and depends on the swimming behavior of the fish. Fast-cruising pelagic fish, such as tuna and marlin, have a lunate caudal fin with a small caudal peduncle (the base of the caudal fin), which is rigid and very efficient at high speed propelling for long durations, but not very efficient at slow speeds or for quick manoeuvring. A forked fin is commonly seen on fast swimmers, although it also functions well at slower speeds too, for example the yellowtail snapper. A more manoeuvrable fin shape is the truncate tail, which functions well at slower speeds, and is seen for example in salmon and herring. The most flexible caudal fin is the rounded fin, which very efficient for manoeuvring at low speed. This is seen on many reef fish, such as the angelfish.

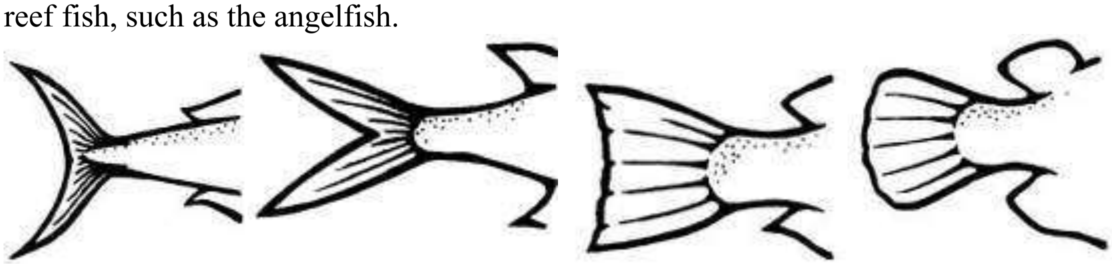


Figure 9.12. Caudal fin shapes, from left to right: lunate, forked, truncate and rounded.

9.4. The Biology of Fishes

9.4.1. Fish coloration and patterns

Most bony fishes use vision as their primary sensory stimuli for finding food and mates, and for communication. Color is therefore extremely important for both species recognition and concealment in the marine environment. Color is derived from specialized cells called chromatophores, which can alter their color by moving pigments around within the cells. Specialized chromatophores, called iridophores, produce the mirror-like silver of many pelagic fish or the iridescent glean in many reef fish. Fish that live in the open ocean, such as billfish and tuna, display a coloration pattern called obliterative countershading, where fish have a dark dorsal surface and a lighter silvery ventral surface. Therefore when viewed from above the dark dorsum blends in with the dark surrounding waters and yet when viewed from below the white belly blends in with the brightly lit surface waters, thus offering these fish camouflage in the open ocean. Many coral reef species (for example, butterflyfish) may exhibit disruptive coloration, in which the background color of the body is interrupted by vertical lines, often passing through the eye, making the fish more difficult to see against the reef. Some fish may also exhibit false eyespots on the posterior part of the body near the caudal peduncle. This eyespot may deceive predators into thinking firstly that the fish may be larger than it actually is and secondly that it is facing the other way, allowing the potential prey to escape. Cryptic coloration allows the fish to be camouflaged into its environment, which is important for many species. Fish such as scorpionfish rely on their irregularly shaped bodies and coloration to blend almost perfectly into their environment whist waiting for their prey to swim within attacking distance. Many fish associated with coral reef environments however, exhibit bright showy color patterns that may advertise territorial ownership, aid in sexual displays or simply warn of toxic defenses.

9.4.2. Locomotion

Water is 1,000 times denser than air, making movement more difficult. For this reason, fish must be streamlined to achieve maximum efficiency of movement. Fish rely on their trunk muscles, arranged in a series of bands along each side of their bodies, to propel themselves through the water column. These bands contract alternatively from one side to the other originating at the anterior end and push the fish along. Elongate fish, such as eels, undulate their entire body while swifter swimmers, such as jacks, flex only the posterior portion of their bodies (Figure 9.13). Other fish such as wrasses or parrotfish use only their pectoral fins, and triggerfish their dorsal and anal fin, to propel themselves about the reef. The highest recorded speeds have been set by swordfish and marlin, reaching 75mph.

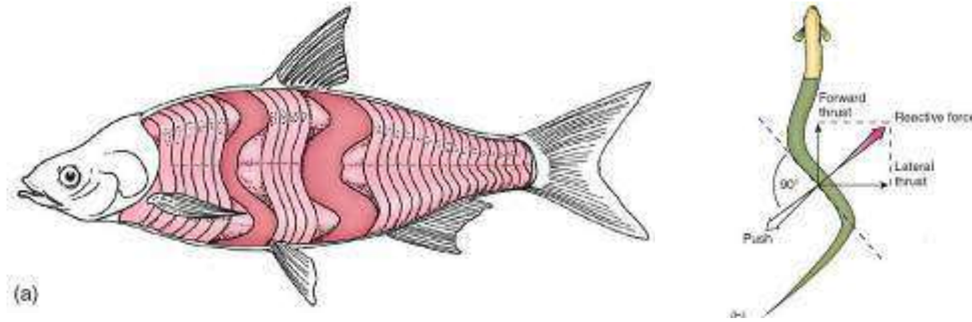
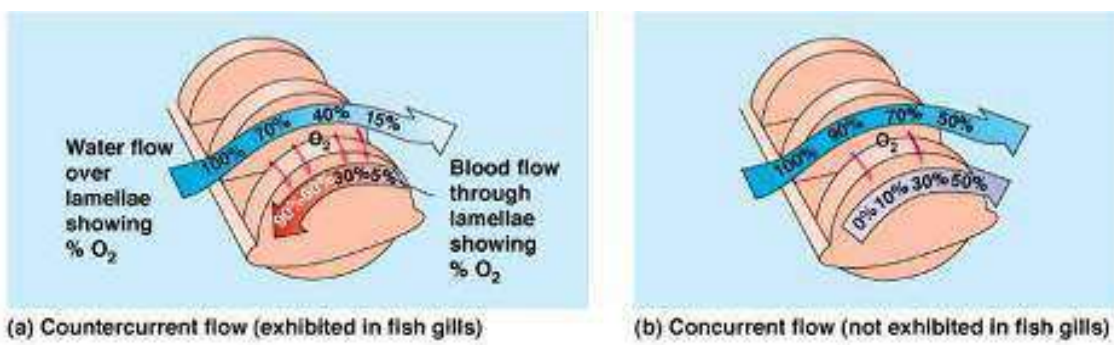


Figure 9.13. (a) Trunk muscles and (b) locomotion in bony fish

9.4.3. Respiration and Osmoregulation

Bony fish use their gills to extract oxygen (O_2) from the water and eliminate carbon dioxide (CO_2) from their bloodstream. The operculum is a hard, bony plate that covers the gills. Gills are composed of thin, highly vascular rod-like structures called gill filaments, attached to a gill arch. The gill filaments are highly folded to increase the surface area for gas exchange, and unfolded can be 10 times the size of the fish. In these structures the blood flows in the opposite direction to the incoming water, creating a countercurrent multiplier system, in which water constantly meets blood with lower O_2 and higher CO_2 concentration maintaining a stable gradient that favors the diffusion of gasses across the membrane (Figure 9.14). This mechanism is very efficient, removing almost 80% of O_2 from the incoming water.



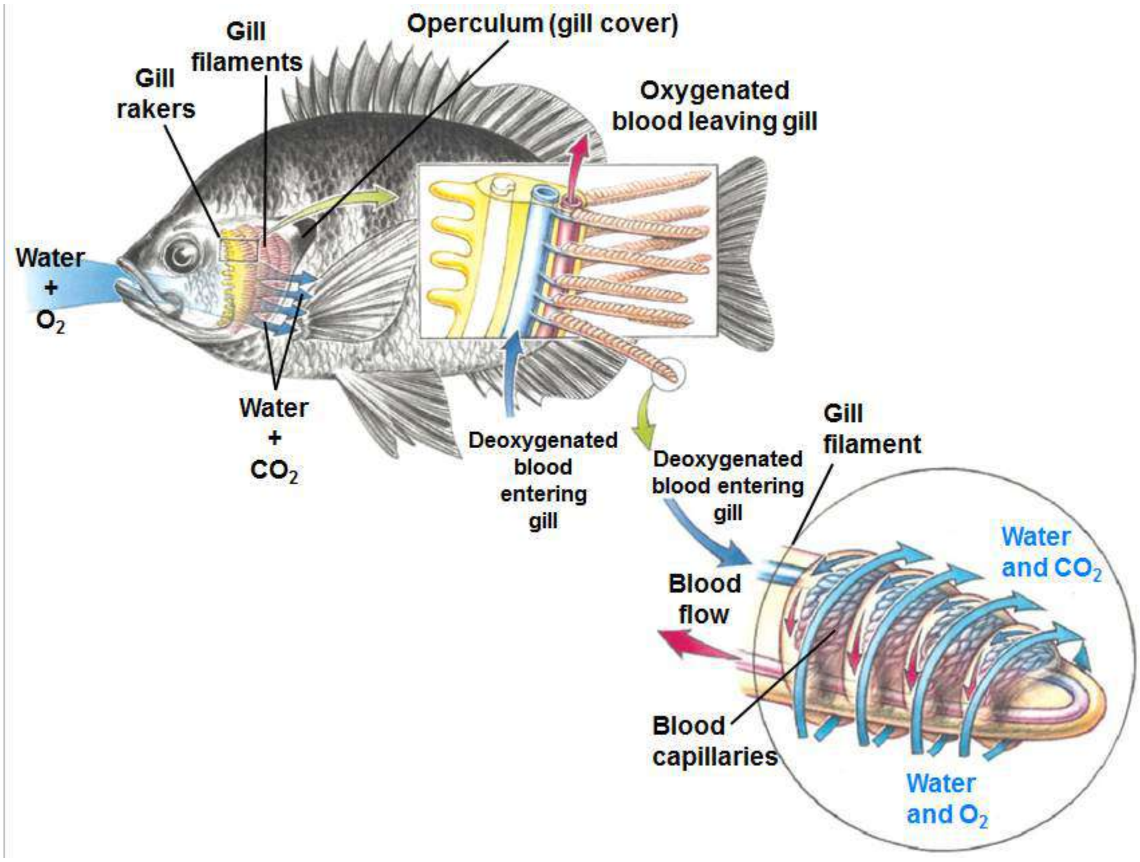


Figure 9.14. Countercurrent exchange system in fish gills.

The gills can be ventilated by taking water in the mouth and actively pumping it through the gills, or in active fish by continuous swimming with an open mouth (ram ventilation). Fish can "suffocate" if their gill arches collapse (e.g. if removed from water and lose the buoyant force provided by it) or if the oxygen levels fall too low (e.g. after an algal bloom, when there are high levels of decomposition).

Except for hagfishes, salt concentration in the blood of nearly all marine fishes is about a third of that of the environment. For that reason, marine fishes tend to lose water across their membranes to the surrounding environment through osmosis. Different groups have different solutions to this problem. Coelocanths and cartilaginous fishes retain urea in their blood and body fluids to increase their internal osmolarity, which ends up being the same or higher than the surrounding water (they are isotonic or slightly hypertonic with the environment). They have unique physiological adaptations to tolerate high levels of urea, which are toxic to most vertebrates. Ray-finned fishes do not retain urea, and therefore are hypotonic and constantly lose water to the environment. To compensate, they drink considerable amounts of seawater, up to 25% of their body weight a day. They remove and excrete the extra salts, primarily through specialized chloride cells within the gills. Salt is also eliminated through the kidneys and digestive tracts and marine fish produce negligible amounts of urine because of their need to retain water (Figure 9.15).

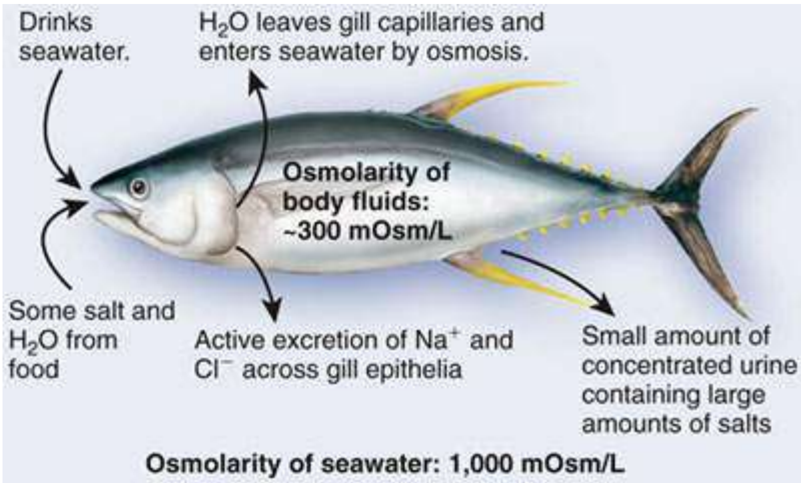


Figure 9.15. Osmoregulation in ray-finned fishes

9.4.4. Cardiovascular system

The cardiovascular system of fish is relatively similar to that of terrestrial vertebrates and contains a heart, arteries, veins and capillaries. Active swimmers, such as tuna, utilize a countercurrent arrangement in their blood vessels to warm up blood coming from their body surfaces and maintaining a core body temperature at 2° to 10° C above that of the surrounding environment (Figure 9.16). In this way they increase the efficiency of their swimming muscles and nerve signals and can reach speeds of 70mph.

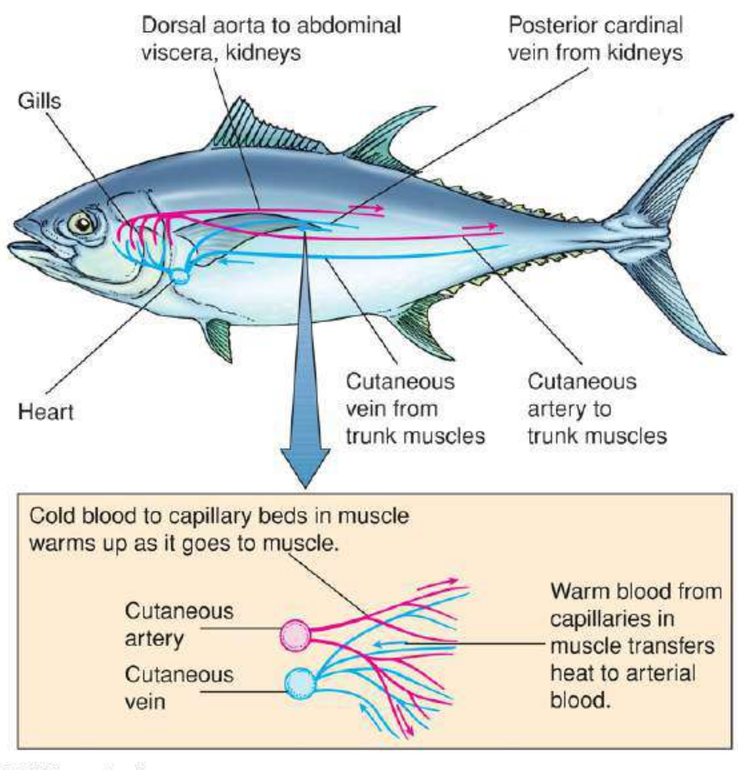


Figure 9.16. Countercurrent exchange system in the cardiovascular system of bony fish

9.4.5. Buoyancy Regulation

Most bony fish, with the exception of some pelagic species, bottom-dwellers and deep-sea fish, use a gas-filled sac located in their abdomen, called a swim bladder, to help them maintain buoyancy in the water column. By adjusting the amount of gas in the swim bladder a fish can maintain its position without any unnecessary expenditure of energy for swimming. Two mechanisms have evolved for adjusting the volume of gas in the bladder. Firstly, an open swim bladder can be filled by gulping air from the surface, for example in herring and eels. Secondly, in a closed swim bladder, gas can be added through a specialized gas gland which fills the bladder from gases dissolved in the blood. This is a derived condition found in fishes such as percids and cod.

Many pelagic fishes which are active swimmers do not have swim bladders because the response time of the bladder is too slow to respond to the rapid changes in pressure, therefore they must continue swimming to maintain their position in the water column. Several benthic dwelling fishes also have no swim bladder, since they have no need to maintain buoyancy as they rest on the bottom. Another method of maintaining buoyancy is to incorporate a greater proportion of low density oils and fats into muscles, internal organs and body cavities.

The swim bladder of bony fish also functions in additional roles, for example as an accessory breathing organ to supplement breathing (e.g. tarpon), or as a sound producing organ amplifying sounds (e.g. drums and grunts).

9.4.6. Nervous System and Senses

Olfaction and taste
Olfaction (smell) receptors are highly developed in sharks and are located in pits surrounding the mouth. Almost two-thirds of a shark's brain is devoted to processing olfactory information. Olfaction in ray-finned fishes occurs through specialized olfactory pits located in nares (nostrils) on the snout. These are open to the external environment, but there is no connection to the throat. Taste receptors are located on the surface of the head, jaws, mouth, tongue and barbels (in goatfish and catfish).

Lateral line system and hearing
The lateral line is a series of canals running the length of the body and over the head, in cartilaginous and bony fishes. At regular intervals the canal is opened to the outside where there is free movement of water in and out of them. Within the canals are neuromasts that can detect vibrations and are used to locate prey and potential predators (Figure 9.17).

The ears of both cartilaginous and bony fishes are internal. There is no external opening or ear drum, instead the sound waves travel through the soft tissues to the internal ear, as the tissue has the same acoustic density as water. The ears of bony fish are composed of three bones called otoliths, which can be used to determine fish age. In some fish the swim bladder lies against the ear and acts as an amplifier to enhance sound detection.

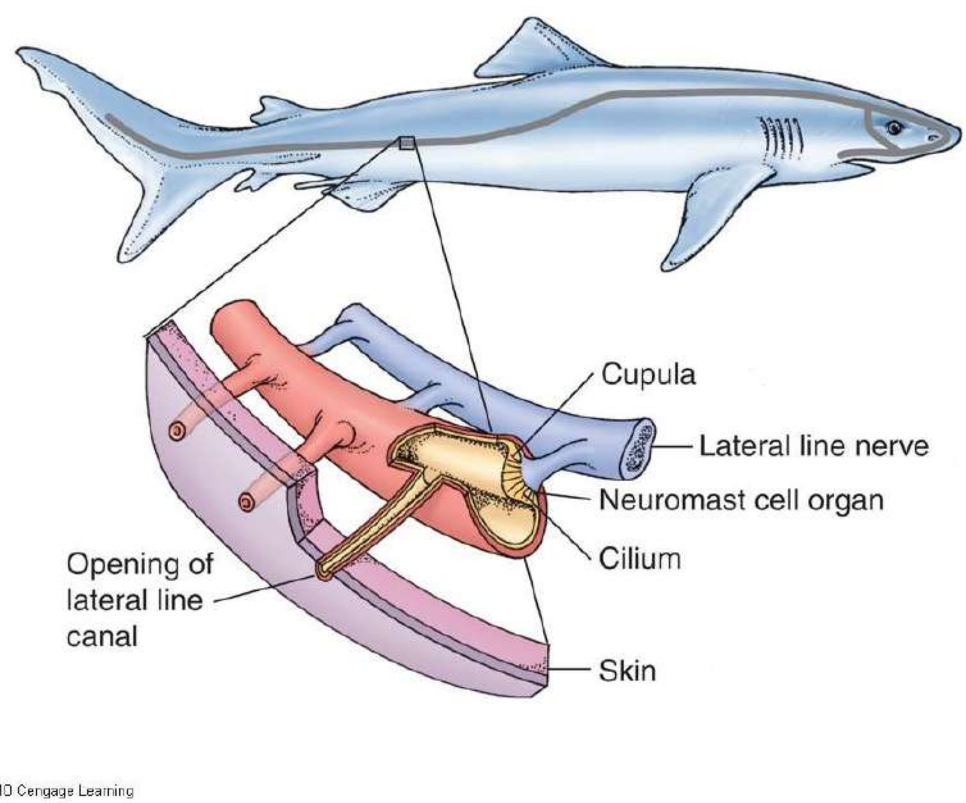


Figure 9.17. The lateral line system

Vision
Sharks are top predators in the oceans and have evolved highly adapted sensory systems. Their eyes are able to see color but lack eyelids, instead having a clear nictitating membrane which covers the eye and protects it from damage. Behind the retina of their eyes is a reflective layer, called a tapetum lucidum, which reflects light back through the retina allowing sharks to see in very low light levels.

The eyes of bony fish also lack eye-lids; they instead have a tough cornea. They do not need to regulate the size of their pupils as the amount of light in water is generally low. Just like a camera, the entire lens moves if needed to adjust for distance. It is thought that fish generally have monocular vision, with each eye seeing its own independent field, and shallow water species may perceive color. Some deep sea fishes have no eyes or non-functional eyes and instead rely heavily on olfaction.

Ampullae of Lorenzini
Sharks can also detect electrical current in the water using a specialized organ called the ampullae of Lorenzini. These organs are scattered over the head and are thought to detect the electrical fields of alternating current created by the muscles of prey. It is also suspected that this organ may detect the earth's magnetic field, assisting the shark in navigation.

9.4.7. Feeding Types

Sharks exhibit a range of feeding strategies, from the predatory great white shark to the whale shark, which strains plankton from the water. The teeth of sharks are composed of modified placoid scales which form several rows of blade-like triangular teeth. These teeth are used for grasping and tearing flesh and are continually lost and replaced in a conveyer belt system. Sharks are unable to move their jaws back and forward to chew and so shake their heads to tear off flesh or devour their prey whole.

The great diversity of bony fish is reflected in their ability to exploit virtually every food resource available. Most bony fishes are carnivores and usually seize and swallow whole prey, since chewing would block the flow of water over their gills. Examples of carnivores include groupers and pufferfish. Butterflyfish are also carnivorous, picking out coral polyps with their tiny mouths. Herbivores feed on a variety of plants and algae and are important in maintaining the delicate balance of algal abundance on coral reefs. The key herbivores on coral reefs are surgeonfish and parrotfish. Herbivorous fishes tend to require longer guts with a greater surface area for digestion and absorption. Filter-feeders such as anchovies rely primarily on plankton. They often travel in large schools and typically use gill rakers to filter out plankton and detritus from the water column.

9.4.8 Adaptations to Avoid Predation

Diverse adaptations have evolved in fish to avoid predation. Porcupinefish and pufferfish can inflate themselves by swallowing large amounts of water and this also causes their spines to stick out making them too large for most fish to swallow. Flying fish

(*Cypselurus* spp.) can leap out of the water and glide for long distances using their enlarged pectoral fins. Some species of parrotfish secrete a mucous cocoon at night to mask their scent from predators while they rest. Surgeonfish have sharp scalpel-like spines located on their caudal peduncle which may be used in defense. Scorpion and stonefish are highly camouflaged and have venomous dorsal spines to avoid predation.

9.4.9. Reproduction

Sharks reproduce through internal fertilization, with male sharks transferring sperm to the female through modified pelvic fins called claspers. There are three different reproductive strategies seen in sharks: oviparity, ovoviviparity and viviparity. Oviparity is the most primitive method with eggs being laid outside the female and development occurring in a protective casing. The offspring usually hatch relatively small due to the limited availability of nutrients in the eggs. This is exhibited in whale sharks. Ovoviviparity is the most common method with eggs developing inside the mother's uterus yet no placental connection is made. The developing young are nourished through yolk stored in the egg but are able to develop within the protection of the mother. This is seen for example in basking sharks and thresher sharks. Viviparity is the reproductive strategy which evolved most recently. In viviparous sharks, the offspring develop inside the mother's uterus, and are fed through a placental connection with the mother. Viviparous sharks give birth to live young, which are relatively large and independent. This is exhibited in hammerhead sharks.

Most bony fish are oviparous, yet they display a wide variety of reproductive behaviors. Some species are pelagic spawners, e.g. cod, tuna, sardines, parrotfish and wrasse, releasing large amounts of eggs and sperm in the water column. There is no parental care and an extremely high mortality rate. In benthic spawning, non-buoyant eggs and sperm are usually spread over large areas of vegetation or other substrate; there may still be a high mortality rate as there is no parental care. Certain species may hide their eggs in some way, e.g. the grunion (*Leuresthes tenuis*) buries its eggs in the sand at high tide. Guarders, such as damselfish, blennies and gobies, exhibit strong parental care, typically from the males, who guard the eggs until they hatch, and thus fewer eggs are produced. In a rarer situation, fish such as jawfish (*Ophistognathus macrognathus*) or seahorses (*Hippocampus*) which are known as bearers, the males will actually carry the eggs until they hatch.

Certain bony fish exhibit hermaphroditism in which individuals have both testes and ovaries for at least some part of their lives. Hermaphroditism may be synchronous (or simultaneous), with an individual possessing functional gonads of both sexes at the same time (for example, hamlets and several deep sea fish), or sequential, changing from one sex to the other during their life. Sequential hermaphroditism may be protogynous, where females change into males (e.g. wrasses and parrotfish) or protandrous, where males later change to females (e.g. anemone fish).

9.4.10. Migrations

There are many instances of migrations in fishes. These migrations are due to physical and biological factors such as temperature variations, following food or mating and spawning requirements. Daily migrations occur to avoid predators or to obtain food, for example grunts migrate from the reefs in the daytime to feed in the seagrass at night. Vertical migration through the water column is exhibited in species such as the lanternfish and is primarily in response to migrating prey species. Seasonal migrations occur primarily in association with mating and spawning. Some fish, like salmon, spend the majority of their lives in salt water and move to freshwater to spawn. These are known as anadromous fish. The reverse, found in freshwater eels which spend their lives in freshwater yet migrate to salt water to spawn, is termed catadromous.

9.4. Review Questions: Fishes

1. What is the skeleton of jawless fish composed off?

2. What are the two extant groups of jawless fish? How are they similar? How are they different?

3. Which fish is able to tie its body in knots to remove excess slime and gain leverage to tear flesh?

4. Give an example of a jawed fish with a cartilaginous skeleton?

5. Do sharks and rays have a swim bladder?

6. Name three mechanisms sharks use to remain neutrally buoyant?

7. How do sharks achieve internal fertilization?

8. What do the Ampullae of Lorenzini detect?

9. Are all sharks predators?

10. Describe the three different reproductive strategies seen in sharks.

11. Why are the eyes and spiracles of a ray on the top side?

12. Give four functions of the pectoral fins in ray-finned fish?

13. Which caudal fin shape is best for high speeds?

14. Which caudal fin shape is best for maneuvering at low speeds?

15. What is the body shape a butterfly fish described as? How is it adapted to their habitat?
16. What are chromatophores?
17. What is an iridiophore?
18. What is the advantage of counteshading?
19. Give an example of a fish showing disruptive coloration?
20. Which fins do parrotfish and wrasses use to swim?
21. What is an operculum? Which groups of fish have one?
22. Explain the counter current exchange system in the gills, and its importance?
23. Compare and contrast osmoregulation in ray-finned fishes and in sharks.
24. Why is it advantageous for active swimmers to have a counter current arrangement of arteries and veins? Which group of fishes displays this?
25. What is a swim bladder and what is its main role?
26. How does a fish with a closed swim bladder control its volume?
27. Why do some active swimmers not have a swim bladder, and how do they achieve buoyancy instead?
28. In addition to providing buoyancy, what other roles does the swim bladder have?
29. What do neuromasts of the lateral line system detect?
30. How are fish ears different to ours?
31. What role does the swim bladder play in hearing?
32. How does the lens in a fish eye adjust for distance?

33. Why does a carnivorous fish swallow its prey whole?

34. Give three adaptations to avoid predation seen in fish?

35. Give an example of a simultaneous/synchronous hermaphroditic fish.

36. Give an example of a protogynous sequential hermaphroditic fish.

37. How do moray eels ventilate their gills?

38. In most fishes, the ___________ fin is used for propulsion.

39. Compare and contrast swimming pattern in a slow-moving eel and in a fast cruising fish like a tuna.

40. Which group of fish is most closely related to land vertebrates?

41. Describe adaptations that cartilaginous fishes and bony fishes have for defense against predators.

10. Marine Reptiles and Birds **(Karleskint Chapter 11)**

10.1. General Characteristics and Adaptations

Reptiles and birds are vertebrates that inhabit both terrestrial and marine environments. They are typically large organisms that are high in the food chain, often at the third trophic level or higher. They feed on a variety of organisms and have relatively few predators. They are adapted to move freely and have highly developed senses. They have proportionally large brains and a high capacity for learning.

The ancestors of marine reptiles and birds were terrestrial, and the reinvasion of the sea by these organisms is reflected in their morphology, locomotion, insulation, osmotic balance and feeding. For example, marine reptiles and birds need to excrete excess salts they gain from their environment, and their nitrogenous wastes are converted to uric acid, which allows for very little water loss with their wastes.

10.2. The Amniotic Egg

The evolutionary success of reptiles and birds in due in large part to the evolution of the amniotic egg, around 340 million years ago (Figure 10.1). Amniotic eggs allow for longer development within a protective covering. This eliminated the need for a free-swimming larval stage and decreased early mortality. It also allowed the egg to be laid in a dry area away from aquatic predators. However, the egg must be fertilized before the shell is added, which required the evolution of copulatory organs for internal fertilization.

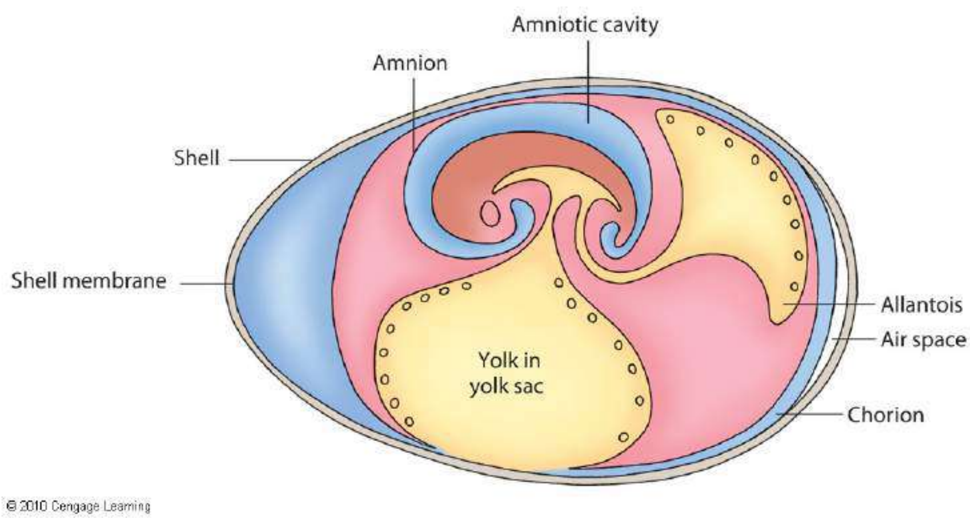


Figure 10.1. Parts of the amniotic egg.

10.3. Marine Reptiles

10.3.1. Adaptations of Marine Reptiles

The ancestors of modern reptiles appeared around 100 million years ago. Reptiles are poikilotherms (their internal temperature varies with the environment) and ectotherm (lose their metabolic heat to the environment). They are commonly referred to as cold-blooded, and their metabolic rate and activity level varies with the ambient temperature; they get sluggish in the cold. For these reasons they are limited to warm areas. Modern-day reptiles include crocodiles, turtles, lizards and snakes, all of which have representatives in the marine environment.

Reptiles have several adaptations that allowed them to survive both on land and in seawater. Circulation through their lungs is nearly completely separate from the circulation through the rest of their body, which is more efficient at supplying oxygen to tissues than the circulatory system of fishes, and helps support their active lifestyle. Their kidneys are efficient at eliminating wastes while conserving water, allowing them to inhabit dry and salty environments. Their skin is covered in scales and generally lacks glands, which minimizes water loss.

10.3.2. Marine Crocodiles

The American crocodile (*Crocodylus acutus*) and the Nile crocodile (*Crododylus niloticus*) both venture in the marine environment to feed, but the Asian saltwalter crocodile (*Crocodylus porosus*) is the one that is best adapted to the marine environment. Asian saltwater crocodiles inhabit estuaries from India and South East Asia to Australia. These are large animals, and can reach 6 m in length. They feed mainly on fish, but can attack sharks and mammals. They drink salt water and excrete excess salts through salt gland on their tongues. Saltwater crocodiles live along the shore and lay their eggs in nests on land.

10.3.3. Sea Turtles

There are seven species of sea turtles, six of which are in danger of extinction. They are mostly found in tropical and subtropical coastal water, but leatherbacks tolerate colder water and have been found in Canada and Alaska. Leatherbacks are able to withstand colder temperatures because of a countercurrent exchange system in their circulatory system: veins (which return blood to the heart) are very close to arteries (which bring blood away from heart to limbs). The limbs of the turtle are colder than the core of its body, and blood cools as it travels to the extremities, but because of the countercurrent exchange system, this blood warms again as it travels back to the heart and heat from the arteries is transferred to the veins (Figure 10.2).

Adaptations to Life at Sea

All sea turtles, except the leatherback, have a protective shell (or carapace) fused to their skeleton (Figure 10.3). The outer layer is made of keratin, which is similar to reptilian scales, and the inner layer is made of bone. The shell of sea turtle is more flattened and streamlined than that of terrestrial turtles. The leatherback sea turtle, the largest of all marine turtles, lacks a shells and its body is covered in a thick hide containing small bony plates. Buoyancy of sea turtles is increased by large fatty deposits beneath the skin and their light and spongy bones. Their front limbs are large flippers used in propulsion, and their back limbs are shaped like paddles and are used in steering and digging nests (Figure 10.4).

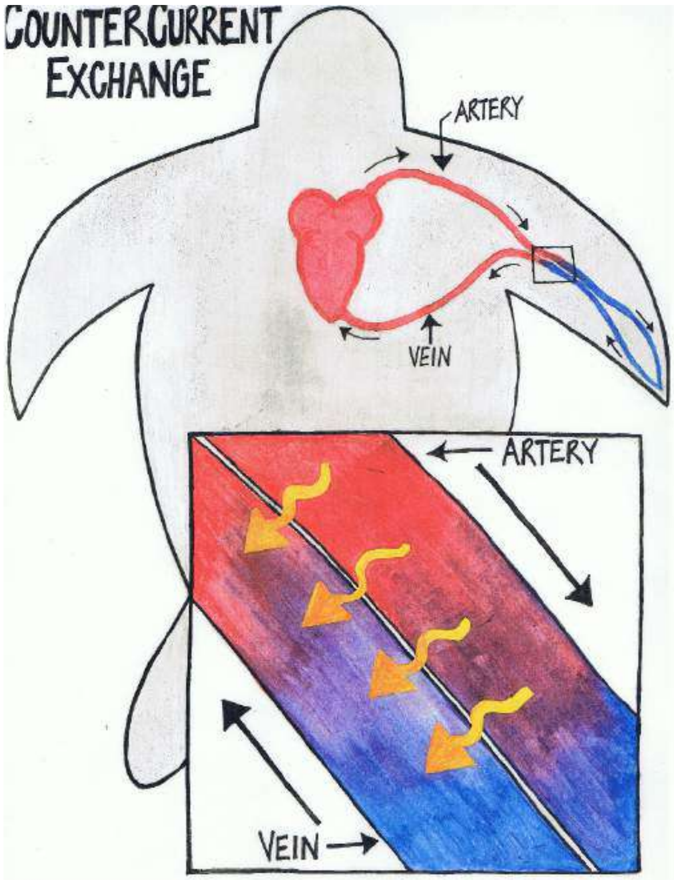


Figure 10.2. The countercurrent exchange system in the leatherback turtle's circulatory system, which allows blood in veins to be warmed as it travels back to the heart. This allows leatherbacks to live in colder water than other species of turtles.

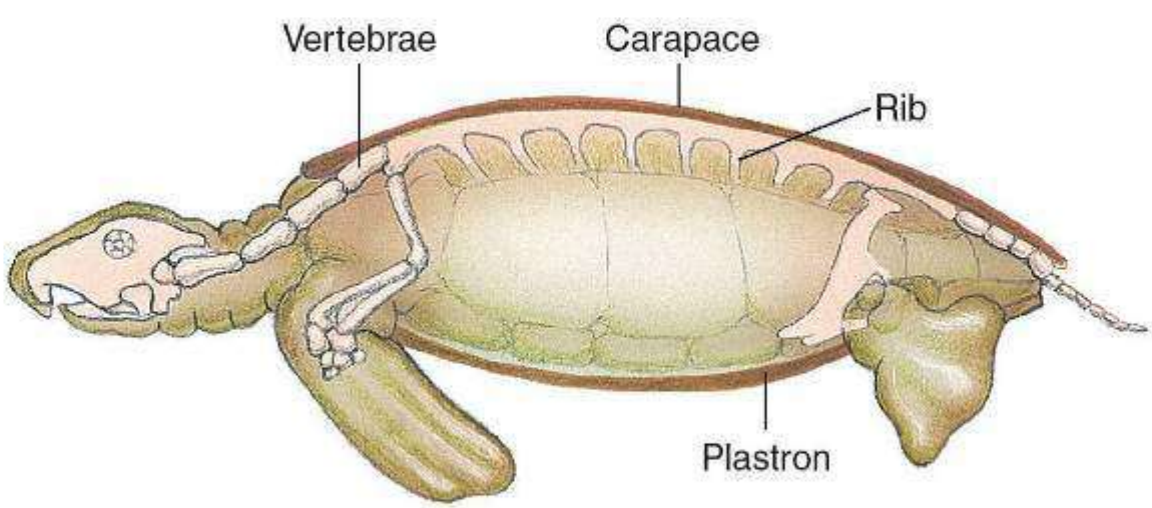


Figure 10.3. Anatomy of a sea turtle.

Figure 10.4. Sea turtles showing flippers and beak-like structure.

Behavior

Sea turtles are generally solitary, and only interact for courtship and mating. They must surface to breathe, but can stay submerged for up to 3 hours at a time. They sleep on the bottom, wedged under rocks and coral, or when in deep water they sleep while floating at the surface.

Feeding & Nutrition

Sea turtles lack teeth, and instead they have a beak-like structure to secure food (Figure 10.4). Most sea turtles are carnivorous, but the green sea turtle is mostly herbivorous. Several species feed on jellyfish; their pharynx is lined with spines to hold the slippery prey (Figure 10.5) and their digestive system is adapted to withstand the stinging cells. Many turtles also ingest plastic bags that they mistake for jellyfish, which often leads to starvation and death. They consume large amounts of saltwater and eliminate excess salts by secreting a concentrated salt solution from the salt gland located above their eyes.

Figure 10.5. Pharynx of sea turtle, showing spines that help swallow prey such as jellyfish.

Reproduction

Mating occurs at sea. Females may mate with several males and lay a clutch with eggs fertilised by different males. When ready to lay their eggs, females crawl out of the water and dig pits on the beach, usually at night. They secrete a mucous on the eggs during laying to keep them moist and they bury their eggs (usually 80 to 150 in a clutch).

The average incubation period is 60 days, but it varies with temperature. The temperature during the development also determines the sex ratio of the hatchlings; warmer temperatures (above 29.9^{o}C) lead to more females and colder (below 29.9^{o}C) to more males. Once hatched, the baby turtles orient themselves towards the brightest horizon and rush to the sea. Once in the water, hatchlings swim several miles offshore until they are caught in currents that take them further out. Early mortality is extremely high and only 0.1% of hatchlings survive to adulthood, becoming prey to birds and crabs on the beach, or large fish and seabirds once out at sea.

Turtle Migrations

Turtles undertake considerable migrations of hundreds to thousands of miles from their feeding grounds to their nesting beaches. They return to the beach where they hatched to mate and lay their eggs. The exact method of navigation for these migrations is unknown; the role of their sense of smell and taste is known to be important, as are audible sounds from other animals. Turtles also probably detect the earth's magnetic field and may navigate using the sun.

Sea Turtles in Danger
Six of the seven species of sea turtles are endangered by human activities. The number one reason cited for the decline and near extinction of sea turtles is getting trapped in fishing nets at sea (particularly shrimp nets), which can lead to drowning and death if hauled aboard in nets. Many areas now require Turtle Exclusion Devices (TEDs), which allow the turtles to escape from the net (Figure 10.6). Beach development destroys nesting sites, and artificial lighting near nesting beaches disorients new hatchlings. Plastics and other types of pollution also greatly affect sea turtles—in particular, many turtles mistakenly ingest plastics (e.g. plastic bags) while hunting for jellyfish. Plastic bags cannot be digested and often does not travel down the digestive tract, instead taking room in the stomach and preventing normal feeding and digestion. Sea turtles are also hunted in many countries for their meat, leather, eggs and shells.

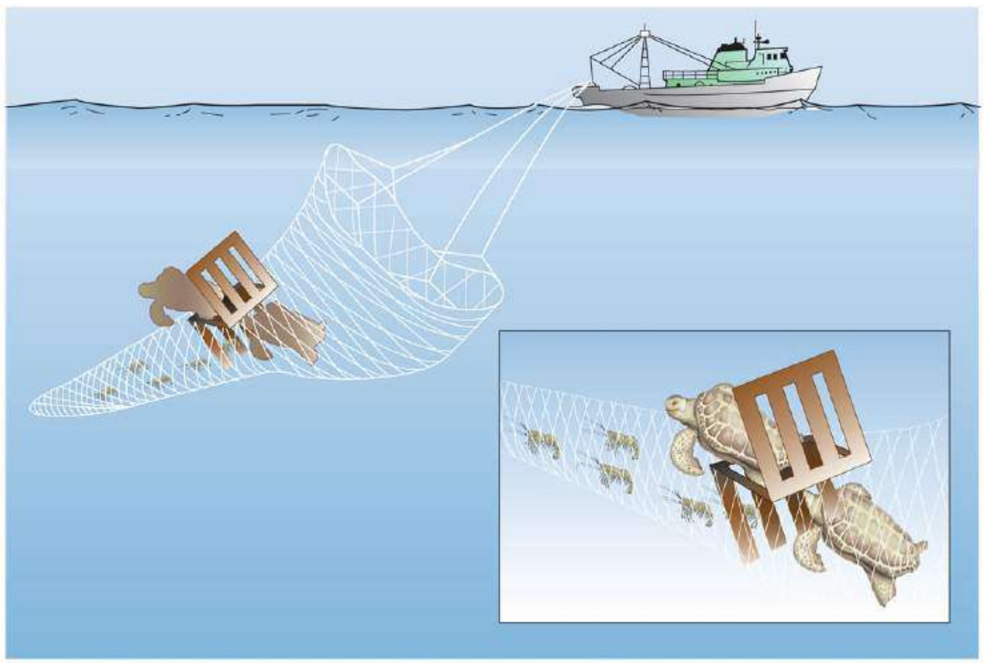


Figure 10.6. All shrimp supplied to the US market must now be caught in nets fitted with TED's.

10.3.4. Marine Iguanas
Marine iguanas are the only species of marine lizard, and they are endemic to the Galápagos Islands. They are herbivores and graze on mats of seaweeds in the shallow subtidal zone. They swallow small stones to decrease their buoyancy and reach their food. They consume salt through water and food, and excrete the excess salts through tear and nasal glands, periodically expelled by nasal spraying. They have a dark coloration, which allows them to absorb heat and warm up faster when out of the cold, upwelling waters that surround the Galápagos.

Marine iguanas are good swimmers, and propel themselves through lateral undulations of their body and tail. Males occupy small territories on shore, and intruders are attacked when they enter this territory. They ride up the swells and touch their tongue to the rocks to locate their territory.

Figure 10.7. Marine iguanas on shore and underwater.

10.3.5. Sea Snakes

There are about 50 species of sea snakes that live in the marine environment. Most remain close to shore in shallow waters of the western Pacific and Indian Oceans; there are no sea snakes in the Atlantic.

Sea snakes have several adaptations for the marine environment. Their scales are absent or reduced to increase streamlining; their tail is laterally compressed to form a paddle; their nostrils are higher on their head than their terrestrial counterparts, allowing them to breathe while drifting at the surface, and they have valves, which prevents water from entering while the snake is submerged. Sea snakes have a single lung that reaches almost all the way to the tail, and their trachea is modified to absorb oxygen, acting as an accessory lung. They can lower their metabolic rate when submerged and can stay underwater for several hours.

Sea snakes feed mainly on fish and eels. Most have venomous fangs, and can swallow prey more than twice their diameter. They are slow swimmers and rely on ambush to capture their prey—mostly small fishes. Their most highly developed sense is eyesight so they feed during the day.

Three species of sea snakes are oviparous and come to land to lay eggs. The rest are ovoviviparous, and the female retains the eggs within her body until they hatch. The young are able to feed and swim immediately upon hatching.

The toxins produced by sea snakes are toxic to other vertebrates, including humans. Luckily they are timid and rarely bite humans, except in self-defense. Humans are more of a threat to sea snakes than vice-versa, and sea snakes are often eaten by humans or hunted for their skins.

10.4. Seabirds

Birds are homeotherms, commonly referred to as warm-blooded; they are able to keep their body temperature constant even with changes in temperature in the environment. They are also endotherms, able to retain some metabolic heat to raise their body temperature. This has allowed birds to live in a wide variety of environments, including colder climates.

Birds eat a lot and have a high metabolism, which allows them to maintain their internal temperature. Their body is covered in feathers, which provide insulation. They also have advanced respiratory and circulatory systems to provide oxygen to active muscles. Their keen senses and large brains help process sensory information effectively.

Of the 8,000 species of birds, about 250 are adapted for the marine environment. Seabirds descended from several groups of terrestrial birds, and as a result, they vary widely in their flying skills, feeding mechanisms and ability to live away from land. Seabirds feed at sea but all must return to land to breed, and most breed in colonies.

Like marine reptiles, seabirds consume large amounts of salt with the food and water they ingest. They have salt glands above their eyes to excrete the excess salt in a concentrated solution through their nostrils. Also like marine reptiles, their nitrogenous wastes are converted to uric acid, which reduces water loss with urine.

Seabirds are commonly nest in large colonies, which offers protection from predators. Birds often nest on deserted islands (also a good protection from predators), and if predators (e.g. rats or goats) are introduced then the majority of the nests on the inside of the colony are likely to survive. Disadvantages of breeding include a higher susceptibility to disease, and that the entire colony is susceptible to disturbance. Seabirds will often abandon nests if disturbed, which can be a huge problem for the population if they all nest together in one particular place and only breed once a year.

10.4.1. Shorebirds

Shorebirds, or waders have long legs and thin bills. They are not seabirds in the strict sense as they do not swim much and do not have webbed feet. They feed mainly in the intertidal zone, and are therefore less common in the tropics where the tidal range is typically less extreme. They typically show countershading, with dark dorsa and light ventral surfaces. Shorebirds include oystercatchers, curlews, turnstones, plovers, avocets, stilts, sandpipers and herons.

10.8. Shorebirds: oystercatcher (left), curlews (middle), turnstones (right)

Shorebirds typically have thin, sharp bills adapted for their particular prey and feeding behavior. The bill of oystercatchers is long, blunt, vertically flattened and orange and used to slice adductor muscles of bivalves, pry limpets of rocks, crush crabs and probe the mud for crustaceans and worms. The curlew a long bill (20 cm) that it uses like forceps to extract invertebrate from burrows. The turnstone has a slightly upturned bill and can use it like a crowbar to overturn stones and debris in search of food.

Avocets, stilts and sandpipers have very long legs and most have elongated necks and slender bodies (Figure 10.9). They wade through the water moving their upturned partially open beak from side to side. The stilt has the longest legs in proportion to its body size than any other bird, except the flamingo. Sandpipers accomplish extremely long migrations of 6,000 miles annually.

10.9. Shorebirds: avocets (left), stilt (middle) and sandpiper (right)

Herons (which includes herons, egrets and bitterns) are represented on every major continent. They have skinny legs and long necks. Most herons hunt by stalking their prey, for example, the Great blue heron quietly waits until small fish or crustacean come into range then spears it with its pincer-like bill as it rapidly extends its neck. The reddish egret uses an interesting technique called canopy hunting, in which it extends its wings to create shade, which lures prey seeking shelter. Other species, such as the little egret are more active hunters, vibrating their feet to scare bottom-dwellers to the surface (Figure 10.10).

10.10. Shorebirds: Great blue heron (left), reddish egret (middle) and little egret (right)

10.4.2. Gulls and their Relatives

This group includes the largest variety of seabirds, with a worldwide distribution including polar regions (Figure 10.11). Gulls and their relatives have webbed feet and oil glands to waterproof their feathers. They are not true ocean-going birds and do not stray far from land. They have enormous appetites and are not very selective eaters (opportunistic feeders). Relatives include terns, skuas, jaegers, skimmers and alcids (auks, puffins and mures).

Of the gulls, herring gulls are the most widespread and well known, probably because they are so vocal and extremely efficient feeders, reaching nuisance proportions in some areas. They are aggressive carnivores, known to eat the eggs and young of other birds, even those of other gulls when food is scarce. They gather in large colonies to breed, nesting in a pile of stones on the ground.

Terns are relatives of gulls found in tropical and subtropical shores. They are similar in color to gulls, but have head feathers projecting back from their heads and are more streamlined. They are not as avid hunters as gulls, but do steal from other birds. The Arctic tern makes the longest migration of any animal, flying solo from north of the Arctic Circle to Antarctica. The royal tern is a gregarious nester, a trait commonly seen in seabirds.

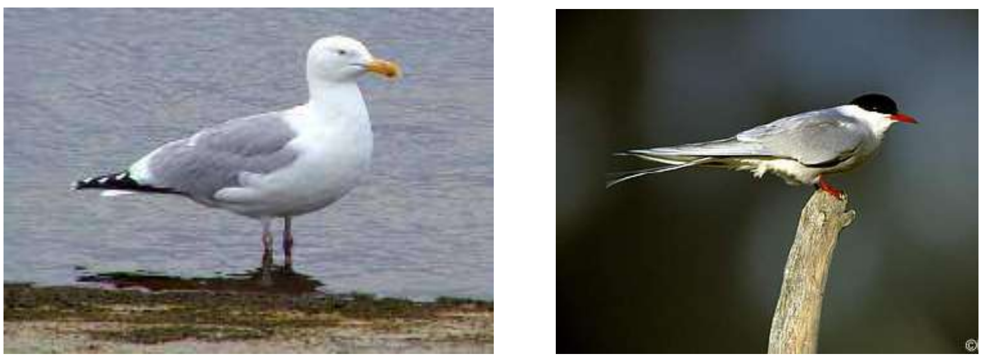


Figure 10.11. Gulls and their relatives: herring gull (left) and tern (left)

Skuas and jaegers are found at high latitudes in colder climates. Skuas are termed the hawks or vultures of the sea, as they are keen predators. The parasite jaeger is known to frequently pursue terns and rob them of their prey. Skimmers (or scissorbills) have a protruding lower jaw and fly with their lower bill just beneath the surface creating a ripple to attract fish (Figure 10.12).

Figure 10.12. Gulls and their relatives: skuas (left), jaegers (middle), skimmers (right)

Although they are related to gulls, alcids (Figure 10.13) look more like penguins, and this a good example of convergent evolution (similar selective pressures brought about similar adaptations in unrelated groups of animals). Both groups evolved independently and are considered ecological equivalents (different groups of animal that have evolved independently along the same lines in similar habitats and therefore display similar adaptations). Alcids live in the northern hemisphere and penguins in the southern hemisphere, but both groups share many characteristics (Figure 10.14). One major difference between the groups is that modern alcids can fly. Alcids nest in noisy colonies high on cliffs of the northern Atlantic and Pacific Oceans. The mortality rate of the young are high as they are frequently knocked off the ledge by their parents or predated by gulls.

Figure 10.13. Gulls and their relatives: puffin (left), auks (middle) and murres (right)

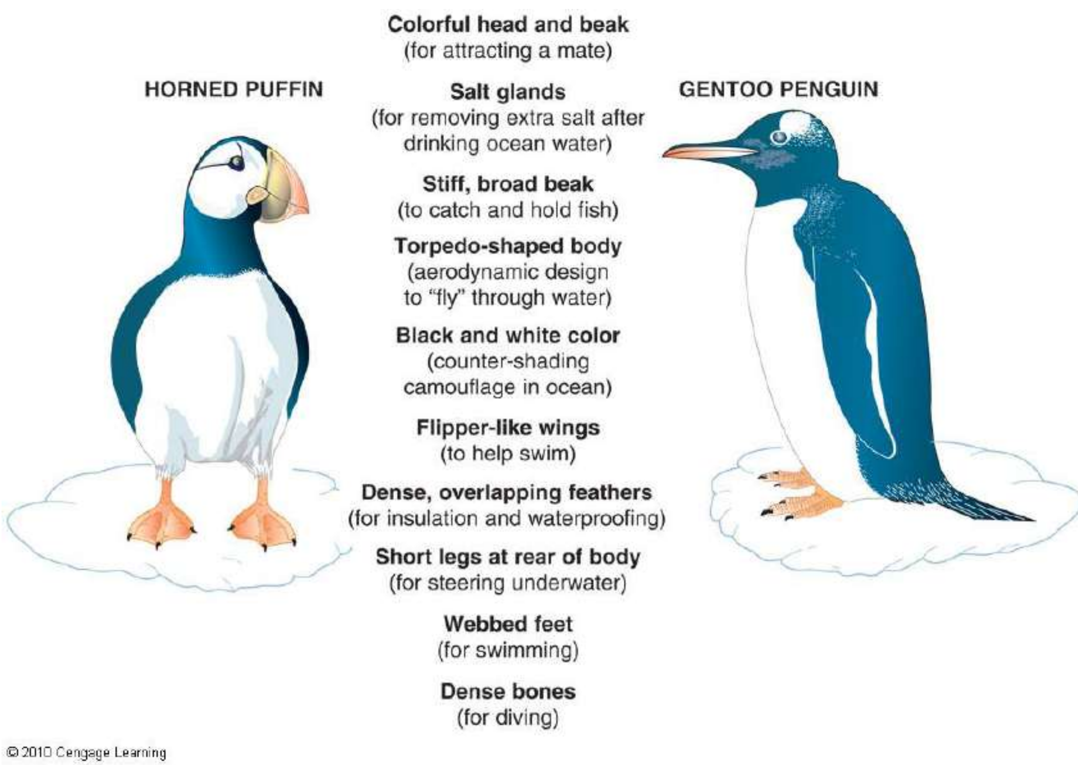


Figure 10.14. Example of convergent evolution between alcids and penguins.

10.4.3. Pelicans and their Relatives

This group includes pelicans, gannets, boobies, cormorants, frigate birds and tropicbirds (Figure 10.15). Many are brightly colored or have head ornaments. Most live in coastal areas or inland waters. They have a worldwide distribution, but are more common in the tropics and warm temperate regions.

Pelicans are large birds and large fish populations are required to support their colonies. Pelicans feed just below the water's surface using their gular pouches (sac of skin that hangs between flexible bones of lower mandible) as nets. The brown pelican is commonly seen in the Caribbean and is the most fully marine pelican. They patrol about 10 m above the water, diving down, folding back their wings and opening their gular pouch when they spot their prey. Their impact stuns the fish and they scoop them up along with about 10 liters of water, which must be drained before they can fly again. It has been suggested that a major cause of death for brown pelicans is loss of eyesight from diving, because once blind they are unable to catch prey.

Boobies have brightly colored faces and feet, and include species endemic to the Galápagos such as the red-footed booby, blue-footed booby and masked booby. The brown booby is commonly seen in the Caribbean. Boobies and gannets can dive into the sea from heights of 18 to 30m to catch fish.

Figure 10.15. Pelicans and their relative: Brown pelican (left), red footed booby (middle), brown booby (right)

Tropic birds are also known as the "bosun birds" because of their characteristic "t'weee-eee" call reminiscent of a bosun's whistle used to call deckies. They have two distinctive long tail feathers and are seen sitting on the surface momentarily after a dive with their tail feathers upright. A familiar example in the Caribbean is the Red-billed tropicbird, which nests on Saba.

Cormorants are impressive divers, and they fish by swimming along the surface while scanning for fish, then plunging to 21-30 m to pursue prey. They swallow their prey headfirst so the scales and spines don't catch in their throat. Cormorants lack oil glands, which decreases their buoyancy and allows them to spend less energy while swimming. The disadvantage of lacking these oil glands is that their feathers are not waterproof like most other seabirds, and they must periodically dry their wings to be able to fly. Cormorants are used by fishermen in Japan and Asia to help catch fish. The bird is fitted with a rope or steel ring around its neck to prevent swallowing and returns to the fishing boat after catching prey, where the fishermen can retrieve the fish. Most cormorants are strong fliers, except the flightless cormorant of the Galápagos Islands. With no natural enemies and abundant food and nesting materials, the need to fly became unnecessary.

Frigatebirds have a lightweight body and a wingspan close to 2 m, which allows them to soars for hours in the lightest breezes. Like cormorants they lack oil glands, and they most likely drown if they settle on water; they feed by skimming the water with their bills, picking up jellyfish, fish, squid or young sea turtles. Frigatebirds regularly pursue and attack other birds to steal their prey. This is termed cleptoparasitism.

Figure 10.16. Pelicans and their relatives: Red-billed tropic bird (left), cormorant fishing (middle), frigatebird (right)

10.4.4. Tubenoses

Tubenoses include albatrosses, petrels and shearwaters, and received their name because of the obvious tubular nostrils on their beaks, the significance of which is unknown (Figure 10.17). Like other seabirds and reptiles, they have salt glands to excrete excess salt. The resulting concentrated solution empties in the nostrils. Their stomach contains a large gland that produces a yellow oil, composed of liquefied fat and vitamin A, which is fed to newly hatched young. Because of its strong unpleasant odor, adults may also use it in defense by regurgitating it through the mouth and nostrils if disturbed. Tubenoses spend months and even years on the open sea, and are very skillful flyers. Male and female tubenoses mate for life and perform elaborate courtship displays. Many undertake spectacular migrations from their breeding grounds to their feeding grounds.

Albatrosses are superb gliders with a wingspan of up of 3.5 m, the largest of any living bird (Figure 10.18). This allows them to take advantage of light winds to keep them aloft, while gliding with minimal effort. Most live in the southern hemisphere, where the winds circle the earth without encountering land. A few species in the Pacific Ocean migrate to the northern hemisphere to breed, but most species are limited to the Southern hemisphere because it is difficult to pass the doldrums. Albatrosses usually come back to land only to reproduce, and courtship displays precede mating, which include gyrations, wing flapping and bill snapping. Long-line fishing is a serious threat to albatross and it is estimated that 100,000 die every year due to this.

Figure 10.17. Petrel (top left), shearwater (bottom left) and albatross (right) showing various types of tubenoses.

Figure 10.18. The wandering albatross (left) is the largest albatross. Many albatross have elaborate courtship displays (right).

Storm petrels are small birds with long legs. They have erratic flight, like a fluttering moth, and are sometimes called the St Peters Bird, as they look like they are walking on water. The Wilson's storm petrel is the most abundant of all the seabirds, with an extremely long life span (20 years) for such a small bird. The diving petrel actually pursues its prey actively underwater as it dives headlong down and continues the chase, emerging after its meal without even missing a wing beat.

Figure 10.19. Tubenoses: Wilsons storm petrel (left) and the diving petrel (right)

10.4.5. Penguins

Penguins are the group of birds best adapted to a marine lifestyle. They are flightless, and their wings are adapted as flippers; while underwater they flap their wings to swim. They only come on land to breed, and are awkward, waddling on their legs or tobogganing on their bellies. Their body is torpedo-shaped and streamlined and their flat, webbed feet are used for steering. Their bones are dense which reduces buoyancy and helps them swim. They breathe by leaping from the water. Penguins live in the southern hemisphere and eat fish, squid and krill. In the water they are preyed upon by leopard seals and killer whales, whilst on land the main threat is predation by skuas, or the freezing temperatures.

Penguins are well adapted for the cold; all but 1 species, the Galápagos penguin, live in Antarctica or other cold regions of the southern hemisphere. They have a layer of fat under their skin and their dense, waterproof feathers trap air that is warmed by body heat. They typically have a large size, and the decreased surface area to volume ratio allows them to better conserve heat.

Life in the extremely cold climates of Antarctica require special adaptations for reproduction. The emperor penguin (Figure 10.20) lays eggs in the middle of the winter, when temperature drop to -63^{o}C and blizzards blow 81-106 mph. The female lays one egg then leaves for the feeding grounds, leaving the egg in the care of the male for two months. Despite the extremely cold temperature, males incubate the egg by balancing it on their feet and covering it with a fold of skin of their lower abdomen. The males fast during the entire incubation period, and if the chick hatches before the mother returns, the male can feed it with undigested food from its crop (digestive organ that stores food before it is processed). When the mother returns with her crop full of fish, she feeds the chick and the male returns to feed. Both parents then help feed the chick. By summer time, the chick can feed itself and can enter the sea. The advantage of laying eggs in the middle of the winter is that the chick enters the sea in the summer, when food is most abundant in polar regions.

Figure 10.20. Colony of emperor penguins

10.5. Review Questions: Reptiles and Birds

1. What is an amniotic egg, and what are the advantages of it?

2. Why was the evolution of copulatory organs important for the evolution of the amniotic egg?

3. How do marine crocodiles eliminate excess salt?

4. What kind of reproductive strategy do marine crocodiles display? Where are baby crocodiles born?

5. How do sea turtles eliminate excess salt?

6. What organ do marine reptiles and birds use to breathe?

7. Which species of turtle is found in cold oceans? What adaptation enables that?

8. What do sea turtles feed on?

9. Where do sea turtles mate? Where do they lay their eggs?

10. How does temperature affect the development of sea turtles?

11. Where would you find the only marine iguana?

12. What adaptation helps marine iguanas live in the cold waters of the Pacific?

13. How do iguanas feed underwater?

14. How do marine iguanas eliminate excess salts?

15. Give five examples of adaptations seen in sea snakes for a marine existence?

16. How do marine birds remove excess salts from their bodies?

17. What do shorebirds eat?

18. How might climate change affect sex ratios in marine crocodiles and sea turtles?

19. Do any seabirds spend their entire life at sea? If so, which one(s)?

20. What do gulls feed on?

21. What are the advantages and disadvantages of nesting in a colony?

22. What is convergent evolution?

23. Give an example of two groups of birds that are ecological equivalents?

24. What is a crop and what is it used for?

25. What species of pelican do we see in the Caribbean most frequently?

26. What is a gular pouch and on which bird would you find it?

27. What is the most common booby in the Caribbean?

28. Which bird is used by fishermen in Asia to help them catch fish?

29. What is cleptoparasitism and which bird exhibits it?

30. Why can a frigate bird not attack prey underwater?

31. Which male birds inflate their throats to attract a mate?

32. Which group of seabird spends most of its life at sea?

33. Give 2 examples of birds that pursue their prey underwater?

34. Describe adaptations of seabirds to maintain their body temperature in cold climates.

35. Which group of seabirds doesn’t have webbed feet?

36. Which seabird migrates from pole to pole?

37. Describe adaptations that penguins have for extensive swimming.

11. Marine Mammals (Karleskint Chapter 12)

Mammals are vertebrates of the phylum Chordata and class Mammalia. Marine mammals live mostly or entirely in water, and are dependent on the ocean for food. They therefore have anatomical features adapted for an aquatic lifestyle, such as fins. In all mammals, the mother feeds her young with milk produced in mammary glands. Mammals are homeotherms and endotherms. Marine mammals have an insulating layer of hair or a thick layer of subcutaneous blubber to help maintain their body temperature, since heat is lost more quickly in water than in air. Like other homeothermic animals, marine mammals expend about 10 times more energy than poikilothermic animals (e.g. reptiles) to support their high metabolic rate, and therefore need a greater amount of food. Being homeotherms, marine mammals can remain active even in the cold and have adapted to a variety of environments including polar waters.

Mammals evolved on land and marine mammals are descendants of terrestrial animals, which is evident from the fossil record. Additionally, the flippers of many marine mammals have the bone structure of a five-fingered hand, and those that do not have hind limbs (sirenians and cetaceans) have vestigial pelvic bones. Mammals in three separate orders have evolved adaptations for the marine environment. The order Carnivora includes sea otters, polar bears and seals; the order Sirenia represents the sea cows (manatees and dugongs) and the order Cetacean includes whales, dolphins and porpoises.

11.1. Sea Otters

Figure 11.1. Sea otters at the surface.

Sea otters are found in the North Pacific. They were nearly hunted to extinction for their thick fur. They lack blubber and rely on their thick fur to maintain their body heat. They have short, erect ears, dexterous 5-fingered forelimbs and well-defined hind limbs with fin-like feet. Sea otters stay near coastal reefs and kelp beds, and eat sea urchins, crustaceans, abalone and some fish. They pick their food from the seabed and carry it to the surface, where they float on their back while they eat (Figure 11.1). They have been seen bringing up stones to smash shells against their reinforced chest, and have powerful jaw muscles and strong teeth to break tough shells on their prey. They can eat 25% of their body weight each day. Sea otters are often found wrapped up in kelp with their feet to stay in the same place while eating or sleeping.

11.2 Polar Bears

Polar bears are top predators of marine food chains in the Arctic region. While they spend much of their time on land and ice, they equally comfortable on ice floes and are excellent swimmers. They have thick blubber and their fur traps an insulating layer of air, which keeps the skin warmer while it swims. Nearly all of their food comes from the sea, with seals being their most important food items. Polar bears are hunted in the Arctic, and are greatly affected by climate change. The Arctic is warming faster than any other ocean, and the amount of sea ice is steadily decreasing. Less sea ice means both lower productivity (less ice-associated phytoplankton, and therefore less food available for higher trophic levels), and less habitat. Because of the lack of sea ice, many more polar bears have been found on the Canadian mainland in recent years, where they have much lower food available.

11.3 Pinnipeds

The pinnipeds include seals, sea lions and walruses. Pinnipeds have four limbs like terrestrial animals but are more at home in water. They are found in all oceans, mostly in cold water. Pinnipeds spend most of their life at sea where they feed, but they must come back to land or sea ice to give birth and molt. Most eat fish and invertebrates but some, like the leopard seal, eat other homeothermic animals. Pinnipeds are eaten by sharks, killer whales and humans.

Pinnipeds are well adapted for life in cold water and have thick layers of subcutaneous fat. They have large brains with well-developed sense, and their two pairs of limbs are modified into flippers. Pinnipeds are fast swimmers and expert divers. They exhale before diving, which reduces the amount of air in their lungs, making them less buoyant and less susceptible to decompression illness. During the dive, their metabolism decreases by 20% and their heart rate slows down, reducing their oxygen consumption. The blood is redistributed to vital organs like the heart and brain so they still receive enough oxygen to function. Northern elephant seals have been known to dive to a depth of over 1500 m.

Pinnipeds mate and give birth on beaches or on sea ice. Most species mate annually. Some species are polygynous, i.e. males mate with several females. This is typically found in species that breed in high densities where it is easy for one male to gain control of several females, and tends to be associated with sexual dimorphism. Polygyny is mostly found in eared seals; true seals (phocids) are usually monogamous. Typically, females give birth to their pups conceived the previous year shortly after arriving on breeding grounds, and then mate again. Gestation is typically 9 to 12 months. The lactation period varies with the species and habitat. The species that live in the coldest habitats, mostly phocids, have shorter lactation periods, from four days to 2-3 weeks. This is in part because female phocids fast while they nurse, and in part due to the nature of the habitat; many phocids breed on pack ice which is unstable. A shorter lactation period means that the pup develops insulation faster, which it needs to enter the ocean in this cold climate. On the other hand, sea lions in temperate habitats may nurse their pups for up to 6 months.

There are three families of pinnipeds: the eared seals (family Otariidae), the true seals (family Phocidae) and the walruses (family Odobenidae).

11.3.1. Eared Seals

Eared seals, as their name suggests, have external ears (Figure 11.2). They swim with their fore flippers while their hind limbs remain motionless and are used for steering. On land, their hind limbs and fore-limbs can be rotated at right angles to their body to help them walk. There are two groups of eared seals: sea lions and fur seals.

Sea lions are highly social animals and congregate in groups when they are ashore. They are the trained seals of zoos and circuses and are intelligent animals. Fur seals have thick, wooly undercoats that are prized in the fur market, and they have been heavily hunted in the past. There is one species of fur seal in the northern hemisphere and eight in the southern hemisphere.

Figure 11.2. Eared seals: sea lion.

11.3.2. True Seals

Phocids, or true seals, lack external ears and swim using their hind flippers only. They are less well-adapted to life on land, as their forelimbs are smaller and closer to their head and cannot be rotated, instead they are dragged behind them on land (Figure 11.3). They drag their body on land, rolling or crawling where possible. True seals congregate on shore or on ice floes when breeding and typically do not establish harems—instead couples form monogamous relationships and remain together all season. The crabeater seal is the most abundant of the phocids, and despite its name it feeds on krill in the Southern Ocean. Harbor seals are found along the cool coasts of the Northern hemisphere. Harp seals are found in the cold waters of the northern Atlantic and Arctic oceans, and their pups have the long, silky yellow-white fur that was highly prized by hunters. The leopard seal is the only phocid that eats homeothermic prey, and it lurks on the edge of ice floes to attack seals, penguins and other seabirds. Elephant seals are very large and show sexual dimorphism. The males have a proboscis, an enlarged and inflatable nasal cavity used to warn rivals and attract mates as it acts as a resonating chamber amplifying their roar. The male southern elephant seal can reach 6m in length and weigh 4 tons. Elephant seals have the deepest dives every recorded for pinnipeds, over 1,500m deep.

Figure 11.3. Harp seal, an example of a phocid.

11.3.3. Walruses

There is only one species in this family (*Odobenus rosmarus*). Walruses lack external ears and have a distinct neck. They use their hind limbs to walk on land. They are found in the Arctic regions of the northern hemisphere. The canine teeth of the upper jaw are developed into tusks (Figure 11.4), and are used in fighting and to hoist the body onto ice floes. The tusks are more developed in males than in females. Their main food source is benthic invertebrates, in particular clams.

Figure 11.4. Male walrus showing tusks.

11.4. Sirenians: Manatees and Dugongs

Sirenians are completely aquatic marine mammals found in coastal areas and estuaries of tropical seas. They get their names from the mythical sirens of Homer's Odyssey and Columbus and other sailors mistook them for mermaids. Like whales, sirenians have streamlined, hairless bodies. Their forelimbs form flippers but they have no hind limbs, only a vestigial pelvis (Figure 11.5). They propel themselves with their tail flukes. There are two families of sirenians: Dungongidae (dugongs) and Trichechidae (manatees).

Dugongs are strictly marine and feed on shallow-water grasses in coastal areas of the Indian Ocean. There is only one species of dugong, *Dugong dugon*; they are hunted for their flesh and now endangered. Dugongs are distinguished anatomically from manatees by larger heads, shorter flippers and a notched tail.

Manatees are found in the Atlantic Ocean and Caribbean Sea as well as nearby inland rivers and lakes. They have smaller heads and longer flippers than dugongs, and have rounded tails. There are three species of manatee and they are strict herbivores. They are slow animals and spend a lot of time at the surface, and for those reasons they are at risk of being struck by boat propellers.

The Steller's sea cow was the only sirenian in polar waters and was found in the Arctic, but it is now extinct due to hunting, overfishing of their prey, climate change and disease.

Figure 11.5. Sirenians: Manatees are found in the Atlantic Ocean (left) and dugongs in the Indian Ocean (right).

11.5. Cetaceans

Cetaceans are the marine mammals most adapted to life at sea, and include whales, dolphins and porpoises. Cetaceans evolved from an ancient group of terrestrial carnivorous mammals, and this is supported by fossil evidence and similarities in the fetuses of cetaceans and terrestrial mammals. Cetacean fetuses have four limbs, and their flippers have the bone structure of a five-fingered hand (Figure 11.6). This five-fingered bone structure is maintained in the flippers of adult baleen whales, and both baleen and toothed whales retain vestigial hip bones even though they don't have legs (Figure 11.7)

Figure 11.6. An embryo of a spotted dolphin, with hind limbs present as small lumps.

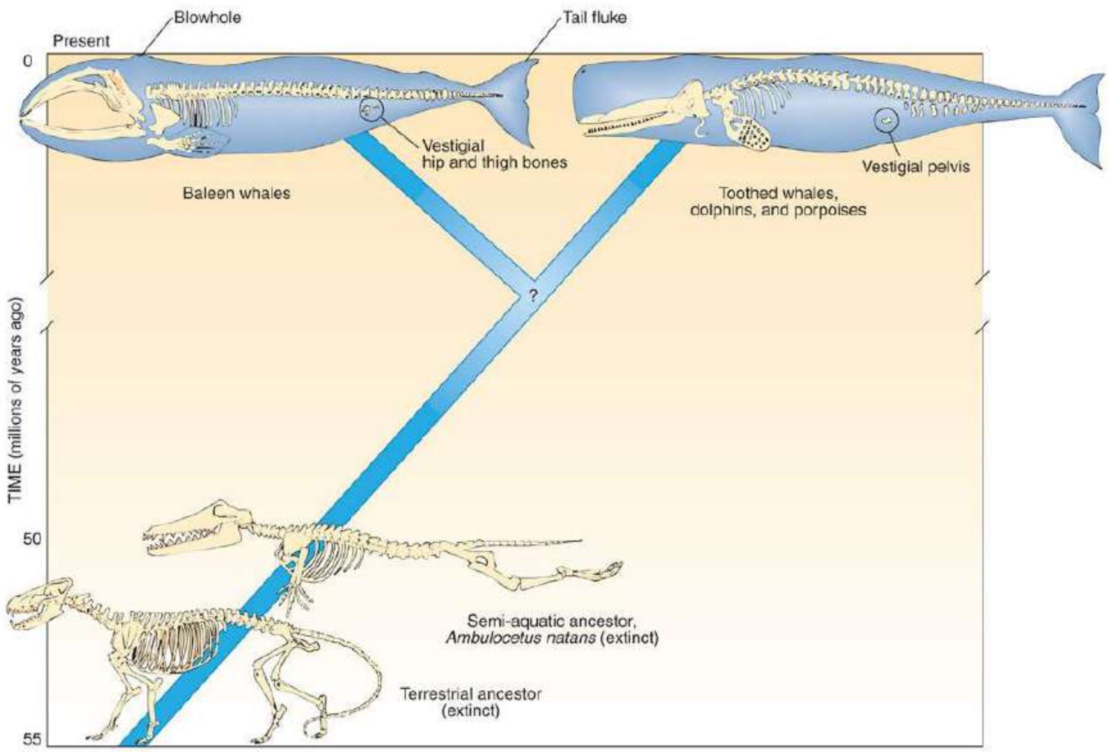


Figure 11.7. Cetaceans evolved from four-legged terrestrial carnivores. Modern cetaceans have adaptations for life at sea including streamlined bodies, flippers and a fluke, but their bone structure is a clue to their terrestrial ancestry: vestigial hip bones or pelvis , and 5-fingered bone structure inside the fins of baleen whales.

The body of cetaceans closely resembles that of fishes because of convergent evolution and it is very streamlined. However cetaceans swim with a vertical motion of their fluke, whereas fishes swim with a side undulation of their caudal fin. The blowhole of cetaceans is the nostril, which migrates to the top of the head during embryonic development. They have a thick layer of subcutaneous fat (blubber), which provides insulation and acts as an energy reserve and a source of water when the fat is metabolized. They have no external ear, but small openings on side of their head which leads to the eardrum. This opening is plugged with wax to prevent water entering and damaging ear drum. The forelimbs are modified into stabilizing flippers. The tail is made of flat dense connective tissue, and is the main organ of propulsion. Like sirenians, adult cetaceans do not have hind limbs though they can be distinguished in the fetus. Cetaceans are hairless like sirenians, and they lack sweat glands which helps them to conserve water.

11.5.1. Adaptations for Diving

Whales have several adaptations similar to pinnipeds that allow them to do extended dives. Prior to a dive, they take a huge breath of air, and oxygen is rapidly transferred to the blood and muscles. The whale then exhales to reduce buoyancy, which also prevents decompression illness from storing air at high pressure. They have proportionately large lungs, which allow them to rapidly absorb a lot of oxygen. Their lungs and rib cages are structured so that they can collapse easily upon descent. During a dive, the metabolic rate and heart rate decrease, and blood is preferentially shunted to vital organs. The brain of cetaceans is less sensitive to carbon dioxide levels in the blood than in terrestrial mammals, so they can stay submerged longer without feeling the urge to breathe. They have a large amount of hemoglobin in their blood compared to terrestrial mammals which allows them to carry a high amount of oxygen in their blood. Cetaceans also have a high level of myoglobin, a molecule that stores oxygen in muscle tissue providing a reservoir of oxygen for muscle activity. When cetaceans surface, they expose their blowhole to the air and emit a spout of vapor condensed from air and mucus droplets. The mucus may help eliminate nitrogen by absorbing it before it gets to the lungs, thus helping prevent decompression illness (the bends).

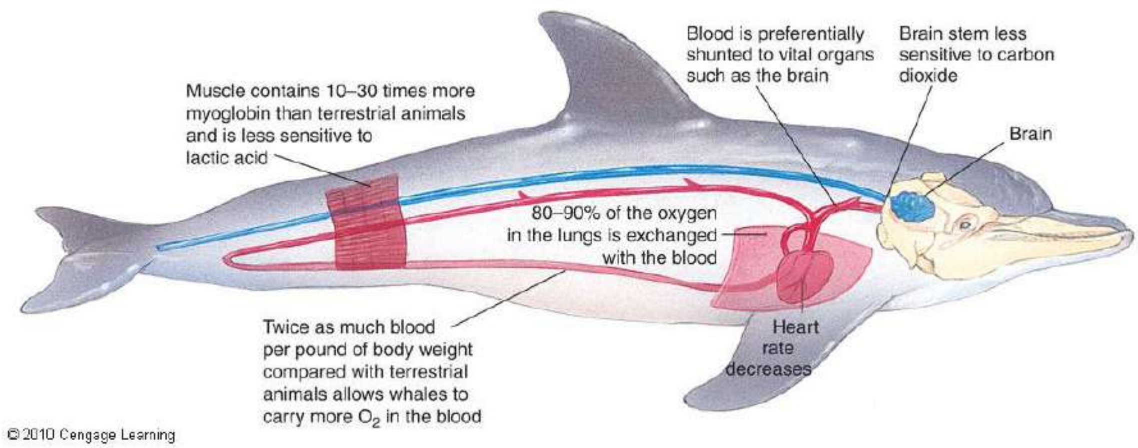


Figure 11.8. Adaptations for diving in cetaceans.

11.5.2. Cetacean Behaviors

Cetaceans are intelligent and curious animals, and they display a range of interesting behaviors. These behaviors are mainly to learn about their environment or play a role in communication, although the meaning of many of them is not fully understood. Spy hopping is when a whale sticks its head straight out of the water. It might occur if the whale is curious about a boat or could help the whale navigate in coastal waters. Breaching is when the whale completely (or almost) leaves the water, which involves swimming vertically very quickly up to the surface, twisting its body and then falling back horizontally (Figure 11.9). Humpback and sperm whales breach regularly and sometimes several times in a row (serial breaching). The significance of this is not well understood, but it may play a role in communication. Breaching has also been suggested to play a role in establishing dominance, knocking off parasites, or purely for fun. Cetaceans also slap the water in a variety of ways, with their pectoral fins or their flukes. Slapping can be aggressive or not.

Figure 11.9. A humpback whale breaching (left) and an Orca spy hopping (right)

11.5.3. Reproduction and Development

Many cetaceans travel in pods, and most have one offspring at a time. Like most marine mammals, cetacean pups are nursed on an extremely rich milk (40-50% fat, 10-12% protein), which allows them to gain weight and increase in size rapidly. Cetaceans give birth in the water, and most do so in tropical areas since the young have a thinner layer of blubber so lose heat quicker.

11.5.4. Baleen Whales

Baleen whales, or mysticetes, are named after the enormous plates of baleen they have in their mouths (Figure 11.10). These are composed of keratin, and hundreds of plates form a tight mesh which is used to sieve water to capture plankton and small fish. The whale feeds by swimming open-mouthed through the water, closing its mouth and then straining out the water through the baleen. Humpback whales create a ring of bubbles (called a bubble net) as they circle around a swarm of krill (or other prey), which concentrates them. The whale then ingests the krill. It is not surprising that the largest animals on earth, baleen whales, feed on such small organisms. Planktonic organisms, being low on the food chain, are present in a larger biomass than organisms higher up on the food chain, allowing the whales to ingest the large quantities of food needed to meet their high energetic requirements.

Figure 11.10. Enormous plates of baleen are used for straining out plankton

Right and Bowhead Whales

Right whales and bowhead whales lack a dorsal fin, and have no ventral grooves. Right whales have strange warts on their head and a downturned mouth (Figure 11.9). They received their name from early whalers because they floated once dead, making them the "right whale" to catch. They have been hunted extensively. The population in the north Atlantic has been heavily depleted and is showing no signs of recovery. The bowhead whale has also been hunted heavily and is the rarest of all whales.

Rorquals

Rorquals have dorsal fins and ventral grooves, which allow their throat to expand as the whale feeds. They are streamlined and fast swimmers. Rorquals include the blue, fin, minke, and humpback whales. The blue whale is the largest of all whales and may be the largest whale that ever lived; it is up to 30m in length and can weigh as much as 1,600 humans (Figure 11.9). The fin whale is the second largest and is rarely seen close to shore. The humpback is easily identified by the hump on its back, and it has very long pectoral fins (its Latin name translates as the "big wing of New England"). Humpback whales spend the summer in the polar seas feeding on krill and other zooplankton, coming to the warmer waters of the tropics in the winter to breed. The numbers of rorquals have also been drastically reduced because of whaling.

Gray whale (*Eschrictius gibbosus*)

Although there used to be several populations of gray whales, only the eastern Pacific population remains today—the others have been hunted to extinction. Gray whales undertake a long migration from their feeding grounds in the Bering Sea to their breeding grounds in Baja California. Gray whales feed on benthic invertebrates and often have large accumulations of barnacles of their skin (Figure 11.11).

Figure 11.11. Baleen whales: Right whale (left), rorqual – blue whale (middle) and gray whale (right)

11.5.5. Toothed Whales

Toothed whales (odontocetes) include sperm whales, dolphins, porpoises, killer whales and narwhals. They have simplified teeth, which may be present in one of both jaws, and can be modified into a tusk (e.g. narwhals)

Sperm Whales (*Physeter macrocephalus*)

Sperm whales are the third largest animal on earth, after the blue and fin whales. They are characterized by a massive blunt snout and have no real dorsal fin. They eat squid and fish and can be aggressive, occasionally attacking whalers (which inspired the story of Moby Dick). They are polygynous: males mate with several females. They are mainly found in the tropics (e.g. Dominica and Guadeloupe) and temperate water, and only occasionally in the polar seas. Sperm whales are named for the spermaceti, a transparent oily substance in the animal's head that is thought to be used in echolocation, which was mistaken for a reserve of sperm by early whalers. Upon contact with air it forms a waxy material which was highly sought after as a high-grade wax at the height of the whaling industry. It was then used in ointments, face creams, luxury candles and lubricants but has now largely been replaced by synthetics. Sperm whales also produce ambergris, a secretion from the digestive tract that is thought to provide protection from undigested squid beaks and cuttlefish bones. When exposed to air, it forms a solid, gray, waxy material with a disagreeable odor, but over time it acquires properties that make it highly prized as a base for most expensive perfumes. Ambergris is even more valuable than spermaceti (Figure 11.12).

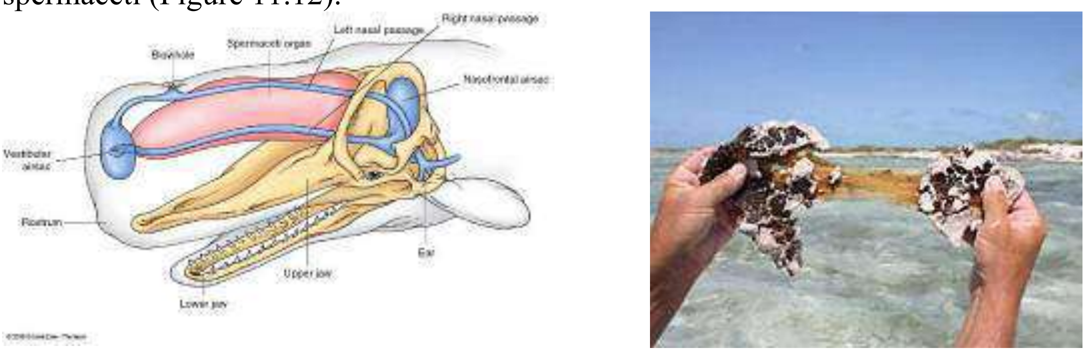


Figure 11.12. Ambergris, a digestive secretion produced by sperm whales, valuable in the perfume industry (right), and spermaceti, an oil used in echolocation that is used in high grade ointments and candles and stored in the spermaceti organ (in pink, left).

White whales

This group contains only two genera with one species each. Belugas (*Delphinapterus leucas*) are unique for their white color, and are found in the northern polar seas (Figure 11.13). The narwhal (*Monodon monoceris*) is a close relative to the beluga and also lives in Arctic waters. Narwhal fetuses have tooth buds, but by birth all but two have disappeared. In males, these develop as a tusk that can reach 3 m. This tusk is used to break air holes in the ice or probe the sediment for food. In the middle ages the narwhal tusk was worth more than its weight in gold, believed to be the magical horns of unicorns. Populations of narwhals suffered severe losses but have now recovered and their only human predators are Inuit (Figure 11.13).

Figure 11.13. White whales: Belugas (left) and narwhals (right)

Porpoises
Porpoises have a rounded head with no definite beak, flat triangular teeth and a triangular dorsal fin. Harbor porpoises are one of the smallest cetaceans (1-2 m) and are known for their great intelligence (Figure 11.14). The vaquita (or "little cow") is endemic to the upper Gulf of California, a rare feature in the marine environment. They face extinction as a result of fishermen depleting stocks of its prey.

Figure 11.14. The harbor porpoise

Dolphins (family Delphinidae)
Dolphins are the most abundant group of cetaceans. In contrast to porpoises, dolphins have a distinct beak, round and conical teeth, and their dorsal fins curve backwards. Common dolphins have a very clear beak and are known for following ships. They are found throughout all temperate oceans and are one of the swiftest cetacean swimmers (Figure 11.15). Bottlenose dolphins are common on the east coast of the USA and in the Caribbean, and have been used extensively in research on cetacean intelligence. They are the performers at aquariums or movie stars and are very sociable (Figure 11.15). The orca, or killer whale, is in the same family as dolphins. It is the largest dolphin (males can reach 10m) and is only cetacean that is known to eat homeothermic prey. They have distinctive black and white coloration and a false eye spot. They are found in all seas, but are most common in the polar regions (Figure 11.15). Pilot whales are dolphins related to killer whales. They are the only whale not protected by international agreements and are still hunted in Bequia (the Grenadines) by traditional mean. They have been exploited by whalers because of their tendency to follow individuals that stray from the pod, allowing whalers to harpoon a couple and tow them to shallow waters then wait for a mass stranding. They live in pods of several hundred individuals that appear to follow a single leader. They frequently beach themselves in large numbers, possibly due to a parasite in their inner ear that affects their ability to navigate.

Figure 11.15. Dolphins: Common dolphins (left), bottlenose dolphins (middle), and orca, killer whales (right)

11.5.6. Echolocation

Toothed whales do not have very good vision, and even in clear water they cannot see more than 30m. To compensate for this, their ears are modified to receive a wide range of underwater vibrations and they use echolocation to distinguish and hone in on objects. Dolphins emit clicking sounds, which are directed by being focused in the melon (an oval mass of fatty waxy material on top of the head). These sounds bounce off objects, and the echoes are picked up in the lower jaw, which transmits vibrations to the inner ear (Figure 11.16). These echoes provide information on the direction, the change in frequency, the amplitude and the time elapsed before the sound returns. In turn, this reveals the range, bearing, size, shape, texture and density of the object.

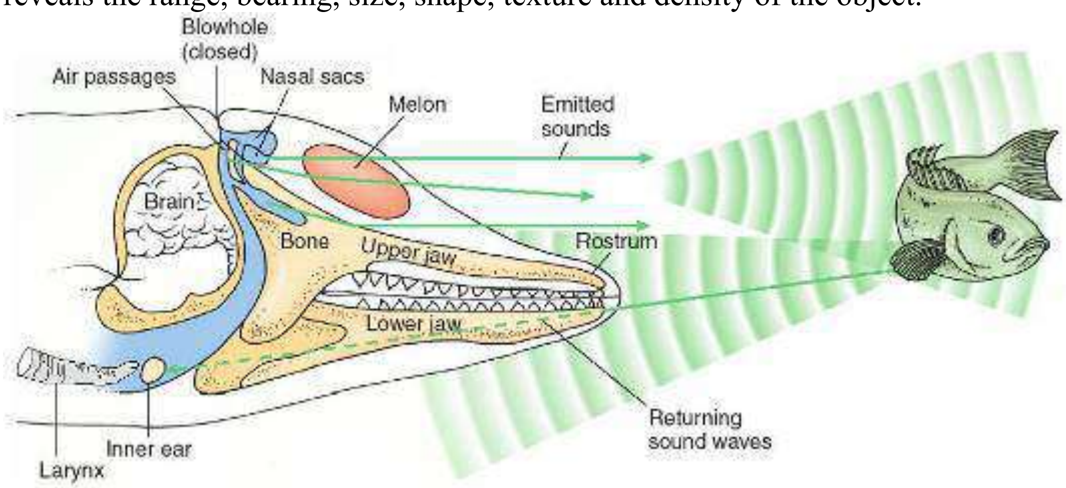


Figure 11.16. Echolocation in dolphins.

11.6. Review Questions: Marine Mammals

1. What are three characteristic of mammals?
2. How do sea otters insulate themselves, do they have blubber?
3. What do sea otters generally feed on and how do they do this?

4. What are the three families of pinnipeds?
5. Explain three adaptations seen in pinnipeds for diving?
6. What provides the propulsive force in eared seals?
7. Are fur seals true seals?
8. What provides the propulsive force in true seals?
9. Which family of Pinnipeds can rotate their flippers to support their weight on land?
10. Which seal is the only one to eat homeothermic prey?
11. Are most seals monogamous or polygamous? Is sexual dimorphism common?
12. Which pinniped has two upper canines evolved into tusks in the males?
13. Where do pinnipeds give birth? Sirenians? Cetaceans?
14. Give an example of a Sirenian.
15. Where would you be most likely to see a Manatee?
16. What is the main food source of Manatees and Dugongs?
17. Cetaceans evolved from a mammal that live in what habitat? Give 3 lines of evidence for this.
18. Give three roles of the subcutaneous blubber in cetaceans?
19. What is a fluke?
20. Describe the adaptations of cetaceans for diving.
21. Why do cetaceans have large amounts of hemoglobin and myoglobin?
22. Why is the medulla oblongata of cetaceans less sensitive to CO_2 levels?
23. What is spy hopping? And what is thought to be its purpose?
24. What is breaching? And what are thought to be its purposes?
25. What is the term used to describe a group of cetaceans?
26. What are the 2 sub-orders of whales, and how do they differ?
27. What is baleen composed of?
28. What is bubble netting, and which cetacean commonly does this and why?

29. Why were right whales considered the correct whale to hunt?
30. What are ventral grooves of rorquals and what is their purpose?
31. Give an example of a rorqual.
32. What is the largest animal on earth?
33. What is the main food source of baleen whales? How might this be related to their size?
34. Give three examples of toothed whales.
35. Which group of marine mammals has very well-developed social systems?
36. Which is the only cetacean to eat homeothermic prey?
37. What is the melon used for?
38. Where are sounds picked up in echolocation?
39. What is the role of echolocation in cetaceans?
40. Describe the migration typical of large baleen whales.
41. Which whale populations have been significantly reduced by commercial whaling/

12. Intertidal Ecology **(Karleskint Chapter 13, Nybakken Chapters 6 & 7)**

12.1. Introduction

The intertidal zone is the part of the marine environment that is between the highest high tide and the lowest low tide. It is therefore alternately submerged and exposed to air. This is a stressful environment with large daily fluctuations in such factors as temperature, salinity, moisture, and wave action. Organisms must have specific adaptations to survive in these environmental extremes. Most organisms in the intertidal zone are marine in origin, so exposure at low tide is physiologically stressful to most.

12.2. Rocky shores

Rocky shores are found in high energy environments, and are often densely populated with sessile organisms well-adapted to the wave action. The distribution of organisms on rocky shores depends on many factors including the amount of wave action, climate, length of exposure to air, amount of light, shape of the shore, and presence of crevices, overhangs and caves that help retain moisture. Rocky shores exhibit a well-defined zonation, a separation of organisms in definite horizontal bands, reflecting their adaptations to specific conditions. Each band is distinct in color and dominant organism, similar to the zonation found on mountains.

12.2.1. Adaptations to life on rocky shores

Avoiding overheating and water loss (desiccation)

As organisms are exposed to air at low tide, they lose water by evaporation. They must be able to either tolerate this water loss, or have mechanisms to reduce it until the tide comes back. Mobile organisms can move in cracks, under seaweeds, or move with the tide. Sessile organisms may occupy selected micro-habitats that retain moisture, such as under seaweeds, or live in dense aggregations. Several high intertidal seaweeds can withstand significant water loss and become dry and brittle at low tide, but quickly absorb water and resume normal functions at high tide. Physiological adaptations that prevent or reduce water loss include closing an external shell (e.g. barnacles, mussels, snails), or producing mucus (e.g. some anemones, hydroids and seaweeds).

As intertidal organisms are often exposed to higher temperatures at low tides, many have adaptations to reduce heat gain and/or increase heat loss.

Reducing heat gain is accomplished by a large body size (compared to similar subtidal relatives), reducing the amount of the body touching the substrate (e.g. mucus threads produced by knobby periwinkles), and light colors.

Increasing heat loss can be done through an increase in surface area to volume ratio (e.g. more pronounced ridges in some mussels and snails), and evaporation; some organisms store extra water that can be used at low tide for evaporative cooling.

Coping with cold
At high latitudes, there can be a risk of freezing in the intertidal zone. Temperate intertidal species show adaptations to retain heat, and in contrast to their warm-climate relatives often have darker, more compact shells that are better at absorbing heat. Moreover, several intertidal organisms produce anti-freeze compounds.

Avoiding wave shock

Many organisms have adaptations to reduce their susceptibility to wave action in the intertidal zone. Many are small in size, squat, with streamlined bodies which minimize drag (e.g. limpets, barnacles, chitons), or live in burrows (e.g. some urchins; Figure 12.1). Seaweeds are flexible and bend with the waves (Figure 12.2). Several organisms such as barnacles, many bivalves and seaweeds are permanently and strongly attached to the substrate. Others have a non-permanent attachment but are strong nonetheless, for example several intertidal mollusks have an enlarged foot to cling strongly to rocks. Mobile organisms can seek shelter in crevices and under rocks (Figure 12.1).

Figure 12.1. Chitons (left) are streamlined to minimize drag, while many urchins (right) create burrows to avoid wave shock.

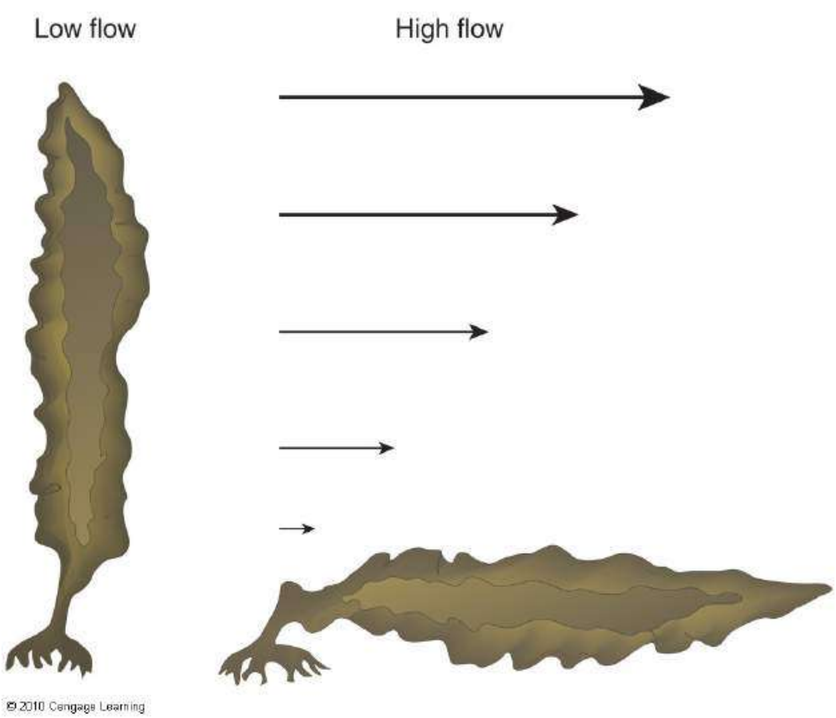


Figure 12.2. Seaweeds are flexible and bend with water movement.

Respiration

Gills of intertidal organisms are typically protected inside a body cavity, which provides mechanical protection and reduces desiccation during low tide. Most organisms must reduce their activity at low tide as they reduce gas exchange. Some gastropods that live high in the intertidal zone (e.g. rough periwinkles, *Littorina obtusata*) conduct gas exchange through their enlarged, well-vascularized mantle cavity, enabling them to conduct gas exchange at low tide (i.e. air breathers), and eliminating the need to protect fragile gills at low tide. Those organisms will drown if submerged for several hours.

12.2.2. Rocky shore zonation

The zonation found on rocky intertidal shores is due to a variety of physical and biological factors. Physical factors include desiccation and temperature, and tend to set the upper limit of the distribution for given organism. Biological factors are typically more important in setting the lower limits of distribution, and are often more complex and subtle than physical factors. Biological factors include competition for space, which can be quite limiting in some intertidal areas, and for light (for seaweeds). Grazing by gastropods, crustaceans, urchins and fishes can limit vertical distribution, affect species diversity and increase patchiness. Similarly, preferential predation can allow a competitively inferior species to dominate.

Zonation patterns in intertidal zones are very similar worldwide in particular in temperate regions and can generally be described by the Stephenson Zonation Classification. This classification of intertidal zones for rocky shores is based on the distribution limits of certain common organisms, rather than tidal heights (Figure 12.3). In this classification, the suppralittoral zone is that above high tide, affected by the ocean only by salt spray. Conversely, the infralittoral zone (or subtidal zone) is covered by water even at low tide. The true intertidal zone is separated into the suppralittoral fringe, the midlittoral zone, and the infralittoral fringe.

The suppralittoral fringe (splash zone) is covered only by the highest spring tide and is dampened by splash. It is dominated by periwinkles (*Littorina* spp.). The midlittoral zone is regularly exposed during low tides and covered during high tides. It is dominated by barnacles, along with mussels and rockweeds. The infralittoral fringe zone extends from the lowest of low tides to the upper limits reached by large kelps (*Laminaria* spp.).

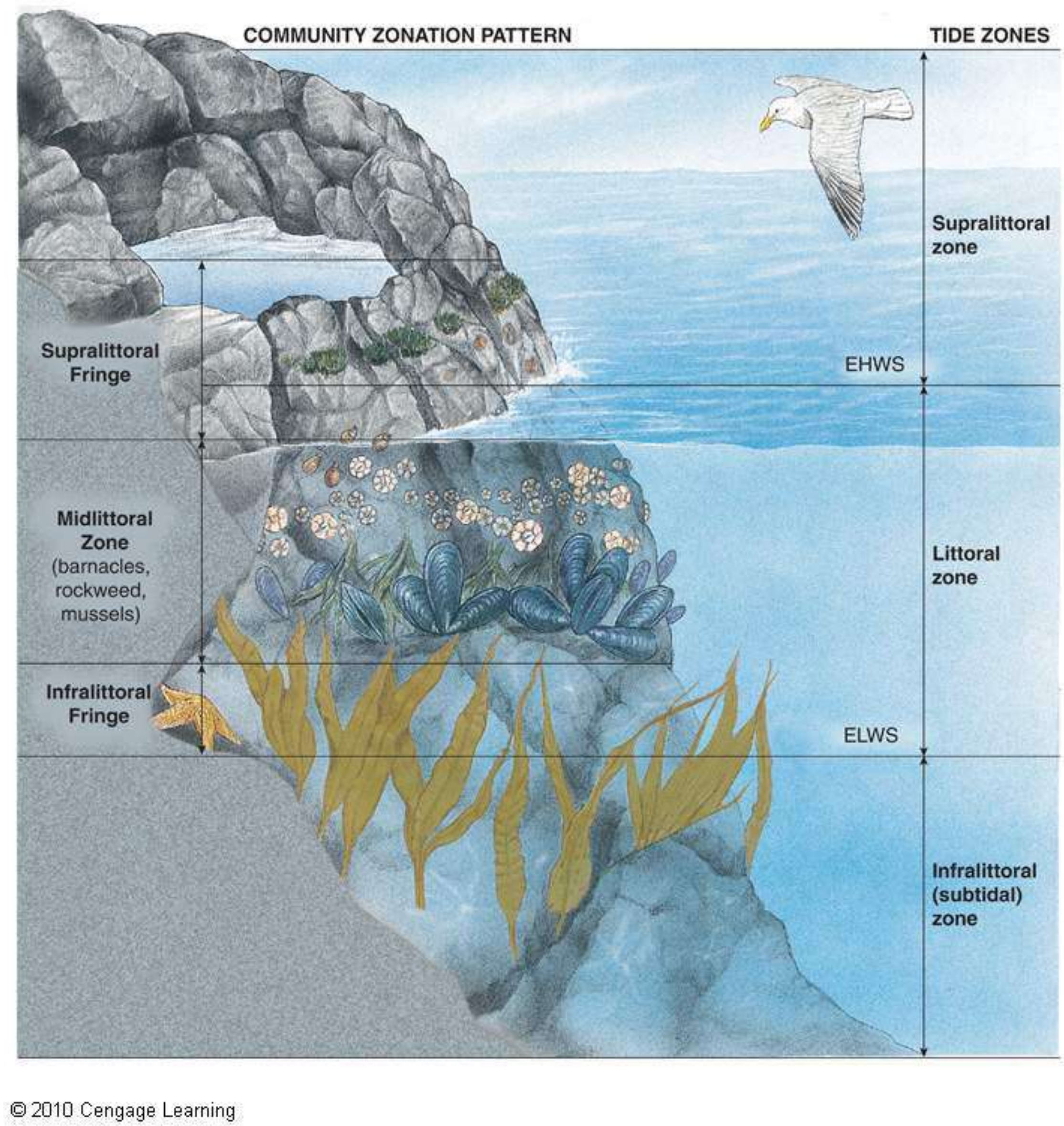


Figure 12.3. Stephenson's zonation classification of the rocky intertidal.

12.2.3. Temperate rocky shores

Temperate rocky shores exhibit well-defined zonation that is comparable in most areas of the world. Below is a description of a typical temperate rocky shore, of the type that would be seen in the western North Atlantic.

The supralittoral fringe is exposed to air for the longest period and is therefore a very harsh physical environment for marine species, with little moisture. Consequently few species have evolved the necessary adaptations to survive in this habitat. As mentioned previously the rough periwinkle (*Littorina obtusata*) exchanges gas across their mantle. Rough periwinkles also hide in crevices and seal the opening of their shell with mucus to avoid desiccation. Lichens form bands or patches that mark the upper part of the intertidal zone. Lichens are a symbiotic relationship between fungi and algae; the fungi receives food from the algae, and the algae benefits because the fungi is able to hold several times its weight in water at low tide. Cyanobacteria form tar-like patches and produce a gelatinous covering that traps water helping them resist desiccation.

In the midlittoral zone, many organisms temporarily suspend feeding as they become exposed at low tide. The upper midlittoral zone is dominated by barnacles (*Balanus* spp. and *Semibalanus* spp.), which are permanently attached to the rock and may be as dense as 9000 individuals/m^2. The middle to lower midlittoral zone is characterized by oysters, mussels, limpets, and periwinkles. Seaweeds are present on rocky shores that experience low wave action, and are dominated by brown algae, specifically rockweeds (*Fucus* sp.). Those are usually small, but can form large mats that trap water and provide a haven for many animals. Seaweeds in this area are well adapted to the problems they face; they produce deterrent chemicals to prevent grazing by herbivores, a gelatinous coating to prevent water loss, attach firmly to the substrate with a holdfast and have flexible blades to withstand wave action.

The infralittoral fringe, the transitional area between the midlittoral and the infralittoral zones, is submerged except during the lowest spring tides. Organisms here can tolerate only brief exposures to air. Dense turfs of seaweeds are often found here, in particular large brown algae, along with anemones, mollusks, sea stars, brittle stars, bryozoans and hydrozoans. This is the most stable area of the intertidal zone, and it exhibits the highest species diversity.

12.2.4. Comparison of temperate and tropical rocky shores

Temperate rocky shores have been studied extensively in a variety of locations worldwide and show striking similarities between locations. In comparison, tropical rocky shores seem to show a greater variation between locations, and therefore it is more difficult to draw generalizations in the tropics. Still there are general trends that can be observed.

Tropical areas tend to harbor more herbivores (generally herbivorous fish), which limit the abundance of fleshy algae. Therefore there are no large seaweeds in the tropical intertidal zone, instead we find bare space or encrusting algae. Predation is also more important, and this limits the abundance of the sessile invertebrates (e.g. barnacles and mussels) that are so important in temperate regions. Because of this, competition for space is much less severe in the tropics than in temperate intertidal areas. Finally, holes and crevices are more important to intertidal organisms in the tropics as they provide shelter from extreme heat and abundant consumers.

12.2.5. Tide pools

Tide pools are depressions in the rock that retain water as the tide retreats. Organisms in tide pools are therefore not exposed to air, but nonetheless need to adapt to particular conditions. Because of their small volume, tide pools heat up in the sun faster than sublittoral water, resulting in large variations in temperature. The anemone, *Anthopleura elegantissima*, found on the Pacific coast is able to tolerate temperatures of up to 13^{o}C above the surrounding water. To survive these high temperatures they retract their tentacles, and attach light colored stones and shells to their tentacles to reflect the heat. Rain decreases salinity within the pool, whereas evaporation on a sunny day leads to increased salinity. As pools heat up they also lose oxygen, which is needed by animals. If there is a lot of algae within the pool, gas concentration tends to change throughout the day: increased oxygen during the day, and decreased oxygen and increased carbon dioxide at night. High levels of carbon dioxide can decrease the pH. Tide pools are therefore also exposed to environmental extremes, but most importantly they experience an instantaneous return to ocean conditions when the tide rises and floods the pool again. Organisms must therefore be able to cope with rapid changes in their environment.

12.3. Intertidal Zones of Sandy Shores

Sandy shores form in areas of lower wave action, where loose sediment accumulates. This loose material commonly includes quartz grains, black volcanic sand, pulverized carbonate plant and animal skeletons. The fauna is less abundant on sandy shores than it is on rocky shores. Competition does not appear to be as important as in rocky shores, as is suggested by the sparse populations, three-dimensional space and abundance of food. There also appear to be fewer predators on sandy shores. The physical factors of wave action, particle size and beach slope may be more important than biological factors in determining the distribution patterns on sandy shores.

12.3.1. Roles of Waves and Sediments

The distribution of organisms on sandy shores is mostly determined by particle size, wave action and slope. Wave action determines the sediment size found on a given beach. High wave action leaves coarse material and low wave action deposits finer sediment. Sediment size influences the size of interstitial spaces (space between particles), which in turn affects porosity and water retention: fine-grained sediments retain water better, and create a better habitat for marine organisms. However, very fine material (silt and clay) do not allow much water exchange, and those sediments tend to become anoxic below the surface, as available oxygen is used up in respiration and decomposition. Sediment size also influences the ability of organisms to burrow; fine sand is easier to burrow into than smaller and larger sediment.

The slope of a beach is determined by the interaction of waves, sediment size, and the relation between swash (water running up beach after wave breaks) & backwash (water flowing down beach). The slope of the beach in turn determines the extent of the intertidal zone for a given tidal range; a steeper beach results in a smaller intertidal area.

12.3.2. Living in the sandy intertidal

Most macrofauna on sandy shores are infauna: they burrow into the sediment. This behavior allows animals to better resist desiccation and heat stress at low tide. With the effects of two stresses reduced, wave action is the single most important factor in determining distribution of organisms on sandy shores. In some fine-grained beaches with limited water flow between grains of sand, oxygen levels can be very low below the very top of the sediment, and thereby limit organism distribution. Several animals have siphons or pumps to oxygenate their burrows and survive in hypoxic or anoxic conditions.

12.3.3. Tides and the activity of organisms

Since the shifting sand prevents the growth of multicellular primary producers in the sandy intertidal, primary production is limited. Benthic diatoms can provide some primary production, but in most cases, the main food source comes from detritus that comes with the tide. The activity of organisms in the sandy intertidal is strongly tied to the movement of the tides. Many organisms wait until high tide to feed and exchange gas, and quickly increase their activities when they become submerged again. High tide also brings a suite of marine predators such as whelks, sea stars and moon snails.

12.3.4. Meiofauna

Meiofauna are microscopic elongate organisms between 62 μm and 0.5 mm in size (Figure 12.5) that are entirely aquatic and live between sediment grains. As such, their existence is dependent on the size of the interstitial spaces, as this regulates water content. Coarser sediments, with greater interstitial volume, harbor larger organisms, yet drain more rapidly. Finer sediments harbor more burrowing forms of meiofauna. The abundance and type of organisms found as meiofauna is also dependent on temperature, salinity, wave action and oxygen availability. They exhibit a range of feeding types; carnivores, suspension feeders and deposit feeders. A unique specialized feeding type is sand licking, in which sand grains are manipulated by the mouth parts to remove minute bacterial growth and thin films of diatoms.

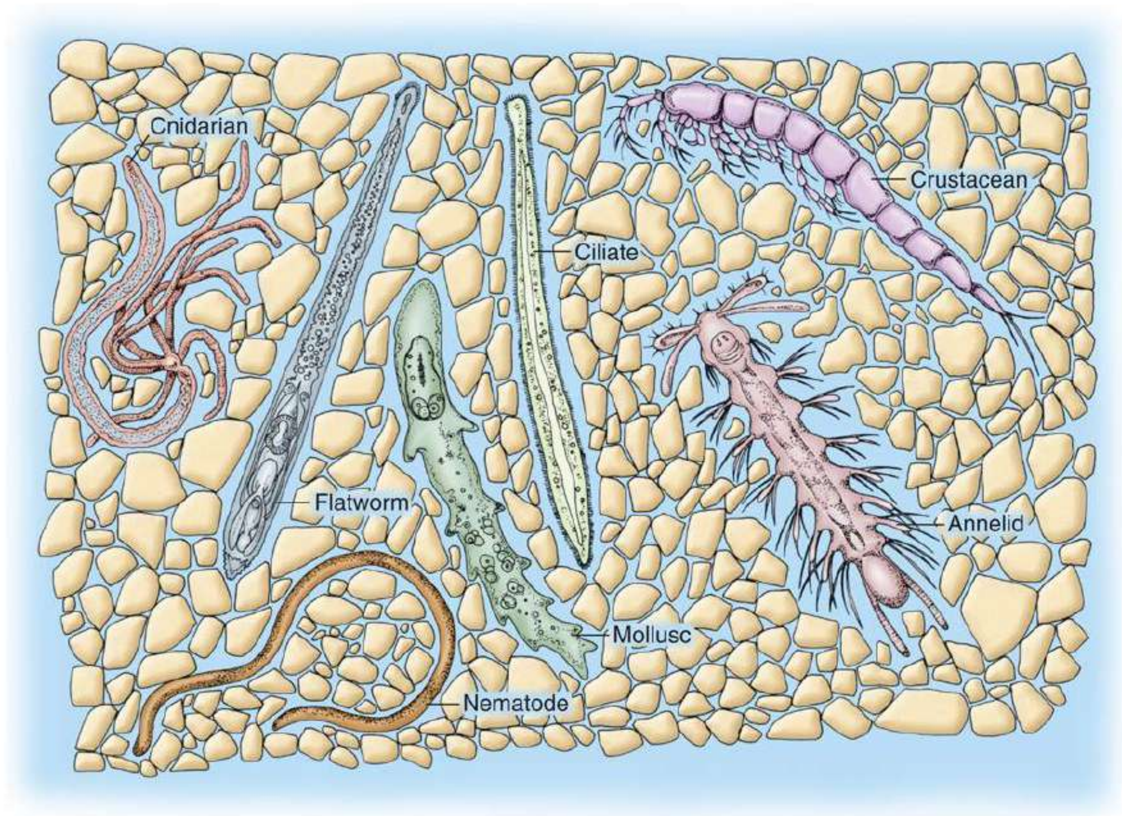


Figure 12.5. Typical meiofauna.

12.3.5. Sandy Shore Zonation

Zonation exists in sandy shores but it is much less defined than on rocky shores. Besides horizontal zonation such as that seen on rocky shores (Figure 12.6), sandy shores also exhibit vertical zonation: from the surface of the sediment down (Figure 12.7). The exact pattern of zonation on a sandy shore depends on many factors, including the amount of water trapped in the sediments, the time of year and the type of beach. The most important factor in determining distribution is wave action. On exposed beaches few organisms can inhabit the surface so organism are typically either mobile or burrow deeply into the sand. Due to shifting nature of sediments few plants exist, and even fewer grazers, therefore the food web is therefore detritus-based in a sandy intertidal zone.

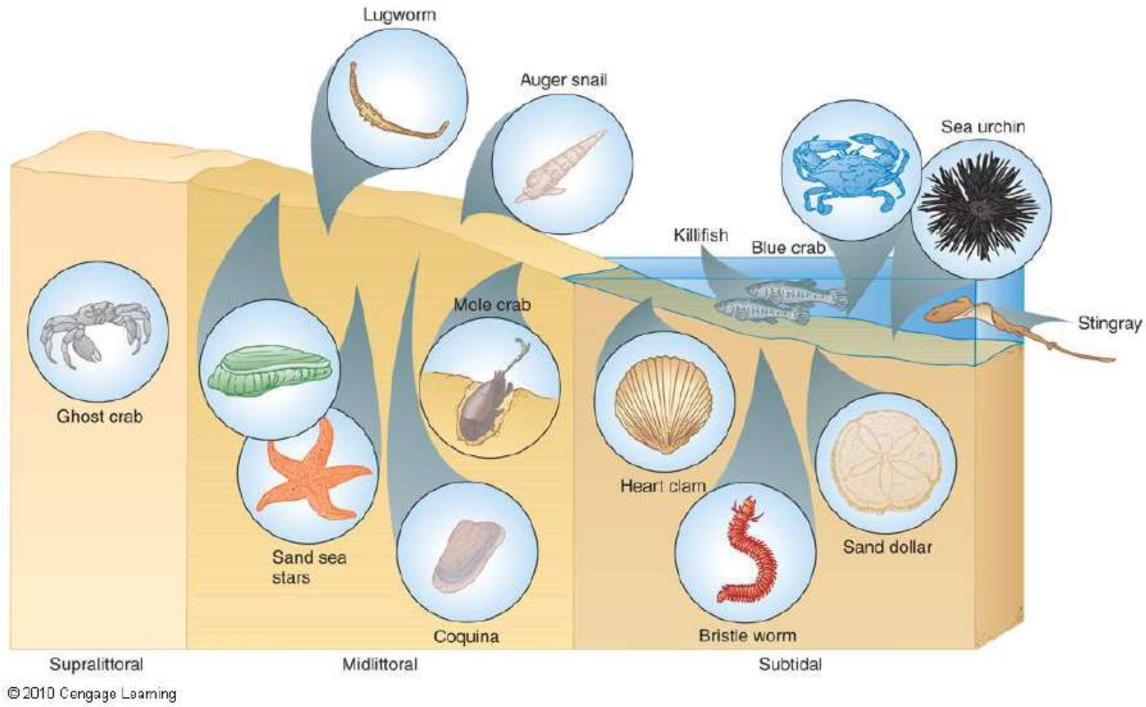


Figure 12.6. Horizontal zonation typical of sandy beaches

The following is a description of a typical horizontal zonation observed in areas such as the east coast of North America, south of Cape Cod.

The supralittoral fringe ranges from the high tide line to the edge of vegetation. Much of this area is uninhabitable as it is too hot and dry because of the sun. Organisms that survive in this zone are mainly arthropods, dominated by insects and isopods in temperate regions, and crabs in tropical regions. An interesting organism found in this zone in tropical regions is the ghost crab, this translucent crustacean scavenges the beach at night, repairing its burrow in the morning and sealing itself in by mid-day to avoid heat and predation. Their burrows often have an alternative escape route.

It is in the midlittoral zone (true intertidal) that vertical zonation is most apparent (Figure 12.7). Moisture reaches the zone of drying sand during the highest tides and gradually evaporates. The zone of retention retains moisture due to capillary action and the zone of resurgence retains water at low tide. The zone of saturation is constantly moist and supports the greatest diversity of organisms, including polychaetes, amphipods, isopods and bivalves. Many of these burrow and retract their feeding and gas exchange appendages during low tide to avoid desiccation and predation. Activity increases at high tide as organisms emerge to feed, find mates, reproduce and exchange gas. Bivalves project their siphons and filter water for food and O_2. Carnivorous snails such as whelks search for bivalves by sensing currents produced by the siphons of clams. Sea stars and sand dollars come out to search for food. Lugworms (*Arenicola* spp.) are deposit feeders that build a U-shaped burrow and leave coiled, cone-shaped casts during low tide. High tide brings food, oxygen, and predators, such as crabs, small fish, and skates and rays. Low tide brings terrestrial predators such as birds.

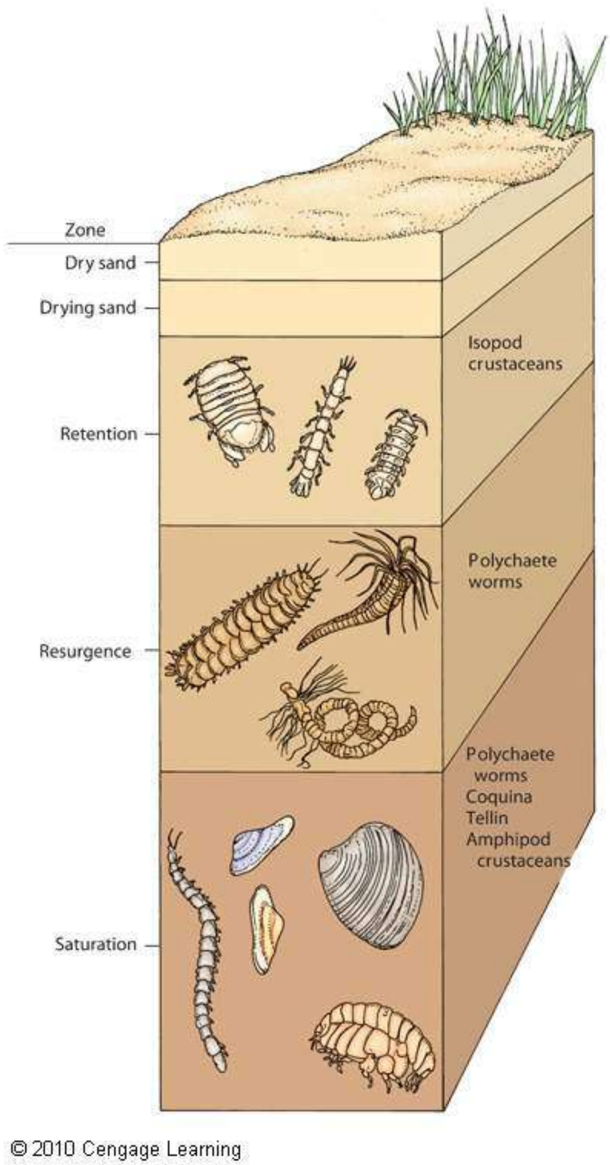


Figure 12.7. Vertical zonation typical of the sandy shore.

The infralittoral fringe is essentially a truly marine habitat, as it is exposed only during the lowest spring tides. This zone is dominated by seagrass beds, with animals such as bivalves, snails, heart urchins, sand dollars and fish.

12.6. Review Questions: Intertidal Ecology

1. What does the term intertidal mean?

2. Which environmental variables fluctuate daily in the intertidal zone?

3. Which areas of the world experience a minimal tidal range?

4. Describe typical temperate rocky intertidal zonation.

5. Describe the adaptations seen in organisms in the mid-littoral zone of the rocky shore to withstand wave shock?

6. Describe the adaptations seen in mobile organisms in the intertidal zone to withstand desiccation?

7. Describe the adaptations seen in sessile organisms in the intertidal zone to withstand desiccation?

8. Give three mechanisms used by intertidal organisms to reduce heat gain?

9. Give two mechanisms to increase heat loss in organisms in the intertidal zone?

10. When are organisms in the midlittoral zone of the rocky shore more active, high or low tide?

11. How do mussels attach to the rock?

12. What is the predominant macroalgae in the midlittoral zone of temperate rocky shores?

13. How do seaweeds in the midlittoral zone overcome problems of desiccation?

14. How can pH vary rapidly in a tide pool?

15. Are rocky intertidal organisms predominantly marine or terrestrial?

16. Give two differences between rocky shores in tropics and temperate regions?

17. Explain the difference between top-down and bottom-up factors, giving examples of each?

18. What kind of sediment (coarse or fine) would you expect to find on a sandy shore with high wave action?

19. How does particle size affect water retention?

20. How is wave action related to the type of animals found on a sandy shore?

21. True or false: you expect to find more deposit feeders on a sandy shore than a rocky shore?

22. If there are essentially no primary producers on sandy shore, what do animals eat?

23. Why is sandy shore zonation less distinct than rocky shore zonation?

24. Is competition more important in determining distribution on a sandy shore or a rocky shore?

13. Estuaries (Karleskint Chapter 14, Nybakken Chapter 8 & 9)

13.1. Introduction

Estuaries are semi-enclosed coastal embayments, formed where rivers meet the sea and freshwater mixes with saltwater, resulting in constant environmental change. The mixing of the various nutrients from freshwater and saltwater often results in high levels of primary productivity, though planktonic productivity may be limited by high turbidity. Much of the organic matter produced is exported and enriches adjacent waters.

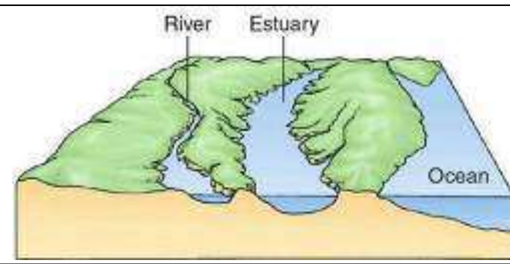
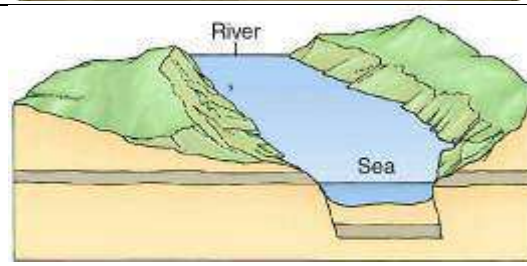
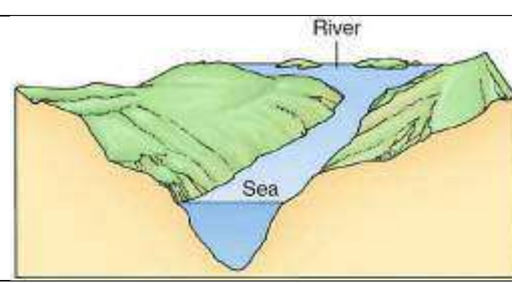
Estuaries are an important nursery habitat for many species; 85% of fish and shellfish sold in commercial markets spend part of their lives in estuaries. They also support commercially important animals such as oysters, crabs, scallop and shrimp.

The size and shape of an estuary can vary greatly depending on the geology of the region. Typically, freshwater flows out of estuaries at the surface while seawater flows in at depth, due to the difference in density between the two. Salinity constantly changes with the tides.

13.2. Physical characteristics of estuaries

13.2.1. Types of Estuaries

The type of estuary formed depends on the geology of the region.

1) **Coastal Plain or Drowned River Valley Estuaries** form when water from melting glaciers raises sea level and floods coastal plains & low lying rivers. E.g. of coastal plain estuaries – Gulf of Mexico E.g. of drowned river valleys – Chesapeake Bay and Long Island Sound	
2) **Tectonic Estuaries** form when geological events, such as an earthquake, caused the land to sink below sea level, allowing the seawater to cover it and becoming natural land drainage channels directing the flow of land runoff into a new estuary. E.g. San Francisco Bay	
3) **Fjords** form when glaciers carve deep valleys into the coast during the last glacial period, and as they retreated the valleys filled with water E.g. Alaska and Scandinavia	

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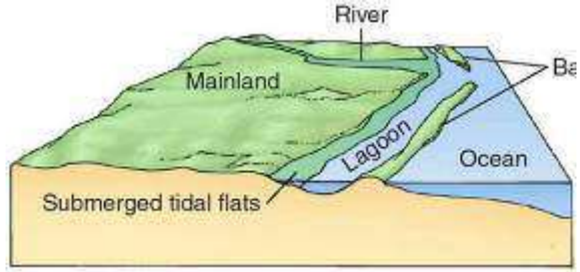
<td>4) Bar-Built Estuaries – tidal flats develop when enough sediment accumulates at mouth of river to be exposed at low tide. The original channel of estuary is then divided. Coast eroded & sediment deposited on the seaward side forming barrier islands, beaches and brackish water lagoons.
E.g. Cape Hatteras region of North Carolina, Indian River complex of Florida’s east coast.</td>
<td>
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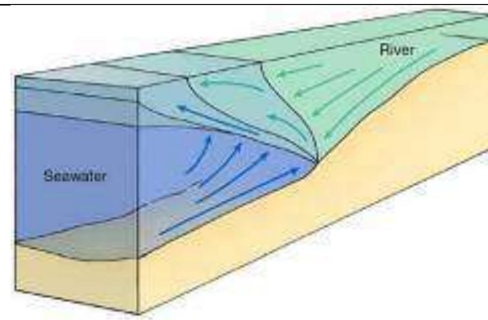
13.2.2. Salinity and mixing patterns

Salinity is constantly fluctuating in estuaries. The pattern of salinity gradient varies with topography, season, tides as well as rainfall.

<table>
<tr>
<td>i) Salt-Wedge Estuary
• Freshwater flows rapidly out at surface, and denser saltwater flows upstream along bottom.
• Strong vertical salinity gradient – halocline
• When tide rises / river flow decreases – salt wedge moves upstream; and vice-versa
• E.g. Mississippi, Amazon, Congo, Sacramento Rivers</td>
<td>
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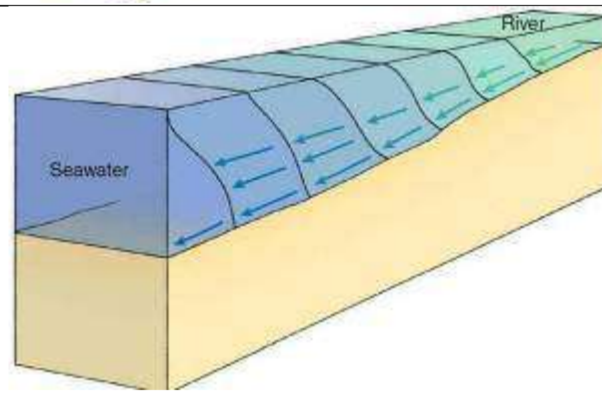
<td>ii) Well-Mixed Estuary
• River flow is low and strong tidal mixing
• Horizontal salinity gradient
• Seaward flow of water at all depths and uniform salinity at all depths, decreasing as it approaches the river.
• Lines of constant salinity move towards land when tide rises or river flow decreases; and towards sea when tide falls of river flow increases.
• E.g. Delaware Bay</td>
<td>
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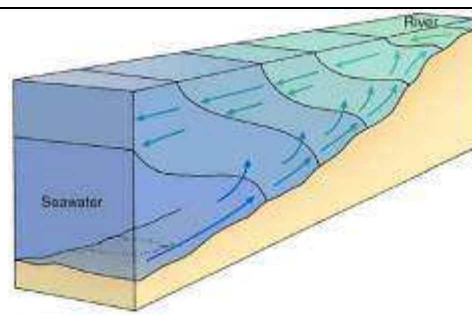
<td>iii) Partially Mixed Estuary
• Strong surface flow of freshwater and strong tidal currents or turbulence (erases salt wedge)
• Oblique salinity gradient
• Tidal currents force seawater upward where it mixes with surface water, producing a seaward flow of surface water.
• E.g. San Francisco Bay, Puget Sound</td>
<td>
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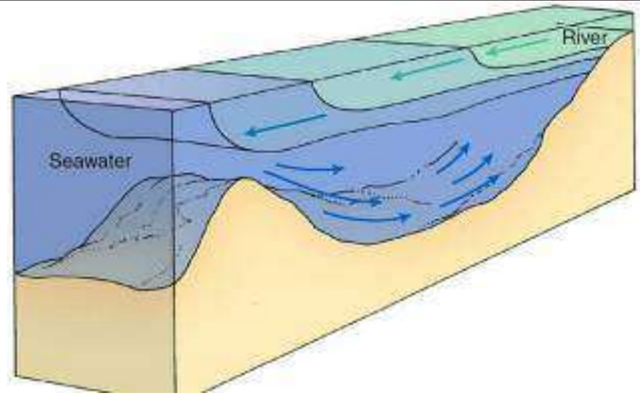
iv) Other Mixing Patterns	

• Don't always exactly fit one category
• Some change with season as rainfall, tides and winds alter the volume of water and strength of currents
• **Fjords** – Mouth of glacier; deep elongated U-shaped valley and a barrier (glacial deposit) at entrance
  • River water remains at the surface and flows seawards, with little mixing
  • Entrance sill isolates deeper saltwater - anoxic
  • E.g. Alaska, Chile, New Zealand, and Scandinavian
	

In a positive estuary, the influx of freshwater from the river more than replaces the amount of water lost to evaporation, so the surface water is less dense and it flows out to sea. The denser saltwater from the ocean moves in along the bottom and is gradually mixed upward into out-flowing low salinity water. This causes estuarine upwelling on a local scale as the nutrient-rich seawater replenishes lost nutrients and promotes growth of primary producers. This is the case in most estuaries.

In contrast, in hot, arid regions estuaries can lose more water through evaporation than the river replaces, and this is described as a negative estuary. Evaporation increases the salinity of the surface water, increasing its density and causing it to sink. The flow is opposite that of positive estuaries; surface water flows towards the river and the bottom water out to sea (Figure 13.1). This type of estuary traps few nutrients, and the surface water from the ocean is generally nutrient-poor, so negative estuaries are usually low in productivity. An example of a negative estuary is the Laguna Madre estuary in Texas.

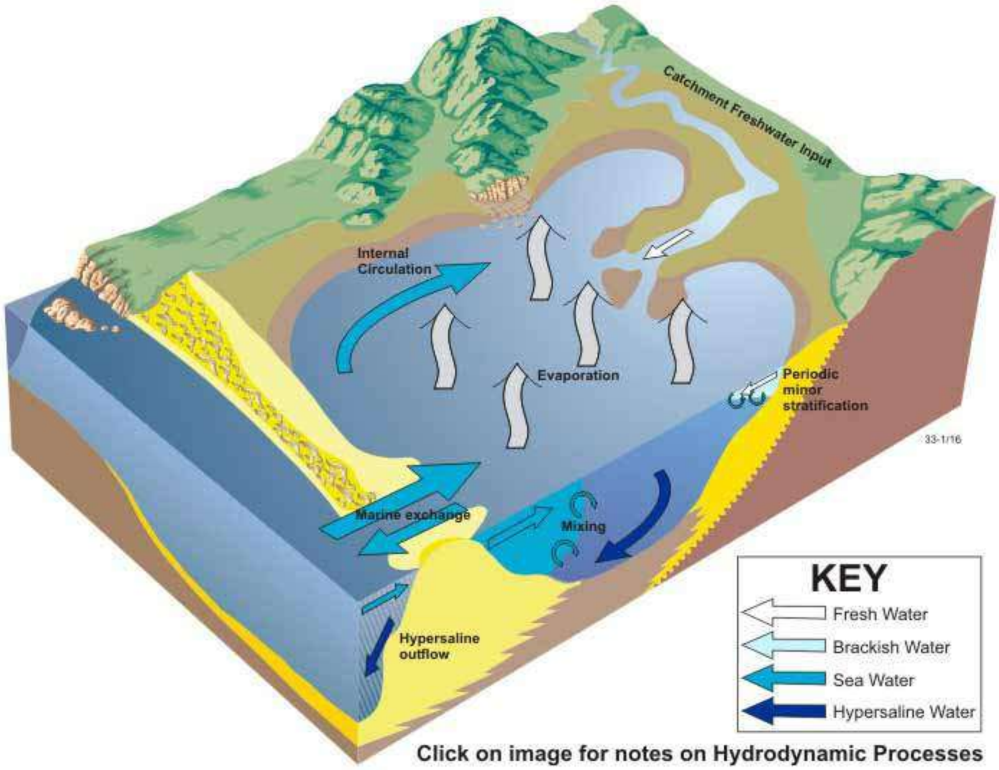


Figure 13.1. Circulation pattern in a negative estuary.

13.2.3. Temperature

Temperature is typically more variable within estuaries than in nearby coastal waters. This is due to their smaller volume and shallower depth, which means that they heat up and cool down more rapidly. Therefore depending on the season, tidal currents either warm or cool estuaries.

13.3. Estuarine Productivity

Estuaries typically have very high productivity, which stem from high nutrient levels in the photic zone. Freshwater runoff carries nutrients from land, including nitrogen, phosphorus and silica, into the estuary. Tides bring in seawater, which typically has less nitrogen and silica but is richer in phosphorus and detritus. The mixing of freshwater and seawater allows a greater spectrum of nutrients to be available in the shallow, sunlit waters. Further, nutrients can be held in estuaries by various processes. Silt and clay transported by rivers readily adsorb excess nutrients and release them when they are in short supply and as such, these sediments act as a nutrient buffer. Moreover, high levels of detritus from adjacent communities such as salt marshes can sink to the bottom, and in deeper estuaries they remain there. These nutrients can be used by certain types of phytoplankton that migrate down at night. High productivity in estuaries is due both to the mixing of nutrients which supports high levels of primary production, as well as the input of detritus from nearby ecosystems.

13.4. Life in Estuaries

13.3.1. General

Conditions are harsh and unstable, and few species have evolved the required adaptations to live here for their entire life. However, because of the high productivity, there is typically a large biomass of those few species that inhabit estuaries. Species found here tend to be generalists and feed on a variety of food, depending on what is available. Dominant organisms also have broad tolerances to environmental factors.

13.3.2. Maintaining an Osmotic Balance

Organisms in estuaries need physiological mechanisms to tolerate varying salinity levels. Some are osmoconformers, which have tissues and cells that tolerate dilution (e.g. tunicates, jellyfish, and anemones). When the environment becomes less saline, osmoconformers gain water and lose ions to the surrounding water (Figure 13.2). These organisms are limited in their distribution by their tolerance for the osmotic change in their body fluids. On the other hand, osmoregulators can maintain optimal salt concentration in their tissues, regardless of the salinity of their environment (Figure 13.2). When salinity decreases in the surrounding environment, osmoregulators concentrate salts in their body fluids in various ways. Some crabs and fish actively absorb salt ions through their gills to compensate for loses (Figure 13.3). Other organisms decrease exchange with the environment by decreasing the permeability of their body surface, e.g. more $CaCO_3$ in their exoskeleton or more mucous on their skin. Yet others have structural adaptations to isolate the body surface from the surrounding water when salinity decreases. For example, snails and bivalves can close their shells by closing their operculum or closing the two valves together, respectively. When isolated in their shell, they switch to anaerobic respiration and await the high tide.

Most estuarine animals are stenohaline, meaning they can only tolerate exposure to a limited range of salinities. A few opportunistic species of estuarine organisms are euryhaline, meaning they are capable of withstanding a broad range of salinities (Figure 13.2).

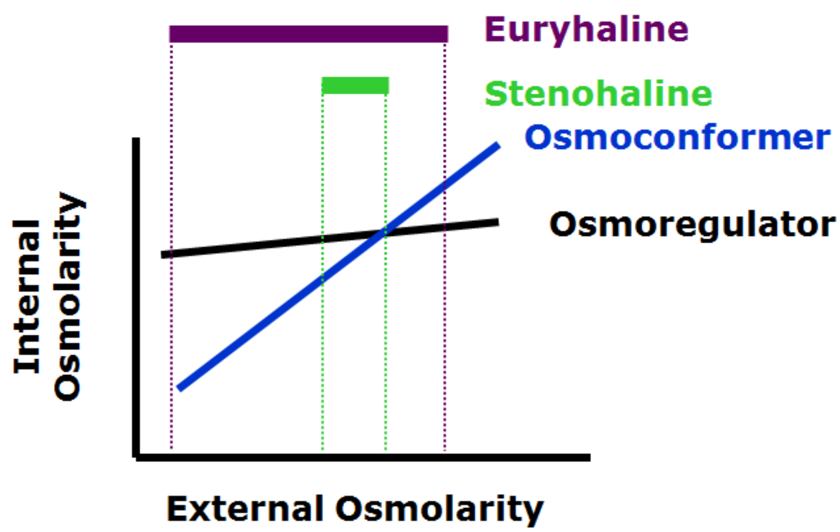


Figure 13.2. Relationship between internal and external osmolarity in osmoconformers and osmoregulators; and range of tolerance of external osmolarity in euryhaline and stenohaline organisms.

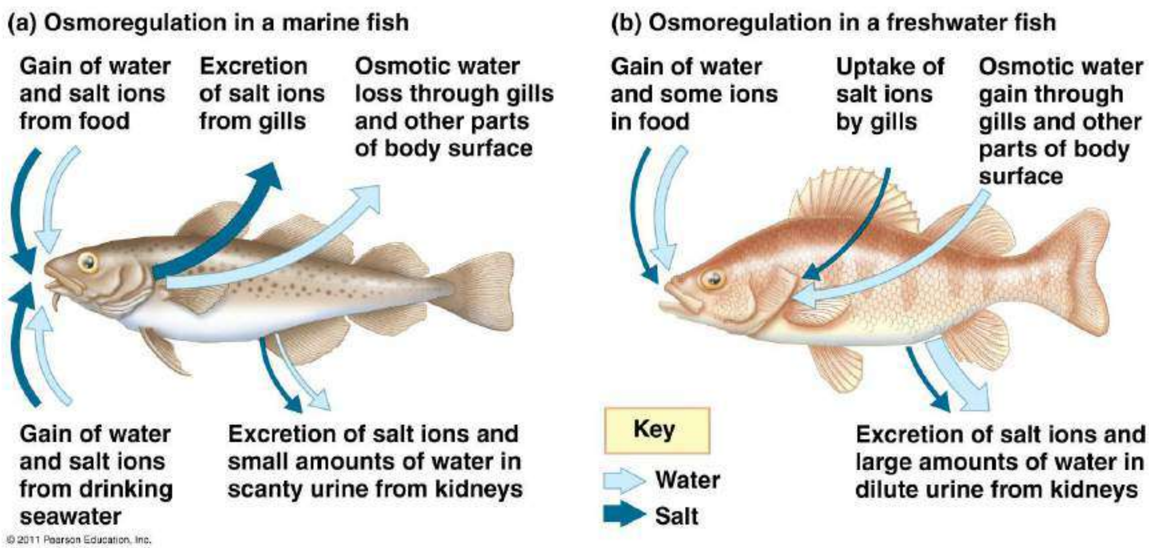


Figure 13.3. Methods of osmoregulation in fish in freshwater and saltwater environments.

13.3.3. Remaining Stationary in a Changing Environment

It may be important for organisms to remain in a given area of estuaries to feed, carry out other activities, or because they have a narrow range of salinity tolerance. However staying in one place can be difficult because of the constant movement of water. Because of this, benthic organisms dominate in estuaries. Marine plants and algae have substantial roots and holdfasts that anchor them firmly to the substrate. Many animals are sessile and are attached on hard bottoms or buried in sediments. Other organisms such as crustaceans and fish tend to move back and forth with the tide, or actively swim to remain stationary.

13.3.4. Estuaries as Nurseries

Estuaries offer a good habitat as nurseries because of a high productivity coupled with a low number of predators. Species such as striped bass, mullet, flounders and various shrimps enter estuaries as juveniles and migrate back to sea after they mature. In contrast, other species (e.g. several species of crabs) can survive the lower salinities of estuaries as adults but their eggs and young cannot. Therefore the females must migrate out to the open ocean to spawn, for their larvae to develop in seawater and the young crabs later migrate back into the estuary.

13.4. Estuarine Communities

13.4.1. Oyster Reefs

Oysters are a dominant invertebrate in the intertidal zone of temperate estuaries. They attach to solid substrates (including existing oyster shells) and form extensive oyster beds, known as oyster reefs. Oysters are filter feeders and typically orient themselves at right angles to tidal currents; incoming tides bring food and take away their waste and sediment. Many other invertebrates live in the structure formed by the oysters, including algae, sponges, bryozoans hydrozoans, polychaetes, mollusks, echinoderms and barnacles.

13.4.2. Mud Flats

Mud flats are found in bays and river mouths where land is protected from wave action. The reduced water motion allows fine sediment particles to settle. Mud flats contain rich deposits of organic material mixed with small inorganic sediment grains. Organic matter carried by rivers and detritus from nearby communities such as salt marshes contribute to the high levels of organic matter in mud flats.

Food Webs in Mud Flats

Benthic diatoms and photosynthetic bacteria are the dominant photosynthetic primary producers in mud flats, but they can only survive in the surface layer where light is available. Diatoms coat the mud with a golden-brown film. The main energy source, however, comes from organic matter brought by rivers and tides. Decomposing bacteria thrive on the high levels of organic matter and are in turn consumed by other organisms (Figure 13.4). When detritus and associated bacteria are abundant, the latter can deplete oxygen levels in the mud through their decomposition, resulting in anoxic sediments. When the sediments become anoxic, certain bacteria produce hydrogen sulphide (H_2S) which has an odor of rotten eggs and colors the sediment black. H_2S is then used as an energy base for chemosynthetic bacteria. The abundant bacteria then become a food source for organisms at higher trophic levels. Bacteria are also important because through decomposition they release nutrients back to the water.

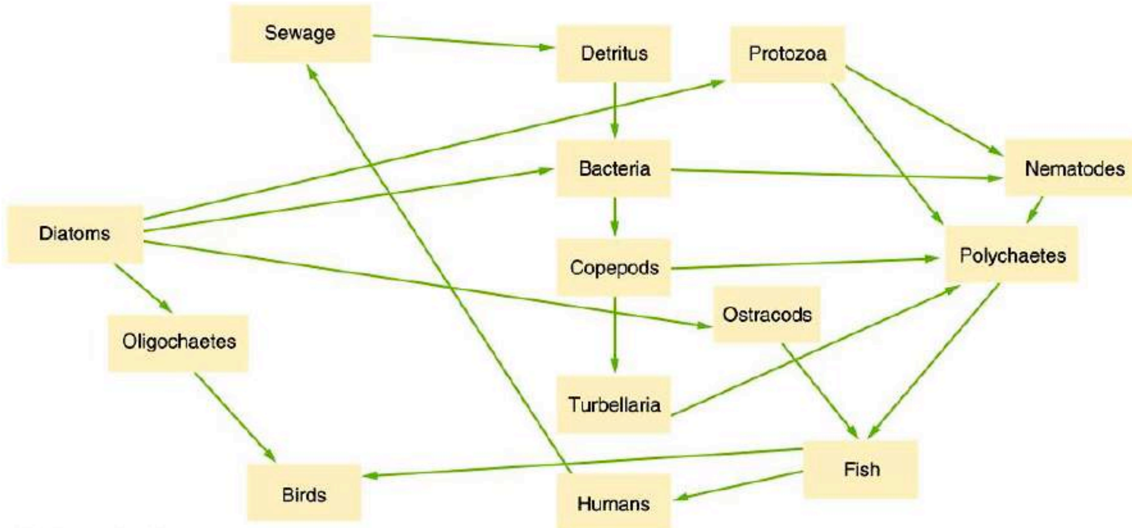


Figure 13.4. Mud flat food webs.

Animals of Mud Flats

Most of the animals on mud flats are infauna: burrowing organisms that live within the sediment. Mud offers protection from many predators, and protection from desiccation at low tide. Moreover, it offers good mechanical support and is therefore home to many organisms with thin shells and soft bodies. Its cohesiveness allows for the construction of permanent burrows.

Few animal species are present on mud flats, but those that are exhibit a high biomass. Animals of mud flats, such as polychaetes, bivalves and shrimps, feed on detritus. Deposit feeders are most abundant; suspension feeders are less important as their filtering appendages can easily get clogged by small sediment particles.

Circulation of water (which carries oxygen) is difficult in mud, as it is not porous like sand. Those organisms that exchange gas through their skin must therefore circulate water through their burrows or maintain a connection with the surface (Figure 13.5). For example, the innkeeper worm maintains a U-shape burrow through which it continuously pumps water, carrying oxygen and wastes. It is named after the variety of organisms that share its burrow, such as tiny pea crabs, gobies and scaleworms. Visitors of mud flats at low tide include the long-billed curlew and sandpipers, and at high tide mud flats are visited by shrimp and fish.

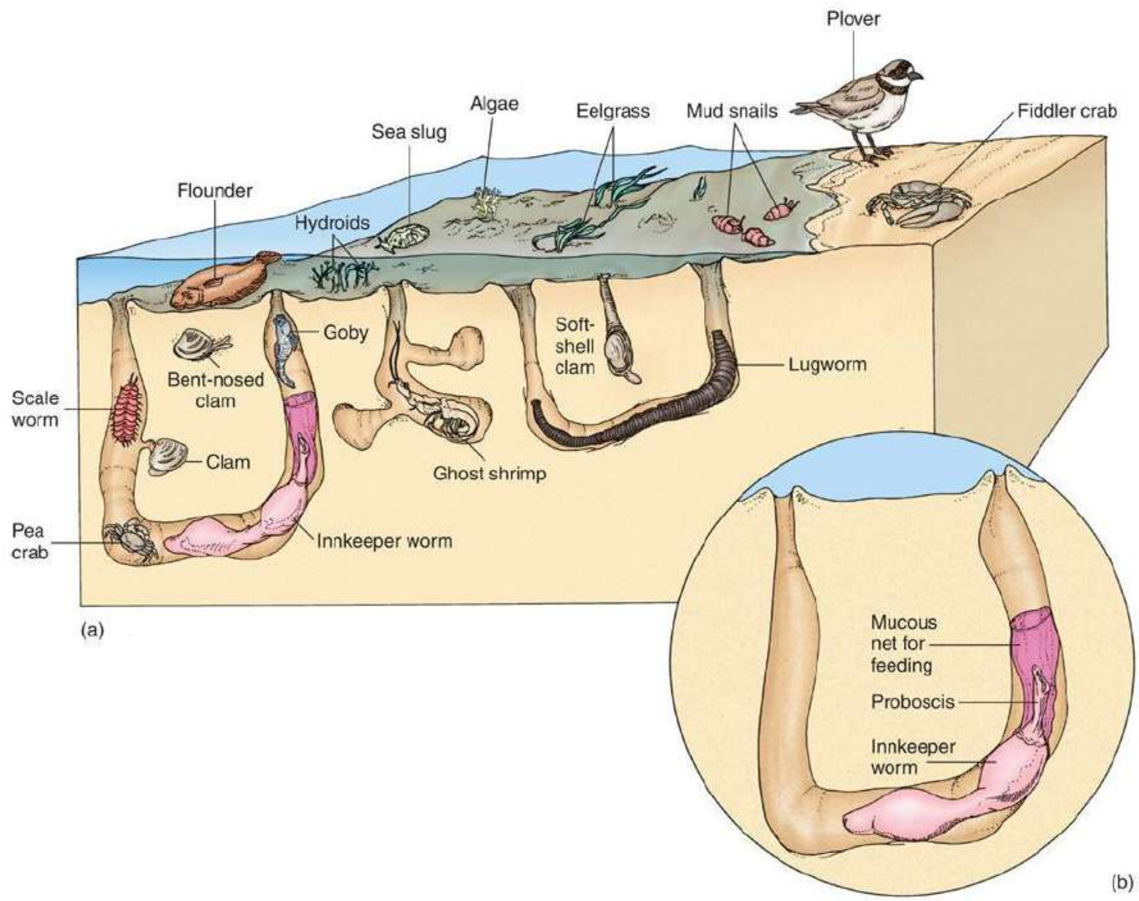


Figure 13.5. Typical animals of mudflats, including the innkeeper worm.

13.4.3. Seagrass meadows

Vast expanses of seagrasses grow in shallow, protected waters, where fine sediment accumulates. Seaweed holdfasts can't easily attach on such substrates, but seagrasses can anchor themselves with their rhizomes.

Seagrasses are highly productive communities. The photosynthesis of seagrasses themselves is limited by their ability to extract nutrients from the sediment. Other photosynthesizers in these communities include green algae which grow among the seagrasses, as well as nitrogen-fixing cyanobacteria which grow right on the seagrass blades. Because the cyanobacteria can utilize atmospheric nitrogen (N_2), they not only boost primary production through their own photosynthesis, but also by increasing the amount of available nitrate.

Most seagrasses are not consumed directly by marine herbivores, who are poorly adapted to digest plant material with such high levels of cellulose. Much of the seagrass biomass, therefore, is channelled through the detrital food web (Figure 13.6). Some proportion of this detritus is also exported to nearby communities through currents.

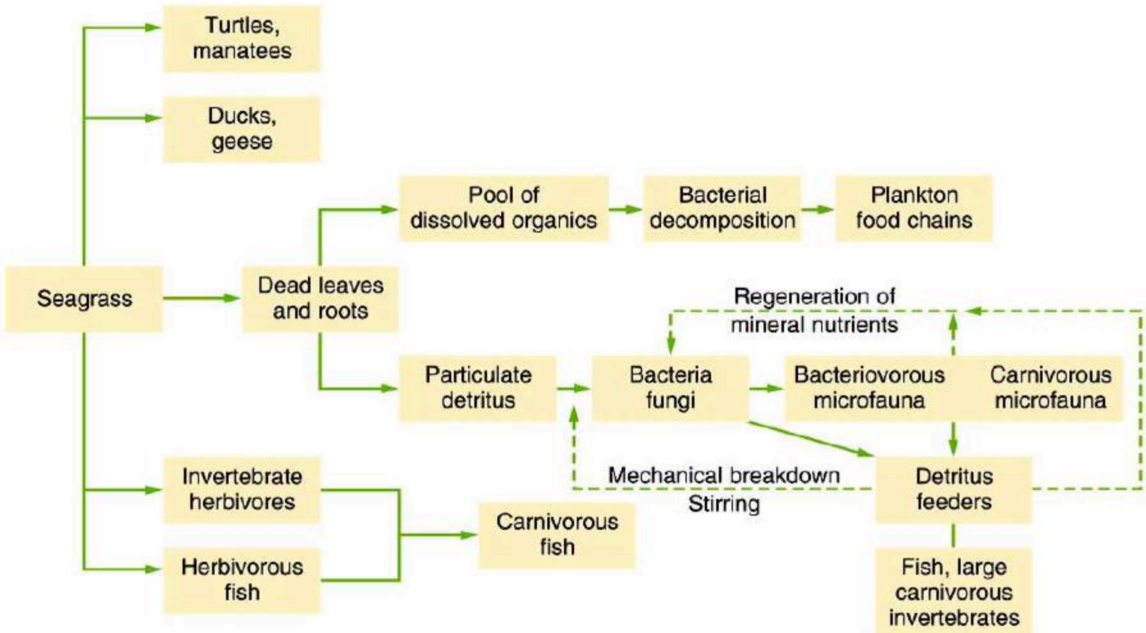


Figure 13.6. Typical food web in a seagrass meadow.

Seagrass meadows provide an important habitat for many organisms (Figure 13.7). Many species of small plants and animals attach directly to the seagrass blades, other species find shelter from predators on the sand between shoots. Seagrasses support a high diversity of organisms, including the larval and juvenile stages of many species. The high productivity and shelter from predators makes seagrass meadows good nursery grounds.

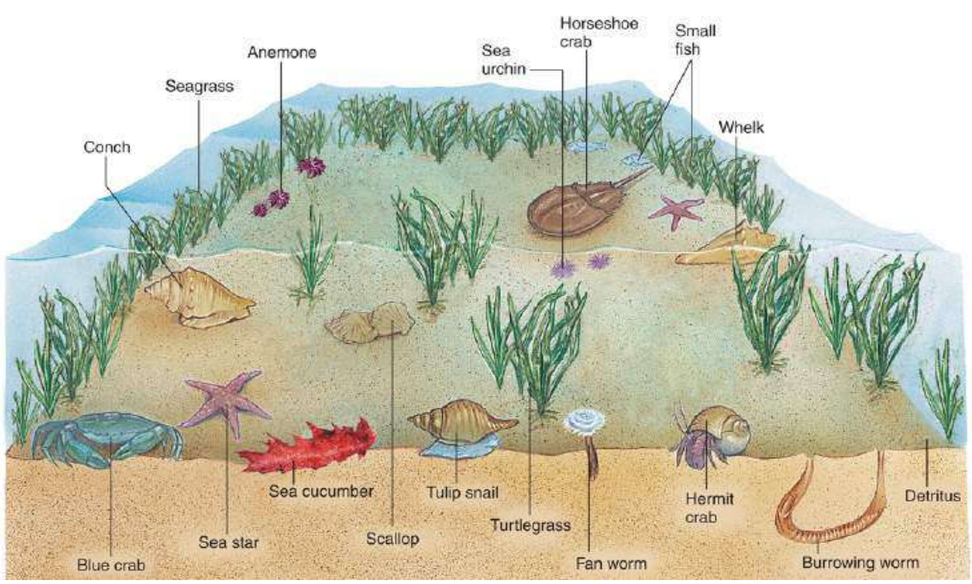


Figure 13.7. Typical seagrass community.

13.5. Wetlands

Coastal wetlands such as salt marshes and mangroves swamps often line the edges of estuaries. They are productive ecosystems that supply a lot of food to estuaries and offshore communities through the detrital food web. Coastal wetlands are also important as a buffer from wave energy during large storms.

13.5.1. Salt Marshes

Salt Communities & productivity

Salt marshes are found on the shoreward side of mudflats in temperate and sub-polar regions of the world, mostly around estuaries. In North America, they are more developed on the east coast than on the west coast, and in both regions are dominated by few species of hardy terrestrial plants such as cordgrass. These plants are known as halophytes: require or tolerate saltwater.

Salt marshes are highly productive and are responsibly for a significant portion of the high primary production of estuaries. Moreover, many commercially important species of fish and shellfish spend a portion of their life associated with salt marshes. Salt marshes are intertidal environments and as such organisms here must be adapted to the particular environmental conditions of the intertidal zone.

Tides replenish nutrients, which support a high level of production by marsh plants, green algae and benthic diatoms. Because marsh plants are difficult to digest, they have few herbivores, and most of this primary production supports detrital food chains (Figure 13.8). Decomposition converts much of this primary production to bacterial biomass, which is then eaten by deposit feeders. The rest is decomposed to a mix of dissolved organic matter and inorganic nutrients. Exported detritus and nutrients support bacteria and deposit feeders in communities nearby.

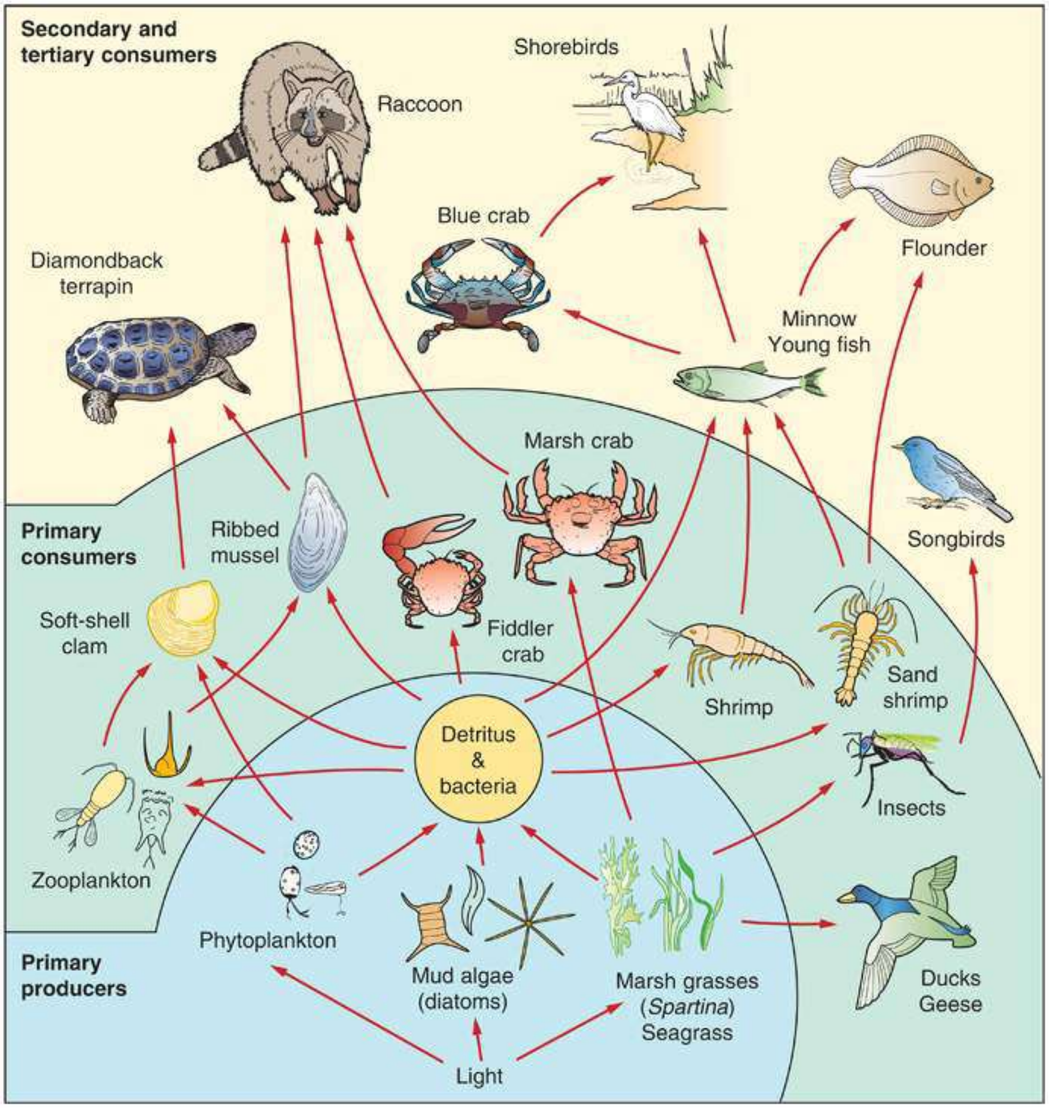


Figure 13.8. Salt marsh food webs.

Animals of Salt Marshes

Permanent residents of salt marshes include snails, mussels and crustaceans (e.g. fiddler crabs, amphipods, marsh periwinkle snail; Figure 13.9). At low tide, terrestrial visitors include predators such as birds, terrestrial turtles, raccoons, otters and minks, and herbivores such as rabbits, mice and deer as well as many insect and spider species. High tide brings many species of fish and crabs.

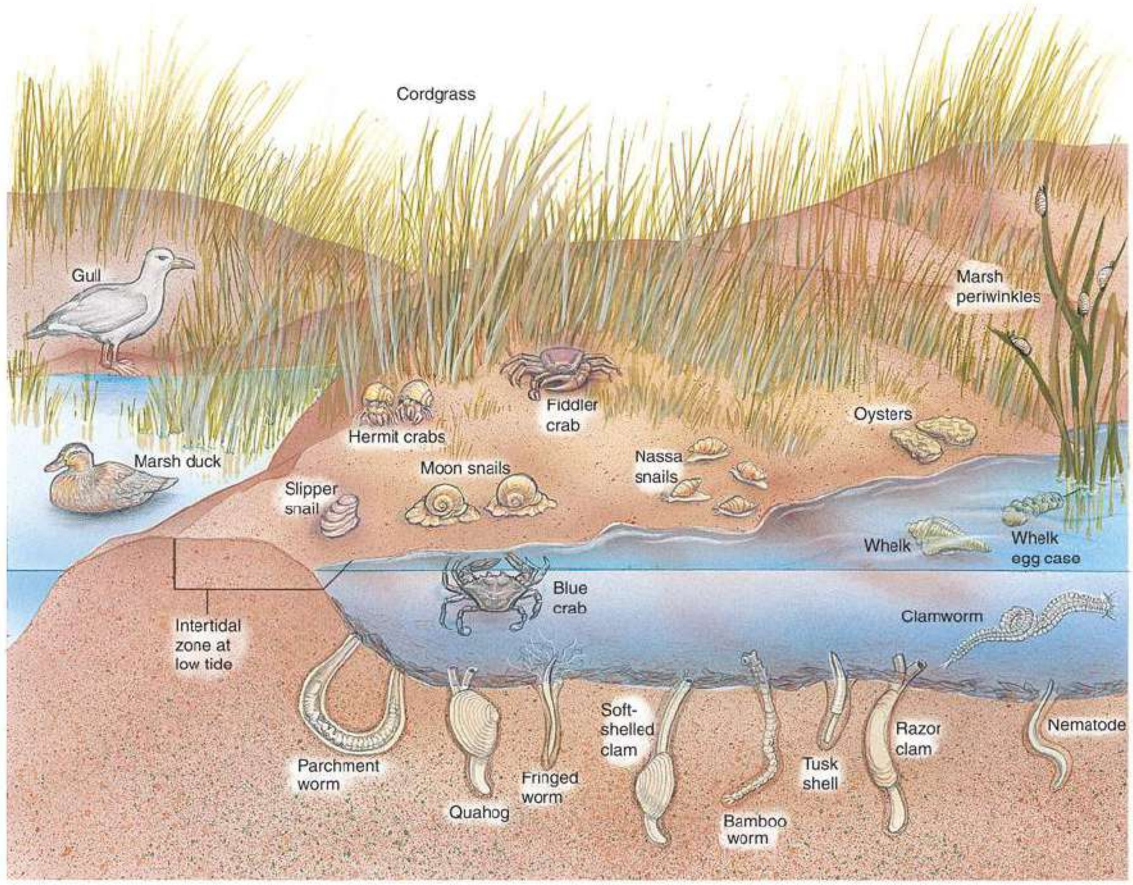


Figure 13.9. Salt marsh community

Succession in Salt Marshes

In addition to providing a significant portion of the high primary production of estuarine communities, salt marsh plants help stabilize soils by decreasing the effects of wave action. Through this, salt marshes can contribute to the process of building more land.

In a typical succession of salt marshes, hardy plants such as cordgrass become established in shallow water and their roots trap sediments. This leads to a build-up of sand and silt, which becomes mud as it gets enriched with decaying material. Small islands of mud appear and as cordgrass traps more sediment, their size increase and they merge. As those islands grow in size and elevation, cordgrass is slowly replaced by land plant that are less tolerant of water and salt, and terrestrial animals appear.

13.5.2. Mangrove Communities

Mangrove forests, also known as mangals, are coastal wetlands found in tropical regions. They are found in estuaries as well as adjacent coastal areas. Like salt marshes, they form in areas of little wave action, where muddy sediments accumulate and become anoxic. The most highly developed mangrove forests are found in Malaysia and Indonesia, which also have the greatest number of species (over 40).

Distribution of Mangrove Plants

There are many different species of mangroves, the most important of which are the red, black and white mangroves. Red mangroves are found closest to the water, in the area of greatest tidal flooding. Their seeds germinate while still attached to the parent, which ensures that the young can develop in a favorable area. Black mangroves are found higher on shore, and experience shallow submersion at high tide. White mangroves and buttonwoods are found highest and closest to land.

Mangrove Root Systems

Because the small grain size in mud impedes water circulation and because of important decomposition, mud tends to be low in O_2. Therefore mangroves must have adaptations to supply oxygen to their roots; most of them exchange oxygen with the atmosphere where the roots are exposed to air through lenticels.

Mud is also soft, and roots must allow the mangrove to anchor firmly for the plant to be stable. To do that, the roots are shallow and widely spread. Red mangroves have prop roots which grow from the trunk and branches and give strong support (Figure 5.12). The roots of black mangroves grow horizontally under the sediment for stability, but have erect, horizontal roots that branch from them, called pneumatophores, that are exposed to air and exchange gas for buried roots (Figure 5.13).

Both these types of roots slow down water flow, and therefore increase sedimentation much in the same way as salt marsh plants do, therefore contributing to building land in a similar way to salt marshes.

Mangal Productivity

Major primary producers in mangals, or mangrove forests, are the mangrove plants, macroalgae and benthic diatoms. Because mangrove leaves are tough, few herbivores can eat them (like those of saltmarsh plants and seagrasses). Most leaves therefore become the basis of the detrital food web in a similar way as salt marsh ecosystems (Figure 13.10). This organic matter supports commercially important fish and shellfish species such as blue crab, shrimp, spiny lobster, mullet, spotted sea trout and red drums.

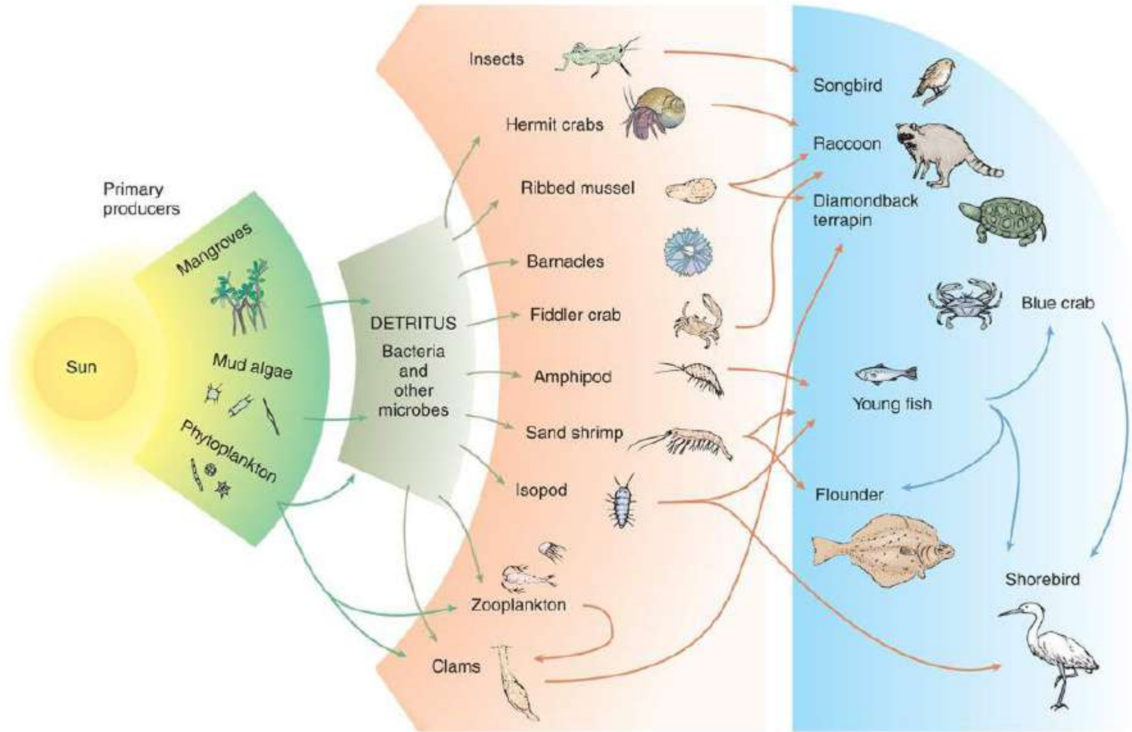


Figure 13.10. Mangrove food web.

Mangroves as Habitat

Mangroves are a habitat to a variety of organisms (Figure 13.11). Roots become encrusted with sessile organisms such as oysters, mussels and barnacles. Herbivorous crabs and snails feed on mangrove leaves or algae on roots.

Many organisms found in mangroves are similar to those found in salt marshes, such as crabs, snails, and shrimps, but there are many organisms not found in salt marshes that can tolerate the more stable environment in mangroves, such as sea stars, brittle stars, sea squirts. Many birds nest in the upper branches of the mangroves, for example, pelicans, egrets, roseate spoonbills.

The sheltered waters in mangroves are also ideal nurseries for many species of crabs, shrimp and fish, and many species found on coral reefs are entirely dependent on mangroves as a juvenile habitat.

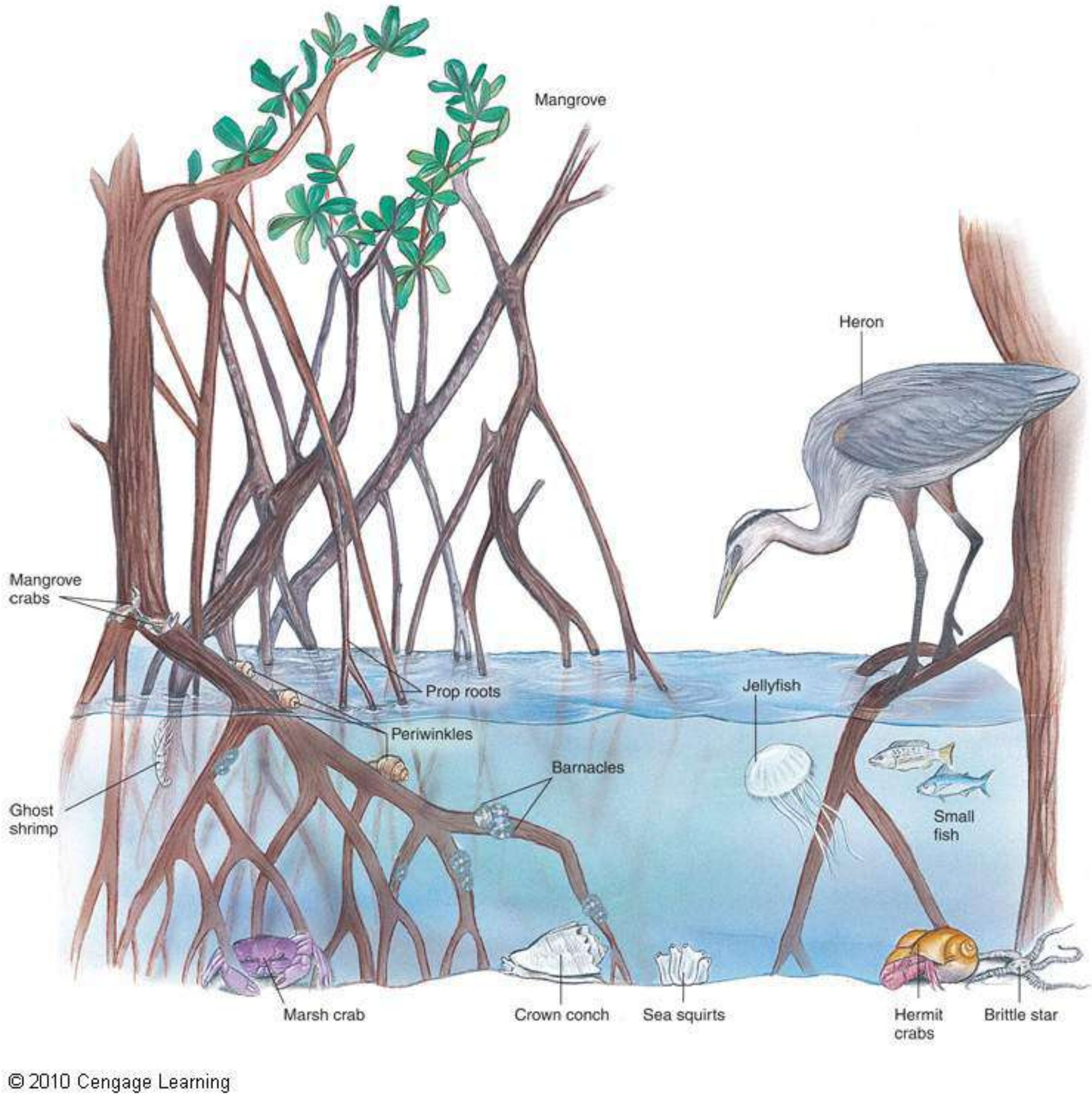


Figure 13.11. Typical mangrove community.

13.7. Review Questions: Estuaries

1. What is an estuary?

2. Is the primary productivity of an estuary typically high or low? Why?

3. Contrast the variation in temperature typically found in estuaries compared to surrounding coastal zones.

4. Why are estuaries ideal nursery habitats for many fish and shellfish?

5. What are the four types of estuaries and how do they differ geologically:

6. Explain the difference between a positive and negative estuary?

7. Give an example of a negative estuary?

8. Are negative estuaries typically high or low in productivity and explain why?

9. What are the 4 different salinity mixing patterns seen in estuaries, and explain each with reference to the angle of the halocline?

10. Is the diversity in an estuary typically high or low?

11. Is the biomass in an estuary typically high or low?

12. Define the term osmoconformer, and give an example of one?

13. Define the term osmoregulator, and give an example of one?

14. Explain how marine and freshwater fish osmoregulate.

15. List three adaptations against excessive water & salt exchange between surrounding environment?

16. What does the term euryhaline mean?

17. Define the term stenohaline?

18. What is the main energy base in mud flats?

19. Is there more infauna or epifauna on a mud flat?

20. What is an epiphyte?

21. Do you find salt marshes in the tropics?

22. True or false: Succession in the salt marsh increases the terrestrial environment?

23. Describe 3 ecological roles of salt marshes

24. Describe the food webs found in salt marshes.

25. Would you expect to find mangroves in temperate regions?

26. Which mangrove (black, white or red) is found growing closest to the sea water?

27. What are the prop roots?

28. What are pneumatophores?

29. Why is detritus such an important part of the food web for salt marsh, mangrove and seagrass communities?

30. Which particular human activity is responsible for the destruction of large amounts of mangroves worldwide?

31. How do mangroves tolerate high levels of salinity?

14. Coral Reef Communities (Karleskint Chapter 15)

14.1. Introduction

Coral reefs are found in the clear warm waters of the tropics and contain a complex community representing virtually every major animal phyla. These waters have relatively low nutrient concentrations, which results in reduced plankton levels and therefore clear blue waters. Coral reefs contain an incredibly high diversity of organisms and have been described as oases in an oceanic desert and can only by rivalled by tropical rain forests in terms of diversity and abundance of organisms. The high biomass in these nutrient-poor environments can ultimately be explained through the symbiotic relationship between the coral polyps and several species of dinoflagellates, known as zooxanthellae, which have the ability to re-use and recycle nutrients. Together with macroalgae they form the basis of a community upon which all other reef animals depend on for food and shelter.

14.2. Reef Corals and the Formation of Reefs

Stony corals (scleractinians) are the dominant organisms that deposit the calcium carbonate structure that makes up basic three-dimensional environment of coral reefs, in or around which all the other organisms to live, hide, feed and mate. Within the stony corals, those species that build reefs are called hermatypic, and are found only in shallow tropical waters. They typically have zooxanthellae living symbiotically within their tissues. Some stony corals are non-reef building, don't have zooxanthellae, and grow below the photic zone in waters throughout the world. Here, we focus on the groups that build tropical coral reefs. While stony corals are the dominant reef-builders in these communities, other groups also precipitate calcium carbonate and contribute to the reef structure, including coralline algae and some hydrozoans (e.g. fire coral).

14.2.1. Coral Colonies

True, or stony, corals (Phylum Cnidaria, class Anthozoa, order Scleractinia) are very simple organisms. Colonies begin when a planula larva settles from the plankton and attaches itself to a solid surface. The planula develops into a coral polyp and secretes a cup of calcium carbonate, a corallite cup, around its body (Figure 14.1). Typically coral polyps have cylindrical bodies, topped with tentacles which are used to capture food from the surrounding water. The polyp reproduces and expands the colony by budding, laying down new skeletal material over existing material. Through an interconnected web of epidermis, the gastrovascular cavity of each polyp remains connected sharing nutritional needs and wastes as each polyp requires. Zooxanthellae are contained within the soft tissues of the polyps giving the corals colorful appearances – red, pink, yellow, green purple or brown colonies are common.

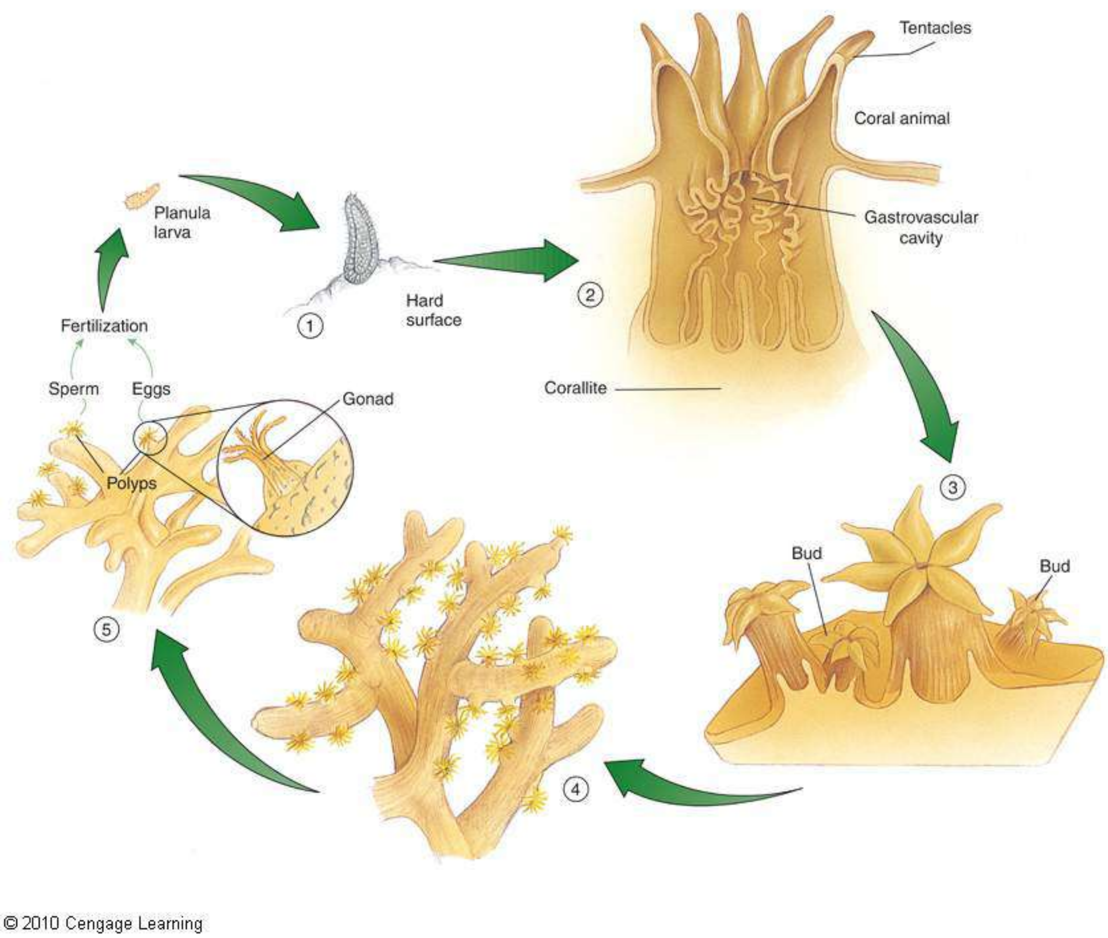


Figure 14.1. Life cycle of a coral colony

Colonies grow upwards and outwards and assume a shape that is partly genetically determined for the species, with some variation due to environmental conditions (e.g. wave exposure and light availability). The larger structures built by colonies can become highly complex shapes, known as life forms, with *massive* (domes), *encrusting*, *branching*, *foliose*, *tabular* or *free-living* colonies.

14.2.2. Coral nutrition

Corals can obtain food in several ways. One is through symbiosis with a type of algae. Most scleractinian corals have a tight symbiotic relationship with dinoflagellates called zooxanthellae, and derive the majority (~90%) of their nutrition from these algae. Whether these zooxanthellae are acquired from their parent or directly from the environment depends on the species. This symbiotic relationship is extremely efficient with virtually no nitrogen waste; the zooxanthellae provide organic molecules and oxygen to the polyp while gaining a stable habitat and metabolic waste materials (including carbon dioxide and nitrate, used as the process of photosynthesis). The removal of carbon dioxide and production of oxygen by the zooxanthellae also seems to improve the growth rate of the coral’s carbonate skeleton. The presence of zooxanthellae is so important to reef building corals that few species can grow below the depth of suitable light penetration for photosynthesis.

Although the symbiotic zooxanthellae provide the majority of nutritional requirements, coral polyps can also be heterotrophic. Using the ring of tentacles surrounding their mouth, which contain stinging cells with nematocysts, the coral polyp can feed on small zooplankton. These small organisms are paralyzed and passed to the mouth using minute finger-like projections called cilia. When not feeding, these cilia can beat in the reverse direction, removing sediment from the surface of the colony. Most corals are nocturnal feeders, extending their tentacles at night and retracting them in the day. Corals may also eat bacteria that grow on their surface, which themselves are small enough to acquire their nutrition through dissolved organic matter in the water column. Finally, corals can obtain organic matter from nearby sediment by extruding mesenterial filaments from their gastrovascular cavity. These filaments secrete digestive enzymes and interestingly, they can also be used to digest coral competitors that venture too close.

14.2.3. Reproduction in Corals

Corals can reproduce both sexually and asexually. Asexual reproduction through budding results in the growth of an individual coral colony. Fragmentation of a colony, also a method of asexual reproduction and common in branching life forms, can lead to a new colony close to the parent. In both budding and fragmentation, the daughter colony is a clone of the parent. Sexual reproduction, on the other hand, occurs through the production of sperm and eggs and results in offspring that is genetically unique. Some species are hermaphroditic, while others may have separate sexes. Most corals are broadcast spawners, releasing their gametes into the water, and this is often synchronized within species and timed with the lunar cycle, to increase the chances of fertilization and decrease mortality due to predation.

14.2.4. Reef formation

A coral reef's framework constantly undergoes some level of accretion and destruction (Figure 14.2). Processes that contribute to accretion (construction) involve not only the growth of stony coral colonies, but also solitary coral species and other reef-building species. Destruction of the reef structure occurs through bioerosion and physical erosion. Boring clams and sponges are important bioeroders that produce tunnels in the reef structure and weaken it. Other species such as parrotfish can remove calcium carbonate from the surface of the reef in the process of grazing films of algae that grow on dead coral colonies. Strong wave action experienced during tropical storm can further break up the reef structure, in particular when it has already been weakened by bioerosion. The rubble and calcium carbonate sediment left behind after a storm can be consolidated by sponges and other reef organisms, and eventually is colonized by coralline algae and new coral larvae. The relative importance of accretion and destruction over geological time will determine the long term changes in reef size and shape.

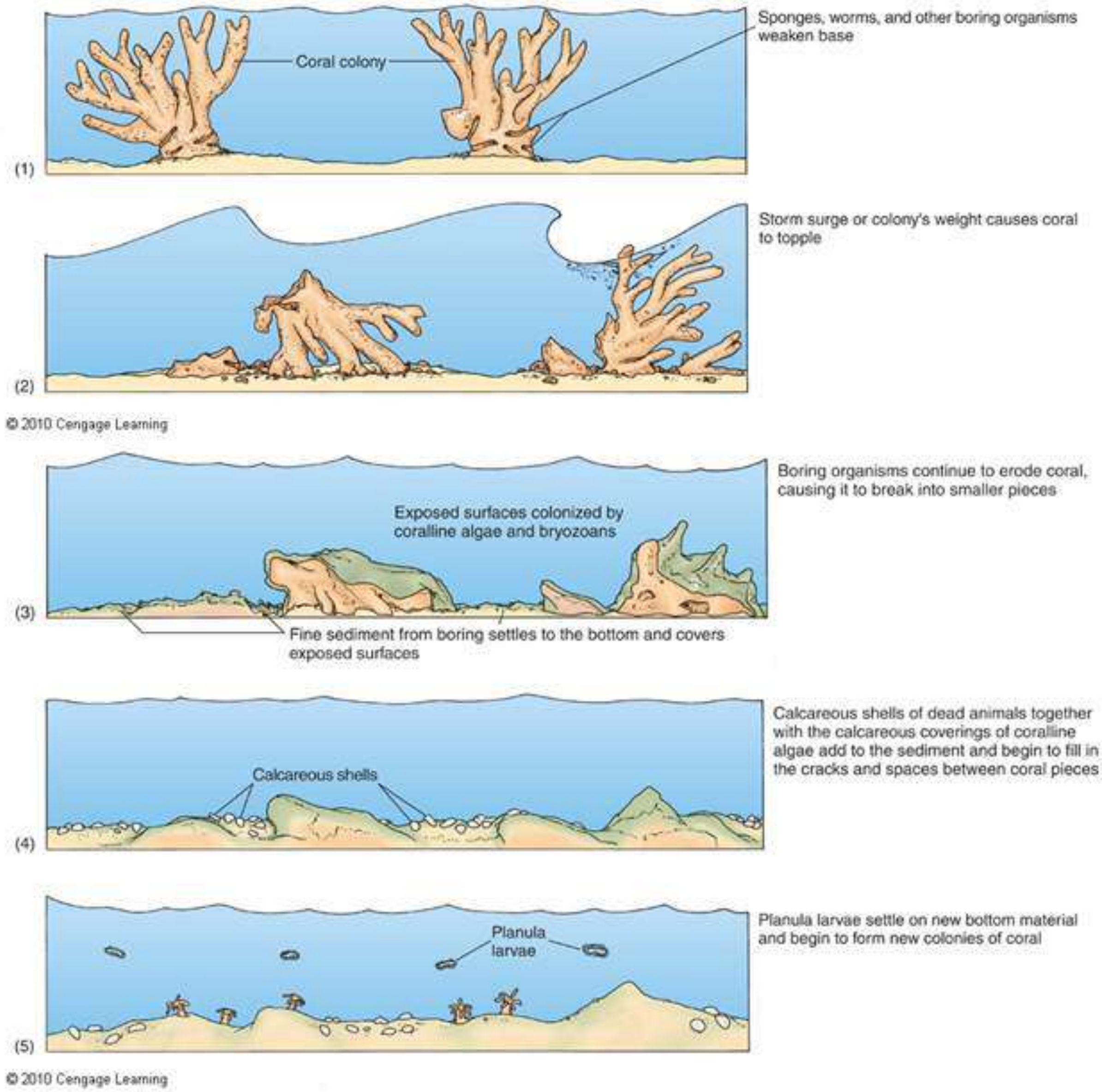


Figure 14.2. Cycle of reef development

14.3. Structure of Coral Reefs

Corals can only grow in warm, well-lit waters and require a solid surface on which to settle. These factors restrict the initial recruitment of hermatypic corals to shallow, rocky substrates in the tropics. As coral colonies grow, they expand both vertically and horizontally, providing further substrate on which recruits can settle. Coral reefs can be divided into four basic category based on their structure and relationship to underlying geological features (Figure 14.3).

14.3.1. Reef Types

Fringing reef

Fringing reefs are perhaps the simplest type of coral reef formation. These develop in the shallow, warm and clear seas surrounding islands and bordering continental land masses. Fringing reefs develop from the upwards growth of corals depositing a calcium carbonate platform to the height of about the level of low tide. These reefs include a shallow platform out to a defined edge, the reef crest, where there is a steeply shelving reef front dropping down to the sea floor (Figure 14.3).

Barrier reefs
Barrier reefs tend to be older structures rising up from a deeper base some distance from the shore, with a lagoon separating them from the coast (Figure 14.3). It is thought that many have their origin from fringing reefs which develop as relative water level increases. Under these conditions the fringing reef continues to grow upwards, but deeper water fills the lagoon between the structure and shore. In other cases barrier reefs may have simply developed in offshore locations, but still remain separated from the coast by lagoons. The largest reef structure in the world is the Great Barrier Reef off the northeast coast of Australia which is approximately 1,200 km long.

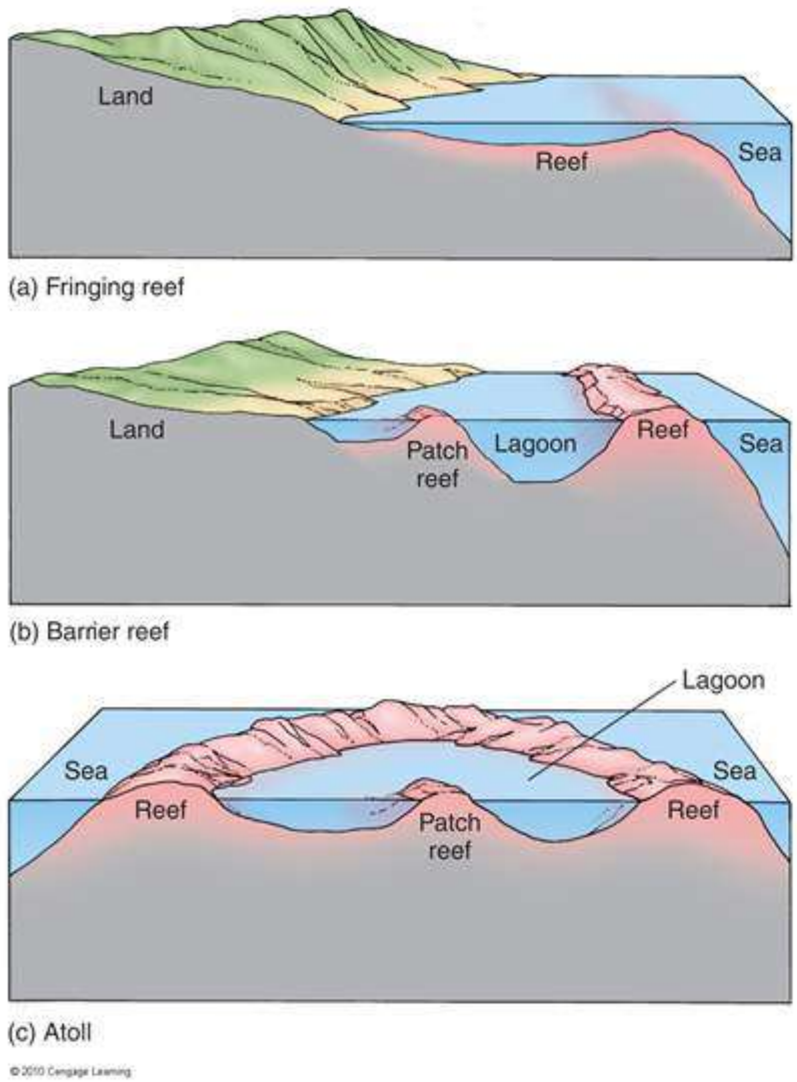


Figure 14.3 Types of coral reef formations

Atolls

Atolls are broadly circular reef formations, which may form sandy cays and enclose a wide lagoon (Figure 14.4). They are typically found offshore, especially in the Pacific and Indian Oceans. Charles Darwin was first to correctly understand atoll formation and his hypothesis is still accepted today. He formulated that they initially develop as fringing reefs around a geologically young, isolated, volcanic island. As the relative sea level rises, possibly due to isostatic adjustments (discussed in OCE 1001), the reefs continue to grow towards the surface, first forming a barrier around the sinking island, but then, as the island disappears beneath the surface, forming a ring of coral just below the surface of the ocean – known as an atoll. Sand may be deposited on the tops of these reefs forming sandy cays whist strong currents often erode and maintain passages through this ring of coral.

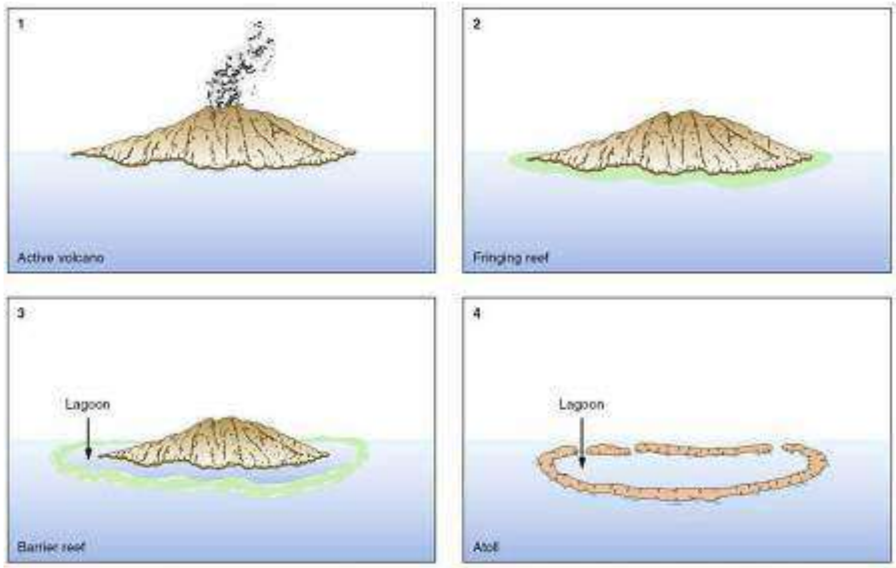


Figure 14.4. Atoll Formation

Patch reefs
Patch reefs are small coral reefs that simply develop where environmental factors are appropriate for coral growth. These are most often located in lagoons where coral recruits have been able to settle on a hard substrate and where currents maintain optimal water temperatures and reduced sediment deposition. Patch reefs are often individually small but may be dotted throughout a larger area.

14.3.2. Reef Structure and Zonation
Moving across a reef from open ocean to shore, environmental conditions vary considerably, and the coral reef community and formation changes accordingly (Figure 14.5). Light and depth, tides, water circulation, wave action, sediments, nutrients, temperature variation and salinity all have a part to play in determining which species are found where on the reef, and a clear zonation can be recognized.

Forereef or Reef Front
On the seaward side, the reef generally falls steeply towards the seabed and represents the area of greatest abundance and diversity of life. The shallowest water may be exposed to considerable wave action, especially during rough seas, and coral growth may be restricted to branching life forms which are typically low and compact, and have a dense and strong skeleton. Wave action often leads to the development of deep channels and high ridges known as spur and groove formations. Diversity is highest just below the shallowest area exposed to the highest wave action. As light further decreases with increasing depth, coral diversity also decreases. The highest abundance of coral is found in the top 15 to 20 m where light is plentiful. Below approximately 60 m is no hermatypic coral growth due to the low light intensities.

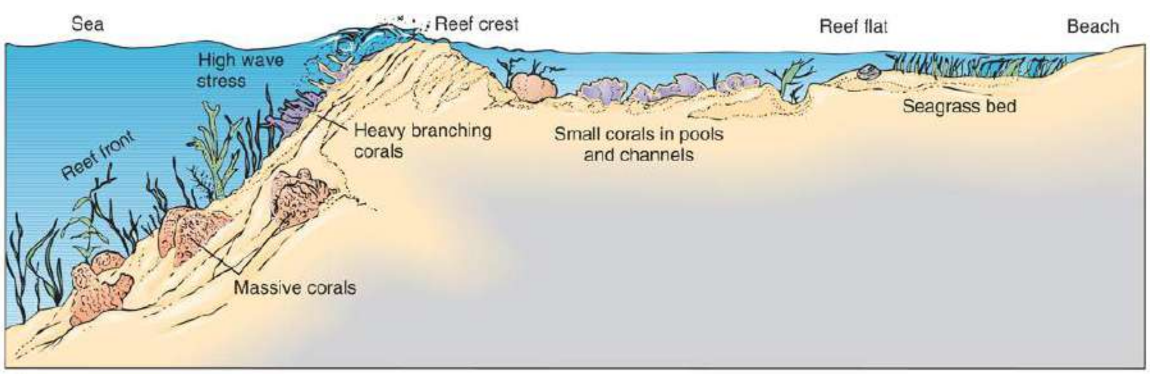
Reef Crest

The reef crest is the highest part of the reef, which receives the highest amount of wave energy. Conditions for coral growth are not ideal here however some species, mainly branching forms, have adapted to them. Where wave action is too high for even those coral species, the reef crest may be dominated by coralline algae in what is called an algal ride. In many cases the spur-and-groove formations extend to the reef crest.

Reef flats

Reef flats are behind the reef crest, and depth here may vary from a few meters to a few tens of meters. The conditions over reef flats can vary considerably, often being dependent on the degree of enclosure. Relatively shallow reef flats may be areas of considerable temperature fluctuation and high nutrient and sediment deposition from river runoff. Generally speaking, reef flats do not exhibit high biological abundance or diversity, with sand and rubble often dominating the reef flat. However this area can provide ideal conditions for certain species. Seagrass communities are a common feature of many reef flats and corals may thrive in patch reefs.

Spur-and-groove formation – is formed as the corals grow out from the reef crest. They form finger-like projections which protrude seawards and disperse wave energy protecting the reef inhabitants. Between some of these projections (spurs) lie sand-filled pockets (grooves) that allow sediment to be channeled down and away from the corals.



(a)

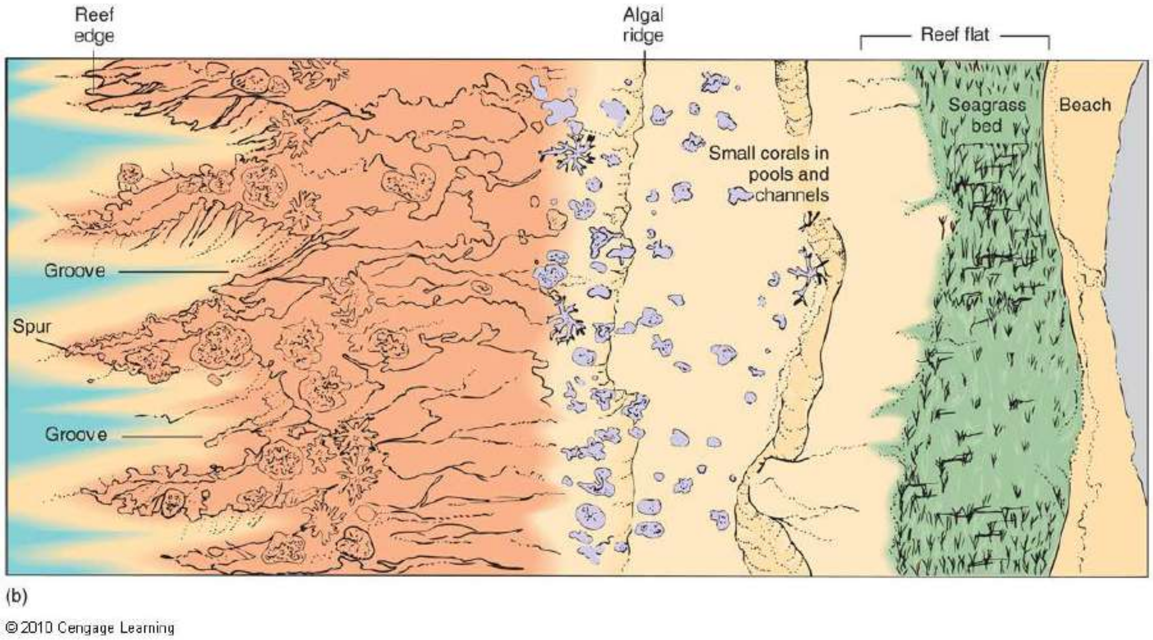


Figure 14.5 (a) Reef structure and zonation (b) Spur and groove formation

14.4. Coral Reef Distribution

The distribution of coral reefs is dependent upon the physical and biological range in which the coral polyp and algal zooxanthellae can survive and flourish.

14.4.1 Temperature

Coral reefs are restricted to a narrow band near the equator (30°N – 30°S), with diversity diminishing fairly rapidly outside of these tropical latitudes (though non-reef building corals can be found in temperate and polar regions). This trend is entirely related to the decreasing temperatures which generally follow increasing latitudes. Most corals cannot grow below ~ 16-18 °C, possibly due to reduced coral growth being smothered by faster growing algae, whereas above ~ 32 °C, corals tend to bleach (see 14.9.4). The optimum temperature for most reef-building corals ranges between 23- 25 °C.

14.4.2. Light availability

The zooxanthellae associated with coral polyps are dependent on light for photosynthesis. As such, hermatypic corals (those that produce reefs, and contain zooxanthellae) can only survive where light levels are high enough. Most reef building corals therefore can only survive above a depth of 60m with the majority thriving in waters of 25m or shallower. Other factors, such as sedimentation and algal shading can also affect the light attenuation in these shallow waters.

14.4.3. Sediment accumulation

As mentioned above, corals require light intensity levels suitable for photosynthesis. Suspended sediment increases the turbidity in the water column and thus reduces the zooxanthellae's ability to photosynthesize. Sediment is introduced into the marine environment primarily though terrestrial run-off from rivers and consequently few coral reefs are found near to large river mouths (also see 14.2.4). Certain species of corals can cope better than others with increased turbidity by actively removing sediments which smother their tissues and block out the light. Removing sediment from the coral's tissues, however, has an energetic cost and when combined with lower light levels due to higher turbidity these factors can greatly reduce a coral's chances of survival.

14.4.4. Salinity

Corals are obligate marine organisms and cannot tolerate fresh water. The absence of corals near major river mouths are at least in part due to the low salinities of these areas (as well as increased sediment load).

14.4.5. Wave action

Healthy coral reefs may act as a buffer to the land from heavy seas and storms. Moderate wave action aids in coral growth as it supplies oxygenated seawater whilst removing any deposited sediment. Heavy wave action, on the other hand, may physically damage the structure of the reef.

14.4.6. Duration of air exposure

Coral reefs are subject to desiccation if exposed above the tide for extended periods of time. During an exceptional low tide some species can sustain exposure for a few hours, however, most will be killed. As such, vertical coral growth is generally limited by low tide levels.

14.5. Comparison of Atlantic and Indo-Pacific Reefs

Reefs in the Indo-Pacific are the most diverse, with around ten times more species than reefs in the Atlantic. One of the reasons for this is that the islands and reefs in the Atlantic are younger and so have had a shorter time for speciation. Reefs in the Atlantic also tend to have a lower average coral cover, usually less than 60%, whereas in the Indo-Pacific coral coverage can reach close to 100% in some places. On Atlantic reefs fire coral, gorgonians and sponges are important non-scleractinian benthic organisms, whereas soft corals (subclass Alcyonaria) are abundant on Indo-Pacific reefs.

14.6 Coral Reef Ecology

Coral reefs are one of the most productive ecosystem on the planet. Their productivity rivals that of tropical rainforest, and is about 30-50 times that of surrounding open ocean. How can such high productivity occur in nutrient-poor tropical waters?

Source of nutrients

Coral reefs receive small amounts of nutrients from outside ecosystems (e.g. runoff from land and small levels of upwelling). The movement of fishes may also be important in supplying coral reefs with new nutrients. Fishes may swim to nearby ecosystems to feed (e.g. seagrasses) and return to the reef for shelter. Fish faeces or decomposition after death can both release new nutrients to the coral reef. But the key to the high productivity of coral reefs is the very tight recycling of nutrients that are already in the ecosystem. The coral-zooxanthellae relationship is particularly important in this process: wastes from the coral animal's metabolism (which include nitrogenous wastes) are quickly taken up by the symbiotic zooxanthellae, rather than lost to the environment. Further, dissolved and particular organic matter in the water column can be aggregated by reef bacteria and later digested by coral. Finally, nitrogen-fixing cyanobacteria are important primary producers on coral reefs, and can supply the important nutrient nitrate.

Photosynthesis on reefs
Photosynthetic organisms of coral reef ecosystems include of course the zooxanthellae of corals, but also benthic macroalgae, turf algae (small filamentous algae that includes many species of cyanobacteria, often with other benthic microalgae such as diatoms), phytoplankton and seagrasses. Many photosynthetic organisms have a close association with an animal which allows for close recycling of nutrients: besides coral and zooxanthellae, cyanobacteria are often found in symbiosis with sponges. Most photosynthetic organisms are either attached to the reef or live in close associate with the reef, such that they are not easily removed by currents.

14.7 Coral Reef Community

Hundreds of species of marine organisms are associated with coral reefs. Not only does the coral provide a foundation for the reef food web, their colonies provide shelter for resident organisms. Space is a limiting factor on coral reefs; corals, algae, sponges and other organisms cover virtually every available surface. Algae, corals and other photosynthesizing organisms require sunlight to survive, so access to light, like space, is also a resource subject to competition. Through predation and competition, many species have become highly specialized to live in tight niches, pushing the coexistence of species to extremes.

14.7.1. Competition among Corals
Fast growing, branching corals grow over the slower growing encrusting or massive corals thereby blocking out the sunlight. These slower growing corals may extend stinging filaments (mesenterial filaments) at night from their gastrovascular cavity and digest their competitor's tissue. As a result of competition between corals differences in species distribution can be observed. Branching corals tend to grow faster and can out-compete massive corals in the upper, shallow portion of the reef whereas the slower growing massive corals are more tolerant to lower light levels and may dominate in deeper area.

14.7.2. Competition among reef fishes
The diversity and abundance of reef fishes is astounding and has led ecologists to ask what mechanisms are responsible for driving and maintaining this diversity. Several hypotheses have been proposed; two of the most important ones are the competition model and the lottery model. The former suggests that competition for food and other reef resources has led to resource partitioning, where species become increasingly specialized for a particular resource (e.g. food type), which allows for the coexistence of

many species. The lottery model suggests that the most important factor controlling reef fish communities on a given reef is simply the chance event of larvae of a given species arriving to the reef at a time where that area is available for colonization. It is likely that no single hypothesis can completely explain the diversity patterns of reef fishes, but it is clear that the high abundance and diversity of fishes leads to high competition for resources.

14.7.3. Effect of grazing

Corals must also compete with other reef organisms for space and light. Sponges, soft corals and algae all grow faster than scleractinian corals and can smother them. At shallower depths, algae often out-compete corals and therefore the distribution of corals at these depths may be dependent upon grazing on these algae by urchins and herbivorous fish species.

The dominant algae on a healthy reef are usually fast-growing filamentous forms or coralline algae, the latter being well protected from grazing by calcification. These species are inferior competitors to the larger, fleshier seaweeds, so grazing on larger seaweeds is an important process that allows them and other inferior competitors to persist. In the Caribbean, overfishing has removed most of the herbivorous fish from coral reefs. Initially algal growth was kept to a minimum by the grazing sea urchin *Diadema antillarum* but in 1982 a pathogen severely reduced the urchin population. As a result, coral cover declined dramatically, from an average of 52% to just 3%, and algae began to dominate the reef, with their coverage increasing from 4% to 92%. Unchecked without grazers, algae was able to overgrow the corals.

14.7.4. Effect of predation

While a few species of fish and invertebrates feed on coral, the ecological effects of these corallivores tend to be limited. One important exception is the crown-of-thorn sea star, which has destroyed an estimated one third of Indo-Pacific corals since 1957. Crown-of-thorns can evert their stomachs to feed on prey outside their body, allowing them to digest coral tissue on colonies of any size. Crown-of-thorn sea star population fluctuations seem to be a normal phenomenon. However in recent years there have been more frequent and severe outbreaks of crown-of-thorns, which seem to be related to the overharvesting of their main predators, the Triton's trumpet (a carnivorous marine gastropod) and other fish species.

14.7.5. Symbiotic Relationships on Coral Reefs

The association between coral polyps and zooxanthellae is only one of many examples of symbiosis between reef organisms. There are three types of symbiotic relationships:

Parasitism – one organism benefits to the others loss.
Commensalisms – one organism benefits while the other is not harmed or benefited.
Mutualism – both organisms benefit from the relationship in some way.

Examples of Coral Reef Symbiosis

a) Cleaning Stations:

Many blue-streaked cleaner wrasses, gobies and small juvenile fish feed on parasites and dead tissue of larger fish at cleaning stations, such as on coral heads or bommies. Larger predatory fish will enter the cleaner's territory and display non-aggressive signals, e.g. colors and postures, to demonstrate their submission. The cleaner fish with then swim throughout the gills, mouth and body of the larger fish removing and eating parasites and dead skin. As such the cleaner receives a constant supply of food whilst the client remains free of parasites and dead skin. Cleaners may also attract fish with their bright colors and movements in a "dance" to display their availability and also to terminate cleaning. This relationship appears to be mutualistic as both organisms gain from their association; however certain species, such as the Sabretooth Blenny, takes advantage of this situation by resembling a cleaner wrasse in body shape, color and display. Mimicking the cleaner wrasse's dance the blenny approaches the larger fish and takes a bite from its unwary victim.

b) Clownfish & Anemones:
Clownfish, or Anemone fish, live within the stinging tentacles of anemones in Indo-Pacific waters. Whilst the anemone fish receives the protection from predatory fish by living within these tentacles, swimming may also stimulate water flow and detritus in and around the anemone, increasing oxygenated water flow and food availability.

c) Pearlfish and Sea-cucumbers
The Pearlfish (*Carapus bermudensis*) and the bottom-dwelling Five-toothed Sea Cucumber (*Actinopyga agassizi*) form an example of commensalisms in the Caribbean. The pearlfish spends its days hiding from predation in the anus of the cucumber, whilst at night it exits the same opening to feed on shrimps and other small crustaceans. The sea cucumbers seem relatively unaffected by this behavior while the fish benefits from its protection.

Other Examples of symbioses on reefs:
a) Conchfish live in the mantle cavity of the queen conch (*Strombus gigas*), emerging at night to feed
b) Gobies & shrimp – shrimp dig a burrow and clear away debris, when a predator appears the goby hides in the burrow; the shrimp may benefit from the predator warnings given by the goby, but gobies are also known to feed on young shrimp
c) Hermit crabs live in empty shells of dead snails, and as they grow they exchange them for larger ones. Some transfer anemones to their shell and move these with them to their new shells, massaging the base of the anemone until they release. The anemone gets carried to new feeding ground and some crabs even feed them with their food scraps
e) Tiny shrimpfish and cardinal fish hide in spines of sea urchins. They hover head down with their striped bodies looking like urchin spines

More information on symbioses in the coral reef ecosystem can be found in Deloach, N. and Humann, P. (1999) Reef Fish Behavior pg 96-121.

14.8 Evolutionary Adaptations of Reef Dwellers

Many interesting adaptations have evolved in reef organisms, making them very well suited to their environment and able to exploit all available niches. The trunkfish, for example, has a tough defensive exterior for protection, although the drawback is reduced mobility and growth potential. Other organisms have protective behaviors, for example, some species of parrotfish wedge themselves into protective crevices at night and secrete a mucous cocoon around themselves to mask their scent from nocturnal predators while they rest. As protection the soapfish will produce a sudsy coating of poisonous mucous with an unappealing taste if threatened.

Color also plays an important role on the reef, often used for concealment, for example, counter-shading in barracuda, disruptive coloration in butterflyfish (see 9.4.1 for more details). Stonefish and trumpetfish combine the use of effective coloration and corresponding behaviors to effectively blend in with their surroundings. Some fish, such as lionfish, use warning coloration to indicate an unpleasant taste or poison to their potential predators. Color is also used to indicate the sex of an individual and help attract mates, e.g. parrotfish.

14.9. Threats to Coral Reefs

Coral reefs are under great stress from natural and anthropogenic (man-made) factors. Whilst these impacts affect reefs to varying degrees, in some places coral reefs have disappeared completely or have been replaced by different ecosystems of lower diversity and productivity. Natural impacts such as hurricanes tend to be most acute, yet these have been present for geological time without greatly affecting reefs. Now reefs are under stress from anthropogenic disturbances, which tend to be chronic in nature. The decreased health of coral reef ecosystems due to anthropogenic impacts makes them more vulnerable to the added impacts from natural disturbances.

14.9.1. Why are coral reefs important?

Coral reefs are important for many reasons. One of the most important being the protection and shelter they provide for many different species of fish. Organisms found on the reef, such as fish and mollusks are an important food source, feeding between 30 and 40 million people every year. Fish provide 90% of the source of animal protein for Pacific Islanders. They also provide a valuable source of income from commercial fishing activities, the tourism industry, the aquarium trade, and they are a source of building materials. Coral reefs are also CO_2 sinks, helping control the levels CO_2 in the ocean as coral polyps take up CO_2 from the water to produce their limestone skeleton. The biodiversity on coral reefs is extremely high, rivaling that of tropical rain forests. These species have many medicinal uses, some of which are possibly still unknown. Coral skeletons are already being used in bone transplants and research is being done on the use of chemicals from sponges in cancer treatment. In addition, coral reefs protect coasts from strong currents and waves by slowing down the water before it gets to the shore, reducing coastal erosion.

14.9.2. Effects of human activities

Unsustainable & destructive fishing

For many traditional cultures, the relationship between human populations and their reefs has been a sustainable one. However with increased population size and improved technology, coral reef fish populations are now being over-exploited in many parts of the world. It is important to remember that tropical waters are nutrient-poor, so the removal of organisms from the reef can affect the long term productivity of the region. Moreover, in some parts of the world, fish are harvested using methods that are detrimental to the reef, including dynamite (which stuns the fish and allow the fisherman to easily collect it), large nets, and cyanide poisoning.

Coastal development

One major pollutant on coral reefs is nutrient enrichment, primarily linked to human waste and agricultural runoff. This increase in nutrients in the marine environment, termed eutrophication, can cause algal blooms which may out-compete corals, create shading and result in de-oxygenation of the water when the algae are decomposed. Moreover, coastal development can lead to runoff with high levels of sediment. Corals are highly sensitive to the impacts of sedimentation. Sediment can be introduced onto coral reefs through increased runoff especially after deforestation and terrestrial development. Suspended matter in the water column will shade underlying corals and may even smother them with a layer of deposit, reducing their ability to feed and causing them energetic requirements to remove this sediment.

Climate Change and Coral Bleaching

Coral reefs are highly sensitive to climatic influences, especially changes in temperature. When temperatures increase (even just 1-2 ^oC) above the upper range of coral tolerance (~32-36 °C) hermatypic corals begin to expel their zooxanthellae, a phenomenon known as coral bleaching, as the coral becomes bright white in the process. If the increase in temperature is short-lived, the corals may re-acquire zooxanthellae and recover. However prolonged bleaching episodes lead to high stress and often coral death. Coral bleaching events have become more prevalent since the 1980s with mass bleaching events being associated with El Nino years.

Coral Disease

Coral diseases affecting scleractinian corals were only discovered in the 1970s. Since then almost 30 diseases have been identified including black band, white band, yellow blotch and white pox. Despite the uncertainty of what is actually causing these coral diseases it is thought that they may have been a major contributor to the decline of some species of corals. Bacteria, which can be linked to human and animal faeces, are often suspected as a cause of these diseases. Moreover, disease outbreaks often follow bleaching episodes, as corals that are physiologically stressed have a lower ability to fight diseases.

African dust hypothesis

As the trade winds blow across the Atlantic they carry with them dust from the Sahara desert. In recent years, increasing amounts of dust have been measured, which may reflect changing land-use practices, a drier climate, and desertification of parts of Africa. The red-iron soils in Barbados have been shown to have originated in the Sahara. This phenomenon was first described by Darwin in 1846, but over the past 40 years amounts of dust have increased and the dust now also carries synthetic chemicals, microorganisms, trace metals and other pollutants of human origin. There are many problems associated with this dust, for example in the Gulf of Mexico the iron in the dust fuels blooms of a cyanobacteria, which can make nitrogen available for dinoflagellates, leading to red tides. In the Caribbean a terrestrial fungus, believed to be carried over in the Saharan dust, causes aspergillosis in gorgonian fans.

14.10. Review Questions: Coral Reef Communities

1. At what latitude would you expect to find coral reefs?

2. What is the key factor contributing to the high levels of productivity found on reefs, in otherwise oligotrophic oceans?

3. Why are coral reefs important? List 4 reasons:

4. Which phylum and class contains hard corals?

5. How does a coral colony grow?

6. What does broadcast spawning mean?

7. What is the name of the symbiotic algae in coral polyps?

8. How do the coral and their symbionts both benefit from the symbiotic relationship?

9. How else do corals obtain food, beside from their symbiotic algae?

10. Describe the differences between fringing reefs, barrier reefs, atolls and patch reefs.

11. How are atolls formed?

12. What is the function of the spur and groove formation in the fore-reef?

13. On which area of the reef would you expect massive corals to dominate?

14. Which area of the reef receives the largest impact of the wave energy?

15. Why are few corals along the west coast of Africa or the northeast coast of South America in the tropics?

16. What is the optimum temperature for coral reef growth?

17. How do slow growing corals compete on the reef?

18. Why did coral cover decline in Jamaica from 52% to 3% in the 1980's?

19. Give 4 examples of threats to coral reefs?

20. What happens during coral bleaching and why does the coral turn white?

21. Can corals recover from coral bleaching?

22. How might agricultural practices in Africa be affecting Caribbean reefs?

23. Why are herbivores important to coral reef health?

24. How do parrotfish protect themselves on the reef at night?

25. How does increased atmospheric CO_2 impact coral reefs, beside by contributing to a warming world?

26. What echinoderm is an important predator of coral in the Indo-Pacific?

27. What invasive fish has had a strong impact on reef fish communities in the Caribbean?

28. What two main physical factors control vertical zonation along a forereef?

Suggested Reading: Spalding et al. (2001). World Atlas of Coral Reefs. – Chapter 1

15. Continental Shelves and Neritic Zone (Karleskint Chapter 16)

Continental shelves and their overlying waters (the neritic zone) are highly productive areas. Their entire water column receives plentiful sunlight since they are shallow, and have abundant nutrients that come from the nearby continents. Most of the marine fish and shellfish consumed by humans are harvested on continental shelves.

15.1. Physical Characteristics of Continental Shelves

Continental shelves vary greatly throughout the world depending on the geology of the area. On average they extend 67km (40 miles) from the coast, but this can range from 1.6km (e.g. western coast of North America) to 1500km (e.g. Arctic coast of Siberia) from the coast. The continental shelf is part of the continental crust, and depth increases gradually in this region, down to about 130m, then dropping off in a steep slope to the oceanic crust (Figure 15.1). The proximity to land means that continental shelves receive high levels of terrestrial sediments. Along with this sediment are abundant nutrients such as nitrogen, phosphorus and silica. Moreover, shelves are shallow and there is little stratification because of tidal currents and wind mixing, which bring nutrients back to the surface. In some areas, coastal upwelling is also an important source of nutrients to coastal seas. It is this high concentration of nutrients, along with abundant sunlight, which makes continental shelves so productive.

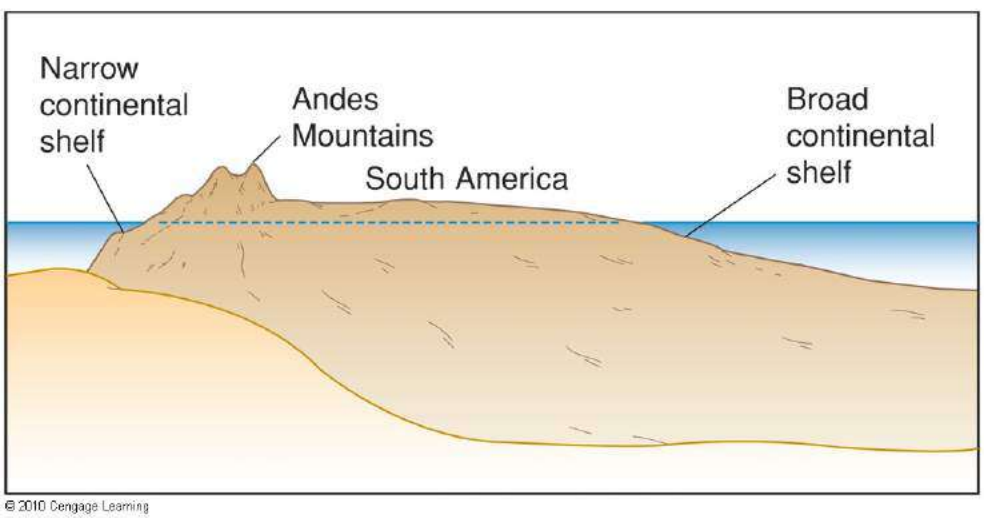


Figure 15.1. Continental shelves, which descend gradually from the coast out until the shelf break, where they end with a steep slope.

15.1.1. Waves, currents, and light

The stability of the environment plays a large role in determining the kind of biological community that develops. In shallow parts of the continental shelf, waves are one factor that plays into this process. On exposed coasts, wave action from large storms can reach

80m deep, with the most important water motion occurring in the shallowest areas. Waves can cause stress and mortality to marine organisms through direct physical damage, or through large movement of sediment.

Strong currents can also affect organisms at all depths of the continental shelf—thought they typically get progressively weaker with increasing depth. Currents not only affect mature organisms, but also the transport of their gametes and larvae. Deposit feeders and sessile organisms with a fragile body do poorly in areas of high water velocity, and for this reason are found in increasing abundance with increasing depth. Other sessile benthic organisms that live in areas of high water velocity have adaptations to deal with the physical stress, such as flexible bodies (e.g. seaweeds) or strong, encrusting growth forms (e.g. bryozoans). Mobile organisms often seek shelter from strong currents, either in crevices or in burrows. Clearly strong currents can limit the distribution of many marine organisms. On the opposite end of the spectrum, areas of the benthos that have very low currents have much lower input of detrital or planktonic food, and here food availability may be a constraint.

The abundant phytoplankton in neritic zones and the high levels of sediment brought from rivers make the water above continental shelves much murkier (turbid) than water in the open ocean. This reduces the depth to which light penetrates and the depth at which primary producers can carry out photosynthesis (compensation depth). Semi-enclosed coastal areas tend to retain more sediment and therefore have higher turbidity; those directly open to the ocean are typically clearer, and sustain photosynthesis at greater depth. This has implications for the growth of both phytoplankton and benthic macroalgae.

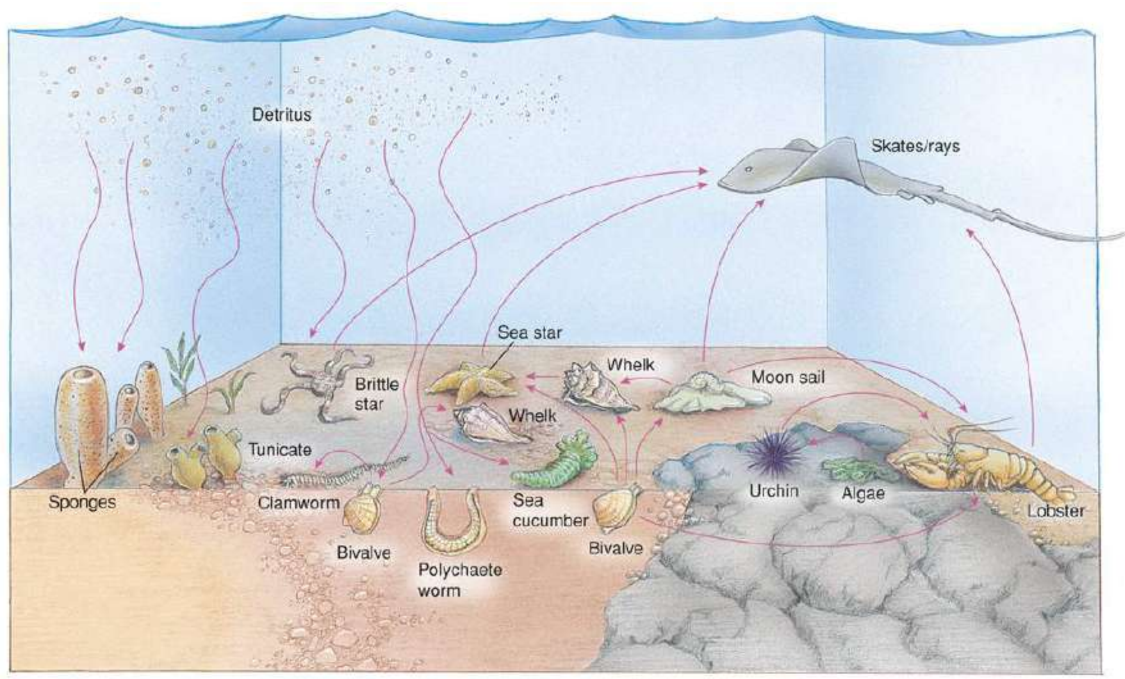
15.1.2. Role of Sediment

The type of substrate is very important in determining the type and number of organisms that inhabit a particular area. Sediment type, in turn, is largely determined by water motion. Where currents are high, sediments of large particle size (sand, rock, gravel) are deposited while much of the fine silt and clay stays in suspension. In many areas there is little sediment deposited and the bedrock is exposed. Areas with strong current also receive high food supply. These areas are not good habitats for infauna, which cannot withstand the abrasion from the constant shifting of sediments. Areas of strong currents are better for epifauna, such as sessile filter feeders (e.g. sponges, anemones, colonial cnidarians) as the coarse sediment provides a firm surface for attachment and the water motion brings a large supply of suspended food particles.

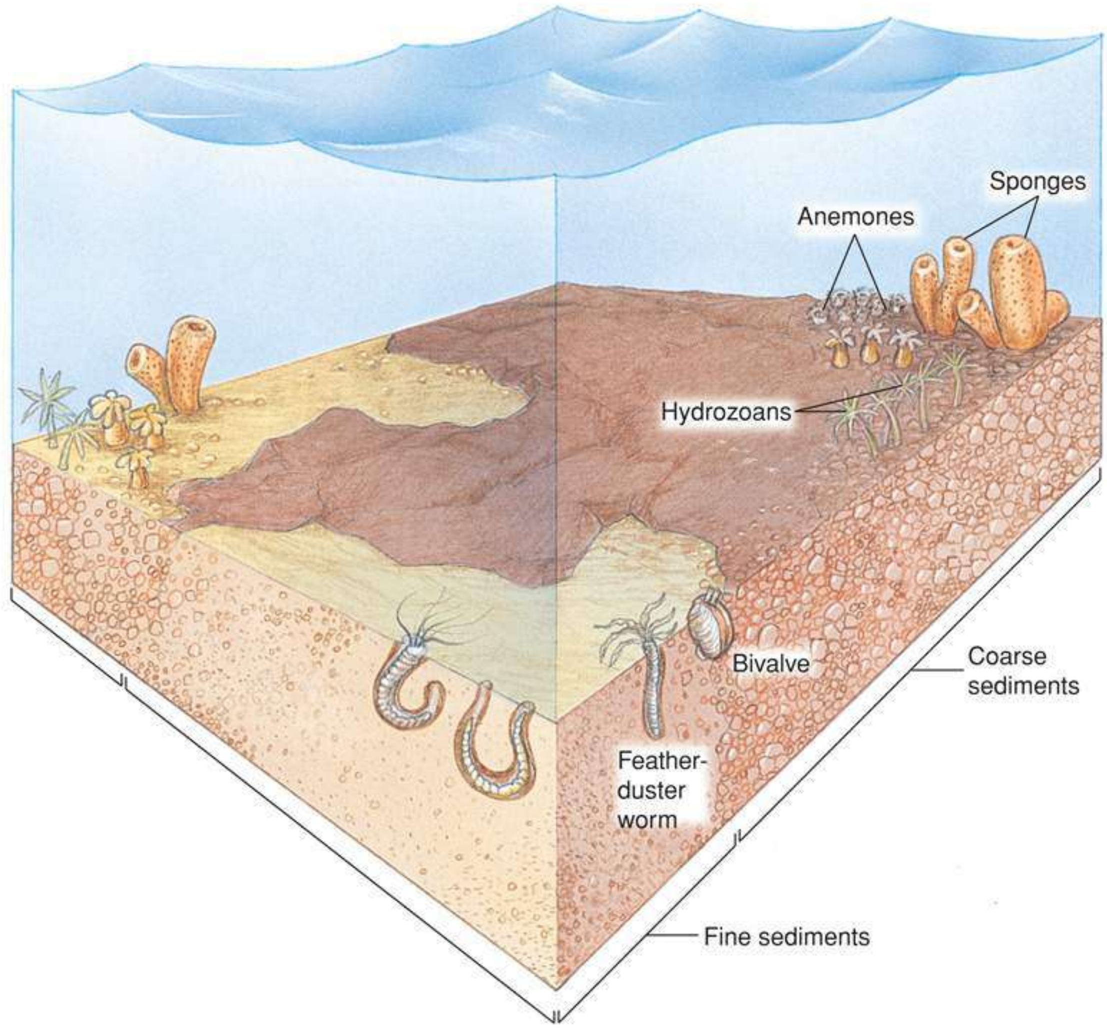
Where currents are weak finer sediment is deposited, creating a stable habitat for a variety of infauna that construct permanent burrows (e.g. polychaetes worms, amphipods, clams). Most are deposit feeders, gaining their nutrition from the organic matter in the fine sediment. Soft sediment bottoms do not support many filter feeders because suspended food is scarcer in the low current conditions, and the fine sediment tends to clog filtering appendages.

15.2. Benthic Communities

Communities on the continental shelf are generally more stable than intertidal zones or estuaries. The food supply is primarily detritus, sinking down from the sunlit waters above, and this is often the limiting factor for benthic communities (Figure 15.2). Benthic communities on continental shelves include many filter feeders and deposit feeders, which themselves are food for other animals. Their distribution is strongly tied to the type of sediment, and can be quite patchy (Figure 15.3).



15.2. Benthic food web typical of continental shelves. Benthic organisms are often limited by detritus that falls from overlying waters or come in with currents.



15.3. The distribution of benthic organisms is in large part determined by the availability of a suitable substrate with the right sediment characteristics. Sediments are often unevenly distributed, leading to patchy distribution of benthic organisms.

15.2.1. Hard-Bottom Communities

Hard bottom habitats are composed of large sediments that cannot be pushed apart, and are most often found off rocky coasts. These areas are dominated by epibenthic organisms such as large seaweeds and sessile colonial animals such as bryozoans, hydroids, sponges and sea squirts. Other abundant invertebrates include sea anemones, crustaceans, bivalves, snails and echinoderms. Sessile organisms are abundant and attach themselves to the rock by cementing their body or using strong thread-like structures.

Benthic communities on the continental shelf tend to be patchy because of small-scale variations in habitat. The uneven distribution of sediment is the most obvious factor controlling the distribution of organisms, but even within hard bottom communities organisms are patchy because of variation in slope, exposure to light, disturbances (e.g. landslides) and patchy larval recruitment. Many invertebrates have short larval stages that lead to short dispersal and allow population to quickly be replenished. Many can reproduce asexually which allows for quick population growth.

Many temperate hard bottom communities are dominated by kelp beds, which are one of the most productive communities on continental shelves. Kelps are brown algae and require a rocky bottom to attach to. They grow in cold water ($<20^{o}$C average) in areas that are high in nutrients. They are normally found in water shallower than 20m, but in clear waters can be found to a depth of 30m.

Kelp forests

Kelp beds are like an underwater forest, in some areas with a canopy and an understory. Kelps are perennial seaweeds, with individuals lasting several years. In the Pacific and the southern Atlantic, the giant kelp (*Macrocystis* sp.) dominates. This is the world's largest algae, and can grow to be 20 to 40m long. The blades have gas-filled floats that offer buoyancy and allow maximum exposure to light. This seaweed is fast growing and blades can grow up to 50cm of new tissue every day. The tall, narrow stipes of *Macrocystis* sp. grow fairly closely together, but there is enough space between them for animals to move, and many swimming animals are found in these forests. The rocky bottom beneath is carpeted with red algae which can photosynthesize in lower light levels. The keystone predator in eastern Pacific kelp forests are otters.

There is no giant kelp in the North Atlantic Ocean, instead smaller kelps of the genera *Laminaria* and *Alaria* sp. dominate. These kelp grow closely packed together and form dense thickets, making it more difficult for large swimming organisms to move freely; instead these ecosystems are dominated by crawling organisms such as lobsters, the keystone predators in this environment.

Kelp Communities

Kelp forests provide food and shelter for a variety of organisms. Their blades slow down currents and decrease the force of waves. The tree-sized algae greatly increase the habitat available for many echinoderms, fish, otters and pinnipeds. Commercially-important species such as abalone (in the Pacific) and American lobsters (in the North Atlantic) live in kelp forests. Herbivores include snails that scrape off the outer layer of kelp cells, and urchins, which can have a very important ecological impact on kelps.

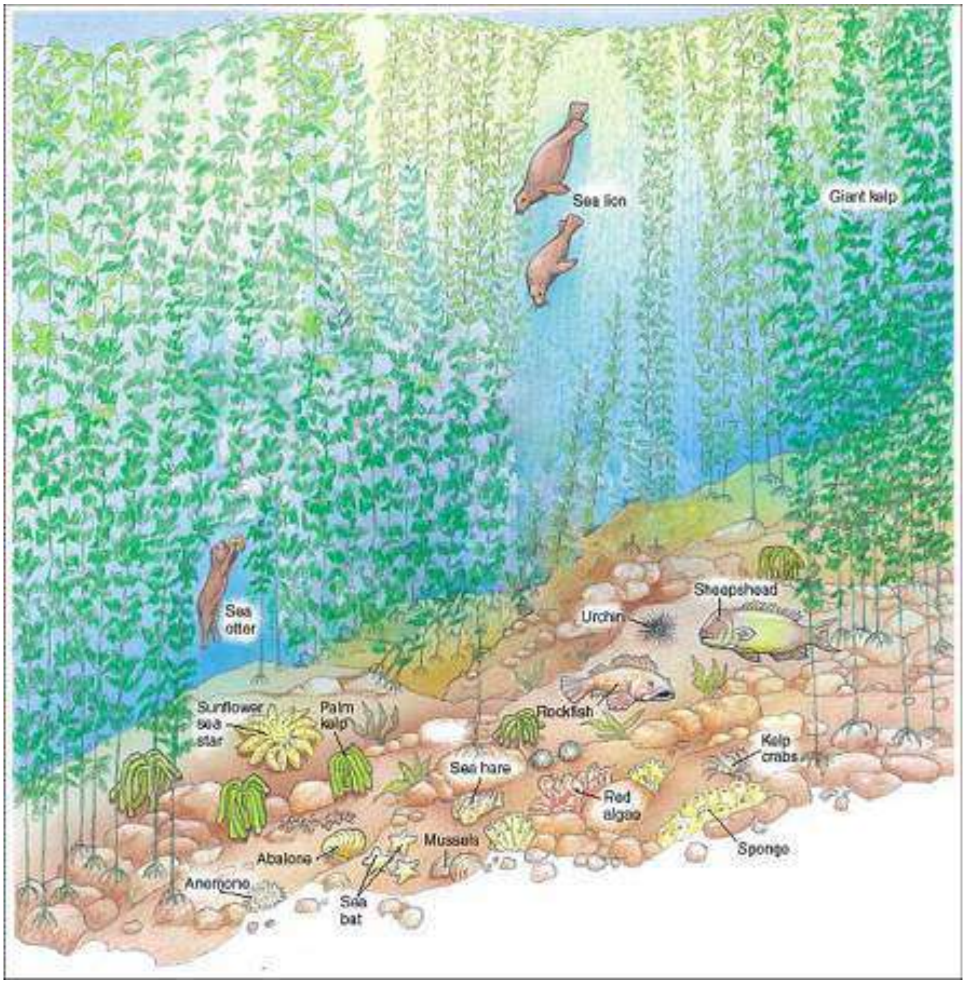


Figure 15.4. Ecosystem in a kelp bed of the giant kelp *Macrocystis* sp. on a hard bottom.

Impact of Sea Urchins on Kelp Communities

Wave action and predation usually prevent urchins from causing significant damage to kelp forests. However in the 1970's urchins became extremely abundant in the shallow subtidal areas along both coasts of North America, in part due to trophic cascades resulting from declining numbers of their predators: sea otters on the west coast and lobsters on the east coast. Urchins cannot eat the upper portions of large kelps, but they can eat young algae and damage the holdfast of larger kelps. When kelp beds are reduced through grazing by urchins, urchins can still survive as they are generalists and can switch to other foods, including other algae and other invertebrates. They then form urchin barrens where it is nearly impossible for kelps to re-establish, and in addition many other species that depend on kelp for food and shelter disappear from the ecosystem. In the North Atlantic, urchins periodically suffer mass mortalities from disease, allowing the ecosystem to return to a state of kelp bed (Figure 15.5).

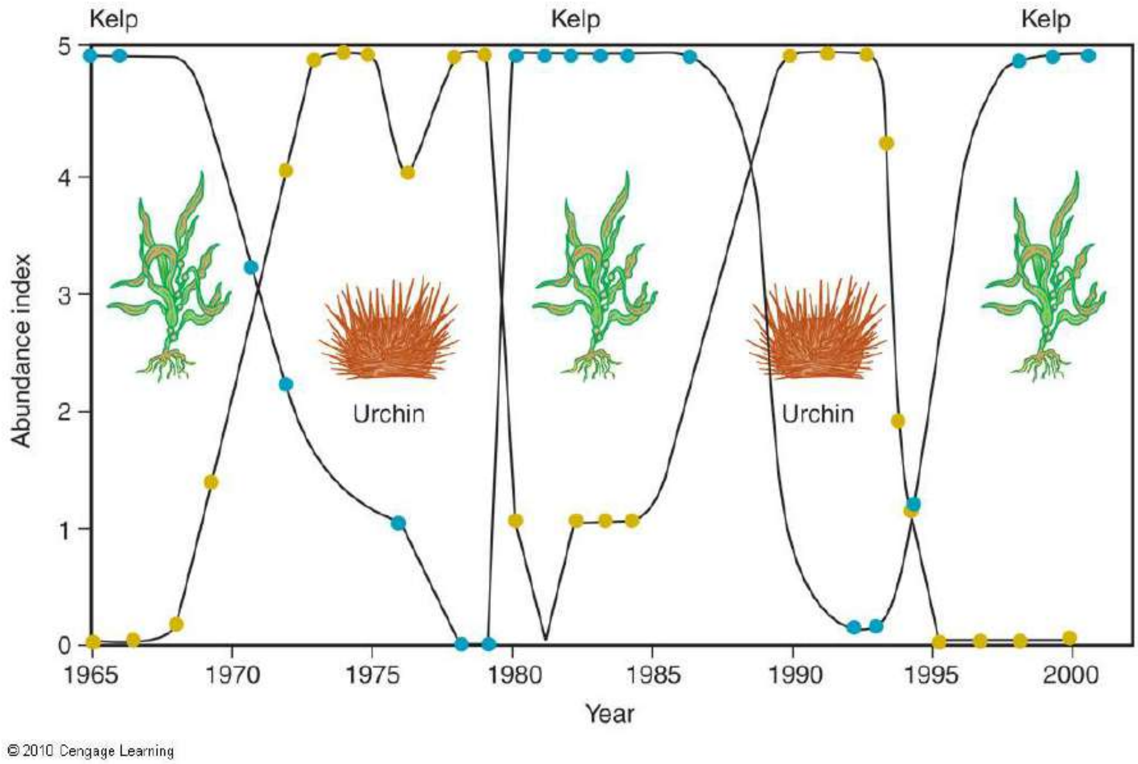


Figure 15.5. Cycles between kelp beds and urchin barrens in the North Atlantic

15.2.2. Soft Bottom Communities

Patchiness in Soft Bottom Communities

Soft bottom communities occur where the bottom sediment is sand, mud, or both. Water motion determines the coarseness of the sediment in a given area; where currents are stronger, sand is deposited, and these areas are dominated by suspension feeders. Where currents are weaker smaller grain-size sediment such as mud is deposit, and those areas are dominated by deposit feeders. Suspension and deposit feeders do not generally occur in the same area. The burrowing and feeding actions of deposit feeders in muddy sediment, increases the amount of suspended sediments, clogging the feeding organs of suspension feeders. Small-scale variations also exist in sediment distribution due to animals feeding, burrowing or by bottom currents creating ripples in sediments (Figure 15.6). The top of crests or mounds experience higher currents and therefore have coarser sediment. There are typically more suspension feeders here where currents bring more suspended food particles. Conversely, the bottom of troughs or depressions experience weaker currents and consequently have finer sediments, and deposit feeders are more common.

Most invertebrates have a planktonic larval stage, and the pattern of larval settlement depends on currents, predation and bottom sediments. Settlement is highly variable and if it is uneven it will result in a patchy distribution of adults.

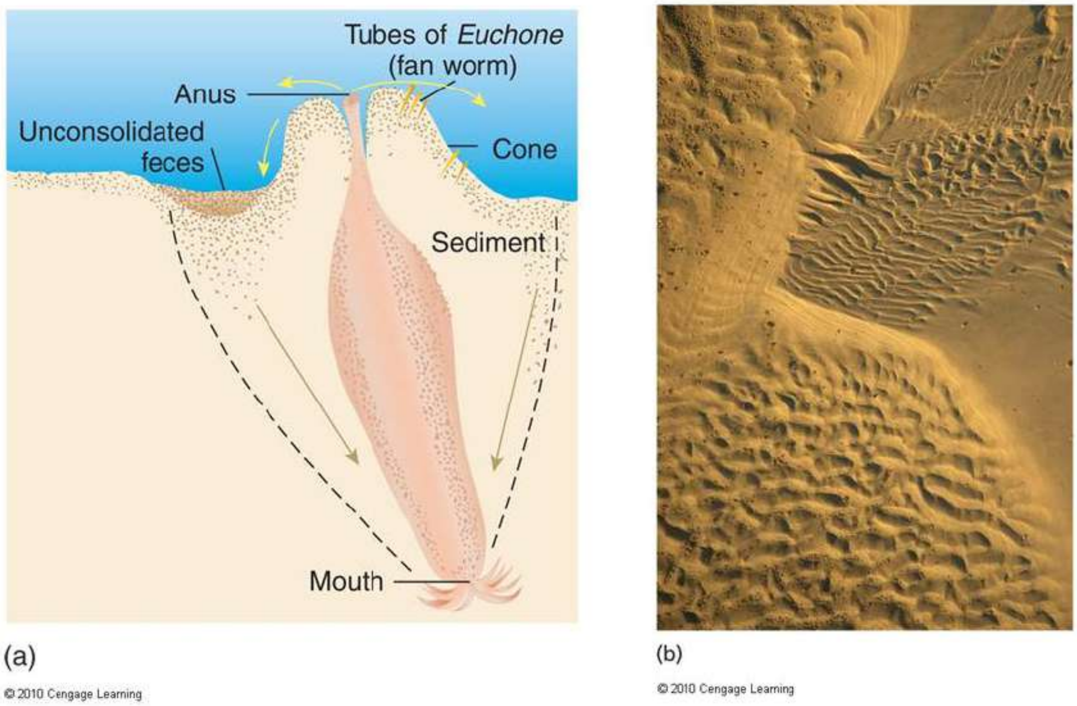


Figure 15.6. Small-scale variations in sediment characteristics can be due to burrowing organisms or currents.

Soft-Bottom Food Chains
The primary food source in soft bottom communities is detritus. Suspension feeders ingest detritus along with plankton, and deposit feeders eat detritus and bacteria. Predators include polychaetes worms and carnivorous snails. Brittle stars can be extremely abundant and may reach densities of up to 80 million/km^2. Fish of soft bottom communities tend to have flattened, compressed bodies and are well camouflaged, for example skates, rays, angel sharks and batfish. Moreover, several commercially important fish such as haddock, hake, pollock, cod and several species of flatfish inhabit soft-bottom environments. Many of these demersal fish feed on benthic invertebrates, and variations it their numbers (e.g. decline through overfishing) can have important effects on the population of their prey. For example the severe decline of cod in the North Atlantic is thought to be one of the primary factors for the high abundance of American lobsters in that area.

15.3. The Neritic Zone

The neritic zone includes the pelagic zone of the coastal seas that lie along the edges of continents and above the continental shelf. The water here has a high density of phytoplankton because of high levels of nutrients, and this high productivity turns coastal waters green (compared to blue water in the open ocean). This phytoplankton is the basis of the neritic food webs; it is eaten by zooplankton, in turn eaten by planktivorous fish, then larger fish, marine mammals, seabirds and humans. The neritic zone covers only

10% of the oceans yet it is so productive that it represents 90% of the world's annual harvest of fish and shellfish.

15.3.1. Food Chains in the Neritic Zone

Runoff from land provides high levels of nutrients, which can support relatively large primary producers such as microphytoplankton (20-200μm) as well as smaller ones like nanoplankton (<20μm). The composition and abundance of the phytoplankton varies with region, season, and grazing by zooplankton. In temperate zones, diatoms dominate the phytoplankton, while in warmer regions dinoflagellates tend to be more abundant.

The zooplankton is dominated by copepods, which can reach densities of 100 000 per m^3. Copepods are the primary consumer of diatoms, and can eat up to 120 000 per day. They have a high reproductive capacity, maturing in 2 weeks and producing a high number of eggs. This allows copepods to increase their population size rapidly when the food supply is abundant.

Food chains in coastal seas are typically 2-3 steps shorter than in the open ocean, for a few reasons. Firstly, because the phytoplankton tends to be larger, there are fewer steps in the food chain until the large consumers. Secondly, because coastal seas are relatively shallow, phytoplankton can be eaten not only by zooplankton but are also eaten directly by benthic filter feeders. The combination of higher productivity and shorter food chains supports larger numbers of higher-level consumers in coastal seas, compared to the open ocean.

15.3.2. Productivity in the Neritic Zone

Upwelling zones are the most productive planktonic ecosystems, supported by a constant supply of nutrients brought back to the surface by currents. For example, upwelling off the Pacific coast of Peru supports large chain-forming diatoms that are directly eaten by anchovies, which in turn are prey for large fish, seabirds, seals, whales and humans. This creates a very short food chain, resulting in high biomass of large organisms. The Pacific coast of Peru, along with the North Atlantic, represents half the world supply of commercial fish. Similarly, the diatoms supported by upwelling on the coast of Antarctica are eaten directly by krill (*Euphausia superba*), supporting a huge biomass of this crustacean and in turn allowing large concentrations of predators such as seabirds and marine mammals.

15.3.3. Other Roles of Plankton in Coastal Seas

Many animal species spend at least part of their life as a member of the plankton (termed meroplankton). Sessile benthic animals such as barnacles, mussels and corals rely on planktonic larval forms to colonize new territories. These animals, for the most part, reproduce externally by shedding their gametes into the water column, where fertilization takes place. Many mobile organisms such as crabs, lobsters, shrimps and fish also have larval stages that are part of the plankton. Mortality is extremely high in these early stages and about one in a million eggs in the plankton survives to adulthood. Consequently, disturbances in the plankton can have important effects on benthic and nektonic populations.

15.4. Review Questions: Continental Shelves and Neritic Zone

1. List two sources of nutrients on continental shelves?

2. Where is the source of detritus for benthic communities of the continental shelf?

3. Are the conditions more, or less stable on the benthic sea floor of the continental shelf than on intertidal shores?

4. List three causes of patchiness on hard bottom communities on continental shelves

5. What type of sediment would you expect when the current on the sea floor is strong? and when it is weak?

6. What type of organisms are favored in a coarse and in a fine sediment environment?

7. Why do you not find infauna if the currents are strong?

8. On which coast of the USA would you expect to find giant kelp (*Macrocystis* sp.), and on which would you find *Laminaria* spp.?

9. What are the keystone predators in kelp ecosystem on the east and on the west coast of the USA?

10. What impact do sea urchins have on kelp communities?

11. Why do deposit and suspension feeders generally not occur in the same areas in the soft bottom communities?

12. How do the activities of burrowing sea cucumbers affect the patchiness of soft bottomed communities?

13. Where is the neritic zone?

14. What is the most abundant type of zooplankton in the neritic zone?

15. Give two reasons why do coastal seas support a larger numbers of higher-level consumers?

16. Why are bigger species of phytoplankton more common in the neritic zone compared to the open ocean?

17. Where are the most productive planktonic ecosystems located?

18. Why can changes in planktonic communities greatly affect populations of benthic organisms?

16. The Open Ocean (Karleskint Chapter 17)

16.1. Introduction

The open ocean represents an immense area that contains 1.4 billion km^3 of water, which is several hundred times the living space of all terrestrial habitats. However while it is large, the open ocean is barren in comparison to coastal seas; the productivity here is limited by low nutrients. There are relatively few large animals because of the low productivity and the lack of hiding spaces.

16.2. Regions of the Open Sea

Coastal waters discussed in the previous chapter represent the neritic zone; the water column above the continental shelf. This chapter focuses on the oceanic zone, the water column over the oceanic crust. The oceanic zone can be further divided vertically based on the depth of light penetration (Figure 16.1). The photic zone, at the surface, receives enough sunlight to sustain photosynthesis. It can reach a depth of about 200m and roughly corresponds to the epipelagic zone. This is where most pelagic animals live. Below the photic zone, the disphotic zone (twilight zone) receives low levels of sunlight, but not enough to sustain photosynthesis. Further below is the aphotic zone, where no light penetrates. In this chapter we focus on the organisms of the photic zone.

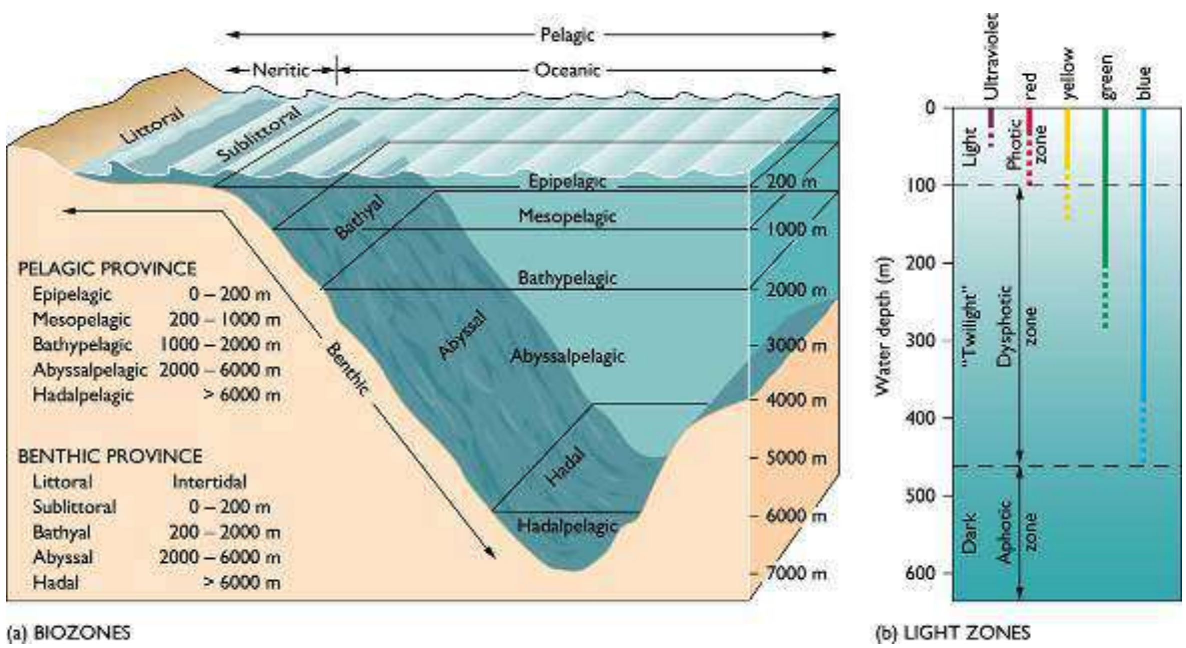


Figure 16.1. Regions of the marine environment.

16.3. Life in the Open Sea

Organisms in the open ocean can be broadly divided in two groups: the plankton and the nekton. Planktonic organisms lack the ability to swim or are weak swimmers and consequently float or drift in ocean currents. Nektonic organisms actively swim and their movements are not governed by the currents. Nekton are large, streamlined and strong organisms, typically higher consumers. There is far more plankton than nekton in the open ocean.

16.3.1. Classification of Plankton

Planktonic organisms can be classified into groups in various ways.

Phytoplankton is the plankton that photosynthesizes. Zooplankton are the animal members of the plankton, which are heterotrophic. Organisms that are planktonic throughout their entire lives (e.g comb jellies, copepods and krill) are called holoplankton. Other organisms, which only spend a part of their life in the plankton (e.g. fish and squid larvae), are called meroplankton.

Plankton are commonly classified based on their size. Phytoplankton are generally small, which creates a large surface area to volume ratio, improving their ability to absorb nutrients and sunlight. Note that the size of plankton ranges from 0.02μm to several meters in size (Table 16.1); plankton does not solely include microscopic organisms.

Finally, plankton can be characterized based on position in the water column. Plankton that live near the surface are called neuston; those that break the surface of the water are called pleuston.

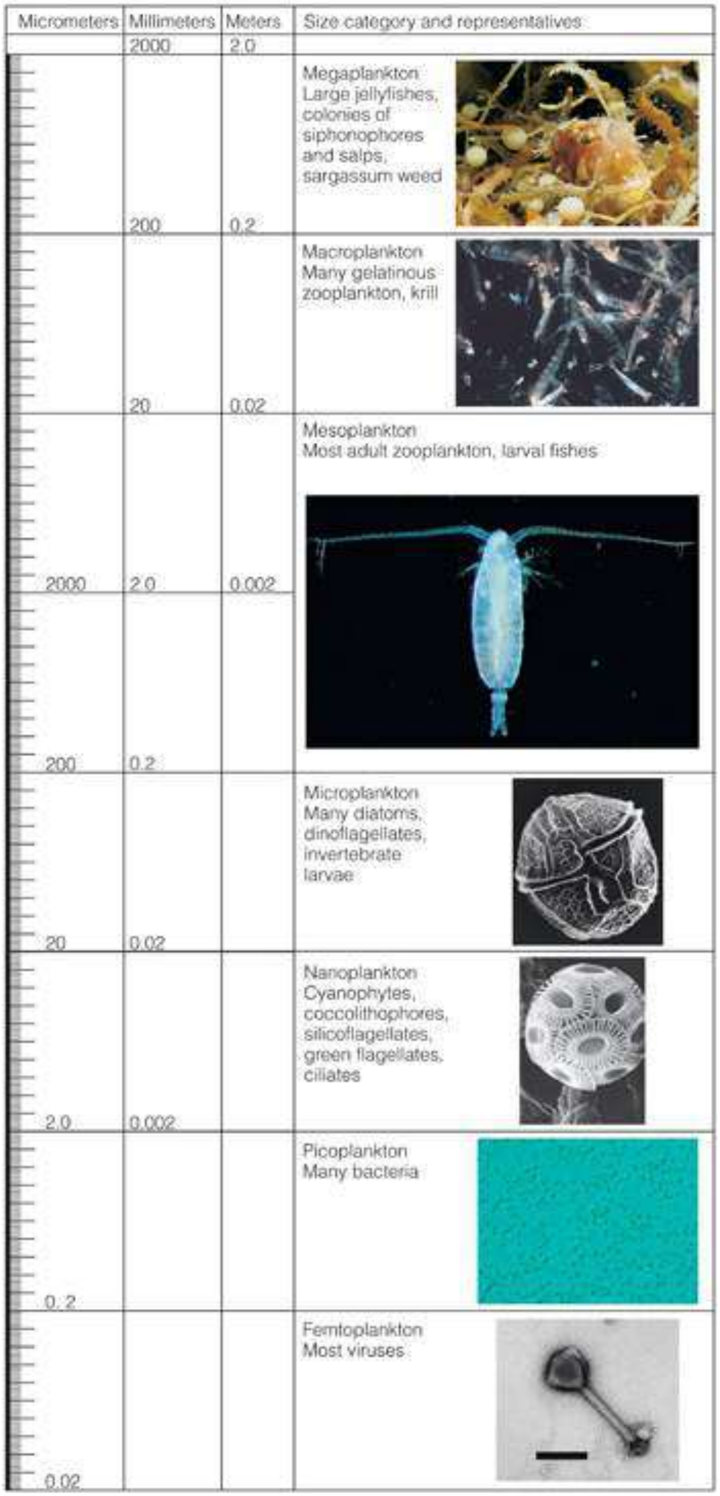


Figure 16.2. Classification of plankton based on size. This particular scheme divides the plankton in 7 size categories, containing plankton of a size within 1-2 orders of magnitude.

16.3.2. Patchiness in the Open Ocean

The distribution of plankton in the sea is not uniform, due to multiple abiotic and biotic factors. Upwelling areas bring nutrients back to the surface and support higher levels of primary productivity, and can cause large scale patchiness in plankton and nekton. Localized variations in sea surface conditions, vertical mixing of water and meeting of water of different densities can also contribute to a higher planktonic population growth in some areas. Nektonic organisms are also distributed unevenly as they follow their planktonic food.

On a small scale, various micro-organisms can attach to particulate organic matter, particularly the gelatinous and mucus secretions from zooplankton. This forms translucent cobweb-like aggregations called marine snow, in which bacteria are 10,000 times more abundant than in adjacent open water. Marine snow particles are important as they greatly increase the small-scale patchiness of the open ocean, are a direct food source, form important microscopic ecosystems, and provide habitat for many organisms. Further, the resulting larger particles of marine snow sink faster than individual small particles, and this may increase the amount of food that reaches the deep sea.

16.3.3. Planktonic Migrations

Many zooplankton in the open ocean undertake a daily migration from the surface to a depth of about 1.6 km (1 mile). This allows them to feed at night in the photic zone (where food is abundant) while reducing the risk of predation during the day by migrating to depth, as planktivorous fish are most abundant in the epipelagic zone. There are added advantages to spending the day in the mesopelagic zone. As the temperature is lower, organisms' metabolic rate will be lower, and they therefore require less food and oxygen. In addition, the low temperature increases the density and viscosity of the water and therefore slows the sinking rate of potential food particles. The migratory zooplankton are often very densely packed and may be picked up as a false bottom on sonar. This is called the deep scattering layer.

16.3.4. Megaplankton

The megaplankton contains many animals (Figure 16.3), but also some plants, such as the floating seaweed *Sargassum* spp. Important members of the megaplankton include cnidarians such as jellyfish, and urochordates such as salps and larvaceans. These urochordates produce extensive mucous structures for feeding, and when discarded these contribute significantly to marine snow.

Pteropods, purple sea snails and nudibranchs are all molluscan zooplankton that show adaptations to a planktonic lifestyle: they have a reduced or absent shell, pteropods have a modified wing-like foot for swimming and purple sea snails reduce their sinking rate by producing bubbles surrounded by mucus.

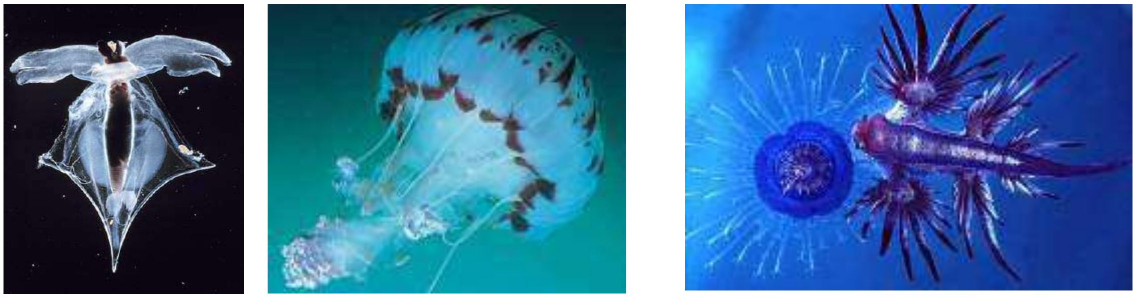


Figure 16.3. Members of the megaplankton: pteropods (left), jellyfish (middle) and pelagic nudibranch (right).

16.3.5. Nekton

Nekton are organisms that can actively swim and whose movements are not governed by currents. This includes large invertebrates, fish, reptiles, birds and mammals.

The most important nektonic invertebrates are squid, which are adapted to life in the open ocean with a stream-lined body and good swimming ability, through jet-propulsion.

Fish of the open ocean are dominated by large, powerful swimmers such as billfish, tunas and sharks. Billfish, such as marlin and sailfish, lack teeth and have a greatly elongated upper jaw that forms a bill used to club prey. Tunas are extremely good swimmers, and can cruise at speeds of up to 27 km/h, with short bursts of speed of up to 75 km/h. They must swim constantly or will sink as they do not have a swim bladder. Tunas are very efficient swimmers with a streamlined body and a smooth body surface (Figure 16.4). Their swimming requires a lot of energy and oxygen. They maintain a good oxygen supply by constantly moving large amounts of water past their gills as they swim. Some tunas maintain an internal body temperature that is 8-10^{o}C higher than the surrounding environment, which allows them to maintain higher metabolic rates and thus higher speeds. Tunas are large and the Bluefin tuna can reach 4 m in length.

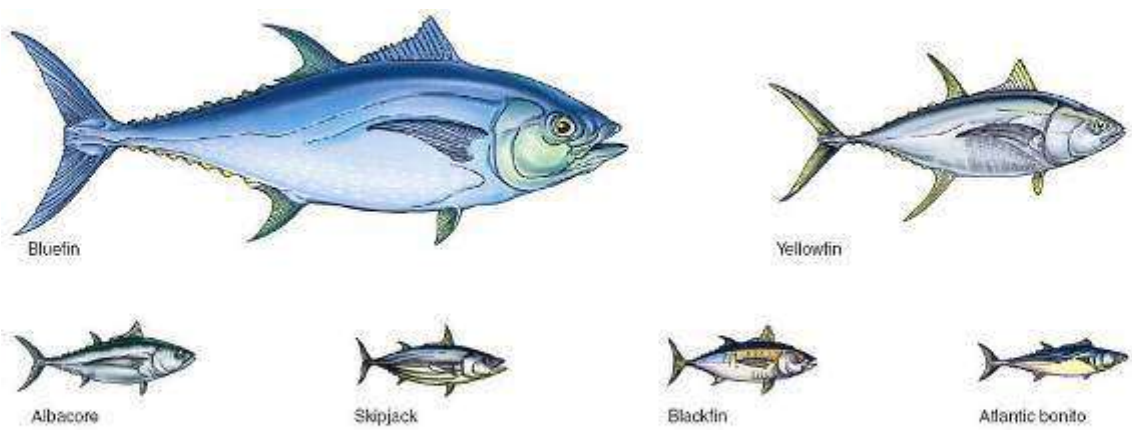


Figure 16.4. Common species of tuna of the open ocean.

In contrast with active fish like tunas and billfish, the ocean sunfish is quite slow-moving. These large fish may weigh up to 1 ton and have very distinctive shape with a modified caudal fin and prominent dorsal and anal fins (Figure 16.5). They feed on zooplankton and are often see lying on their side at the surface. The cause of death for these fish is often large internal and external parasites loads, and it is believed that they come to the surface when diseased to be cleaned in a mutualistic relationship with seabirds.

Sharks are important predators of the open ocean. They have streamlined bodies and many species display internal fertilization, an adaptation for life in the open ocean, where mates are less abundant and success rates of external fertilization lower. Moreover, several species, such as hammerhead sharks, are viviparous, which ensures a higher survival rate for the young.

Manta rays (Figure 16.5) channel small fish and plankton into their mouths. They are large, growing up to 6m in diameter and are one of the few rays to inhabit the open ocean.

Most sea snakes are not very abundant in the oceanic nekton, but the yellow-bellied sea snake can be found in high densities in the Indian and Pacific Oceans. An accumulation of algae and fouling organisms creates a need to shed their skin, unable to rub against the sea floor like their coastal relatives, the open ocean sea snakes must tie their body in knots.

The only oceanic birds that can really be included in the nekton are penguins, found in the southern hemisphere. These flightless birds are very good swimmers and consume large amounts of krill, squid and fish.

Whales are the largest members of the nekton. Baleen whales filter small invertebrates and fish, while toothed whales feed on squid and larger fish.

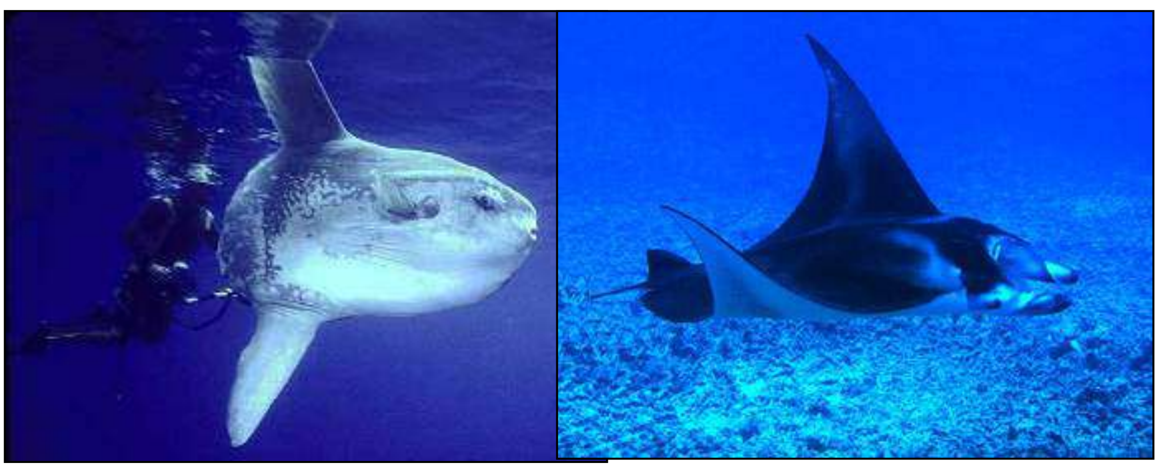


Figure 16.5. Ocean sunfish (left) and manta ray (right)

16.4. Environmental Conditions of the Open Ocean

The open ocean is generally a very stable environment. There are no sudden fluctuations in temperature or salinity. However, organisms face other challenges. Living in well-lit surface waters with no hiding places means a high susceptibility to predation. Moreover, organisms must remain in the photic zone where light and food is more abundant.

Nutrients are a lot less abundant in the open ocean than they are in coastal areas as there are no nutrient inputs from land. This influences the type of primary producers that can survive here.

16.5. Adaptations of Organisms in the Open Ocean

16.5.1. Competing for limited resources

Nutrients needed by photosynthetic organisms are present in very low concentrations in the open ocean, compared to coastal zones and upwelling areas. Open-ocean microorganisms have a few adaptations to cope with this low nutrient concentration. First, groups of microorganisms that are successful in the open ocean tend to be those that require no or little silica for their cell walls, thereby reducing the need for this nutrient. Further, the most common open-ocean species have a low metabolic needs for other nutrients such as nitrates and phosphates. Finally, open-ocean microorganisms tend to be very small and therefore have a high surface area to volume ratio, which enhances the rate of nutrient uptake.

16.5.2. Remaining Afloat

Phytoplankton must remain in the photic zone where light levels are high enough to sustain photosynthesis. In turn, the distribution of phytoplankton dictates the distribution of zooplankton and other predators. Plankton have a tissue density greater than seawater and will therefore eventually sink, and as they are weak swimmers they must have methods to stay in the upper part of the water column.

Swimming

Many organisms, whether planktonic or nektonic, can actively swim. Organisms swim using flagella, cilia, or appendages, or by jet propulsion or undulations of the body (Figure 16.6).

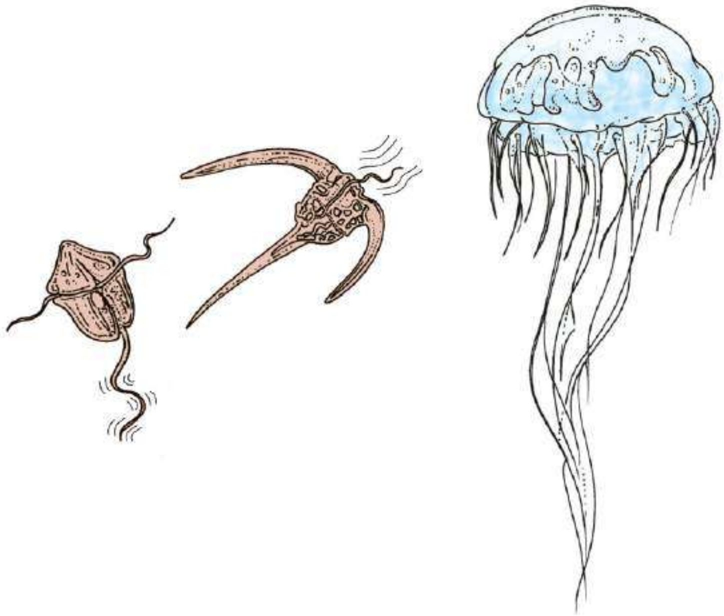


Figure 16.6. Dinoflagellates and jellyfish can remain afloat by actively swimming

Reduced Sinking Rates
Organisms can reduce their sinking rate by increasing their surface area to volume ratio, with flattened bodies or appendages like spines (which also deter predators; Figure 16.7). However this only slows down the sinking, it does not prevent it. This strategy is found in many types of phytoplankton and zooplankton (e.g. diatoms, radiolarians, crustaceans) but it is disadvantageous to most nekton, which need to minimize drag.

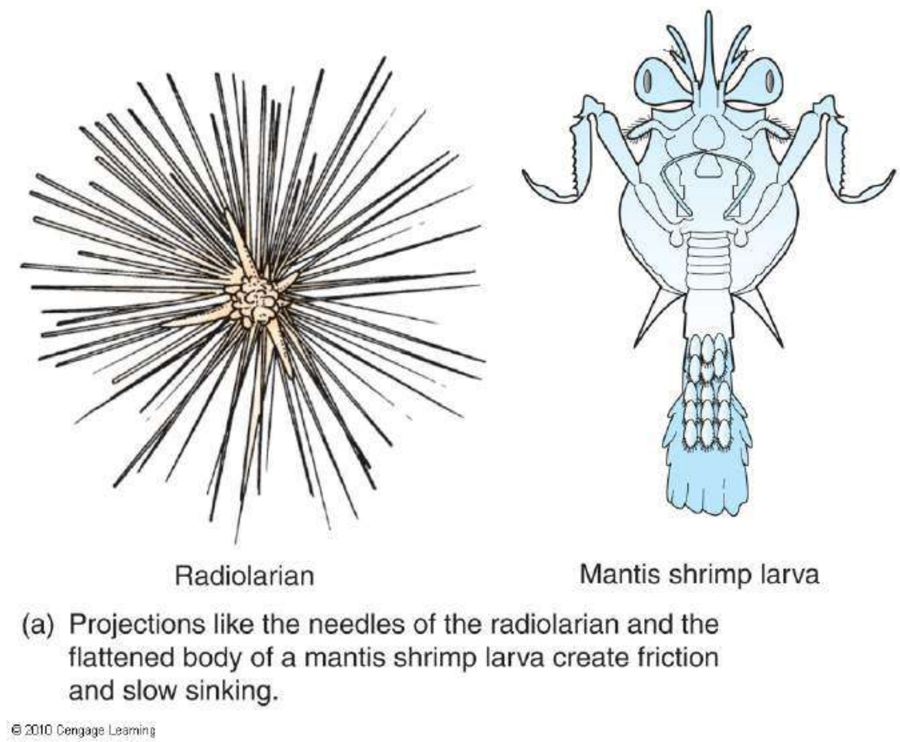


Figure 16.7. Examples of adaptations to reduce sinking rate.

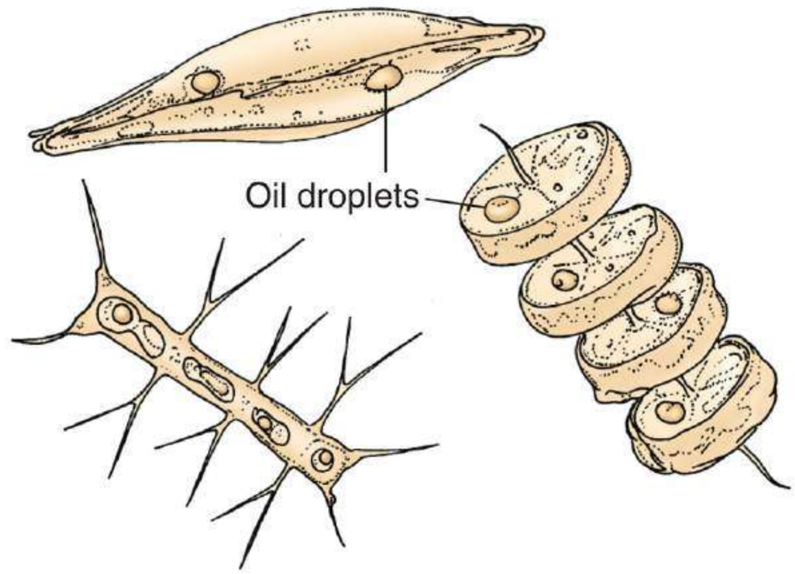
Increased buoyancy

Organisms can increase their buoyancy through the storage of low-density materials such as oils, fatty acids or other lipids (Figure 16.8). This adaptation is seen in phytoplankton, zooplankton as well as large nekton such as whales and sharks.

Other organisms, such as gelatinous zooplankton, dilute their proteins and minerals with water, reducing their overall density. This adaptation would not be suitable for nekton, which need strong muscles and skeletons for locomotion.

Some organisms such as squids and some dinoflagellates, replace heavier ions with lighter ones, creating a lower density without affecting their osmotic properties.

Finally, many planktonic and nektonic organisms reduce their buoyancy by storing gases in gas bladders, chambers, or in the vacuoles in the cytoplasm. For example, Portuguese man-o-war, *Sargassum* spp, nautilus, radiolarians, diatoms and fishes with swim bladders.



(b) Diatoms store their food reserves as oil. The oil makes them more buoyant and offsets some of the weight of their shells.

Figure 16.8. Diatoms have oil droplets which help them remain afloat.

16.5.3. Avoiding Predation

As there is no place to hide in the open ocean, different mechanisms of predator avoidance are required. Many organisms have stinging cells, such as jellyfish. Others avoid predators by swimming fast or taking to air (e.g. flying fish and squid). Many organisms find safety in numbers, and schooling is an important behavior of oceanic fish. Similarly, some pelagic invertebrates such as salps or Portuguese man-o-war live in colonies.

There are two main types of camouflage displayed in the open ocean. Counter-shading is a coloration where the dorsal surface is dark and the ventral surface is light, allowing the fish to blend well with both the darker ocean beneath them and the lighter layers from above (Figure 16.9). Other organisms, such as copepods, jellyfish and salps, are camouflaged by being nearly transparent.

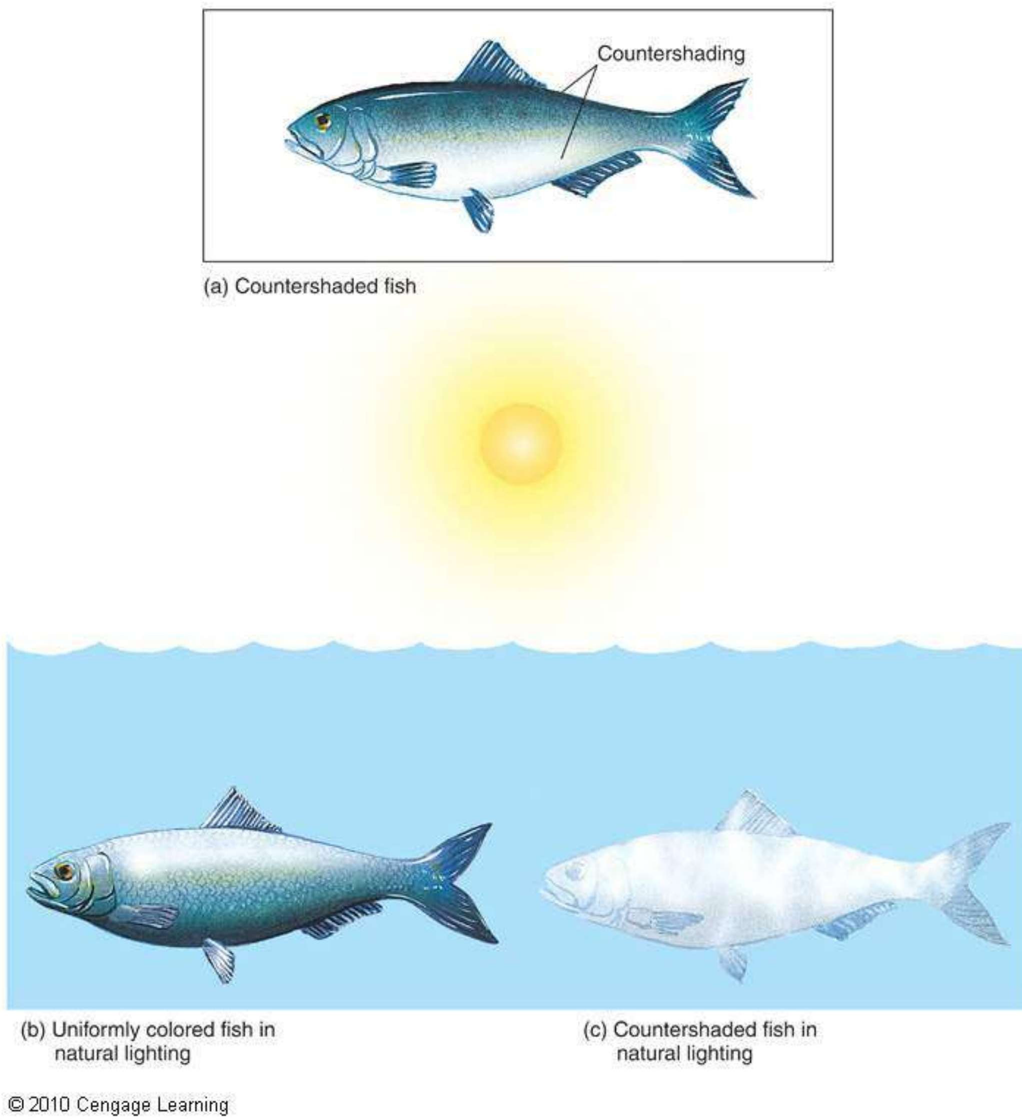


Figure 16.9. Countershading, a type of camouflage in the open ocean.

16.6. Ecology of the open sea

16.6.1. Productivity of the Open Sea

The base of the food chain in the open sea is phytoplankton, as there are very few seaweeds (only floating species such as *Sargassum*) and no vascular plants. The primary producers are small; their higher surface area to volume ratio allows them to absorb nutrients more readily. These smaller primary producers are therefore well-adapted to survive in the low nutrient levels of the open ocean.

All higher forms of life in the open sea rely on plankton for food. Nutrients are scarce in the photic zone because of the distance from land, except in upwelling areas (along some coasts and along the equator, discussed in more detail in OCE 1001). The open ocean therefore supports low numbers of phytoplankton compared to coastal seas, and an even fewer zooplankton.

16.6.2. Food Webs in the Open Sea

Most of the phytoplankton in the open ocean is nanoplankton due to the low levels of nutrients, and may include cyanobacteria, small diatoms, dinoflagellates, coccolithophores and silicoflagellates.

Phytoplankton provide food for herbivorous zooplankton, and also leak some of their photosynthetic products into the surrounding environment. This dissolved organic matter (DOM) is made up of small particles that can't be taken up by larger organisms. However bacteria are able to metabolize some of the DOM and return it to an inorganic form. This allows nutrients to be returned more rapidly to the water and be used by phytoplankton again. Moreover, bacteria become a food source for small zooplankton and channels energy into the food web that would otherwise be lost with the DOM. This microbial loop (Figure 16.10) is quite important to increase the efficiency of open ocean ecosystems.

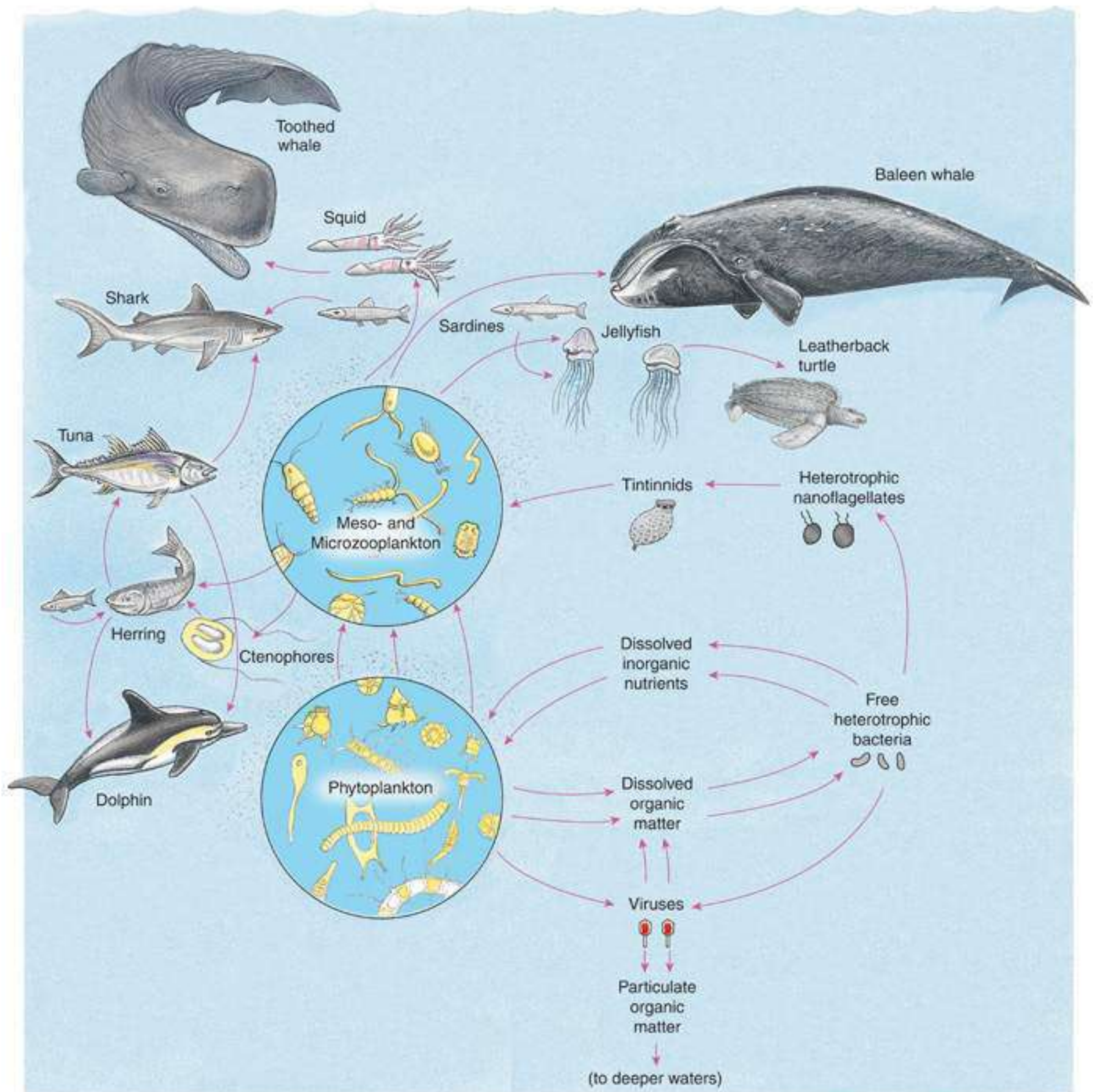


Figure 16.10. Food webs of the open ocean, showing the microbial loop, important in channelling more biomass to higher levels of the food chain.

16.6.3. Efficiency of Open-Ocean Food webs

The nutrient-poor open seas typically have long food chains that may reach 5 or 6 links (Figure 16.11). The food chains are longer than in coastal seas because of the smaller size of the primary producers. Energy and biomass are lost with each trophic levels, so these longer food chains support lower numbers of large animals. Therefore both the low levels of nutrients in the open sea (therefore low primary productivity) and the long food chains contribute to the low biomass of large animals at the top of the food chain.

Isolated areas of upwelling, with higher levels of nutrients and primary production, can sustain a high biomass of large animals but are an exception in the open ocean.

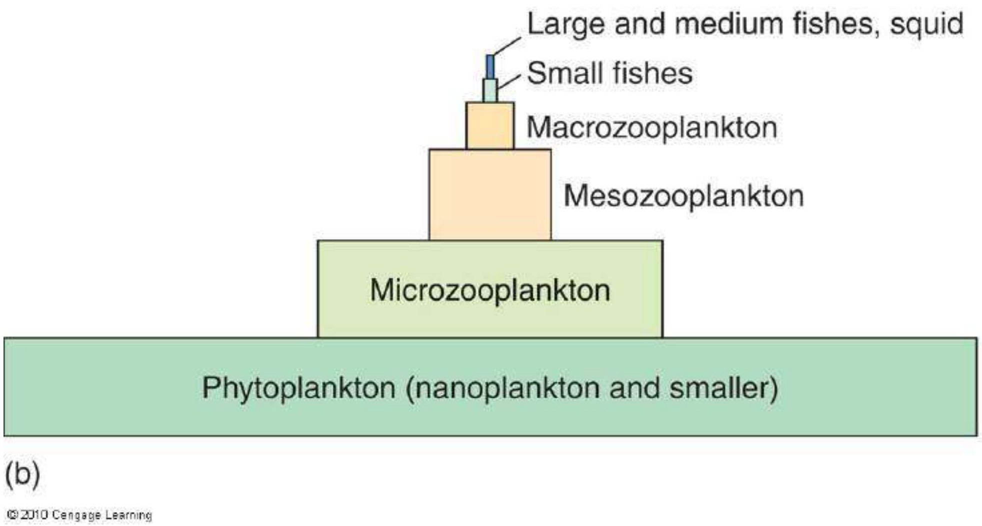


Figure 16.10. Long food chain, typical of the open ocean. Because energy and biomass are lost with each level, these long food chains support a small number of oceanic predators.

16.7. Review Questions: Open Ocean

1. Explain the two main reasons why are there relatively few large animals in the open ocean?

2. How does the size and abundance of the primary producers differ between the open ocean and coastal seas? Why is this?

3. What are the three vertical zones of the open ocean, based on light levels?

4. What is the difference between plankton and nekton?

5. What is meant by the terms holoplankton and meroplankton? And give an example of each?

6. What is marine snow and why is it important?

7. Why do zooplankton migrate vertically to the surface at night?

8. What is the deep scattering layer formed by?

9. Which oceanic fish maintains its body temperature 8-10^{o}C higher than surroundings? And what are the advantages of this?

10. Do tuna have a swim bladder? If not, how do they maintain buoyancy

11. Which organism that makes up part of the nekton is full of internal and external parasites?

12. How do sea snakes in the open ocean shed their skin?

13. Which group of seabird is considered to be part of the nekton?

14. Give an example of an organism that has spines to increase it frictional drag and reduce its sinking rate?

15. Give 3 methods of increasing buoyancy?

16. How do organisms in the open ocean avoid predation?

17. What are two types of camouflage seen in the open ocean?

18. What is the microbial loop and why is it important in the open ocean?

19. Do some organisms eat bacterioplankton?

20. Name three organisms found in the megaplankton

21. What type of seaweed does not attach to the benthos and is found in the open ocean?

22. In which vertical zones of the open ocean is most of the biomass concentrated? Why?

23. What is plankton distribution patchy?

17. Life in the Ocean's Depths (Karleskint Chapter 18 and Nybakken & Bertness Chapter 4)

The deep sea is the most extensive habitat on the planet, comprising 90% of the volume of the oceans. The deep sea is the part of the marine environment below the photic zone. It comprises the disphotic zone (twilight zone) and the aphotic zone (permanently dark). Due to difficulties in sampling at great depths, the deep sea is much less studied than other ocean zones. It is however important to better understand processes and organisms of the deep sea. The deep sea has an immense volume and can play a very important role in global ocean current, carbon sequestration and nutrient cycling. It may contain minerals and other resources of economic importance, and new species are discovered on nearly every deep sea expedition undertaken.

The deep oceans are broadly characterized by three major physical variables: lack of light, intense cold and high ambient pressure. Moreover, there is a scarcity of food. Animals in the deep sea show intriguing adaptations for these conditions (Figure 17.1)

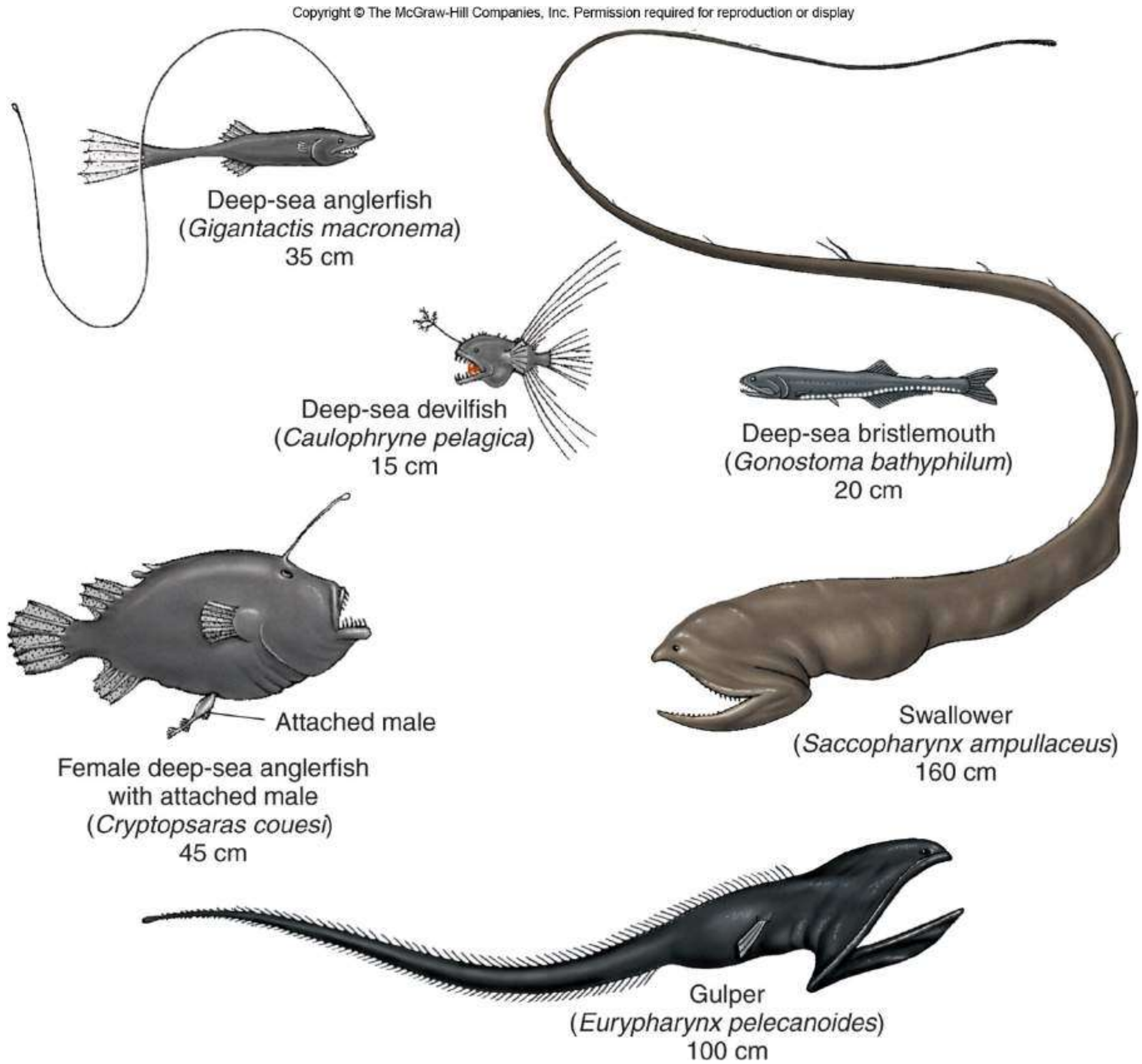


Figure 17.1. Some inhabitants of the deep.

17.1. Survival in the Deep Sea.

Edward Forbes proposed in the mid-19th century that no life could survive below 550m. This was an extrapolation of the observation that in the shallow waters he sampled, plants and animals became progressively less abundant as depth. We know today that there is life at all depths in the ocean, but life if the deep sea requires adaptations for very particular conditions. Even in the clearest oceans sunlight cannot penetrate sufficiently below 200m to support photosynthesis. By about 1000m deep, all sunlight has been absorbed. Added to this, heat energy is quickly absorbed in the surface waters causing the deep ocean to be cold throughout the year. The ambient pressure of these waters is extremely high; the surface pressure is 1 atmosphere (atm) and with every10 m descent the pressure increases by 1 atm. Thus the pressure exerted on an organism at 1,000m will be 101 atm (510 kg/cm^2) or at 10,000 m 1,001 atm (5,100 kg/cm^2). In addition there are other problems to life in the deep, such as finding food or mates in total darkness. The conditions in the oceanic depths may be some of the most extremes experienced by any organism, however, they are stable and have not changed for millions of years. Therefore, there is a high diversity in deep-sea communities as they have had a long period of time for speciation events to occur.

17.1.1. Adaptation to Pressure

Most of the deep sea is under pressures of 200-600 atm, and pressure can be up to 1,000 atm (at 10,000m). Several thousand species, including echinoderms, annelids and mollusks, tolerate the high pressures of the deep sea. These organisms endure high pressures by maintaining a fluid pressure within their tissues that correspond exactly to that in the ambient water. In this way the organism's tissue fluid pushes against the surrounding pressure with an equal but opposite force, preventing the organism from being crushed. Proteins and membranes affected by high pressure and must be modified to work. Another effect of depth is that as pressure increases and temperature decreases, the solubility of $CaCO_3$ increases, so at depths it is harder for organisms to create shells, and those that can tend to have thin shells.

17.1.2. Adaptations to Cold

At any depth in the deep sea the temperature remains constant, there are no seasonal or annual variations. Below 3,000-4,000m the temperature is 1-4°C. However, there are a few deep sea environments with higher temperatures, e.g. the Mediterranean has a bottom temperature of ~13°C and the Red Sea ~20°C, which is due to their separation from main ocean basins and the sinking of warm saline water from surface.

The cold water temperatures of the deep ocean require organisms to adapt to this extreme. Nearly all animals inhabiting the deep have body temperatures closely resembling these cold surrounding waters. As a result of these low body temperatures, metabolism in the deep tends to be very slow; organisms move slowly, grow slowly and reproduce less frequently and later in life. An advantage of this slow metabolism is that these organisms require less food, live longer and may grow larger than their shallow water counterparts. Another advantage to the intense cold at these depths is the increase in density of the surrounding water. Therefore organisms do not need to expend large amounts of energy to prevent sinking and many do not have a swim bladder, since their density is very similar to the surrounding water.

17.2. Life in the Dark

Of the three major physical factors that affect animals living in the deep oceans, the lack of light has had the greatest evolutionary impact.

17.2.1. Color in Deep-sea Organisms

In the region from approximately 200 – 1,000 m, known as the disphotic, or twilight, zone there is still enough light for color to be important. Countershading can be a useful camouflage strategy, and several species of fishes in this zone have light-producing organs called photophores on their ventral surface to further lighten it and help in this camouflage. Other fishes are silvery grey or deep black in color, thus making them difficult to see in low light conditions. Invertebrates are often purple, bright red, or orange, which appear as shades of black and grey at depths due to absorption rates of different wavelengths of light. One reason for red colorations might be because most bioluminescent light is blue, therefore red pigments protect organisms from the revealing bioluminescent flashes from predators. In the aphotic zone (abyssal and bathyal zone) at depths of 1,000-6,000m, where there is no light, coloration becomes less important. Here the organisms tend to lack pigments and are often colorless or a dirty white, particularly benthic organisms.

17.2.2. Roles of Bioluminescence

Even though sunlight does not penetrate to the depths of the oceans, some organisms are able to produce their own light in the form of bioluminescence (Figure 17.2). This characteristic is particularly common in organisms between 300 – 2,400 m deep. In fact, 90% of mesopelagic organisms have ability to produce light. Bioluminescence can be produced either though luminescent organs (photophores) or some animals harbor symbiotic bioluminescent bacteria. This is an example of mutualistic symbiosis, as the host animal benefits through light production, while the symbiotic bacteria receives a secure place to live and a constant food supply. Some organisms are able to regulate the bioluminescence by altering the amount of oxygenated blood flow to the regions where the bacteria reside. Bioluminescence occurs when a protein, called luciferin, is combined with oxygen in the presence of an enzyme called luciferase and adenosine triphosphate (ATP). During these reactions the energy from ATP is converted into light energy and is almost 100% efficient, with very little heat loss. Most bioluminescence in marine organisms is blue and green, although red and yellow have also been reported.

The location and role of bioluminescence in the deep sea varies between organisms. Luminescent organs can be located in rows along their sides or ventral surface, on depressions or growths from their heads, on tentacles or even around organism's eyes.

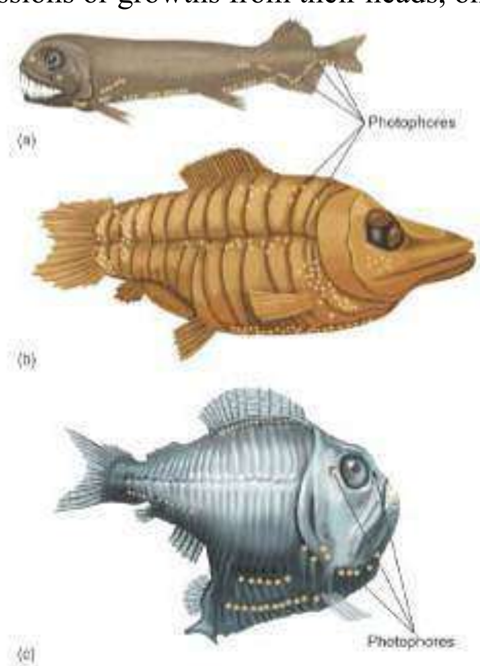


Figure 17.2. Loosejaw (a), spookfish (b) and hatchetfish (c) all possess photophores.

Camouflage – In the twilight zone (150-450m), bioluminescence is primarily used as camouflage against the light surface. The presence of luminescent organs on the ventral surface of an organism may aid countershading in camouflaging the animal. If the intensity of illumination matches the intensity of sunlight then the animal will not appear as a shadow or silhouette. Hatchet fish (*Argyropelecus* spp.) and mid-water squid A*albraliopsis* spp.) use bioluminescence that way.

Mating & Species Recognition – Bioluminescence patterns may play an important role in identifying other animals of the same species and what sex they are. For example, male lanternfish (*Myctophum* spp.) have bright photophores on top of their tails, whereas females of the same species have weak lights on the underside of their tails. Although this might increase the dangers of predation to these organisms, the evolutionary benefit of finding a mate and producing offspring outweighs this disadvantage. Once a mate is found, a series of light flashes may signal readiness to mate.

Attracting Prey – Certain species may utilize bioluminescence to attract prey. The anglerfish (*Melanocetus johnsonii*) attracts prey using bioluminescent lures extending like a fishing rod from its head. Small fishes whose normal prey are luminescent are attracted to these lures, and may become a meal for the waiting anglerfish. Some species of stomiatoid fish have photophores around their eyes to illuminate whatever prey they look at. They have been known to fix krill in their beam of light and rapidly devour them.

Defense – Bioluminescence is also utilized as a mechanism for defense. Some deep water squid species release a cloud of bioluminescent fluid when they are disturbed. The opossum shrimp actually releases a chemical which explodes into clouds of stars. These sudden bursts of light may frighten and confuse potential predators, allowing the animal to escape. Another example is the hatchetfish which has highly reflective side surfaces of the white pigment guanine that functions as a mirror. When a predator approaches it sees light reflected that is of the same color and intensity as the background

17.2.3. Seeing in the Dark

The British biologist N.B. Marshall made extensive observations on the brains and eyes of deep-sea fishes to answer the question of whether these animals are able to perceive any light in the disphotic zone. Studying fishes living as deep as 1,000 m, he concluded that although there is virtually no light at these depths certain species may actually be able to see their food, mates and predators with what little light is available. Fish in this region have large eyes, to maximize their light collecting abilities in low light conditions. It has been found that the presence of large eyes is often correlated with the presence of light organs. Many organisms of the mesopelagic zone will also migrate vertically to the surface waters at night, and therefore benefit from having large eyes. In the permanent darkness of the aphotic zone eyes become largely unnecessary. Below 2,000m fish eyes become smaller and less functional, or they lack them completely, instead relying on chemical and tactile stimuli to find their prey and mates, and to avoid predation.

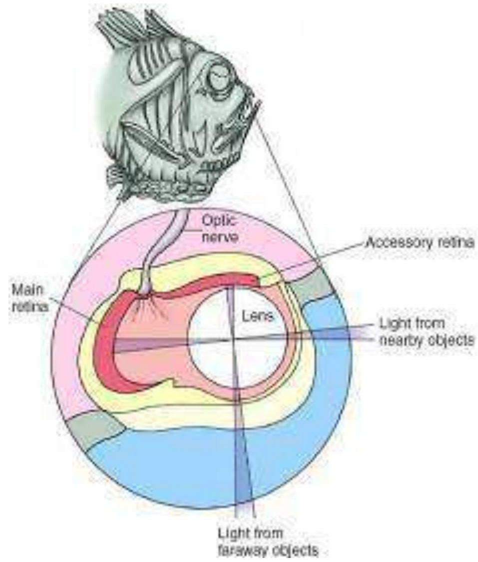


Figure 17.3. Tubular eyes typical of fish in the disphotic zone.

Several families of deep sea fish have tubular eyes, these give the fish a bizarre appearance as they consist of a short black or silver cylinder topped with a spherical, transparent end. These eyes may also contain two retinas, one to focus on distant objects and the other to see closer things (Figure 17.3). This gives the fish wide binocular vision, enabling them to see better in dim light and have better depth perception than possible with the spheroid eye of other vertebrates. The anglerfish has well developed eyes during its early life, which is spent in well-lit shallower waters, but as it grows and descends into the depths (1,800m) its eyes stop growing and may begin to degenerate. Other organisms in the deep may have barrel-shaped eyes which are stalked or unequal in size, e.g. deep sea squid. It is thought that these eyes probably adapt to the amount of light available in their habitat.

17.2.4. Finding Mates in the Dark

Due to the low abundance of organisms in the deep it may often be difficult for organisms to find receptive mates to reproduce with. Hermaphroditism is common in deep-sea fish and increases the likelihood of finding a suitable mate in this habitat where population densities are low. Some species of deep water anglerfish have found a unique and extreme solution to the difficulty of finding a mate. When a male encounters a female of the same species, he bites her and remaining attached, sometimes for the rest of his life. The skin around the male's mouth and jaw fuses with the female with only a small opening on either side of the mouth remains for gas exchange. The eyes and most of the male's internal organ degenerate and his circulatory system becomes connected to the female's, effectively becoming a life-long sperm-producing appendage.

17.2.5. Finding Food in the Dark

In the depths of the ocean, food is scarce. There are no photosynthetic organisms to produce food, therefore much of the food web depends on detritus and organic matter which drift down from surface water supporting benthic detritivores and scavengers. The amount of food in the deep sea is correlated with the amount of primary productivity in the surface waters above, or the proximity to a secondary source, such as organic debris from terrestrial habitats. This organic matter is continuously consumed as it sinks down from shallow water, and therefore the amount of food that reaches the deep sea floor decreases with increasing depth, as does the quality. A portion of the sinking particles are not directly suitable as food, and must first be acted on by bacteria (e.g. chitin, wood and cellulose). This leads to a high abundance of bacteria in deep benthic sediments and this allows a greater number of larger organisms to survive. Other potential sources of food are Dissolved Organic Matter (DOM) and marine snow.

A few processes help increase the flow of food from shallow to deep water. Although unpredictable, the large carcasses of dead mammals and fish that sink quickly before being consumed in shallow water are quickly detected by deep-sea organisms and bring consumers from great distances. Some organisms, including small fish and invertebrates, swim to shallow waters at night to forage. These daily vertical migrations bring more nutrients and organic materials to the depths.

Even at the best of times food is scarce in the deep sea and many animals have evolved bizarre adaptations to survive. Many deep-sea fish have huge teeth and large mouths with expandable stomachs, and only a small tail for slow swimming. As food is rare at these depths, this adaptation allows an organism to consume a large proportion of species which it encounters. For example gulper eels (Figure 17.4), which are common below 1,500 m, have jaws that are hinged like a trap-door and stomachs that can expand to several times their normal size to accommodate prey that is larger than the eel itself.

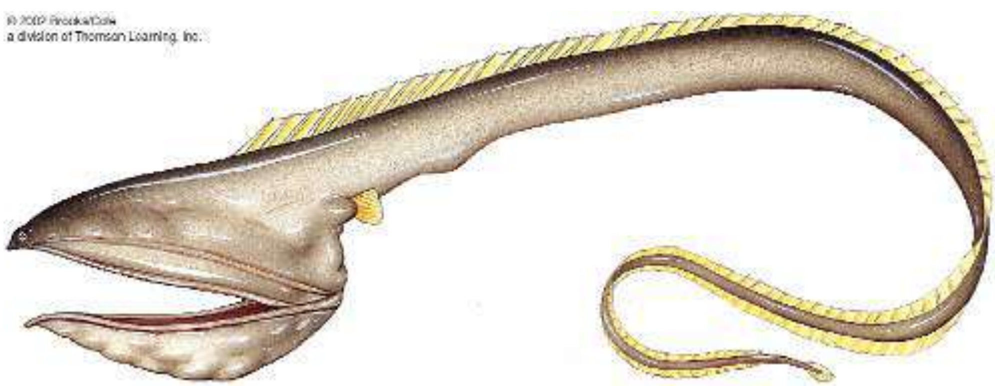


Figure 17.4. Gulper eel, common below 1,500 m.

Stomiatoids are also able to ingest prey larger than themselves, which gives them the advantage of being able to take advantage of rare food items. Most species are 15 –18cm long, have large heads with curved, fang-like teeth and elongated bodies that taper into a small tail. They also have a fleshy projection called a barbel that dangles below the chin. The barbel can act as a lure, is used to probe the sediment, or is used in species recognition.

The deep-sea anglerfish uses a highly modified spine of its dorsal fin as a luminescent lure. When the prey is close enough it suddenly drops lower jaw creating a suction which draws the prey in its mouth. It then impales the prey on its long curved teeth before it swallows it whole. Many carnivorous fish have black linings to their digestive tracts so bioluminescence from prey will not shine out and attract their predators.

17.3. Giants of the Deep

In general most deep-sea organisms are smaller compared to their shallower counterparts, however giants of the deep have been found among some invertebrate groups – abyssal gigantism. A combination of low temperatures and scarce food reduces growth rate but increases longevity and the time it takes for organisms to reach sexual maturity, so they have more time to achieve such gigantic sizes. Natural selection may also favor large size, since a large size, long life and delayed sexual maturity leads to production of larger eggs and subsequently larger young, which can then feed on a wider range of food sizes. In addition, large organisms are more mobile so can cover larger areas in search for food and mates, and a longer period of sexual maturity gives more time to find a mate. Sea urchins that live on the ocean floor have bodies up to 30 cm in diameter, compared to just a few centimeters in their shallow-water relatives. Biologists have also found sea pens over 2m high and shrimps 20 – 30cm long.

Perhaps the most spectacular of the deep-sea organisms is the giant squid, which can reach lengths of up to 16 m long including their tentacles. Their arms are as thick as a human thigh and covered with thousands of suckers, while each of their two tentacles can be 12 m in length and have 100 or more suckers with serrated edges. Although little is known about the natural history of giant squids, it is thought that they spend most of their lives below 180 m. They use jet propulsion for movement although this may be weak, and it seems probable that they cannot capture active prey. Much of what is known of giant squids is from their remains found in the stomach of sperm whales which are their major predators, as well as scars, from serrated suckers, found on the whale's bodies.

17.4 Relicts from the Deep

Environmental conditions in the deep sea are believed to have remained very stable for more than 100 million years. As such it is thought that the deep sea contains organisms that have undergone little evolutionary change from their early ancestors. Several organisms have been discovered which appear to be extremely similar to specimens found only in fossil records, becoming known as living fossils.

17.4.1 *Spirula*

This cephalopod mollusk named for its spiral shell was thought to be extinct until the Challenger expedition in 1872-1876 caught living specimens. They average 7.5 centimeters in length and have barrel shaped bodies with short thick arms. Its internal shell is divided into gas-filled chambers which aid in buoyancy (Figure 17.5).

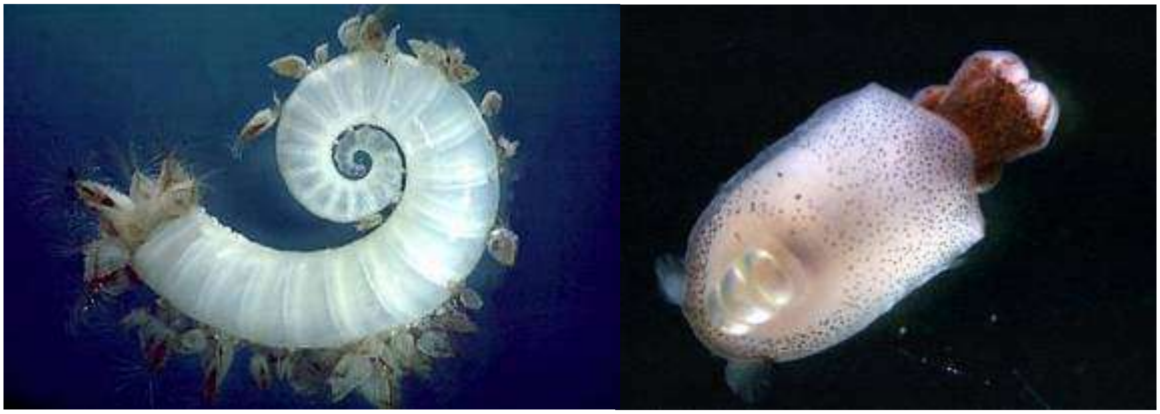


Figure 17.5. Spirula, a deep sea cephalopod.

17.4.2 Vampire Squid

Discovered alive in 1903, the vampire squid had only previously been found in fossils, dating back to 100 million years ago. Receiving its name from to the dark color and the webbing between its arms, the vampire squid lives between 900 – 2,700 m deep in tropical and temperate regions. It is small, reaching a maximum size of 13 cm. It has two long arms which are coiled into pockets in its web when not used, it is thought that these play a role in sensory function. The vampire squid is a phylogenetic relict and possesses features of both octopods (cephalopods with 10 arms, like octopus) and decapods (cephalopods with 10 arms, like squid and cuttlefish). In addition, it has some adaptations for the deep-sea, including the loss of the ink sac and most active chromatophores, development of photophores and the gelatinous consistency of the tissues. It is thought to represent the order Vampyromorpha, being somewhat of an intermediate between an octopus and a squid.

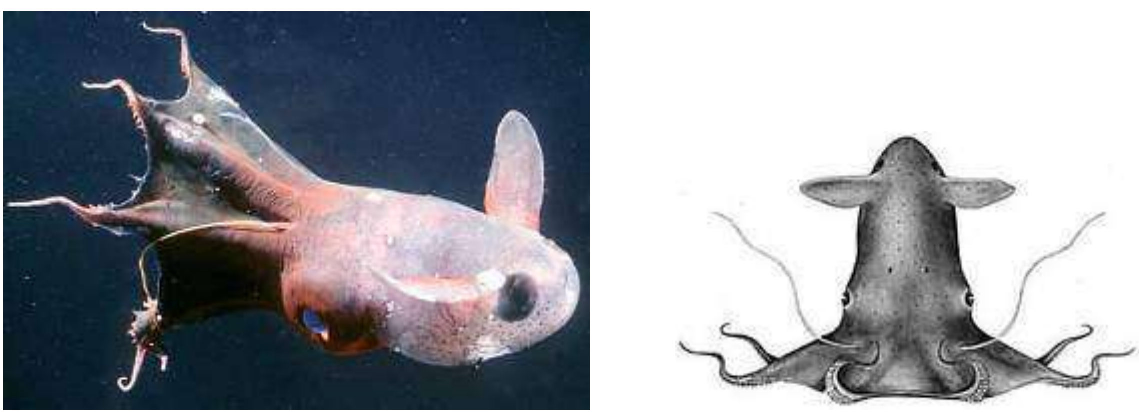


Figure 17.6. Vampire squid.

17.4.3. Coelocanth

Thought extinct for 70 million years, the coelacanth (Figure 17.7) was first discovered alive off South Africa in 1938. This fish of approximately 2m in length, has large thick scales and fleshy bundles between its body and fins and is thought to be an ancestral connection between fish and tetrapod vertebrates.

Figure 17.7. A coelacanth.

17.5. Life on the Sea Floor

The deep sea floor has been described as a barren landscape with few living organisms. Life on the sea floor is challenging, and like pelagic animals of the deep, benthic fauna has evolved to this unique habitat of extreme pressure, cold temperatures and scarce food.

17.5.1. Benthic Organisms

Sources of food for benthic organisms
In the depths of the oceans floor there is no light to support photosynthesis and the extreme cold slows the growth of bacteria and other microorganisms. Generally speaking the minerals and organic matter that sustain benthic organisms are derived from detritus such as feces and decaying tissue from the surface that rains down onto the substrate. What is not intercepted by pelagic animals accumulates and is concentrated on the sea floor. Near the margins of the continental shelves, turbidity currents may deliver organic matter from the relatively thick sediment of the continental shelves to the abyssal plains and trenches. Occasionally, food may arrive on the bottom in the form of carcasses of larger pelagic animals, such as whales, which sink to the bottom faster and therefore with little interference from pelagic scavengers.

Benthic Food Chains
If sufficient nutrients are present in benthic communities, bacteria can grow yet growth is often slow due to extreme pressures and low temperature. Meiofauna, organisms that live in the spaces between sediment particles, such as foraminiferans, nematodes and other small worms, feed on the bacteria, the limited organic matter and even on each other. Large worms and bivalves living within the sediments (infauna) feed on the meiofauna, but the majority of animals (80% by number) are large deposit feeders such as sea cucumbers, brittle stars and urchins that feed on the surrounding detritus. In areas where

coarser sediment such as sand dominates the sediment, suspension feeders such as giant crinoids and sea pens feed on organic matter suspended in the water column. However, less than 7% of species of the deep sea benthos are suspension feeders, because of the slow water movement and scarcity of food, they would expend more energy creating a current than they would receive in the food.

Predators in these communities are primarily fish, squid and sea stars. Herbivores are present in low numbers, feeding on plant remains, such as wood. Further away from the margins of continental shelves the food availability diminishes even more. There may still be enough organic matter to sustain bacteria, meiofauna and infauna, although large deposit feeders are generally absent. In mid-ocean trenches, the deepest recesses of the ocean, food may be so scarce that even tiny organisms are rarely found.

Diversity of Benthic Organisms of the Deep

Although the density of organisms in the deep benthos is only a fraction of that found in the shallow seas, there is in fact a surprisingly high degree of diversity. There are alternative hypotheses to explain this high diversity. It is proposed that because highly stable environmental conditions have persisted over long periods of time it has allowed species to evolve that are highly specialized for a particular microhabitat or food source, therefore fewer organisms go extinct creating an accumulation of viable species (Stability-Time hypothesis). Another alternative is simply that diversity is highest in the deep sea because it covers the greatest area. Finally, organisms do not disperse as readily in the depths as they do in the shallows, which contributes to isolation and aids in speciation. None of these hypotheses can individually explain all the diversity patterns seen in the deep sea, and several of these hypotheses are likely acting simultaneously.

17.5.2. Hydrothermal Vent Communities

In 1977 oceanographers discovered a thriving community along deep-sea volcanic ridges near the Galápagos. Mineral-rich water, heated by the earth's core sustains some of the most productive self-contained communities in the oceans and demonstrates that ecosystems can exist without solar energy. The primary producers at hydrothermal vents are chemosynthetic organisms that extract energy from chemicals dissolved in the water. Since 1977 other hydrothermal vent communities have been found in the Gulf of Mexico, Gulf of California, mid-Atlantic Ridge system, North Fiji and many other sites. Not all deep sea chemosynthetic communities are associated with hydrothermal vents; for instance communities associated with cold-water seeps, which utilize methane as a source of energy, have been discovered off the coast of Oregon and the west coast of Florida.

Formation of Hydrothermal Vents

Hydrothermal vents form at spreading centers (mid-ocean ridges) where cold seawater seeps down through cracks and fissures in the ocean floor. The water comes into contact with hot basaltic magma, where it exchanges minerals, picking up sulphur, iron, copper and zinc. The superheated water, rich in hydrogen sulphide, returns to the ocean through chimneys formed by mineral precipitation (Figure 17.8). These chimneys are divided into two groups: white smokers, which emit a stream of milky fluid rich in zinc sulphides at temperatures less than 300°C, and black smokers which release water rich in copper sulphides at temperatures between 300 – 400°C.

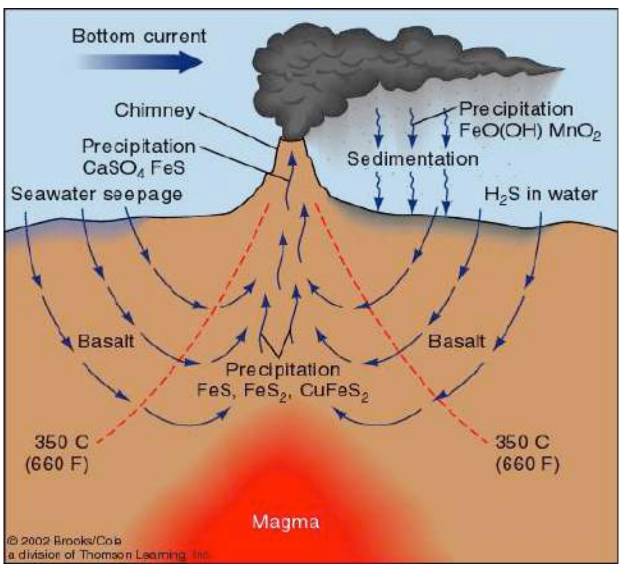


Figure 17.8. Circulation of water and minerals at a hydrothermal vent.

Vent Communities

Surrounding hydrothermal vents are rich communities, supporting a biomass of up to 3,000 times that of the surrounding area, including large clams, mussels, anemones and barnacles amongst other organisms. Clams of the genus *Calyptogena* exhibit the fastest known growth of any deep-sea organism, approximately 4cm/yr. Vestimentiferan worms, of the phylum Annelida (*Riftia* spp.), can grow to as long as 3 m and be several centimeters in diameter. The primary producers in these communities are chemosynthetic bacteria which oxidize hydrogen sulphide (H_2S) to provide the energy for producing organic compounds from carbon dioxide. Hydrogen sulphide is toxic to most life forms, however vent organisms have special blood protein that bind to H_2S preventing it from interfering with O_2 uptake and respiration. Consumers such as clams, mussels and worms filter bacteria from the water or graze on the bacteria on rocks. Many species also have symbiotic chemosynthetic bacteria associated with their tissues. For example, *Riftia* spp. worms have no mouth or digestive system as adults, obtaining all their nutrition from chemosynthetic bacteria living within the tissues of their body cavity. Mussels (*Bathymodiolus* spp.) and clams (*Calyptogena* spp.) also have lots of bacteria in their gills. Nearly all vent organisms are endemic, meaning they are found in no other environments.

The Rise and Fall of Vent Communities

It is estimated that vent communities are rather short-lived and may only proliferate for approximately 20 years or so. Shortly after a new vent forms, colonization is rapid and organisms thrive until geological changes deactivate the vent and it becomes dormant. For the species of vents to continue, colonization of other vents needs to occur. It is thought that larvae of vent species may stay suspended in the water column for several months, travelling hundreds of kilometers in deep water currents before finding another suitable habitat. Large carcasses, such as that of whales, may also be used as an intermediate habitat where these species can grow and obtain nutrients before reproducing asexually and colonizing new vents.

17.6. Review Questions: Life in the Ocean's Depths

1. What are the physical characteristics of the deep sea?

2. How much does the pressure increase with every 10 m down?

3. Are the conditions more or less stable in the deep sea, compared to shallower ecosystems?

4. Describe adaptations of deep sea organisms to deal with the high pressure.

5. Describe adaptations of deep sea organisms to deal with the cold temperature.

6. Describe an advantage of the cold temperature in the deep sea.

7. What is the disphotic zone?

8. What type of camouflage is seen in the disphotic zone?

9. What is the name of light-producing organs?

10. What are 4 roles of bioluminescence?

11. What type of eyes would you expect on a fish that live at 800m deep? And on one that lives at 3000m deep?

12. Describe the mating strategy of the male deep sea angler fish?

13. Why do deep sea organisms often have large mouths and expandable stomachs?

14. Describe typical deep benthic food chains.

15. What kind of benthic organisms are most abundant in the deep sea?

16. Why is diversity high in the deep sea?

17. Where are hydrothermal vents mostly found?

18. What are the primary producers in vent communities?

19. How do organisms colonize new vents once one hydrothermal vent dies?

20. What is the ecological role of whale falls in the deep ocean?

21. Why are there hydrothermal vents of various color?

22. What colors are most often seen in deep sea animals? Why?

18. Marine birds and mammals in polar seas (Sumich & Morrissey Chapter 12, Nybakken & Bertness Chapter 5)

18.1. General Characteristics of Polar Seas

Polar regions exhibit a drastic change in photoperiod throughout the year. They have long winters without sunlight that prevent photosynthesis, and a period of constant sunlight during the summer. It is cold, and the sea surface temperature is around 0^{o}C, even in the summer. Polar seas are therefore dominated by sea ice. Certain areas have a permanent ice cover called fast ice. The larger area which freezes in the winter is called the pack ice. As ice is less dense than water, it floats at the surface and insulates seawater from the cold. For that reason, the ice never becomes more than a few meters thick.

The presence of sea ice has important consequences for the ecology of polar seas. First, it provides a stable and nearly predator-free platform for organisms to give birth and raise their young. Moreover, sea ice increases productivity, as many species of primary producers (e.g. diatoms) live attached to the ice on its underside where it is not too thick, or live in the water in close association with the ice. Diatoms can reach such high densities that their photosynthetic pigments color the underside of ice floes brown. Finally, sea ice greatly reduces the abundance of intertidal organisms in the winter through ice scouring of rocky shores.

18.2. Physical comparison of the Arctic and the Antarctic

The Arctic is an ocean surrounded by continents. It has only two outlets: the Bering Strait and the Fram Strait, both of which are relatively shallow (70 and 400 m respectively). The entire central core is covered by permanent fast ice and every winter the ice area is increased with pack ice, some of which is the result of multiple years of freezing. The pack ice is therefore fairly thick (3-4 m). Several large rivers from the surrounding continents empty into the Arctic, discharging a significant sediment load. This large discharge of freshwater also creates a halocline and a pycnocline. Because of this pycnocline and the surrounding continents there is little to no upwelling in the Arctic which, combined with shading from the thick ice, results in a lower productivity in the Arctic (~25 g/C/m^2/yr) compared to the Antarctic.

The Antarctic, on the other hand, is a frozen continent surrounded by an ocean which is covered by pack ice seasonally. This pack ice is typically no older than a year and is relatively thin (1-2 m). The continental shelf is narrow and falls off rapidly to deep water. The Antarctic is open to the Atlantic, Pacific and Indian oceans, and the circulation pattern in the area results in upwelling around Antarctica. There are few rivers and therefore no halocline or pycnocline is created and this, along with the substantial upwelling, results in high levels of productivity in the summer (~100 g/C/m^2/yr).

Shallow subtidal areas are generally devoid of permanent communities, down to the level to which ice extends. This is due to the mechanical action of ice grinding or by freezing the animals. Another problem for benthic subtidal communities is anchor ice. Ice platelets begin to form on bottom (down to 30m) around nuclei. As the platelets increase in size they may surround invertebrate living on bottom. As ice is less dense, it rises up to the thick sea ice above, carrying with it the trapped invertebrate, and as a result they are permanently lost from the community.

As may be expected, the differences in physical characteristics between the Arctic and the Antarctic lead to differences in the ecology of organisms that live there.

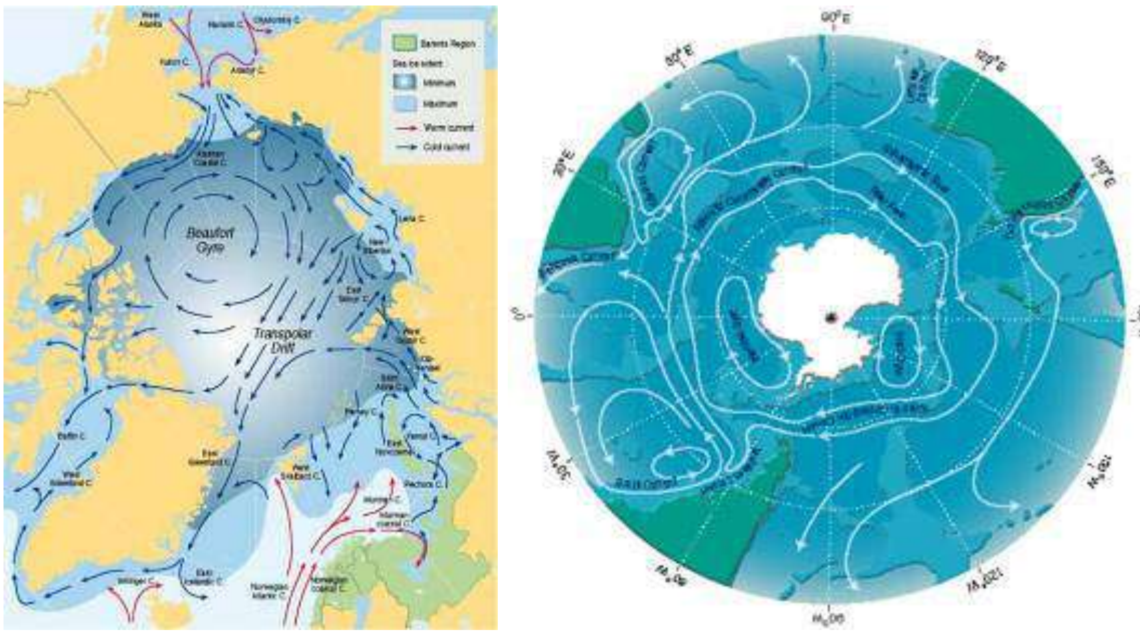


Figure 18.1. Maps of the Artic (left) and the Antarctic (right).

18.3. Benthic communities

In the Arctic, the benthic fauna is impoverished and consists mainly of organisms derived from Atlantic Ocean. Benthic communities tend to be dominated by one or only a few species. Due to the extensive areas of sediments, the benthic fauna is mainly infauna. In contrast, in the Antarctic the diversity of benthic organisms is far greater and there is a high degree of endemism. This could be due to a long evolutionary history and isolation, and the presence of both hard and soft substrates. Antarctic waters support a benthic biomass of twice that of the Arctic, which is related to the nutrient-rich water and high offshore productivity. In contrast to the Arctic, several species dominate benthic communities and organisms tend to be epifauna.

These differences in benthic communities between the Arctic and Antarctic could also partially be due to different disturbance regimes. In the Arctic there are more disturbances, such as increased scour from fast ice, large variations in salinity due to river runoff in the summer and sinking water with a high salinity during winter freezing. There are also more biotic disturbances from the presence of bottom-feeding crabs, fish and marine mammals, absent from the Antarctic.

18.4. Marine Homeotherms in Polar Seas

This chapter focuses on marine homeotherms, those organisms that maintain a constant internal temperature. Maintaining a high core body temperature in a cold environment is energetically costly, but there are two main benefits to living in polar seas: the availability of abundant food in the summer, and near predator-free platforms for reproduction. Marine homeotherms have several adaptations for this extreme environment. Most have large bodies with a low surface area to volume ratio and can store lipids for extended food-poor seasons. Some fast for extended periods during the winter, while others undertake long migrations to polar seas while food is abundant in the summer and spend the rest of the year at lower latitudes (Figure 18.2). Those that do long seasonal migrations are streamlined and have a low energy cost of transportation. Finally, most polar homeotherms have an insulating layer of blubber.

18.4.1. Marine Mammals in Polar Seas

Young cetaceans can swim at birth, whereas the young of pinnipeds and polar bears cannot. Newborn arctic mammals tend to be very large (blue whales weigh 3 tons at birth!), but they have a higher surface area to volume ratio than their parents and have less blubber. Newborns therefore lose heat quicker than adults. To solve this problem, pinnipeds give birth on land or on ice, and larger cetaceans migrate to give birth in tropical seas.

Newborns have an astonishingly high growth rate. Blue whales have a growth rate of 100 kg/day in their first few months of nursing. Hooded seal pups complete their lactation in just 4 days. These high growth rates can be achieved because the milk of polar mammals is very high in fat: seal milk is up to 60% fat, compared to 3-5% for cows. These high growth rates are important for the survival of the young, but the energy demands on the female are very high. Because of this, polar mammals typically have long gestation periods, which can be over a year; they do not reproduce more than once a year, and except for polar bears only have one offspring at a time.

Pinnipeds

Polar pinnipeds give birth in the spring, which allows their young to grow quickly in milder temperatures before the winter arrives. They give birth on fast or pack ice, which is a very large area compared to temperate pinnipeds that are concentrated over small beaches. Because breeding females are scattered over this large area, males cannot easily gain control of many females and polar pinnipeds are generally monogamous. Polar seals also tend to be monomorphic, since monogamous males do not have to compete as much for access to females.

Cetaceans

Baleen (Mysticete) whales are the largest animals on earth. They are filter feeders and use their baleen plates to filter plankton and small fish from the water, or benthic invertebrates from the sediments (e.g. grey whales) (Figure 18.3). Rorquals, which have throat grooves, can fill their mouth with an amount of water equivalent to 2/3 of their body weight.

Baleen whales undertake long migrations: they feed in the polar seas in the summer and mate and calve in the winter in the tropics whilst fasting. Many mysticete whales exhibit reverse sexual dimorphism (females are bigger) associated with the large energy cost of reproduction. Gray, bowhead and right whales are thought to have sperm competition, where copulating males compete with previous copulators by attempting to displace or dilute their sperm in the female's reproductive tract.

Baleen whales create loud, low-frequency pulses that may be used to communicate over large distances. These sounds may also be used for echolocation; the wavelength they use doesn't allow for good resolution but could be used to discern large oceanography features or swarms of krill

Toothed whales (Odontocetes) have representatives that are permanent (e.g. belugas, narwhals), or transient (sperm whales, killer whales) inhabitants of polar seas. Most feed on fish, though some populations of killer whales regularly feed on homeothermic prey (e.g. penguins and seals). Toothed whales often have well-developed social systems, and use acoustics for extensive communication and echolocation.

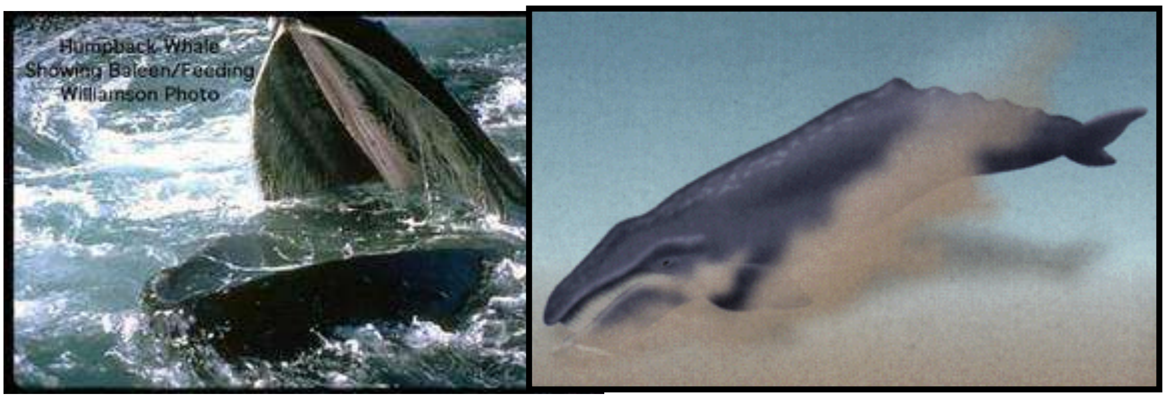


Figure 18.2. Mysticete whales using baleens to feed. Blue whale filtering plankton from the water (left) and grey whale filtering benthic invertebrates from the sediment (right).

18.4.2. Seabirds in Polar Seas

Seabirds obtain their food from the sea, and excrete excess salt through nasal glands. Most polar birds undertake long migrations to nest at high latitude during the summer when food is abundant and go to lower latitudes in the winter when it gets very cold in polar regions. More seabirds nest in polar regions in the southern hemisphere than in the northern hemisphere.

Almost all polar seabirds must forage while raising chicks, often far from their nesting areas. They have several adaptations for this. They are good flyers with long wings, which allows them to conserve energy while flying long distances. Their core body temperature is $2-3^{o}C$ lower than most other birds, which also helps conserve energy. Many have sub-dermal fats and oils in their stomachs, which allow them to last a long time without food. Their eggs are less sensitive to chilling, and many have a good olfaction which allows them to forage at night when marine organisms are more abundant near the surface.

18.5. The Arctic

The Arctic is characterized by short burst of primary production in the summer. Arctic phytoplankton tends to be larger than temperate phytoplankton, and this creates short food chains with seasonal aggregations of large mammals and birds. There are very few euphausiids in the Arctic; copepods are a dominant herbivorous zooplankton.

18.5.1. Arctic Pinnipeds

As with most polar pinnipeds, Arctic pinnipeds are mostly monogamous and monomorphic. The most abundant pinniped in the Arctic is the Ringed Seal, which gives birth in snow caves on fast ice. Harp seals are the second most abundant seal in the Arctic, even though their population was greatly reduced because of hunting for the white fur of their pups. The hooded seal is the only polygynous Arctic seal; males mate with several females. They show sexual dimorphism, where males have a “hood” in their nasal cavity that can be inflated for sexual displays. Hooded seals have the shortest nursing period of any pinnipeds, and the pups gain 7 kg/day over their 4 days of nursing. Right after weaning, the female mates again and returns to feed. Walruses are also polygynous and dimorphic, with males being twice the size of females. The tusks of walruses are present in both sexes and are used for defense and to help the individual pull itself up on ice floes.

18.5.2. Polar Bears

Though polar bears are not strictly marine, their diet is comprised mainly of marine organisms and they are very good swimmers. Their paws are large, which improves their swimming and distributes their weight better on ice. Polar bears are found on ice in the Arctic (there are none in the Antarctic) where their white fur gives them good camouflage. Polar bears prey on seals, walruses, belugas and birds, securing most of their year’s energy from ringed seal pups. Polar bears endure long seasonal fasts when the food supplies decrease or when reproductive activities prevent foraging. Females reproduce only once every 3-4 years, but usually give birth to two cubs. Male polar bears compete aggressively for access to females. Polar bears are induced ovulators, and females must repeatedly mate to trigger ovulation. After fertilization, implantation is delayed until the fall.

18.5.3. Baleen Whales

Baleen whales that visit the Arctic include rorquals (blue, fin, humpback and minke whales) as well as grey whales, which all undertake migrations between the poles and the tropics. They are found in the Arctic only in the summer when the food is most abundant. The bowhead whale, on the other hand, is a permanent resident of the Arctic and adjoining seas, seldom occurring below 45 degrees latitude.

18.5.4. Toothed Whales

Belugas and narwhals are permanent residents of the Arctic (Figure 18.3). Belugas are medium sized, white whales with small flippers and very thick blubber. They have no dorsal fin but have a dorsal ridge that can be used to break through thin ice to breathe.

Narwhals have a long spiral tusk, which is formed from a modified upper tooth and was the basis of the legend of the unicorn. The tusk is longer in males, and they are sometimes seen "tusking"; rubbing tusks as a means of communication and identification. Narwhals are found in remote polar areas covered with heavy pack ice.

Killer whales as a species have a worldwide distribution but individual social groups (pods) occupy a narrower geographical range and pods are regularly seen in the Arctic. Killer whales feed on a wide variety of prey including fish, marine mammals, birds, cephalopods and turtles. They are the only cetacean known to eat other marine mammals consistently. Killer whales are apex predators, they are not preyed upon in the wild as adults under normal circumstances, and therefore play an important role in maintaining and determining the health of ecosystems. There are interesting differences in diet between pods, with some being solely piscivorous while other pods eat mammals. Killer whales use echolocation and vocalizations extensively when feeding on fish, but less frequently when feeding on mammals, to avoid detection.

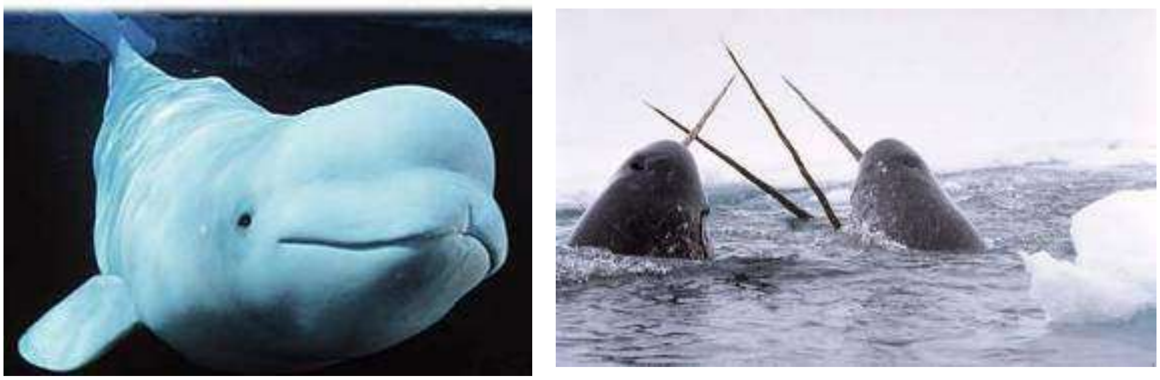


Figure 18.3. Beluga (left) and narwhal (right), toothed whales resident of the Arctic.

18.5.5. Arctic Birds

There are no penguins in the northern hemisphere. In the Arctic, auks (Figure 18.4) are the ecological equivalent to penguins. Their short wings make them poor flyers, but excellent swimmers and divers, able to pursue their prey underwater.

The Arctic tern (Figure 18.4), which looks like a small gull, undertakes the longest migration of any bird, from the Arctic to the Antarctic, to take advantage of the plentiful summer food supply in both poles.

Figure 18.4. Puffin, a type of auk (left) and an Arctic tern (right).

18.6. The Antarctic

The Antarctic experiences a higher summer primary production than the Arctic due to upwelling and the lack of a halocline and pycnocline. Biologically, Antarctic organisms are more diverse and endemic than those in the Arctic. Amazingly, nearly all Antarctic species depend in some way on one species of large, herbivorous euphausiid shrimp: the krill *Euphausia superba*, which is approximately 6 cm long. This species filter feeds on the abundant pelagic diatoms, or scrapes algae from the underside of the ice. The standing stock of krill (biomass at a given time) can reach 250,000,000 metric tons. Krill is in turn prey for benthic invertebrates, pelagic fish, squid, seabirds and marine mammals (Figure 18.5). The key to the evolutionary success of krill is that during periods of no light and little food in the winter they can reduce their metabolic rate and survive 7 months without food at depths of 250-500 m. During this time they metabolize structural proteins and stored lipids, which reduces their body size, eliminating the need to molt.

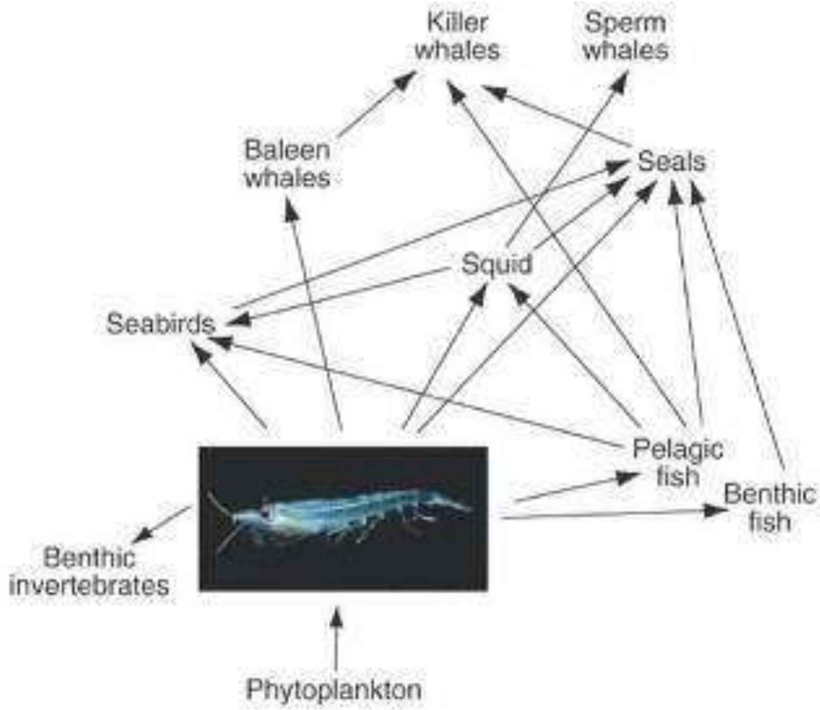


Figure 18.5. Antarctic food web with krill, *Euphausia superba*, at 2nd trophic level.

18.6.1. Antarctic mammals

The vast area of sea ice in the Antarctic is the permanent home to several species of seals, and in the summer to several species of large whales. The Antarctic population of krill is thought to support about half the world's population of seals and a large proportion of whales and seabirds.

Pinnipeds

The crabeater seal is the most abundant seal on earth, with approximately 10 million individuals. Despite their name, crabeater seals feed almost exclusively on krill, and have modified teeth that are used to strain water and catch krill much in the same way as baleen plates. They remain in Antarctica year-round and are monogamous, enhancing the prospect of paternity by guarding their female partner. Crabeater seal pups are an important food source for leopard seals and approximately 80% die before their first birthday.

Leopard seals feed on krill, which comprises about half their diet, and they also eat homeothermic prey (penguins and crabeater seal pups) and are the only pinnipeds known to regularly do so (Figure 18.6).

Weddell seals are found around cracks in fast ice, which they keep free of ice as breathing holes by constantly abrading the edge with their teeth. They feed on squid, fish, krill and benthic invertebrates. Males defend a breeding territory under the ice near a breathing hole and display to the females. They are very good divers, and can stay for up to 80 minutes at 600 m.

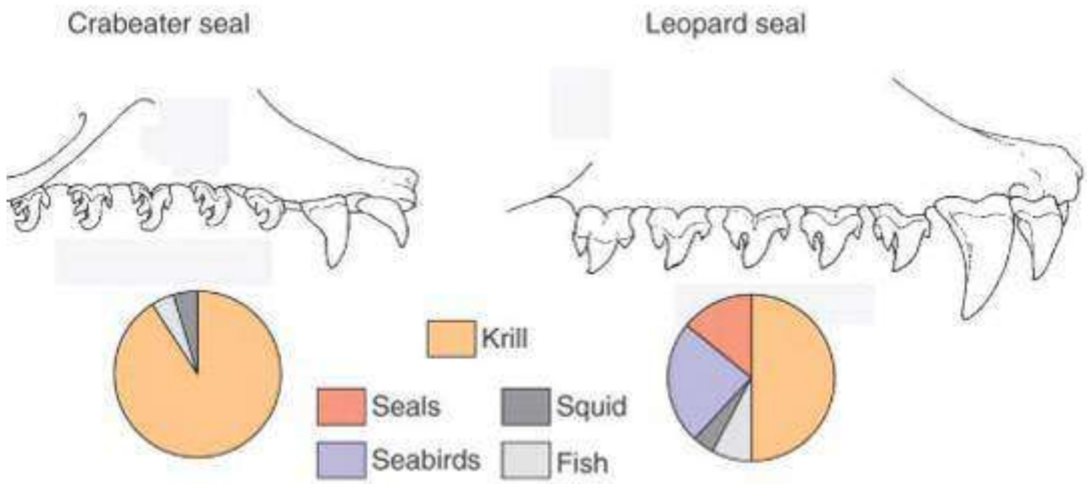


Figure 18.6. Crabeater seal (left) and leopard seal (right) teeth specialized for filtering krill, with the proportion of krill in their diet indicated below.

Mysticete whales

Rorquals such as blue, fin, humpback and minke whales come to Antarctic waters in the summer to feed. Like other Antarctic species, they all eat krill *Euphausia superba*. The blue, fin and humpback whales were all heavily depleted through whaling. For example, 29,000 blue whales were harvested each year in the first half of the 20th century, and 1.4 million whales had been removed by 1960. Today about 2,000 individuals remain in Antarctic waters. The Minke whale, because of its smaller size, was largely exempt from this large-scale whaling. Reduced numbers of the large whales have resulted in important ecological changes, including changes in the reproductive rates and increase in the number of Minke whales, Adelie penguins, crabeater seals, leopard seals and many species of fish. All those species feed on *E. superba* and a reduction in competition from the large whales allowed more food for the latter species.

Toothed whales

There are no toothed whales that are permanent residents of the Antarctic. However killer whales, sperm whales and beaked and bottle-nosed whales visit the Antarctic seasonally when food is abundant.

18.6.2. Antarctic birds

18.7. Adelie (left) and Emperor (right) penguins.

Several species of birds visit the Antarctic seasonally, including the Antarctic prion, which has modified teeth used to strain water and feed on krill. However only a few species of penguins are found in the Antarctic throughout the year. Adelie and Emperor penguins are abundant on pack ice. They are both large birds (Adelie 75 cm, Emperor 1.1 m), which allows them to survive the cold temperatures of the winter. They are flightless and their wings are modified as narrow flippers which are very efficient for swimming. They are awkward on land and often slide on the ice. Both species feed in the water and migrate south to about 70°S to find nesting sites. Though they have a lot of similarities, Adelie and Emperor penguins have very different reproductive strategies. Adelie penguins lay their eggs in the spring so the chick can grow during the milder months of the summer and enter the water to start foraging in the winter. Emperor penguins, on the other hand, lay their eggs in the winter, which allows the chick to be large enough to start foraging in the summer, when food is abundant. In both species, the parents take turn foraging and taking care of the young until the chick is large enough to enter the water.

18.7. Polar Seas in the Future

With global climate change and warming of sea surface temperatures, the area covered by pack ice at each pole is gradually getting smaller. This in turns reduces primary production, as much of the primary producers (e.g. diatoms) are found associated with ice. Lower primary production means reduced populations of critical herbivores such as euphausiids and copepods, causing a loss of biomass at all higher trophic levels. The loss of ice also has important consequences for those organisms such as seals and birds which use ice for reproduction, molting and resting, and for polar bears which use ice as a hunting platform.

18.8. Review Questions: Marine Homeotherms of Polar Seas

1. What is pack ice?

2. What is fast ice?

3. Describe three physical differences between the Arctic and the Antarctic?

4. Is productivity higher in the Arctic or the Antarctic, and why?

5. Describe the two main benefits of polar seas for marine mammals and birds.

6. What is the main advantage of pupping on pack ice rather than in the water?

7. How do newborn polar marine mammals achieve very high growth rates?

8. Why are polar pinnipeds mostly monogamous?

9. Do most pinnipeds show monomorphism or sexual dimorphism?

10. Where and when do polar cetaceans give birth?

11. Which seal has white pups with highly prized fur?

12. Explain the sexual dimorphism seen in hooded seals?

13. Are hooded seal polygynous or monogamous?

14. Do both male and female walruses have tusks?

15. What is the name of the white toothed whale that has a dorsal ridge to break the ice from below, and is preyed on by polar bears?

16. Is the tusk on a narwhal longer in males or females?

17. Do you find narwhals in the Arctic or the Antarctic?

18. Are there penguins in the Arctic? If so, what species? If not, what is their ecological equivalent?

19. What is the organism on which all species in the Antarctic depend either directly or indirectly? What is the phylum and class of this organism?

20. How does the Weddell seal maintain an ice-free breathing hole?

21. How does the reproductive strategy of Adelie penguins and emperor penguins differ?

22. Why does the presence of sea ice increase polar primary productivity

23. In which season is polar productivity highest/

24. Which toothed whales are permanent residents of the Arctic? And of the Southern Ocean?

25. Which seal eats homeothermic prey?

26. What do crabeater seals eat?

19. Marine Biodiversity, fisheries and climate change

19.1. Diversity in marine ecosystems

Species diversity has two components: the number of different species found in an ecosystem (the species richness) and how equal the abundances of each species are (the species evenness). Communities with a greater number of different species have a higher richness than communities with fewer species (Figure 19.1). Species diversity increases with richness and with evenness, such that communities with the highest diversity have a high number of different species (high richness), and the relative abundance of each species is fairly equal (i.e. similar biomass/density—high evenness). Therefore, for the same richness, the community that is more even has greater diversity (Figure 19.2).

Figure 19.1. The fish community on the left, with 3 different species, has a higher richness than the fish community on the right, with only 2 species.

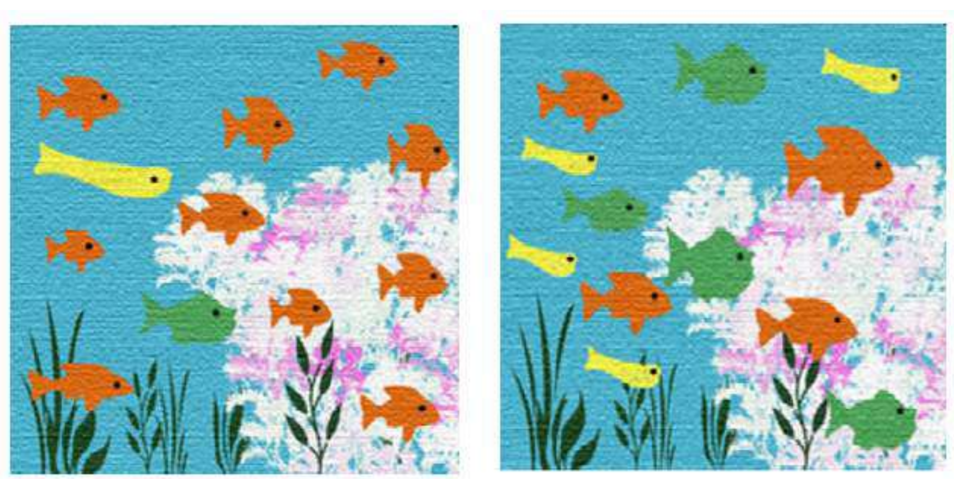


Figure 19.2. Both fish communities have a richness of 4 (4 different fish species) but the community on the right is more diverse, because there are 3 individuals of each species while the community on the left has just one individual of the yellow fish species and one individual of the green fish species.

There is a lot of variation in the levels of species diversity in marine ecosystems. Typically, tropical ecosystems have greater diversity compared to cold water ecosystems; this trend is seen across multiple taxonomic groups (see Figure 19.3 for patterns of bivalve richness with latitude). Coral reef ecosystems, in particular, are extremely diverse tropical ecosystems. Yet, there is a lot of variation in the biological diversity of coral reef communities. Coral reefs in the Indo-Pacific are much more diverse than those in the Atlantic (Figure 19.4)—because the Atlantic is a much newer ocean, therefore there have been fewer speciation events in the Atlantic. On the other end of the diversity spectrum, we find that estuaries tend to be less diverse than fully marine habitats. This is because few species have the adaptations to tolerate the physical conditions of estuaries, and because estuaries are nearshore environments that tend to be quite dynamic (i.e. can change rapidly), which leads to high rates of local extinction. When looking at patterns of species diversity with depth, we find that diversity tends to be highest in bathyal zone (around 2000-2500m; Figure 19.5). The reason for the greater diversity in the bathyal zone compared to shelf habitats is likely because it is an extremely stable environment—free of the environmental extremes that may cause extinctions in shallow waters. Diversity decreases below the bathyal zone because few species can survive at the low population densities that are dictated by the low food density found there.

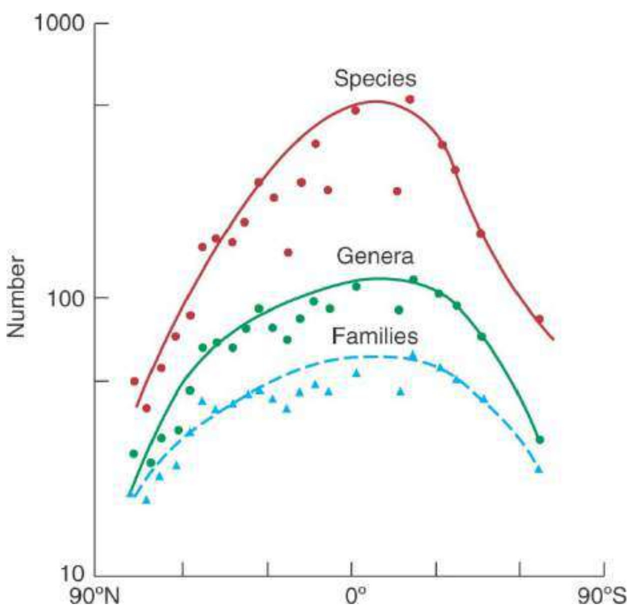


Figure 19.3. The relationship of bivalve mollusk taxon diversity and latitude. Points are average number of species, genera, and taxonomic families.

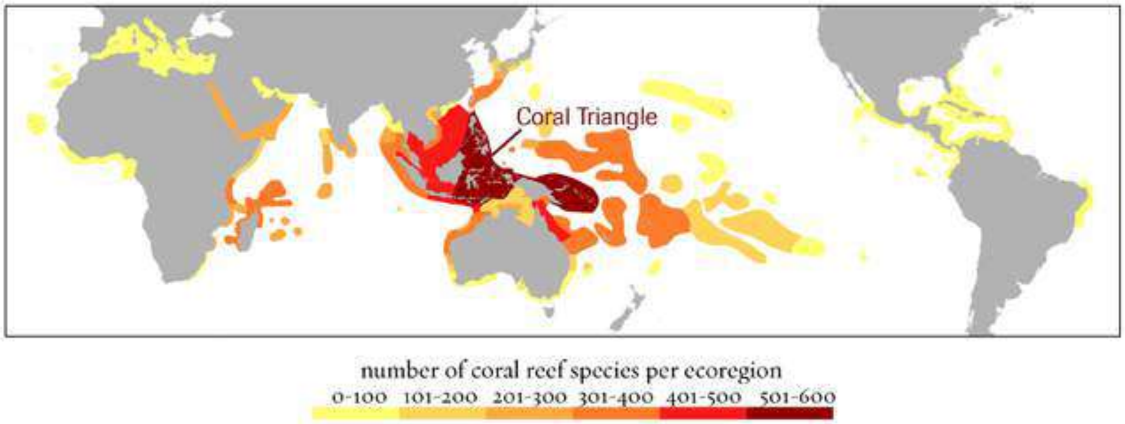


Figure 19.4. This map shows that the coral triangle in the Western Pacific/Eastern Indian has the highest coral richness (it also has the highest coral diversity). The Indo-Pacific has much higher diversity than the Atlantic because it is much older. The coral triangle also has high diversity because it straddles the equator, has many coral reefs in close proximity (which leads to low extinction rates), and because dominant current patterns bring larvae from distant reefs (which increases the immigration of new species, and lowers the risk of local extinction).

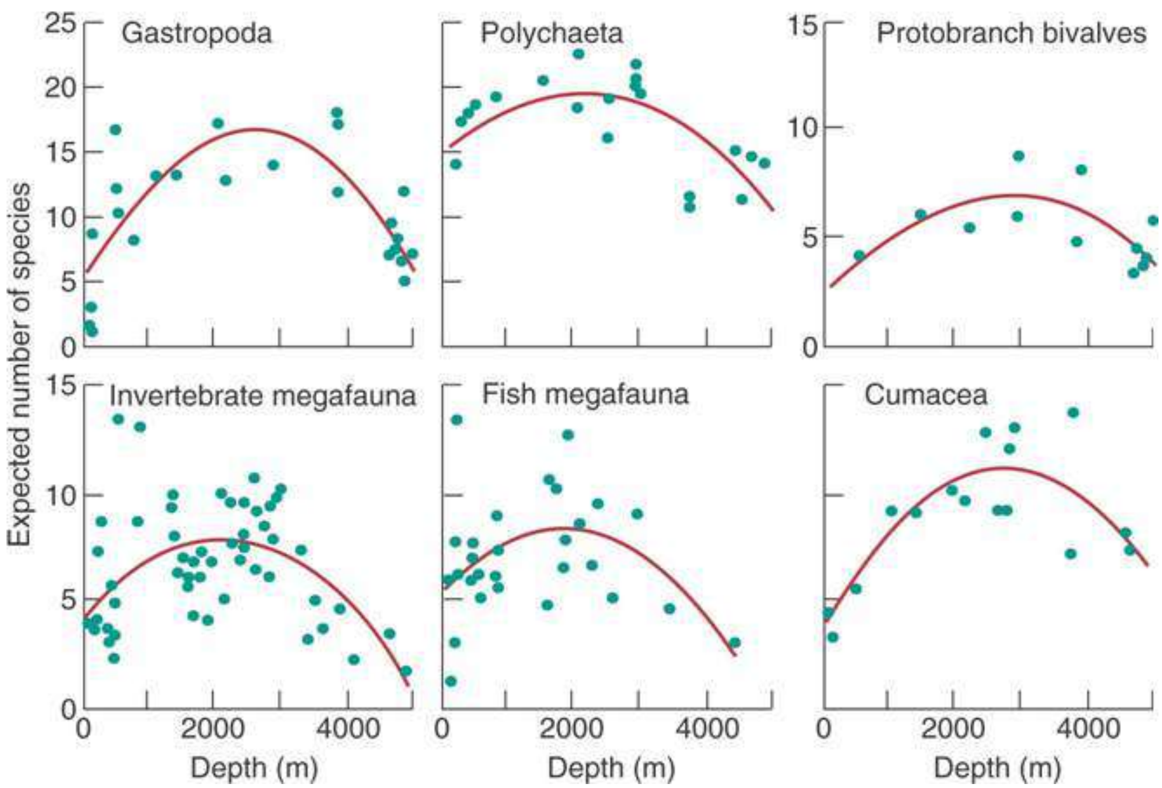


Figure 19.5. For many groups of animals, richness peaks in the bathyal zone.

Conservation biologists are concerned with preserving species diversity within ecosystems. They are also interested in preserving high genetic diversity within populations, since genetically diverse populations tend to be more resilient to disturbances and have a lower risk of extinction. Finally, conservation biologists are aim to preserve a high diversity of communities and ecosystems in landscapes or regions.

19.2. Value of biological diversity

The marine environment is extremely valuable to human populations. Here are some of the reasons why humans should be concerned with protecting marine biodiversity:

- Because of its aesthetic value. People around the world enjoy watching marine organisms, whether through snorkeling/diving, glass-bottom boats, or in aquaria.
- A lot of pharmaceutical compounds are derived from marine organisms. For example, new research shows that the debilitating venom produced by cone snails could be used as a new oral pain reliever. Bioprospecting studies are ongoing and new promising compounds are discovered every year.
- Many industrial products are derived from marine organisms. For example, sand filters commonly used in pools are in fact made diatomaceous earth, sediment rich in silica shells created by diatoms.
- Marine ecosystems are an important source of food around the world.
- Loss of species that are near the top of food chains can have drastic top-down effects on marine ecosystems. For example, the North Atlantic has seen a dramatic decline in large sharks, losing around 90% of great shark biomass over the past few decades. This decline in great shark set off a large trophic cascade in which mesopredator biomass increased, and the prey of mesopredators declined (Figure 19.6).
- Loss of species that are structural elements in a community (e.g., corals, seaweeds, seagrasses) might cause loss of many more species in that community.
- More diverse communities may be more resilient to environmental stressors and disturbances. For example, in a coral reef community with few species of dominant coral, one bleaching event or one hurricane can have a devastating impact the overall amount of coral if the few dominant species happen to be vulnerable to high temperatures or strong wave action. On the other hand, in a diverse community with dozens of common species it is likely that a few species can survive the disturbance well and therefore the overall impact on coral cover will likely be lower.
- Marine ecosystems provide us with many ecosystems services. For example, coral reefs and mangrove forests reduce wave energy and therefore protect coastlines. Mangroves and saltmarsh grasses trap a lot of sediment before it reaches the coastal zone, and also take up nutrients—therefore can reduce the impact of land development on nearshore marine environments.

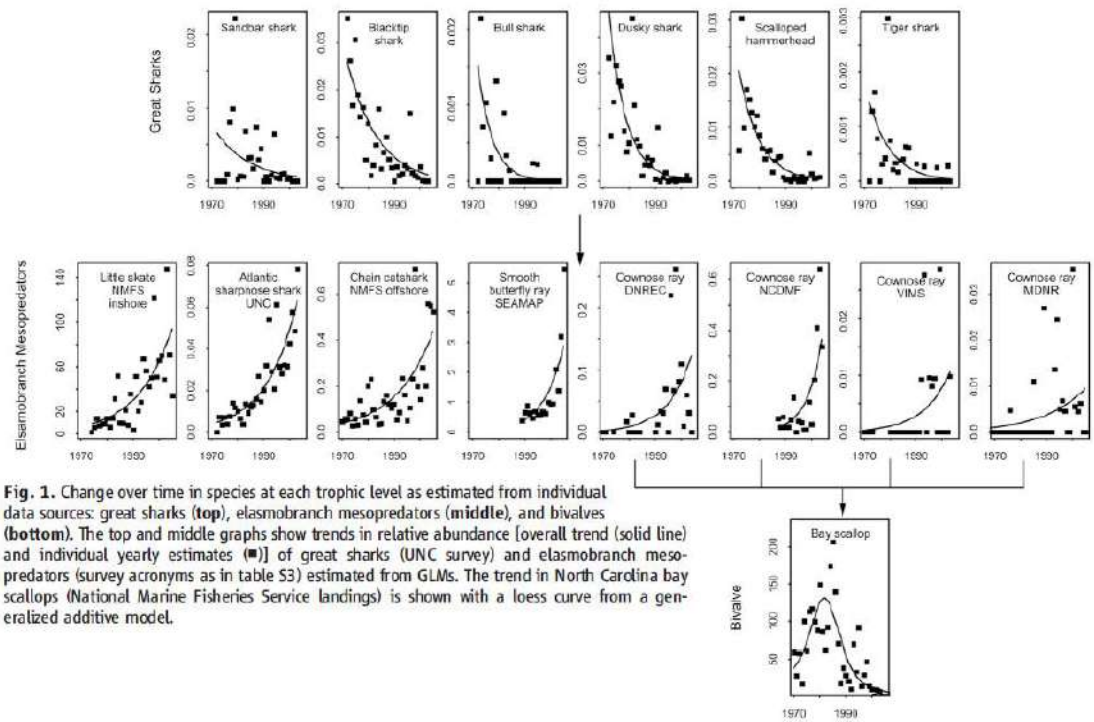


Figure 19.6. Change in abundance of top predators, mesopredators, and prey in the North Atlantic from 1970 to 2007. From Myers et al 2007, Science 315: 1846-1850.

There is broad worldwide agreement that we should increase efforts to protect biodiversity. The United Nation's Convention on Biological Diversity (CBD), signed in 1993, has 3 broad objectives: 1) the conservation of biological diversity; 2) the sustainable use of the components of biological diversity and 3) the fair and equitable sharing of the benefits arising out of the utilization of genetic resources. Under the CBD, the Aichi Biodiversity Targets (ABT) provide a specific framework for action to protect biodiversity. The ABT lists 20 specific targets under five strategic goals:

- Strategic Goal A: Address the underlying causes of biodiversity loss by mainstreaming biodiversity across government and society
- Strategic Goal B: Reduce the direct pressures on biodiversity and promote sustainable use
- Strategic Goal C: To improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity
- Strategic Goal D: Enhance the benefits to all from biodiversity and ecosystem services
- Strategic Goal E: Enhance implementation through participatory planning, knowledge management and capacity building

19.3. Impacts of fisheries on marine populations and communities

A detailed analysis of the status of marine fisheries is done in *Introduction to Oceanography* (Chapter 17). Here, we will focus on the impact of fisheries on marine populations and communities.

Humans have fished in oceans for thousands of years, but the scale and impact of marine fisheries has greatly increased over the past 100 years—as technology has allowed us to be more efficient at finding, catching and processing fish and other marine organisms. The catch of marine fisheries steadily increased throughout the 20th century until around 1990, at which point it started plateauing despite continued high fishing effort (Figure 19.7). This plateau indicates a decreased in catch per unit effort, one of the key signs of overfishing. Fisheries biologists estimate that around 70% of marine stocks are overfished—i.e. we are harvesting them in an unsustainable manner.

Overfishing can have obvious negative consequences for the targeted population, and there are many examples of marine stocks driven to very small proportions of historical stock size. One of the most obvious example is that of the North Atlantic cod in Newfoundland, which was fished so heavily for decades the stock eventually collapsed and showed few signs of recovery for over 2 decades. Some fisheries scientists estimate that if humans continue fishing at current rates, all fish stocks will have collapsed by 2048. While this specific estimate has been hotly debated, it is clear that current fishing practices are largely unsustainable. Fishing activities can therefore greatly alter the composition of marine ecosystems. In some areas, multiple species are heavily harvested; in others, fishing effort may be concentrated on just one or a few species, but this can still have a significant effect on the entire communities. For example, the decline of the North Atlantic cod on the Eastern Scotian Shelf set off a trophic cascade and community-wide effects. As cod (and other demersal fish) declined, the biomass of their prey significant increased. This included small pelagic fish, as well as benthic shrimp and snow crab. The increase in those species, in turn, led to a decline in zooplankton, and an increase in phytoplankton (Figure 19.8). The increase in biomass of pelagic fish on the Eastern Scotian shelf also created a "predator-reversal" situation: the large biomass of pelagic fish created significant predation on planktonic cod larvae, resulting in very low cod recruitment which largely prevented cod stocks from recovering.

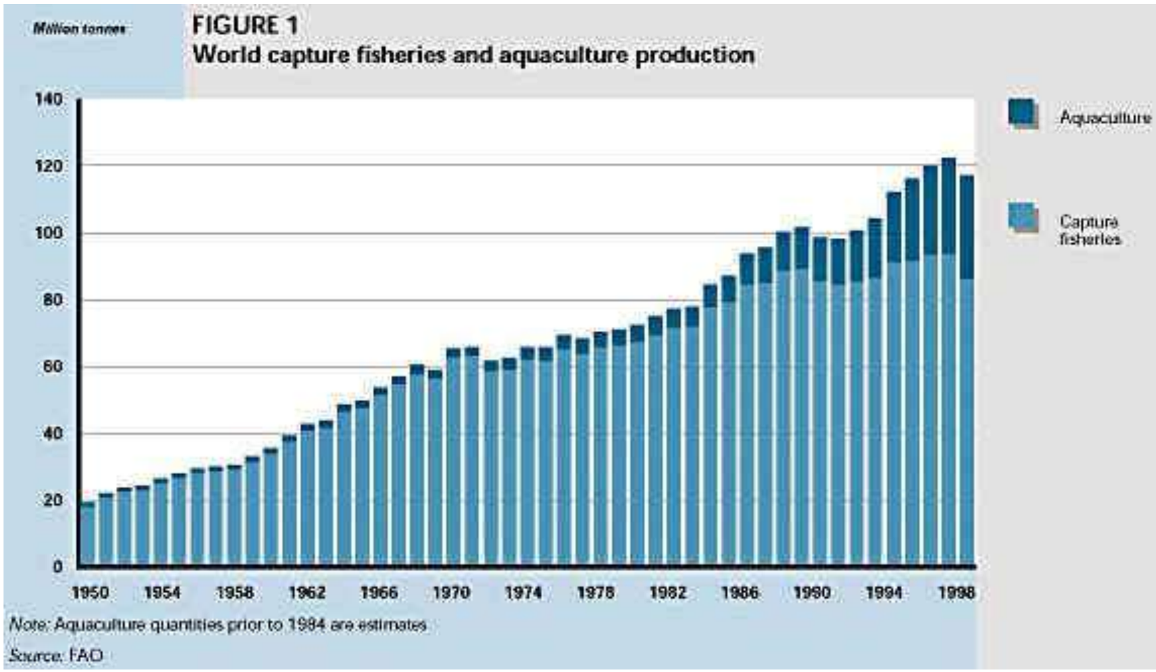


Figure 19.7. Catch of global fisheries (light blue) from 1950 to 1998, showing an increase in catch until ~1990.

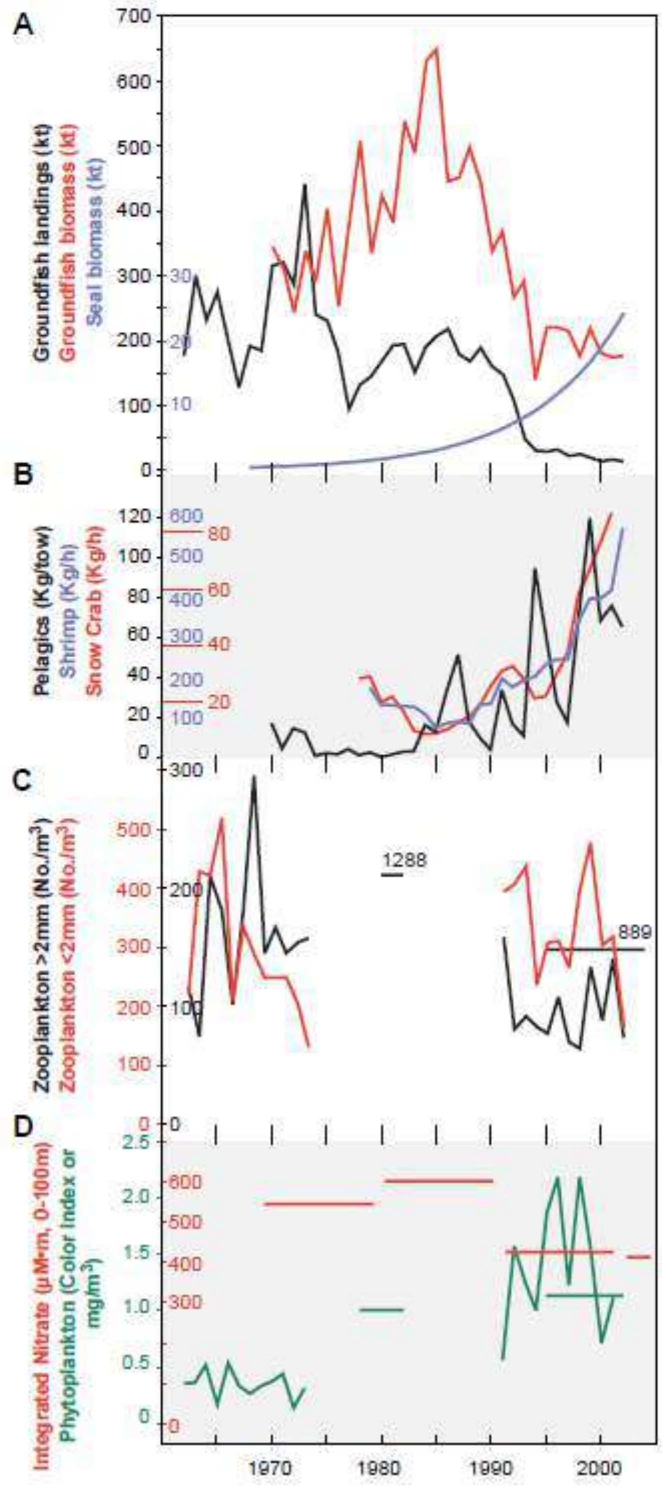


Figure 19.8. Trophic cascade on the Scotian Shelf caused by the overfishing of groundfish (demersal fish). From Frank et al 2005 Science 308: 1621-2623.

Fisheries can also lead to a decline in species other than the target species through bycatch and habitat destruction. Bycatch refers to the catch of organisms other that the target organism—e.g. dolphins caught in purse seine nets intended to catch schools of tuna. While organisms caught as bycatch are typically released in the environment—they are often dead by the time they are released, hence bycatch can have strong impacts on some marine populations. Additionally, some fishing activities can have a large impact on benthic habitats and thereby affect entire communities in the fished area. Benthic trawls are notorious for having a significant impact on benthic communities (e.g. Figure 19.9).

Figure 19.9. Benthic community on a continental shelf, with a healthy community of deep water coral before trawling (left), which is largely removed by trawling activities (right).

19.4. Impacts of climate change on marine populations and communities

The causes and consequences of climate change are covered more thoroughly in Introduction to Oceanography (chapters 19-20). Here, we will focus on some key biological impacts of ocean warming and ocean acidification.

19.4.1. Ocean warming

As oceans are becoming warmer, there can be several consequences for marine populations. In some cases, populations may shift their latitudinal or depth ranges to remain in a zone of suitable temperature (e.g. Figure 19.10). While this has been recorded in several species of fish, dispersal and range shift may be more limited in some sessile species. Additionally, some organisms may be limited in range shifts due to their tolerance to other environmental parameters. For example, biologists predict that corals are unlikely to thrive at increasing high latitudes with warming temperatures, because the light levels they require are only found in the tropics.

In many cases, populations will be limited in their range shifts as oceans warm and will experience increasingly high temperatures—in many cases higher than the optimal temperature range for a species. This can lead to physiological stress or mortality, e.g. coral bleaching episodes often cause extensive coral mortality. Those bleaching events that don't cause mortality are often followed by coral disease outbreaks, as the stressed and weak coral have a lower ability to fight infections. Warmer temperatures can also lead to an increased frequency of tropical storms, which can cause population declines in many tropical ecosystems.

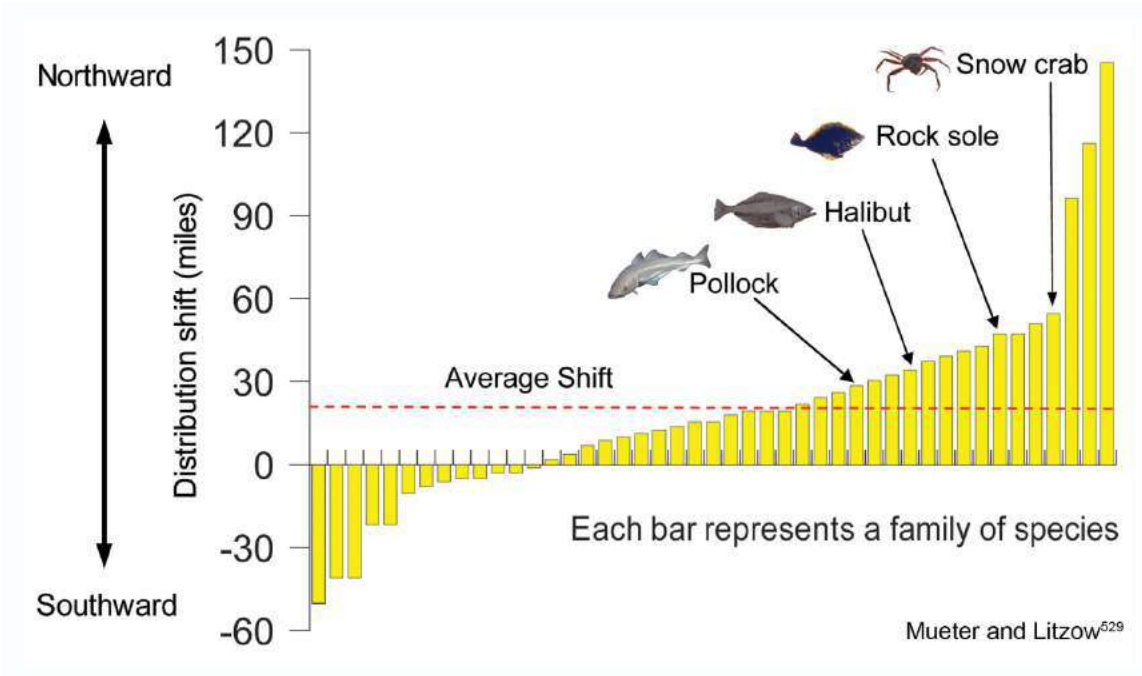


Figure 19.10. Latitudinal range shift for several marine families in Alaska from 1982 to 2006. On average, populations moved 19 miles north over the 24 year period.

The consequences of ocean warming are likely to be especially dramatic in polar seas, where melting of sea ice leads to lower salinities, lower productivity, and decrease habitat for many animals. Sea ice is an integral component of polar marine ecosystems, and oceanographers have documented a severe decline in sea ice at both poles over the past several decades. Melting of sea ice leads to lower surface salinities, and if a strong halocline and pycnocline is established, it may lower the supply of nutrients to the photic zone—therefore lower primary productivity. Loss of sea ice also lowers primary productivity in a more direct way—since a large portion of polar primary productivity is from diatoms that attach to the underside of thin sea ice. Decreased biomass of producers can lead to food limitations for their predators and therefore limit biomass at higher trophic levels. Loss of sea ice also has a strong impact on those organisms that use the sea ice for breeding and foraging (e.g. penguins, seals, polar bears).

19.4.2. Ocean acidification

Over the past 300 million years, ocean pH has been slightly basic and rather stable, averaging about 8.2. Today, because of an increased amount CO_2 in the atmosphere, there is a greater concentration of dissolved CO_2 in the oceans. In oceans, CO_2 reacts with water to form carbonic acid (Figure 19.11), and this has led to a decrease in ocean pH to around 8.1. This drop of 0.1 pH units represents a 25% increase in acidity (e.g. free hydrogen ions) over the past two centuries.

Ocean acidification has an especially strong impact on calcifying organisms since free hydrogen ions react with carbonate ions and this process results in lower calcification rates (i.e. formation of calcium carbonate structures). Calcifying organisms impacted by this includes corals, mollusks, echinoderms, among many others. Ocean acidification also impacts non-calcifying organisms. For example, it has been shown that lower pH negatively affect the sense of smell and hearing in fish larvae, and reduces learning and predator recognition.

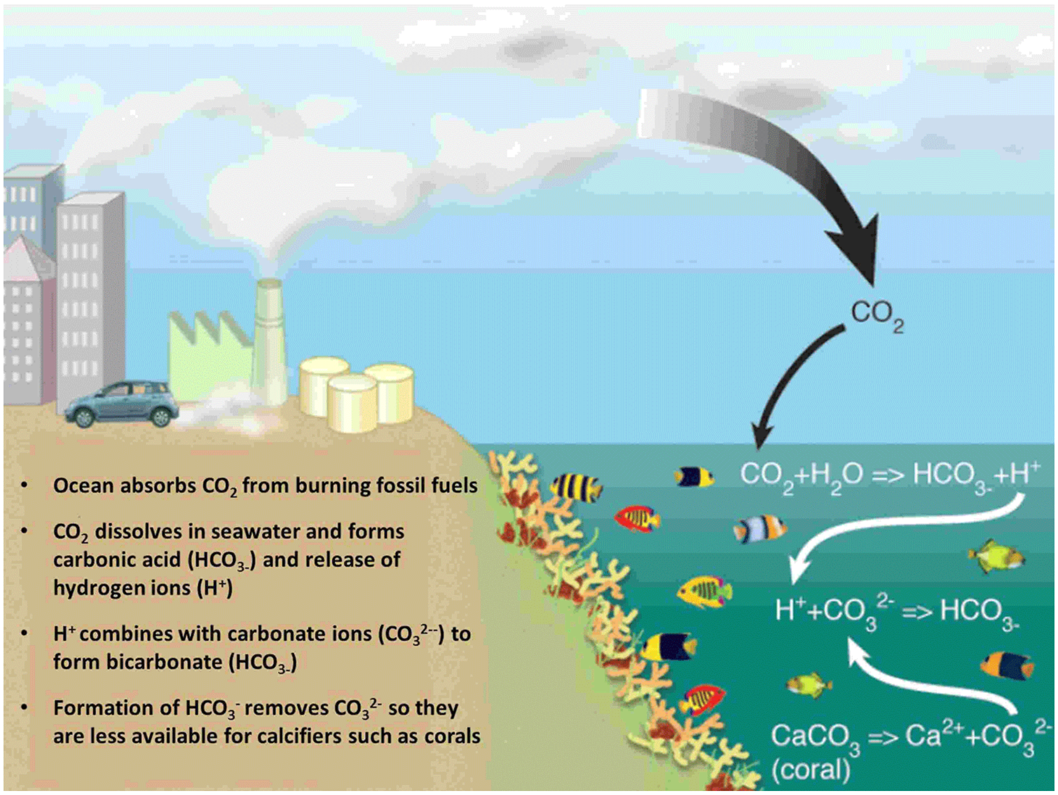


Figure 19.11. As CO_2 dissolves in water, it decreases ocean pH. Free hydrogen ions react with carbonate ions, which are then less available to react with calcium to form calcium carbonate.

20. Other Threats to Marine Biodiversity

20.1. Habitat destruction

Habitat destruction is the most important cause of biodiversity loss, worldwide. When no other suitable habitat is found nearby, loss of habitat can lead to local extinction. Habitat fragmentation, in which large, continuous habitats are divided into smaller patches of lower total area, often results in smaller populations, which are at greater risk of decreased genetic diversity and local extinction. Many human activities can lead to habitat loss and fragmentation, especially in shallow coastal zones.

20.1.1. Fishing and aquaculture activities

As mentioned in chapter 19, some fishing activities negatively impact benthic habitat. Benthic trawls are notorious for their destruction of benthic habitats (Figure 19.9). On coral reef ecosystems, dynamite and cyanide fishing destroy coral habitat in the process of harvesting fish. In some cases, the increase traffic associated with fishing (including anchors, lines and traps) can also damage habitat as this gear comes into contact with fragile benthic organisms.

Aquaculture activities can also destroy habitats. This is most obvious with shrimp farming, which is largely done by raising shrimp in coastal ponds built on mangroves. About a fifth of mangroves worldwide have been lost since 1980, and shrimp farms are the leading cause of this decline. Most shocking is that a large proportion of shrimp farms that are built are soon abandoned due to problems with disease and pollution, yet the clearing of mangroves is long-lasting.

20.1.2. Coastal Development

Wetlands are commonly dredged and filled in to accommodate urban, industrial, and agricultural development—with associated loss of species that live within them. Cities, factories, and farms thus created also produce various wastes that can impact downstream habitat. For example, dredging activities and dock construction can lead to excess sediment and the shading of corals. The extended cruise ship port currently (2017) proposed in Grand Cayman is expected to destroy 15 acres of reefs, and potentially harm another 15 to 20 acres through increased nutrient input, shading and/or sedimentation. 4 Dredging within the Port of Miami in recent years has led to extreme sedimentation and a 93% mortality of nearby coral. Waste products from coastal development can also include sewage, excess fertilizers, toxic chemicals (see section 20.3).

20.1.3. Tourism and recreation

Tourism is one of the fastest growing economic sector in the world, and there are many recreational activities that can impact the marine environment.

Scuba diving

Scuba divers may damage habitats as they come in direct contact with coral or other organisms, or as their movements resuspends sediment in the water column. Some studies have estimated that divers in coral reef environments cause on average one coral break per dive. Whether or not this is problematic largely depends on the density of divers. Some popular sites (e.g. Eilat, Red Sea) see over 30,000 divers per year, and the damage from divers is measurable with 100% of coral showing signs of breakage.

Boating

Boats can impact benthic habitats in a few ways. Anchors dropped on coral reefs can damage coral colonies, and anchor chains can damage an even larger area of reef as they may be dragged back and forth on the reef. Boat hulls or propellers striking the benthos can also represent significant problems. A striking example of this occurred in March 2017 when a small cruise ship ran aground on a reef in Indonesia, destroying a large section of the reef (Figure 20.1). Unfortunately, such damage from ships is not uncommon. In 2015, a mid-sized cruise ship's anchor was videotaped as it dragged across a reef in the Cayman Islands (Figure 20.2). Many other examples of coral damage caused by vessels of all sizes have been recorded. In shallow seagrass habitats, propeller scars occur when a boat's propeller tears and cuts up seagrass roots, stems and leaves, leaving a long, narrow furrow devoid of seagrasses. This damage can take 8 to 10 years to repair, or in several cases the area may never completely recover. Although linear features are most often associated with prop scars, some areas of seagrass habitats have been completely denuded by repeated scarring. In other instances, a linear scar can become a larger feature if the sediments are scoured to undercut the seagrass bed. This erosion can result in detachment of large sections of seagrasses that then float away leaving behind patches of bare sediment wider than the original prop scar.

Figure 20.1. Healthy corals just outside the impact zone, left, compared with those destroyed in the impact, right. Source: news.mongabay.com/2017/03/cruise-ship-wrecks-one-ofindonesias-best-coral-reefs/

Figure 20.2. The anchor of the cruise ship Zenith damaging a reef in Grand Cayman. Source: youtu.be/U3l31sXJJ0c - Scott Prodahl

20.1.4. Climate change

As the earth warms due to anthropogenic activities, habitats are modified and sometimes lost. For example, polar bears are heavily dependent on sea ice in the Arctic as a hunting platform. With declining ice cover (Figure 20.3), more polar bears are moving onto nearby landmasses and have much reduced access to potential prey (e.g. seals and whales). Similarly, polar seals and birds that breed on ice are likely to face much lower reproductive success with loss of sea ice. Climate change can also affect tropical ecosystems, and we have documented extensive loss of coral due to warming-induced bleaching events in recent decades. This loss in coral leads to a decline in reef fish that rely on coral for habitat. Climate change may also modify the salinity of marine ecosystems, e.g. some high latitude ecosystems may see declines in salinity as ice melts, to a degree that renders them unsuitable for some marine species.

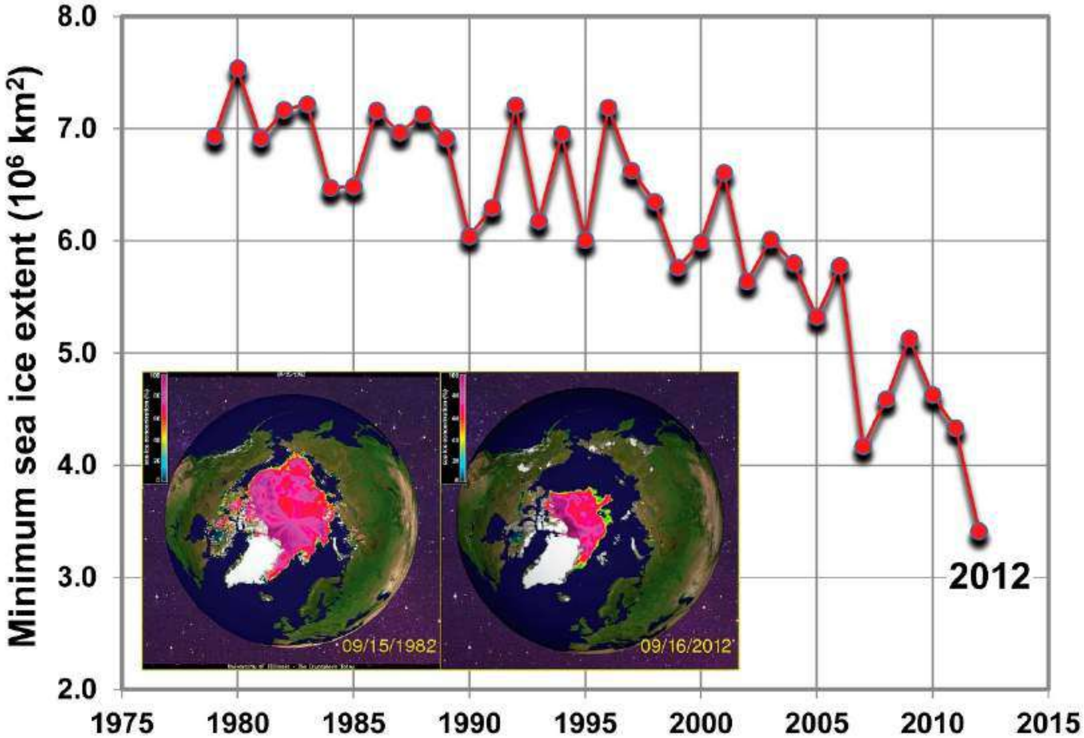


Figure 20.3. Decline in Arctic sea ice from late 1970s to 2012, leading to habitat loss for polar bears and other sea ice animals. Source: USGS Alaska Science Center.

20.2. Introduced species

Introduced species, also called non-native, exotic or alien species, are those species that have been moved by humans beyond their historical range. Thousands of marine species have been introduced to various areas around the world (Figure 20.4)

20.2.1. Vectors of introduced species

Introductions can occur intentionally or unintentionally via different vectors: attached to the hull of ships, inside ballast waters carried by ships, released from aquaria, through man-made canals (e.g. the Suez Canal), moved with various aquaculture products, among others (Figure 20.5). Marine introductions have become more frequent as human travel by ships, along with other vectors, have accelerated. Given the importance of shipping as a vector of marine introductions, it is not surprising that large shipping ports have a high number of invasive species. The San Francisco Estuary is thought to be the most invaded aquatic ecosystem in the world. There are at least 212 introduced species in the estuary, most of which invertebrates.

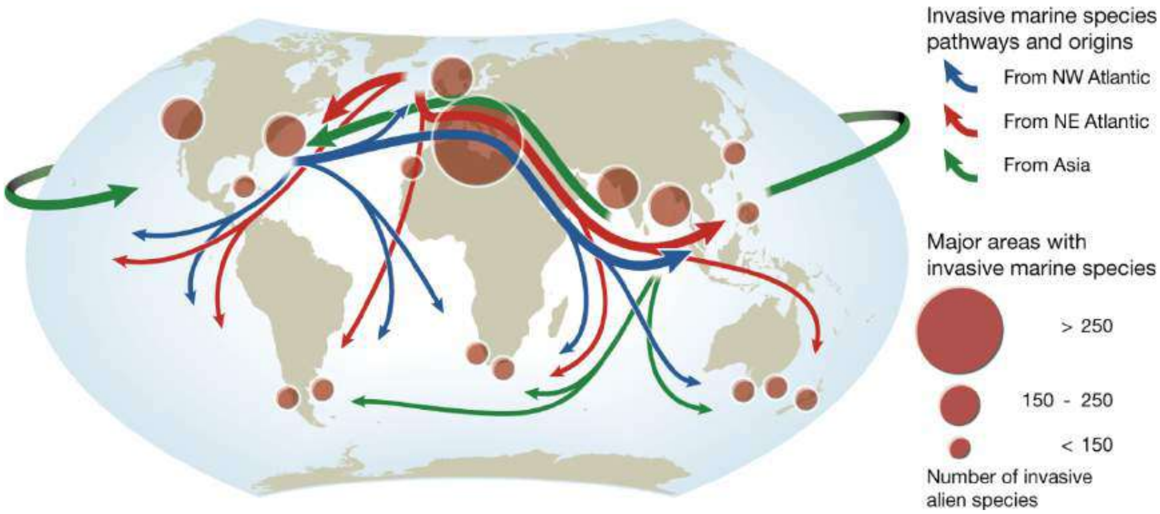


Figure 20.4. Major pathways and abundance of marine invasive species. Image from UNEP/GRID-Arendal Maps and Graphics Library

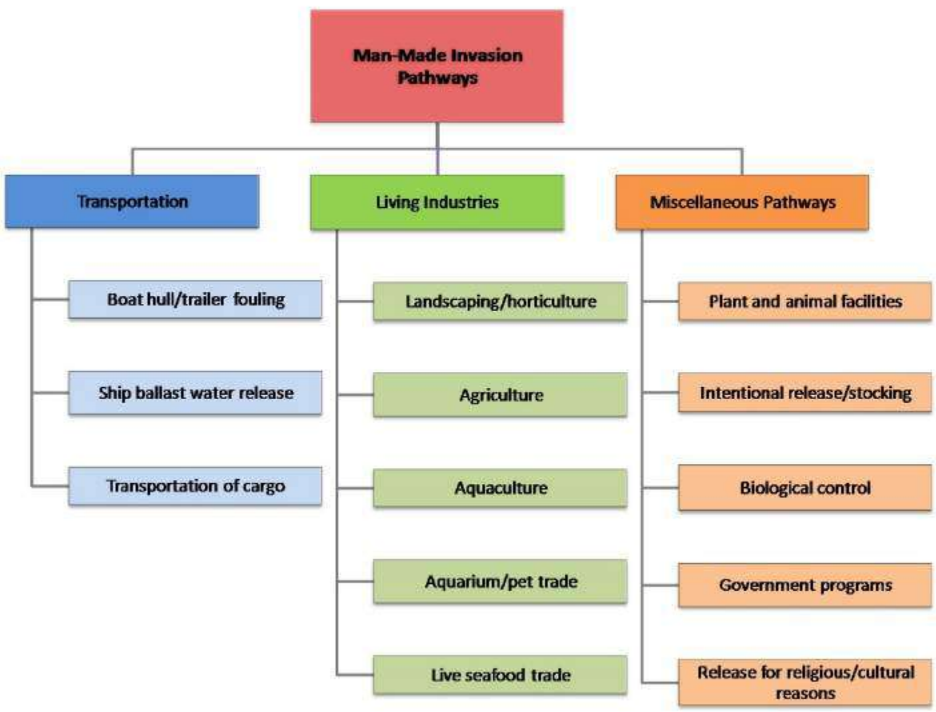


Figure 20.5. Various vectors (invasion pathways) for introduced species. Source: http://gulfcoast.harc.edu

20.2.2. Problems associated with introduced species

In their new location introduced species may be free from the native predators, parasites and diseases that controlled their population in their native range, and in some cases populations of introduced species grow and spread rapidly.

Invasive species are non-natives that have a negative economic or ecological impact in the new locale. Invasive species can have a strong impact on native communities: they may compete with native species for various resources; they may prey on native species; or they may introduce new diseases or parasites to the community; they may cause local extinctions and reduce species diversity. Invasive species may also affect human activities. For example, an invasive species that changes the native community may impact fisheries catch or ecosystem services in the region. Or invasive fouling organisms may increase the cost of maintenance for boats, piers, and underwater pipes.

The invasion of the Indo-Pacific lionfish on Caribbean coral reefs is a great example of the large impact that invasive species can have. Lionfish are thought to have been first introduced to the east coast of Florida in 1992 during hurricane Andrew, when six individuals escaped from a broken aquarium. It is possible that additional releases from other aquaria after this initial introduction sped up the range expansion and population growth. The introduced lionfish population grew fairly rapidly, in large part due to the high reproductive potential of this fish: females can reproduce every 55 days throughout the year, and produce hundreds of buoyant eggs that can be carried by currents. Lionfish are also generalists that can live from the surface to almost 500ft deep. They are voracious predators and compete with native predators for prey. They have venomous spines and while some native Atlantic/Caribbean species consume lionfish occasionally, this consumption is not high enough to control the lionfish population. Additionally, parasites common on the gills of native fish do not seem to infect lionfish. The lionfish invasion has been especially dramatic in the Bahamas, where the population increased rapidly from 2006 to 2008 (Figure 20.6). Lionfish have had a negative impact on the native fish prey they consume, as well as on the native predators of those small fish, which are now competing with lionfish for this limited food source.

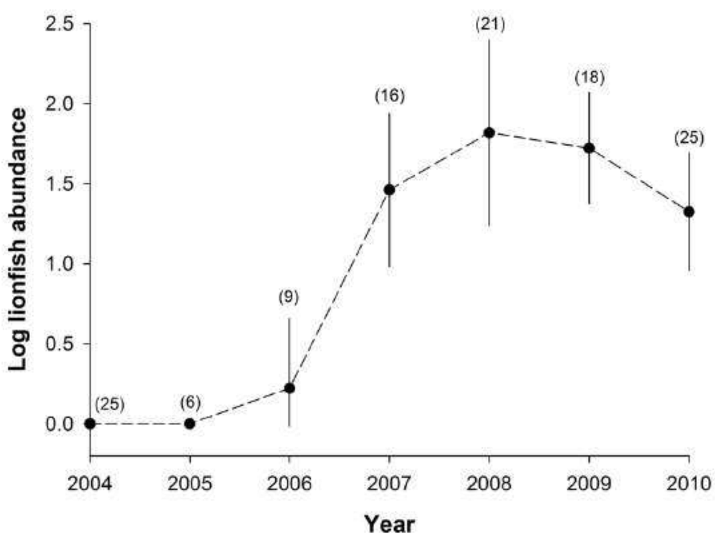


Figure 20.6. Abundance of Indo-Pacific on coral reefs off southwest New Providence, Bahamas. Abundance is the number of lionfish sighted during each roving survey, recorded in log 10 scale. Points represent log-scale means, bounded by 95% confidence intervals. The yearly number of surveys is given in parentheses. From Green et al 2012 PLOS One e32596. doi:10.1371/journal.pone.0032596.g001

20.2.3. Predicting and controlling invasions

A staggering number of species have been introduced around the world, yet many of those never establish a viable population in the new range. Of the introduced species that do get established in the new locale, only a small proportion are considered invasive. Whether or not an introduced species becomes established, and whether or not it becomes invasive, depends on many factors including the timing of the introduction, number of individuals released, whether the species is released in an environment similar to its native range, etc… Yet there are certain inherent species traits that increase the likelihood of successful invasion. Typically, successful invaders tend to be generalists—species that can eat a variety of food and live in a wide range of habitats. They tend to be r-selected species with the potential for a high population growth rate. And many successful invaders have long planktonic larval phases. This includes the likelihood of surviving long periods of time in ballast waters (one of the most important vector of marine invasions), and increases the chances of rapid spread in the invaded range. While these traits are typical of successful invaders, it is difficult to predict whether an introduced species is likely to get established, and whether it is likely to be detrimental to the native community. In early stages of establishment, most invaders either go unnoticed or appear harmless. However, rapid reproduction and spread over time can lead to exponential increases in both the total area infested and associated control costs. Hence, prevention of introductions if by far the best strategy to mitigate the impact of invasives. The cost of control and the likelihood of eradication both decrease with increasing population size, size of invaded range, and time since invasion (Figure 20.7). While prevention is the most effective and cost-efficient strategy for managing invasive species, in an introduction does occur, early detection and rapid response can help limit the scale of an invasion and the cost of control.

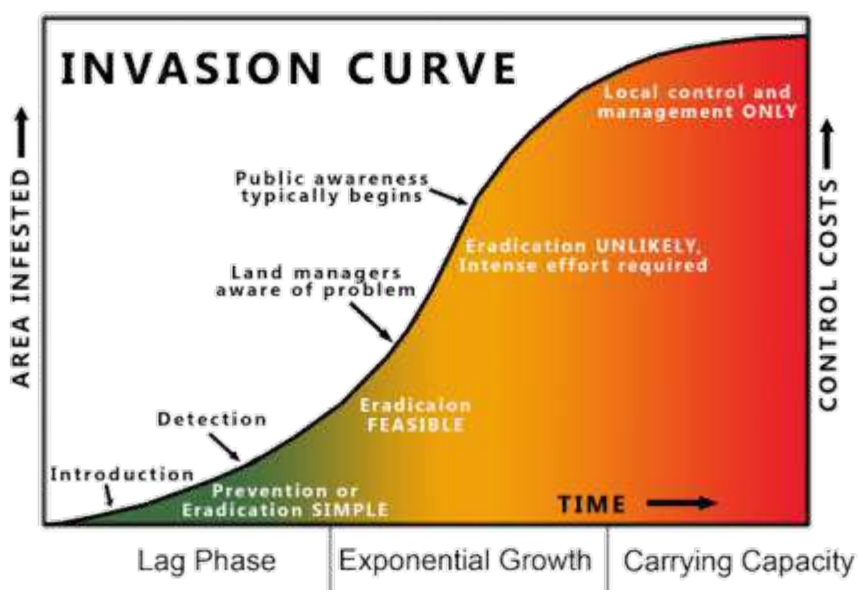


Figure 20.7. Typical pattern of invasive species in their invaded range. Population size and size of invaded area initially grow slowly in the lag phase, then at a more rapid rate in the exponential growth phase. Finally, population size and range both level off in the

carrying capacity phase. Notice this pattern is much like that of logistic population growth (Figure 2.6)

Prevention of introductions focuses on controlling the major vectors for introduction. For example, ballast waters are known to be responsible for hundreds of aquatic invasions, including ten of the most detrimental aquatic invaders (Figure 20.8). Because of this, the International Maritime Organization now mandates, since September 2017, that all ships manage their ballast water to remove, render harmless, or avoid the uptake or discharge of aquatic organisms and pathogens within ballast water and sediments. Ballast waters may be treated using electrolysis or UV light; or ballast waters can be exchanged in the middle of an ocean crossing, where the density of organisms is much lower and there are few coastal species present in the plankton. In Australia, hull fouling is an important vector of marine invaders and therefore the Australian government mandates that ships coming into Australian waters should (1) clean the vessel's hull within one month prior to arrival; or (2) apply antifouling paint within one year prior to arrival; or (3) book the vessel to be hauled out and cleaned within one week after arrival.

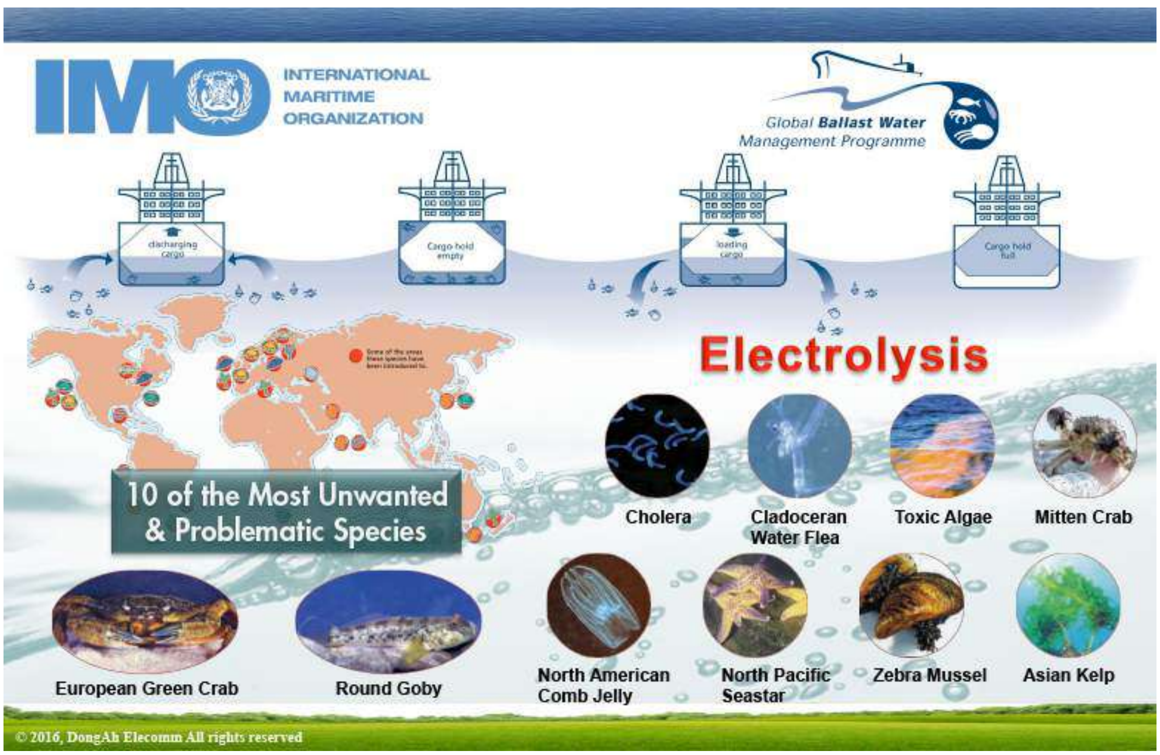


Figure 20.8. Ballast waters, used to stabilize ships when they have no cargo, have led to many problematic aquatic invasions. New regulations mandate that ships treat their ballast waters.

Once an introduced species is established, managers may attempt to eradicate it before the population becomes too large. However, complete eradication is typically difficult and unrealistic in the marine environment, where many species have planktonic stages that cannot easily be controlled. Moreover, marine species may be more difficult to locate and remove, compared to freshwater and terrestrial organisms. Therefore, management efforts typically focus on keeping population sizes below a certain level, to minimize the impact of the invader. For example, lionfish derbies have been organized in Florida and the Caribbean to bring together recreational divers who compete to remove the most lionfish (Figure 20.9). Just in South Florida, over 18,000 lionfish have been removed through these derbies, and research shows that if these lionfish removal efforts occur often enough, the population of lionfish can be kept at a level at which it has a limited effect on native communities.

Figure 20.9. Lionfish derbies in Florida and the Bahamas.

20.3. Marine pollution

Pollution is the presence in or introduction into the environment of something that has harmful effect. Chronic pollution is permanent pollution caused either by repeated or continuous emissions of pollutants, or the presence of very persistent pollutants. For example, the presence of pesticides in the environment from their use in agricultural fields is a form of chronic pollution. On the other hand, acute pollution occurs suddenly, and is often severe, e.g. an oil spill following the grounding of an oil tanker. If there is a single identifiable source of pollution from which pollutants are discharged, such as a sewage discharge pipe, it is considered point-source pollution. Non-point source pollution comes from many diffuse sources, e.g. the combined impact of many septic systems in a watershed (Figure 20.10).

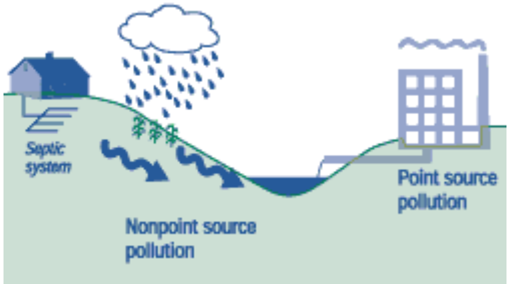


Figure 20.10. Nonpoint source vs point source pollution.

20.3.1. Toxic substances

Many types of heavy metals have been introduced to the marine environment, mostly through industrial processes. These include methylmercury, which is strongly linked to birth defects in humans, and lead, which has neurotoxic effects and is linked to aggressive behavior. Other toxic substances (e.g. PCBs and DDT) have been used as pesticides in agriculture. Polycyclic aromatic hydrocarbons (PAHs) are added to the environment largely through oil spills and coal mining. These toxic substances cannot be metabolized by biological organisms, therefore they tend to accumulated within tissues of individuals exposed to them, in the process of bioaccumulation. Since there is decrease in biomass with increasing trophic level, toxins tend to become more concentrated in the tissues of predators—a process known as biomagnification. Biomagnification is the reason doctors advise against eating a lot of predatory fish (e.g. tuna), in particular for pregnant women.

20.3.2. Oil pollution

Oil can leak from terminals and loading pipes in harbors; it can leak from offshore drilling platforms and from the wrecks of oil tankers. These may all lead to acute oil pollution and many regulations aim to limit these inputs of oil in the environment. However, by far the most important contribution of oil to the marine environment if the chronic, nonpoint source of oil from gas stations and other small leaks, which eventually reach the oceans via storm drains (Figure 20.12). Oil in the marine environment is problematic because the PAHs it contains are toxic—they impair cell membrane, and have neurotoxic and behavioral effects on many animals. Crude oil generally less toxic than refined oil, because it contains a lower concentration of PAHs. Oil spills are also detrimental to the marine environment because of the physical effect of oil on organisms. Birds are especially affected by this; oil coats contour (outside) feathers and collapses their interlock, allowing water to penetrate to down feathers beneath the contour feathers. Once this occurs, birds lose insulation and may die of hypothermia. Unfortunately, efforts to clean-up oil are often more detrimental than the spill itself. These efforts may include using dispersants which may themselves be toxic, or sometimes the use of steam on beaches, which kills organisms living in the sediment. One of the most promising way to manage an oil spill is through bioremediation, using biological organisms (such as certain bacteria) to remove the oil.

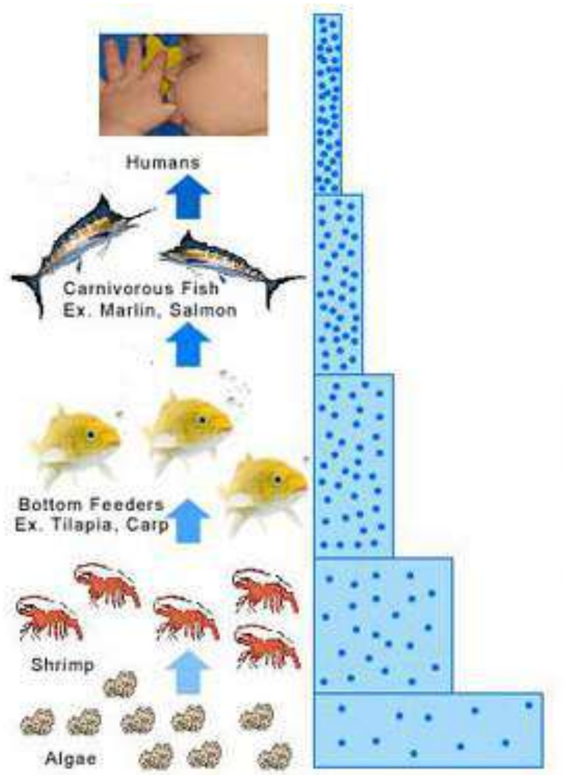


Figure 20.11. Biomagnification of toxins from low to high trophic levels. Blue rectangles represent the biomass at each trophic level; dark blue dots represent the concentration of a toxin.

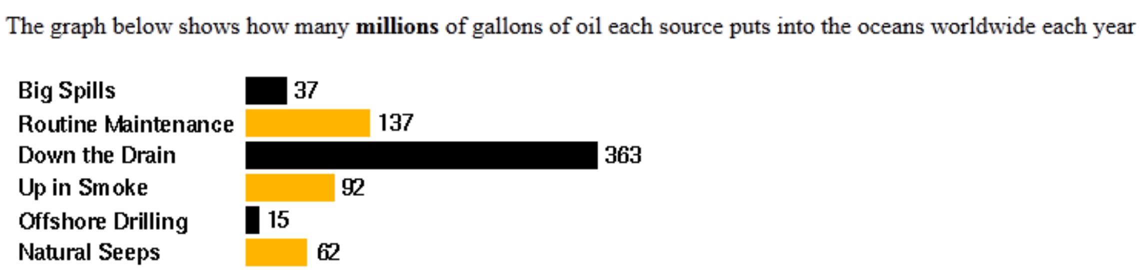


Figure 20.12. Relative importance of various oil inputs to the marine environment.

20.3.3. Plastic

Plastics are inexpensive and durable hence their widespread use by humans. Unfortunately, their durability also means that they do not biodegrade, and with over ¾ of plastics not recycled, this leads to a large amount of plastic waste every year. In coastal zones, plastic pollution can be quite high in some parts of the world with high plastic use and limited recycling facilities. Asia leads the world in plastic pollution with China in the lead and give SE Asian countries (Indonesia, Philippines, Vietnam, Thailand, Malaysia) in the top 10 producers of plastic waste. Once they enter the marine environment, plastics tend to float with surface currents and for this reason, there are large accumulations of plastics in most oceanic gyres.

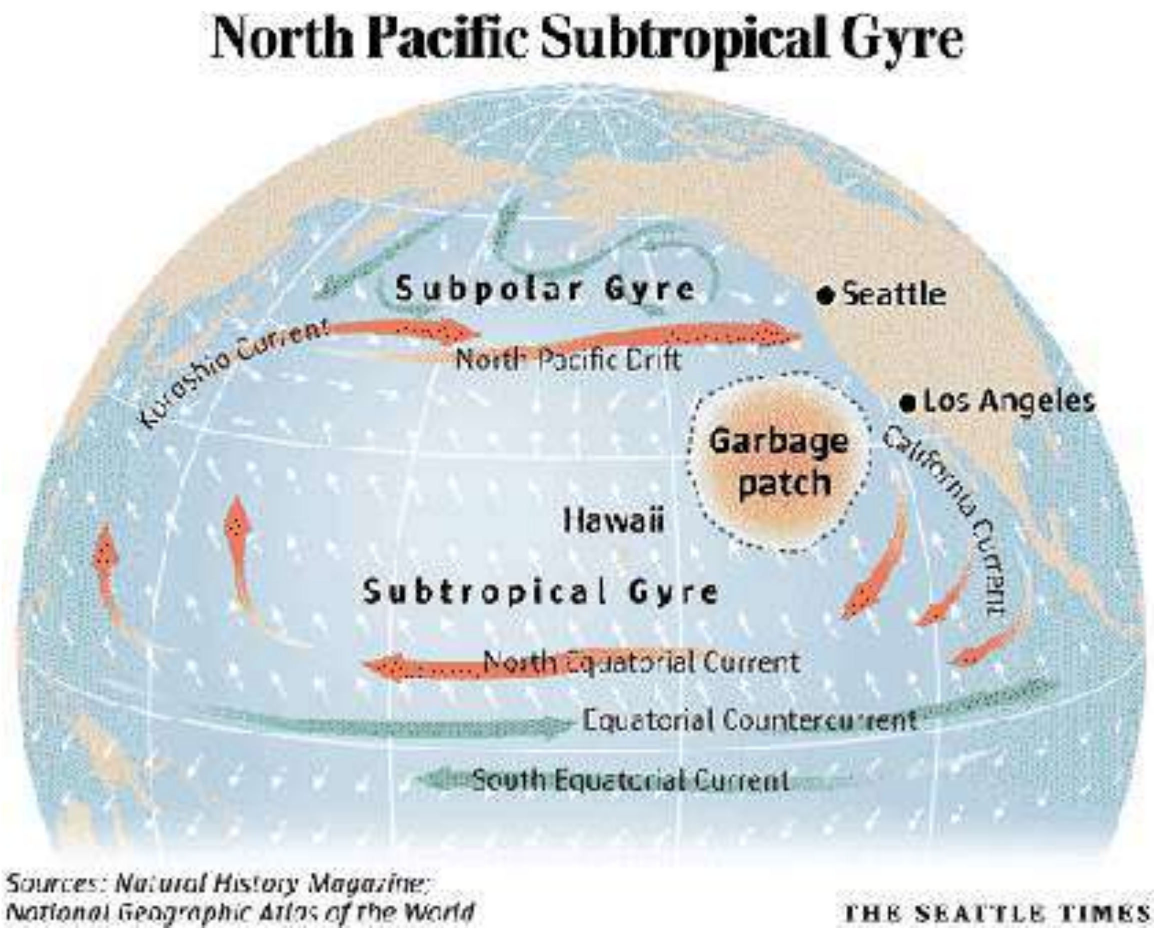


Figure 20.13. The North Pacific Subtropical Gyre concentrates plastic waste into a garbage patch.

Plastic pollution can lead to the death of marine organisms as they get trapped in larger debris, or if they ingest enough plastic to prevent proper digestion of food. (Figure 20.14).

Figure 20.14. Top: seal trapped in plastic debris. Bottom: carcass of seabird found with plastic filling its digestive tract. It is highly likely that this bird die of starvation due to this plastic.

Plastics may also have toxic effects on marine life, as plastics readily absorb and concentrate toxins and persistent organic pollutants (POPs). Because much of marine plastic pollution is from plastics of very small sizes they can ben ingested by organisms as low trophic levels and may contribute to the biomagnification of toxic compounds.

20.3.4. Excess nutrients

Eutrophication refers to the anthropogenic addition of dissolved nutrients to coastal waters. This mostly occurs through agricultural activities as nutrients added to fields as fertilizers can wash downstream, and through the release of sewage. The nutrient stimulation of primary production in coastal waters often results in hypoxia through the decomposition of plankton following blooms (Figures 20.15 and 20.16). Aquaculture activities have also been associated with eutrophication and hypoxia, due to excess feed added in pens and waste from high densities of fish (Figure 20.17).

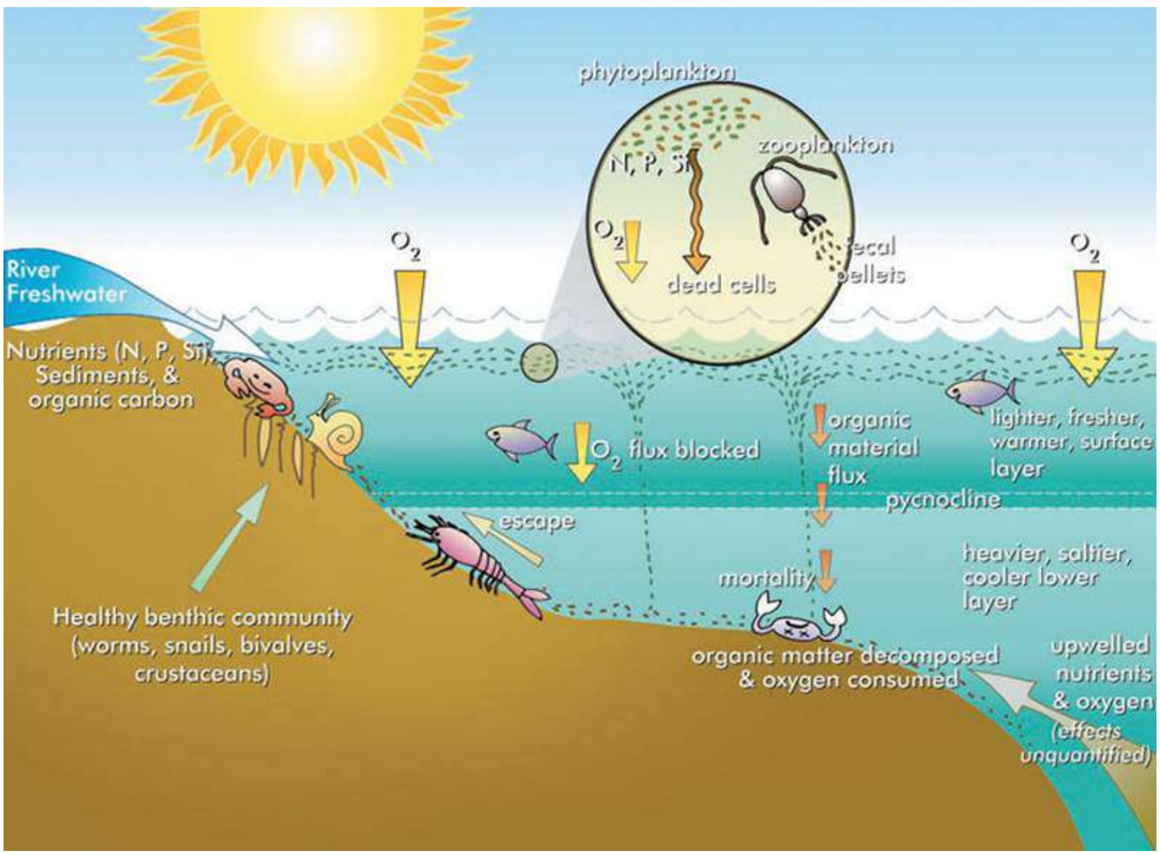


Figure 20.15. Nutrients brought to coastal zones through rivers lead to increased productivity. Organic material in surface waters (dead plankton, fecal pellets) eventually sinks below the pycnocline and decomposition of large amounts of organic matter can lead to very low levels or oxygen near the benthos.

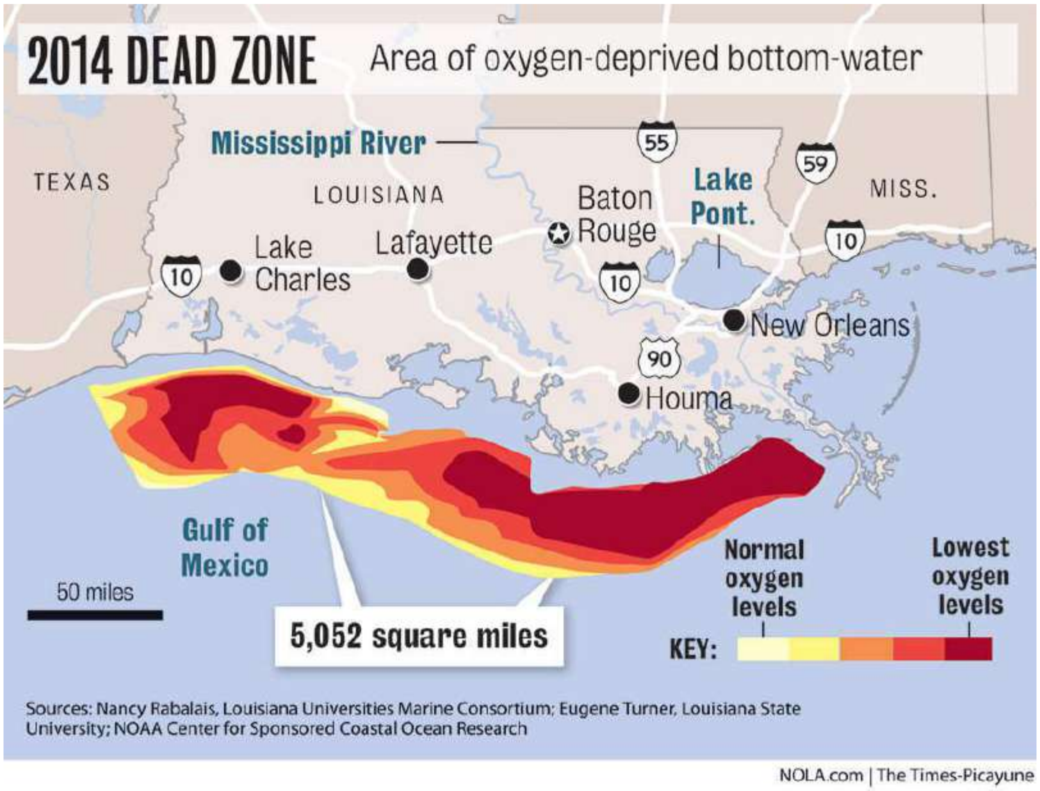


Figure 20.16. Eutrophication from agriculture through the Mississippi watershed leads to hypoxic zones in the northern Gulf of Mexico, often called dead zones.

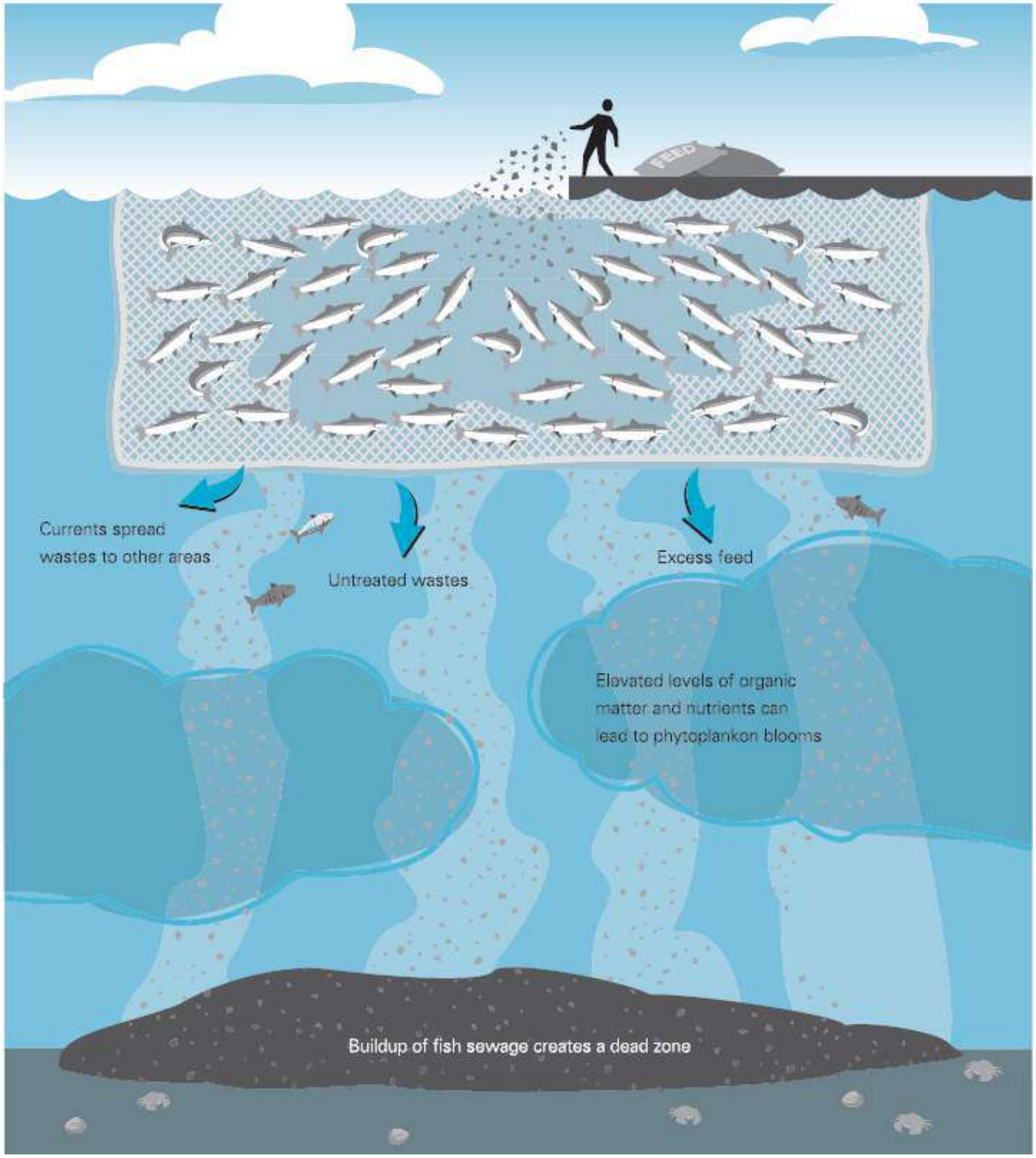


Figure 20.17. Mechanisms by which aquaculture can lead to eutrophication and hypoxia.

21. Marine Conservation

21.1. Marine Conservation Strategies

Environmental managers and conservation biologists may employ various strategies to conserve the marine environment. The best strategy may vary with location, specific ecosystem, and history of human impact. In many instances, conservation efforts focus on biodiversity hotspots—areas that have a high level of species diversity. By focusing on those areas, we might protect a greater number of species for a given effort, and maintain high species diversity. In other cases, conservation might focus on particular species—perhaps those that are endangered or at high risk of becoming endangered. Focusing on one particular species can still be beneficial for other species for example by maintaining key trophic interactions or ecosystem processes, or in the case of umbrella species, because protecting the species indirectly protects many other species in its habitat.

When establishing conservation goals, it is important to remember that many ecosystems were already substantially changed centuries ago by human activities, and continue to be modified by humans. For example, the Stellar Sea Cow went extinct in 1768 and the Caribbean Monk Seal was extinct in the eastern Caribbean by the early 1700s. Corals on the Caribbean coast of central America show a record of impact from deforestation-associated sediment as early as the 1800s. In the 20th century, overexploitation and climate change have had strong impacts on the composition of marine ecosystems, but often the extent of these changes are not entirely understood. This is the problem of shifting baselines—the fact that the “baseline” against which we measure ecosystem health may not represent a pristine state (Figure 21.1). Therefore, as managers attempt to assess the impact of their strategies on marine ecosystems, it is important that they keep in mind how ecosystems have changed over time.

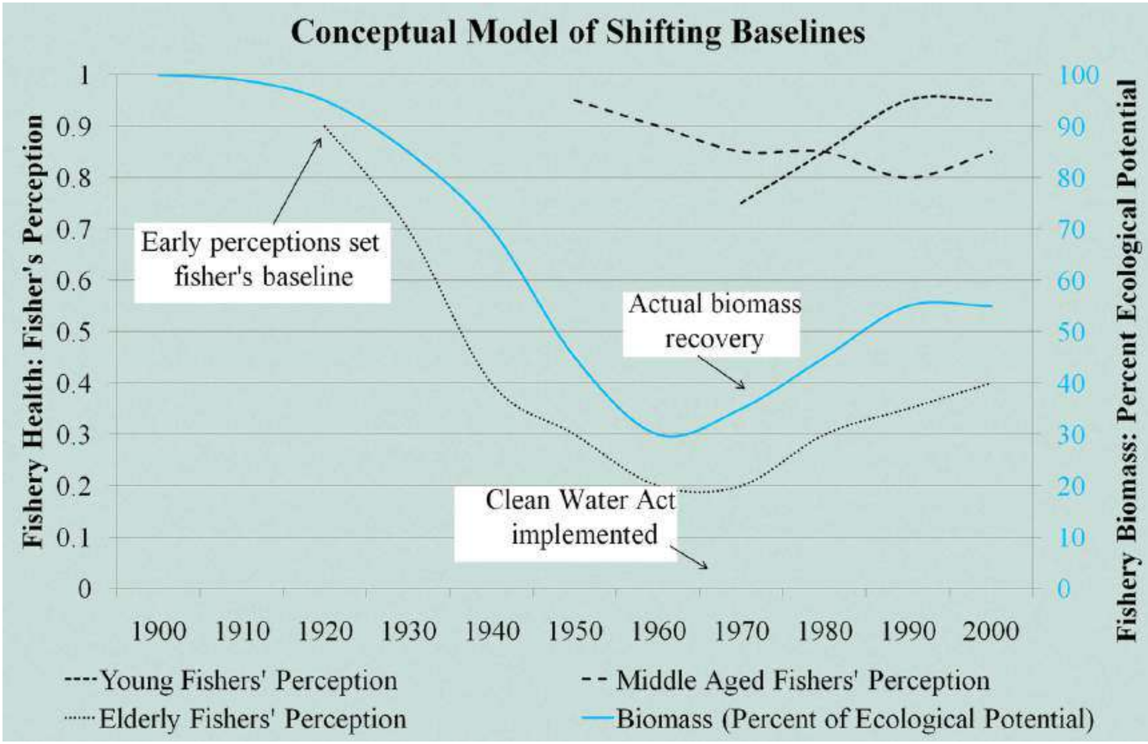


Figure 21.1. The concept shifting baseline suggests that each generation tends to evaluate change (e.g. environment change such as population or biodiversity decline) based on its own experience. This can mask the big declines that might be seen if a longer time frame were analyzed. In this graph, elderly fisher's perception of the changing fish biomass is correct, while young fishermen only see an increase in biomass and interpret this to mean that the fish are close to their full ecological potential.

21.2. Marine Protected Areas: Spatial Protection

A marine protected area (MPA) is essentially a space in the ocean where human activities are more strictly regulated than the surrounding waters - similar to parks on land. These may be managed by local, state, territorial, native, regional, or national authorities. There are many kinds of MPAs which can have a wide range of conservation objectives. Such objectives can include

- To ensure the long-term viability and maintaining the genetic diversity of marine species
- To protect depleted, threatened, rare or endangered species and populations
- To preserve entire ecosystems, including habitats considered critical for the survival and/or lifecycles of species, including economically important species
- To provide for the continued welfare of people affected by the creation of marine protected areas;
- To preserve, and manage historical and cultural sites and natural aesthetic values of marine areas

MPAs may be forbid extractive activities altogether (no-take zones or marine reserves), or may allow some level of fishing (e.g. during certain times of the year, or at some low rate. Many MPAs are multiple-use areas, where some areas are no-take zones while others allow some fishing activities (e.g. Figure 21.2).

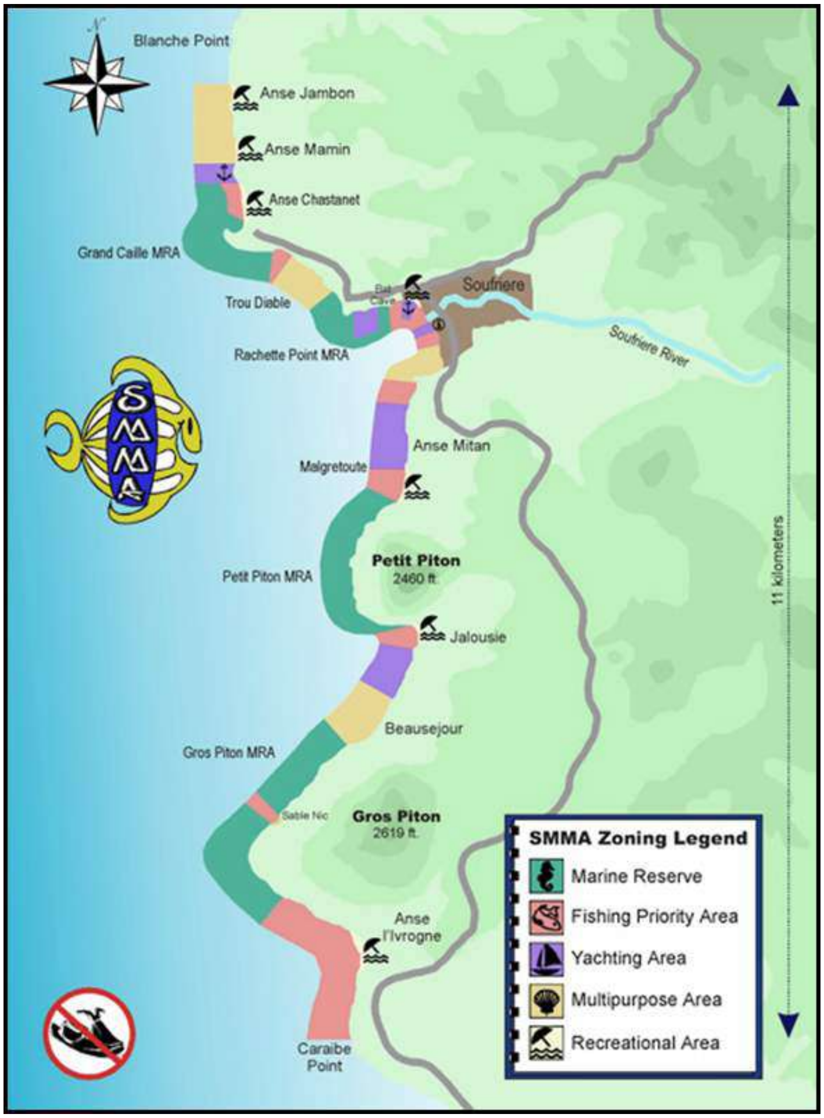


Figure 21.2. Zones of the Soufriere Marine Management Area in Saint Lucia. Green areas indicate marine reserves (no-take zones), while others allow some fishing activities.

21.2.1. Benefits of Marine Protected Areas

Marine reserves have been shows to increase the size of populations inside their boundaries even at relatively small sizes (Figure 21.3). Marine reserves have also been shown to increase biodiversity and to increase the average size of fish. Further, these benefits may also extend beyond the boundaries of the reserves through a process called the spillover effect: as populations protected from harvesting grow in size and reach carrying capacity, a greater number of larvae will drift out of the reserve and more adults will migrate out. Therefore, while the establishment of a marine reserve can lower the total area that fishermen can fish, it can increase overall catches (Figure 21.4). However, it can take 15 years or more for the benefits of MPAs to be measured—hence managers and communities must commit to a significant effort to yield the potential benefits of MPAs.

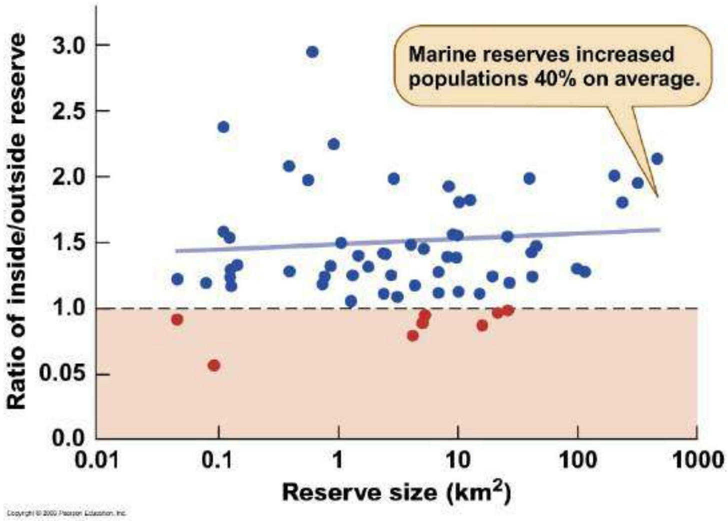


Figure 21.3. Marine reserves across a range of size lead to larger fish densities inside their boundaries compared to outside their boundaries.

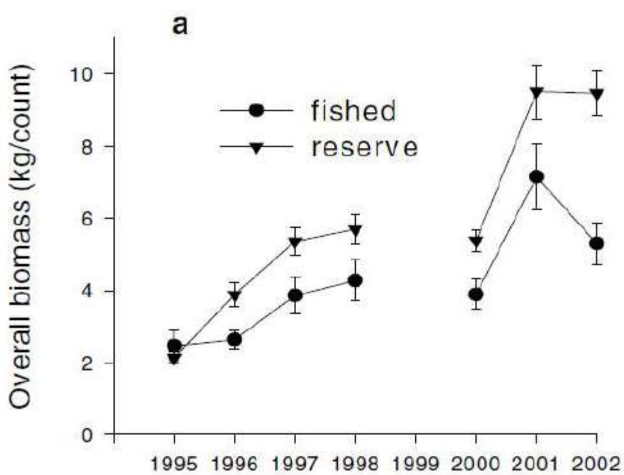


Figure 21.4. Change in fish biomass inside reserves and in nearby fished zones following the establishment of a network of marine reserves in Soufriere, Saint Lucia. Note that fish biomass increased both inside and outside reserves, though the increase was more pronounced inside the reserves. From Hawkins et al 2006, Biological Conservation 127:487-499.

21.2.2. Reserve size and design

While every situation is different, there are general principles that tend to increase the efficacy of reserves. Larger reserves tend to work better than small reserves (Figure 21.5b), as they protect larger populations which have a lower risk of extinction. Large and unfragmented reserves (Figure 21.5c) reduce the edge effect, changes in population or community structures that occur at the boundary of two habitats. Typically, a greater number of reserves should be preferred over a smaller number (Figure 21.5d), especially if the reserves in the network are in close enough proximity to one another. I cases where reserves are isolated, habitat corridors or stepping stone can increase connectivity (gene flow, through larval export or migration) between reserves and thereby increase effective population size and genetic diversity (Figure 21.5e and f). Finally, reserves that protect entire ecosystems, or connected ecosystems, may have greater success than those that only focus on a narrow part of an ecosystem (Figure 21.5a). For example, reserve protecting coral reef ecosystems near tall volcanic islands may have much greater success if they have some jurisdiction over the upstream watershed and can work to prevent erosion and excess sedimentation. Additionally, since many coral reef fishes spend their juvenile stages in nearby mangrove or seagrass ecosystems, marine reserves will likely be much more successful if they also include those areas.

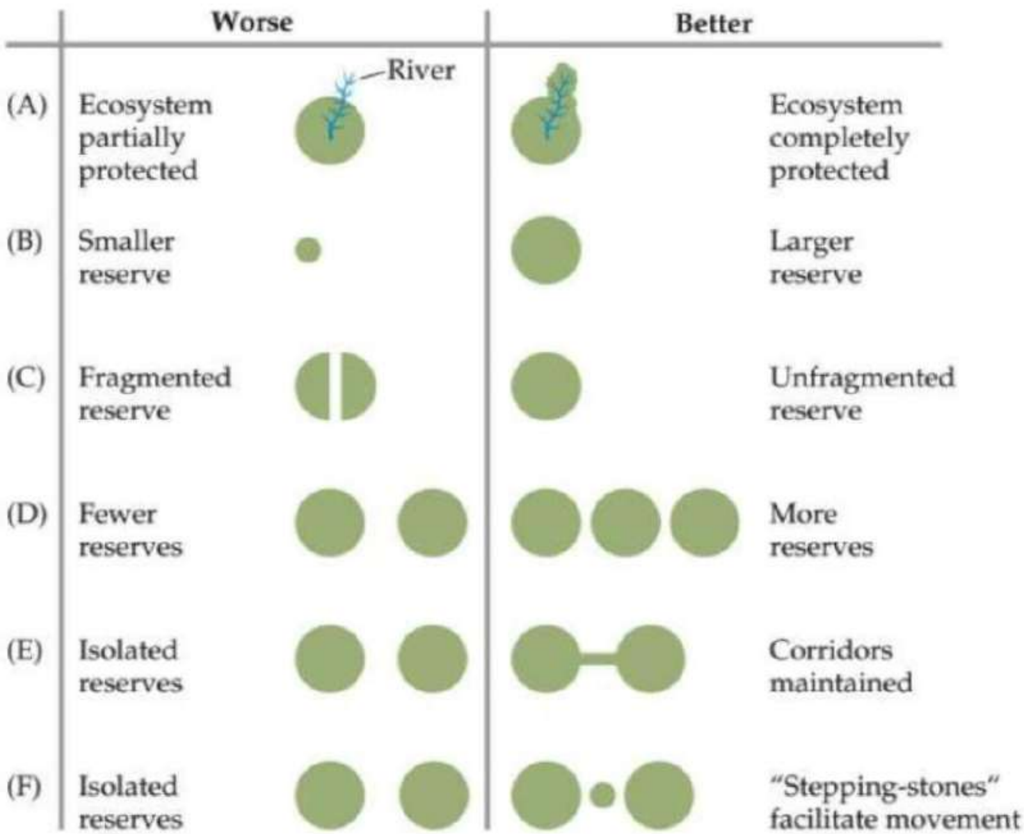


Figure 21.4. General principles of reserve design.

21.2.3. Community involvement and co-management

Like terrestrial parks, marine protected areas have historically been planned and implemented through a top-down, legislative approach by federal or state government agencies. However, these government-managed MPAs have been criticized for excluding resource users (e.g. local fishermen) in the decision-making process, and have often caused or exacerbated conflicts in coastal human communities. Marine resource managers are increasingly including more bottom-up, community engagement in their management strategies. Involving all stakeholders in the establishment process can lead to easier enforcement, reduced conflicts, and greater exchange of information at all levels. Many MPAs are thus "co-managed", with strong involvement from both government and the community. In some cases, communities entirely lead the creation and enforcement of small MPAs, and in many cases these community MPAs have been shown to increase the biomass and size of fish, though not to the same extent as older and often larger government MPAs.

21.2.4. Limitations of MPAs

Regulations dictated by MPAs primarily focus on fishing limitations and MPAs do help increase the biomass of harvested species. However, MPAs may not be adequate in protecting entire ecosystems, in particular if significant stressors remain. For example, MPAs may be beneficial to corals by helping maintain healthy populations of herbivorous fishes, which in turn reduce the cover of macroalgae that competes with coral for spaces. Yet corals inside MPAs remain vulnerable to threats such as runoff, storms, disease, increasing water temperatures and ocean acidification, which originate outside reserves. For example, Therefore, to achieve the greatest success, MPAs should either have some jurisdiction over activities in upstream watersheds and nearby ecosystems, or be located in an area with low levels of external stressors. Global stressors such as climate change will also need to be addressed for the long-term persistence of marine ecosystems, inside and outside MPAs.

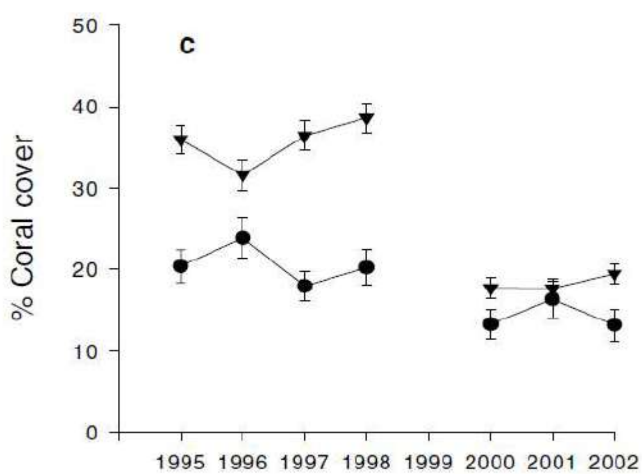


Figure 21.5. Change in live coral cover inside reserves and in nearby fished zones following the establishment of a network of marine reserves in Soufriere, Saint Lucia. Note that even though fish biomass increased over time (Figure 21.4), coral declined at all sites—largely from sediment stress due to uncontrolled erosion in upstream watersheds. From Hawkins et al 2006, Biological Conservation 127:487-499.

21.2.5. Very large MPAs

Under the CBD's Aichi Biodiversity Targets, Target 11 specifically aims to protect 10% of all marine waters by 2020. Since 2000, several very large MPAs have been established (or expanded from a previously smaller MPA, in the case of the Great Barrier Reef Marine Park) which directly contributes to this goal of protecting a larger proportion of our oceans. Very large MPAs include a variety of habitats and species assemblages and inherently connect various ecosystems and communities without the non-protected areas found in networks of small reserves. Many large MPAs encompass significant portions of the range of large and highly migratory species, such as tuna and marine mammals, thereby providing such species with protection measures not afforded by smaller MPAs. Those very large MPAs that are established in remote areas also protect ecosystem that have had little fishing pressure and are generally in good condition. Yet it can be difficult to establish and manage large MPAs. Several large MPAs have faced significant political and economic objections from powerful lobbies such as the industrial fishing interests, due to the value of the resources that may no longer be extracted. Large MPAs also have a greater overall cost of surveillance and management, frequently require coordination between many agencies, and are more difficult to enforce. However, despite these difficulties, there is broad agreement that very large MPAs are a necessarily tool to help achieve our biodiversity conservation goals, and there seems to be political momentum to support existing and future large MPAs.

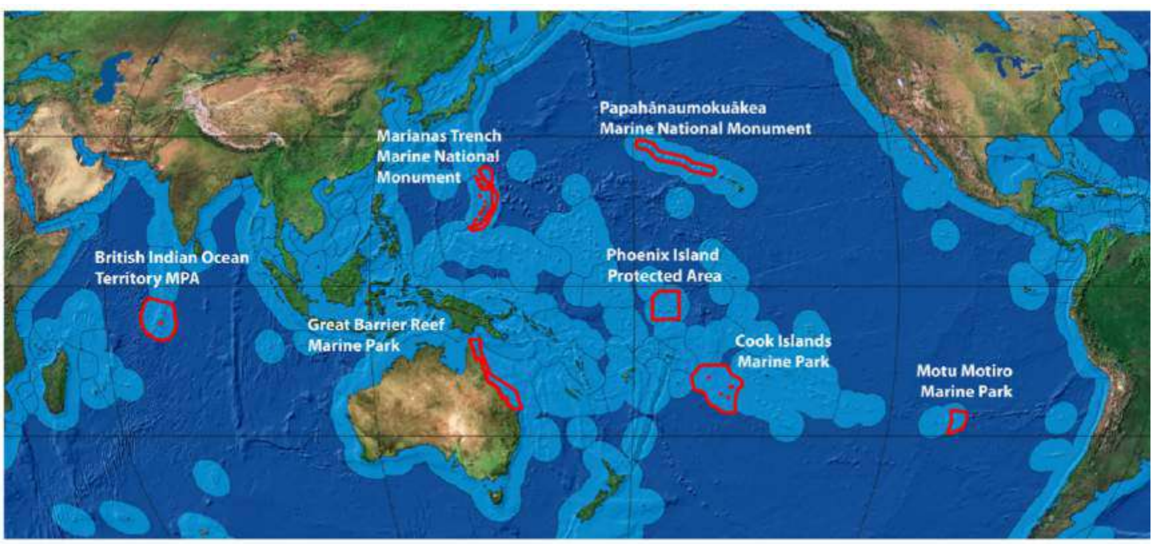


Figure 21.6. Map showing the location of the seven pioneer large-scale MPAs (from Wilhelm et al 2014, Aquatic Conserv: Mar. Freshw. Ecosyst. 24 (Suppl. 2): 24–30)

21.3. Controlling marine pollution

Regulations to reduce marine pollution vary from country to country. Given that the sources and nature of pollutants are quite varied, there are many different types of laws and strategies to limit marine pollution.

21.3.1. Marine Plastics

United Nation's International Convention for the Prevention of Pollution from Ships (MARPOL), prohibits the dumping of plastics anywhere in the ocean. Most countries also have federal regulations that prohibits intentional dumping of plastics. While this is a positive step, it still doesn't prevent much of the plastic pollution that enters our waters, e.g. plastic bags and bottles improperly disposed of, and accidental release of plastic nurdles during shipping (pre-production microplastic resin pellets typically under 5 mm (0.20 in) in diameter), and microbeads from cosmetics. Recycling programs have played an important role in reducing plastic waste, as have programs to reduce the use of plastics (e.g. banning single use plastic products, introduction of biodegradable options). There are also large-scale initiatives to actively remove plastics from ocean, e.g. the Ocean Clean-Up Project (Figure 21.7).

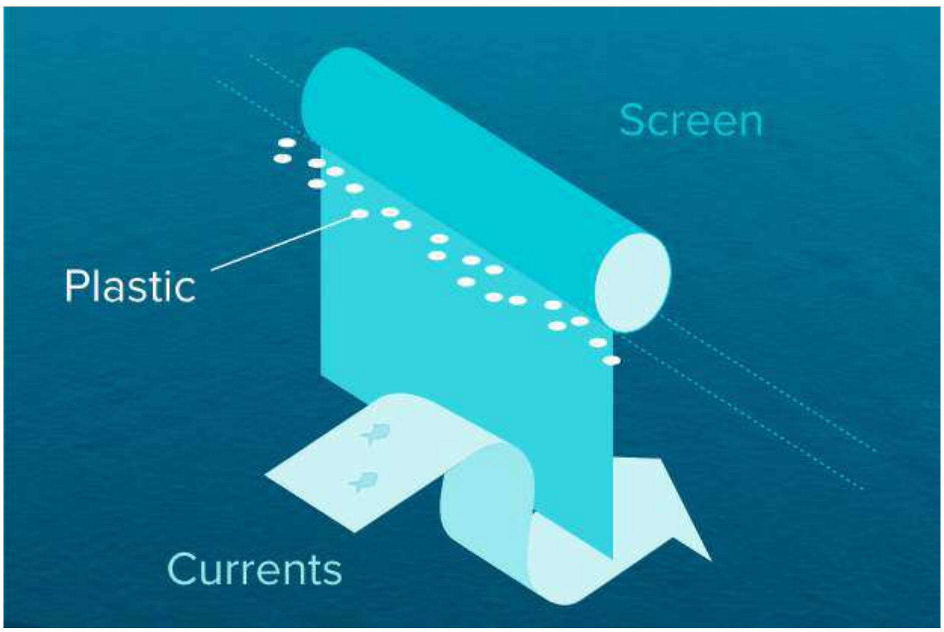


Figure 21.7. Diagram of plastic-catching screen deployed as part of the Ocean Clean Up project, to remove plastic from ocean gyres. From www.theoceancleanup.com

21.3.2. Heavy Metals

Sources of heavy metals include mining, industrial production (foundries, smelters, oil refineries, petrochemical plants, pesticide production, chemical industry), untreated sewage sludge and diffuse sources such as metal piping, traffic and combustion by-products from coal-burning power stations. Antifouling paints used on vessels is also a concern, especially in areas of high vessel density. According to a United Nations report, an increasingly serious global problem is the management of electronic waste, particularly the disposal of used computers and mobile phones, which contain over 1 000 different materials, many of which are toxic to humans. Lead, methylmercury, copper and cadmium are some of the most important heavy metal pollutions, and all can pose serious health risks as they magnify up the food chain.

One of the great difficulties in reducing heavy metals concentrations for any one government is that heavy metals can readily be transported for long distances in the atmosphere and through rivers. Some of the regions worse affected by heavy metal

pollution are far removed from the greatest production of these chemicals. For example, zooplankton in the Arctic have a higher concentration of methylmercury than similar species at mid-latitudes, and concentrations of methylmercury are so high foods of Inuit children (including seal and beluga meat) that it appears to have caused a decline in IQ of 5 points. For this reason, international regulation is highly desirable.
There are many international conventions that regulate the emission, use and disposal of heavy metals and other toxic chemicals. Copper is now banned from use in anti-fouling paint. The removal of lead in gasoline was also part of an effort to reduce environmental contamination.

21.3.3. Oil
While much of oil pollution is chronic non-point source pollution, regulations can more readily target acute leaks and spills. Specific regulations vary from country to country, but broadly address prevention, containment/removal at sea, and clean up in coastal areas.

Prevention
The International Maritime organization has established several regulations aimed at reducing the likelihood of hull breaches in oil tankers (e.g. through grounding or collision with another vessel) and reducing the likelihood of an oil leak, should the hull be compromised. The navigation equipment and steering gear on oil tankers must be replicated, so that in the event of failure of the main equipment, the tanker can still navigate safely. Additionally, tankers of 20,000 tons and above have to be fitted with an emergency towing arrangement. The International Convention for the Prevention of Pollution by Ships (MARPOL) includes regulations regarding subdivision and stability which are designed to reduce the risk of oil being spilled, in the event of collision or grounding. For example, ships are prohibited to carry oil in the forepeak tank - the ship's most vulnerable point in the event of a collision. Tankers of 5,000 tons and more must be fitted with double hulls, which reduce the chance of damage to oil tanks in the event of an accident. Finally, all tankers and bulk carriers aged five years and over have been subject to an enhanced inspection program which is intended to ensure that any deficiencies - such as corrosion or wear and tear resulting from age or neglect - are detected.

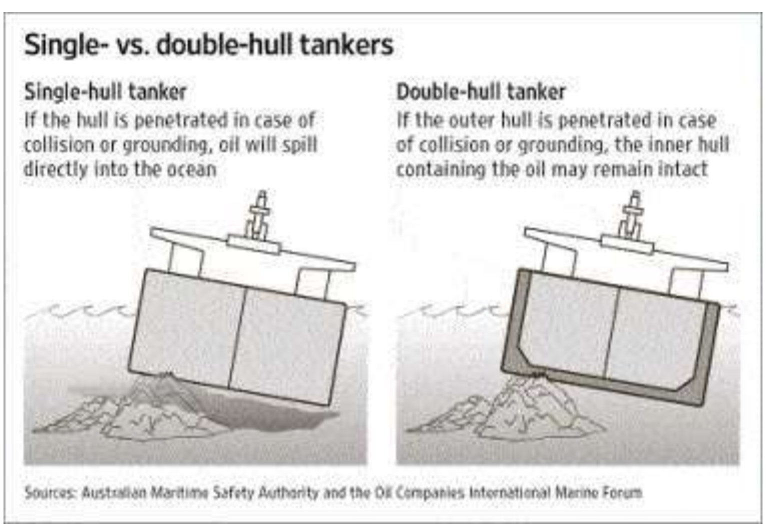


Figure 21.8. Double hulls on oil tankers are design to reduce the chance of an oil spill in the event of damage to the outer hull.

Containment and clean up/removal in open water

Once a spill has occurred, the spread of an oil slick can be limited with various kinds of equipment and tactics. Booms are floating, physical barriers to oil, made of plastic, metal, or other materials, which slow the spread of oil and keep it contained. Booms are deployed using mooring systems, such as anchors and land lines. Skimmers are boats and other devices that can remove oil from the sea surface before it reaches sensitive areas along a coastline. In some cases, response teams burn oil slicks before they reach the coast. To do this, responders corral some of the oil from the slick in a fire-proof boom, then ignite it. This technique works best when the oil is fresh and the weather relatively calm. Oil burning is controversial, however, because of the impact of the smoke emissions on air quality. One concern is that in situ burning merely substitutes one pollution problem (air) for another (water). However, it is important to recognize that unburned spilled oil presents air quality problems of its own. The volatile fraction of crude oil (approximately one third by volume) contains many toxic hydrocarbons which would normally evaporate and could create hazardous air concentrations in the vicinity of the spill. In situ burning would eliminate most of these vapors. Therefore, whether in-situ burning is of value will depend on many factors, including location and extent of the spill, weather conditions, and the chemistry of the oil spilled. Finally, chemical dispersants can be applied by boats and aircrafts, to help disperse the oil into the water column, so that much less stays at the surface, where it could affect beaches and tideflats. Chemical dispersants are extremely controversial, because they can be highly toxic to ecosystems and humans, and while they may reduce the impact of oil on surface/intertidal organisms, they may increase the impact at depth and the overall incorporation of oil compounds into the ecosystem.

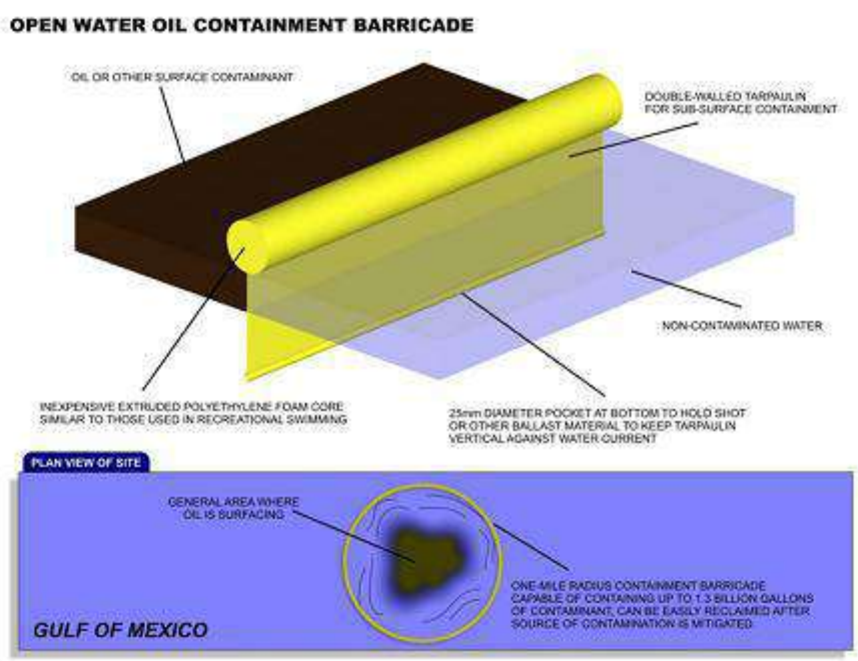


Figure 21.9. Oil-containment booms may be made of different materials (plastic, metal, oil-absorbent materials). The diagram here shows one possible type of boom, with a tarpaulin attached to a foam float.

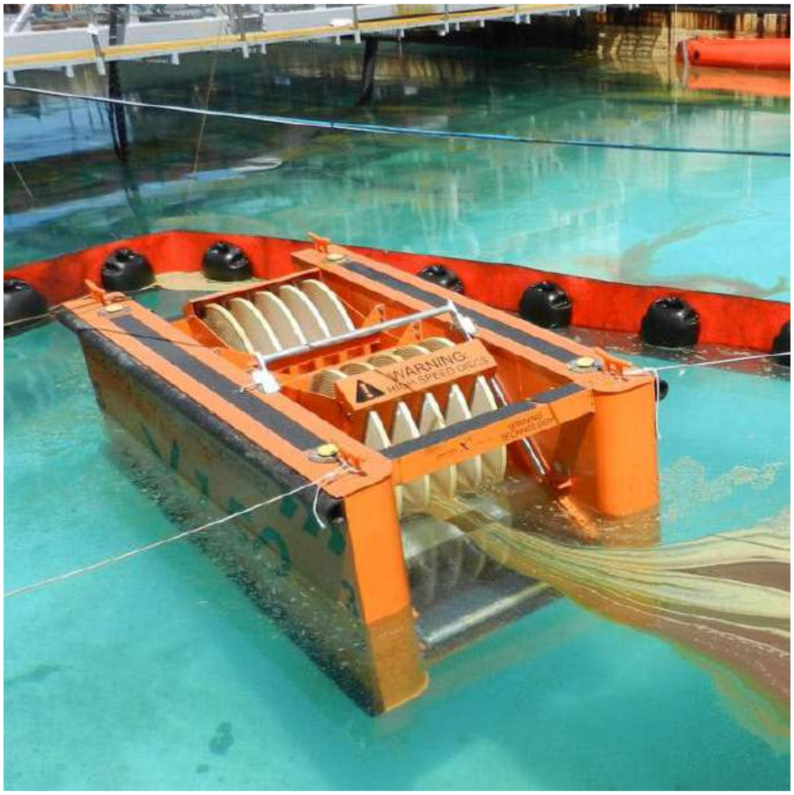


Figure 21.10. This skimmer is made with an oil-attracting material, which means oil adheres to the drum or disc and is separated from the water's surface. This type of selective skimmer recovers a high concentration of oil and very little water.

Clean up in coastal areas

Once oil reaches shorelines, high-pressure, hot-water washing is often used for removing stranded oil from hard surfaces, like large rocks and seawalls. However, while effective, it can directly and indirectly injure and kill plants and animals in the treated zone, both in the short-term and long-term. Additionally, when it is used incorrectly, high pressure water streams may drive oil into the beach sediments where oil may become trapped or further contaminate clean areas. Finally, using high pressure or large volumes of water can wash away fine sand and silt from shorelines and disrupt the structure of the beach. For these reasons, steam washing is now rarely used to clean up spills.

Because birds can be particularly affected by oil, in many cases clean-up efforts will include specific efforts to clean oiled birds. Oil is removed from feathers with a series of tub washes with low concentration of Dawn liquid detergent. Once oil is removed, birds are rinsed and dried. Birds are allowed to preen their feathers back into place, which is necessary for their insulation to be effective. Birds are then placed in warm tubs to continue preening while the natural waterproofing of their feathers returns, and are closely monitored for good health and normal behavior before being released.

Bioremediation

Bioremediation involves using biological organisms to consume and break down environmental pollutants, in order to clean up a polluted site. Most hydrocarbons in crude oil are biodegradable, and some species of bacteria can even convert polycyclic aromatic hydrocarbons (PAHs, the most toxic to plants and animals) completely to biomass, CO_2, and H_2O, if oxygen is added to the system. Bioremediation efforts may involve introducing bioremediation organisms to a spill area, and/or involved adding nutrients (e.g. nitrates (NO_3^-), phosphates (PO_4^{3-}), and iron (Fe)) to speed up the rates of oil biodegradation. Bioremediation may be done in open water or along coastlines.

21.3.4. Eutrophication

Specific measures to prevent nutrient overload depend on the activities responsible for eutrophication in a given area. Where agriculture is important, excess nutrients can be avoided through limiting the use of artificial fertilizers in fields. In aquaculture facilities, placing the facilities in areas with fast currents, using low stocking densities and only using the amount of feed needed are some of the practices that can control eutrophication. Excess nutrients caused by sewage can be controlled through more extensive treatment of sewage, and/or using sewage sludge as agriculture fertilizer.

21.4. Ecosystem restoration

Since climate change is a global phenomenon, one could argue that there are no truly pristine ecosystems in the world (i.e. ecosystems that show no impact from human activities). Yet some marine ecosystems, in particular those very far from large human populations, are relatively pristine. Others are so heavily degraded that even with regulations that address the causes of the degradation, the ecosystem may take some time to recover. In many instances, humans can speed up with process through ecosystem restoration efforts. Ecosystem restoration is a broad concept that includes many different activities. Here, we will go over a few of the most important ones.

21.4.1. Habitat rehabilitation

When degradation affects the biotic and abiotic components that create a habitat for many species in an ecosystem, the ecosystem is unlikely to recover until these species or structures are re-established, hence restoration efforts may focus on habitat rehabilitation. For example, Tampa Bay (Florida) saw massive declines of seagrasses in latter half of the 20th century, largely due to eutrophication and boating activities. By the turn of the century, the eutrophication problem had been largely solved, and there was an aggressive effort to plant seagrasses throughout the bay, in order to speed up the recovery. This was a massive success, and seagrass biomass is now back to levels not seen since the 1950s. In many areas, similar efforts have been done with planting mangroves on shorelines.

Restoration of coral reef habitat can be done in a number of ways. In many instances, new colonies are grown from coral fragments broken from larger colonies. In other cases, eggs and sperm are collected during mass spawning events, and new, genetically unique colonies are grown from the fertilized gametes. Small coral colonies may be grown in the lab or suspended in shallow waters that offer optimum growing conditions and are monitored for signs of stress and disease. Eventually, the growing colonies are attached to a living reef—typically with some type of cement.

Figure 21.11. Fragments of *Acropora cervicornis* coral, growing in shallow water before being transplanted on the reef.

21.4.2. Artificial reefs

When the lack of available hard structure is an important limiting factor for the health of a biological community, marine managers may opt to build artificial reefs—which can provide a substrate for the attachment of encrusting organisms (e.g. corals, sponges, bryozoans, etc…) and shelter for many fish and invertebrates. Submerged shipwrecks are the most common form of artificial reef. Oil and gas platforms, bridges, lighthouses, and other offshore structures often function as artificial reefs. When repurposing a shipwreck or other structure into an artificial reef, it is important that the wreck for be stripped of and fuel, oil, and other toxic materials. Purpose-built artificial reefs are also commonly used, and may be as simple as a structure of cinder blocks fastened together. In other cases, cement is used to make artificial reefs of various shapes, from dome structures promoted by the Reef Ball foundation (Figure 21.12), to works of art that may be quite attractive to some snorkelers or divers (Figure 21.13). Recently, artificial reefs have also been created by putting low electrical voltage through a metal structure, which causes the deposition of calcium carbonate onto the structure. The artificial reef can then readily be colonized by settling coral. This process, called electro-mineral accretion, can be powered by solar panels, and has been achieved successfully in many locations to speed up the colonization or artificial reefs by coral (Figure 21.14 & 21.15).

Figure 21.12. Artificial reefs created based on the mold/process promoted by the Reef Ball foundation. The holes in the balls are to facilitate the movement of small fish and invertebrates in and out of the Reef Ball.

Figure 21.13. One of many underwater sculptures located in Grenada. Others can be found around Cancun.

Figure 21.14. Artificial reef created by electro-mineral accretion.

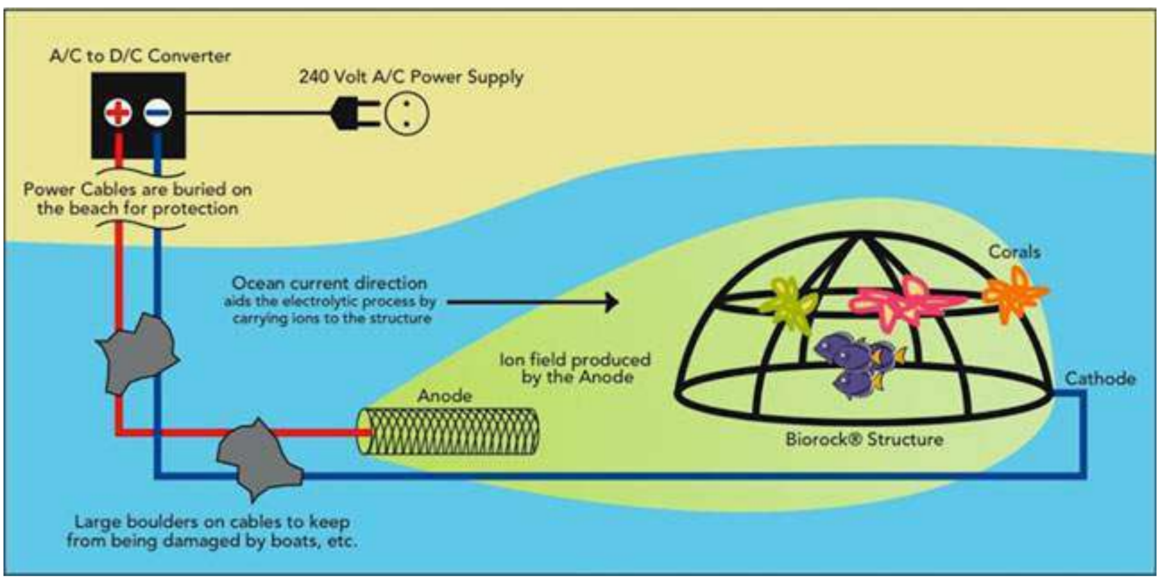


Figure 21.15. Process of electro-mineral accretion. This process has been popularized under the name BioRock, by the Global Coral Reef Alliance.

21.4.3. Captive breeding

Captive breeding programs with the goal of reintroduction into wild ecosystems have existed since the 1960s. These programs have historically focused on terrestrial species and several of these species would now be extinct if not for captive breeding. However, captive breeding of marine organisms for conservation purposes has been much more limited. Dolphins and other small marine mammals have been bred successfully in aquaria, but these programs are typically aimed at keeping offspring in aquaria, rather than at reintroductions to wild populations. Some captive breeding programs may have beneficial impacts on marine ecosystems, even if the offspring are not reintroduced to the wild. For example, many fish species that are popular in the aquarium trade are now bred in captivity rather than harvested in the wild—clownfish being one of the most important of these species. This will reduce pressure on wild populations, and on the coral reefs (and other habitats) that are often damaged in the process of catching these fishes. Finally, there are a handful of programs that breed marine species in captivity, for the specific purpose of reintroduction to the wild. These include several species of tropical and temperate fish, crustaceans (including shrimp) and mollusks, such as the endangered white abalone in California.

21.5. Endangered species legislation

While the conservations measures discussed so far in this chapter may affect entire ecosystems, in some cases there is a need to enact legislation for specific species within an ecosystem. This is often the case in fisheries management, where quotas set for individual species. It is also the case when species are threatened or endangered. In the US, the Endangered Species Act (ESA) provides a program for the conservation of threatened and endangered plants and animals and the habitats in which they are found. Once a species is in the endangered species list, the law not only prohibits the harvesting, import and export of the species, but also mandates that federal agencies ensure their actions are not likely to jeopardize the continued existence of the listed species or result in the destruction or adverse modification of its designated critical habitat. This means that the Endangered Species Act allows from a wide variety of specific regulations to help conserve listed species. At an international level, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) is an agreement signed by 183 countries that regulates the trade of plants and animals. There are over 35,000 species on the CITES list, and once a species is listed, it cannot be traded between countries without special approval.

22. Marine Conservation in Small Island Developing States

The United Nations recognizes 52 countries and territories as Small Island Developing States (SIDS; Figure 22.1). The vast majority of them (43) are found in the Caribbean and Pacific regions. SIDS vary greatly in size, environmental features, and economic status, but as a group they tend to share the following challenges:

- Production sectors heavily dependent on their limited natural resource base (e.g., agriculture, forestry, fishing, tourism).
- Scarce land resources.
- Increasing pressures on coastal and marine environments and resources.
- High transportation and communication costs.
- Serious vulnerability to extreme climate events and other natural disasters (e.g. tropical storms, tsunamis, volcanic eruptions.
- Shifting patterns of rainfall and tropical storm activity
- Small domestic markets.
- Limited ability to develop economies of scale.
- High import content (especially of strategic imports such as food and fuel).
- Limited economic diversification possibilities.
- Dependence on a narrow range of export products.

In short, SIDS have an exceptionally dependence on their limited natural resources. Therefore, effective management of marine ecosystems is especially critical for the long-term well-being of these nations. Since the SIDS recognized by the UN are all located in the tropics, we will focus here on the issue of marine management in tropical SIDS.

List of Small Island Developing States (UN Members)			
1	Antigua and Barbuda	20	Federated States of Micronesia
2	Bahamas	21	Mauritius
3	Bahrain	22	Nauru
4	Barbados	23	Palau
5	Belize	24	Papua New Guinea
6	Cape Verde*	25	Samoa*
7	Comoros*	26	São Tomé and Principe*
8	Cuba	27	Singapore
9	Dominica	28	St. Kitts and Nevis
10	Dominican Republic	29	St. Lucia
11	Fiji	30	St. Vincent and the Grenadines
12	Grenada	31	Seychelles
13	Guinea-Bissau*	32	Solomon Islands*
14	Guyana	33	Suriname
15	Haiti*	34	Timor-Lesté*
16	Jamaica	35	Tonga
17	Kiribati*	36	Trinidad and Tobago
18	Maldives*	37	Tuvalu*
19	Marshall Islands	38	Vanuatu*

List of Small Island Developing States (Non-UN Members/Associate Members of the Regional Commissions)			
1	American Samoa	8	Guam
2	Anguilla	9	Montserrat
3	Aruba	10	Netherlands Antilles
4	British Virgin Islands	11	New Calendonia
5	Commonwealth of Northern Marianas	12	Niue
6	Cook Islands	13	Puerto Rico
7	French Polynesia	14	US Virgin Islands

*** Also LDCs**

Figure 22.1. The United Nation's list of Small Island Developing States. From: Small Island Economies: from Vulnerabilities to Opportunities. In: Brussels Rural Development Briefings A series of meetings on ACP-EUEU development issues.

22.1. Importance of tropical marine ecosystems to small island nations

22.1.1. Coral reefs

Coral reefs represent one of the most important natural resources of many tropical islands. They are a source of food, beach sand, and in some cases building materials. They function as natural breakwaters along the coasts of many tropical islands. They also provide habitats for many fish and invertebrates, and generate significant revenues for many small island economies through avenues such as tourism (e.g., snorkeling and scuba diving).

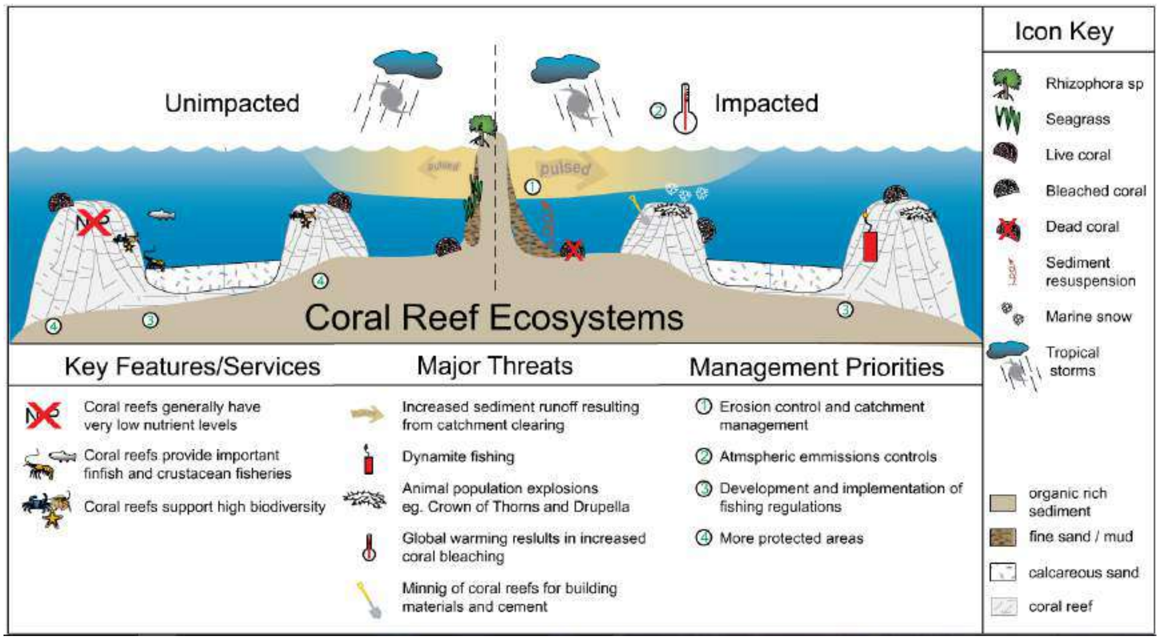


Figure 22.2. Some key characteristics and ecosystems services of coral reefs, and how they change in coral reefs heavily impacted by human activities. Source: Land Ocean Interactions in the Coastal Zone (LOICZ).

22.1.2. Mangroves

Many coral reef fishes spend their juvenile stages in mangrove roots, therefore hence any loss of mangroves is likely to also impact nearby coral reef ecosystems. Moreover, mangroves provide a diverse array of ecosystem services: they increase coastal protection against tropical storms, reduce coastal erosion, and function as a sink for sediment and nutrient runoff from the watershed.

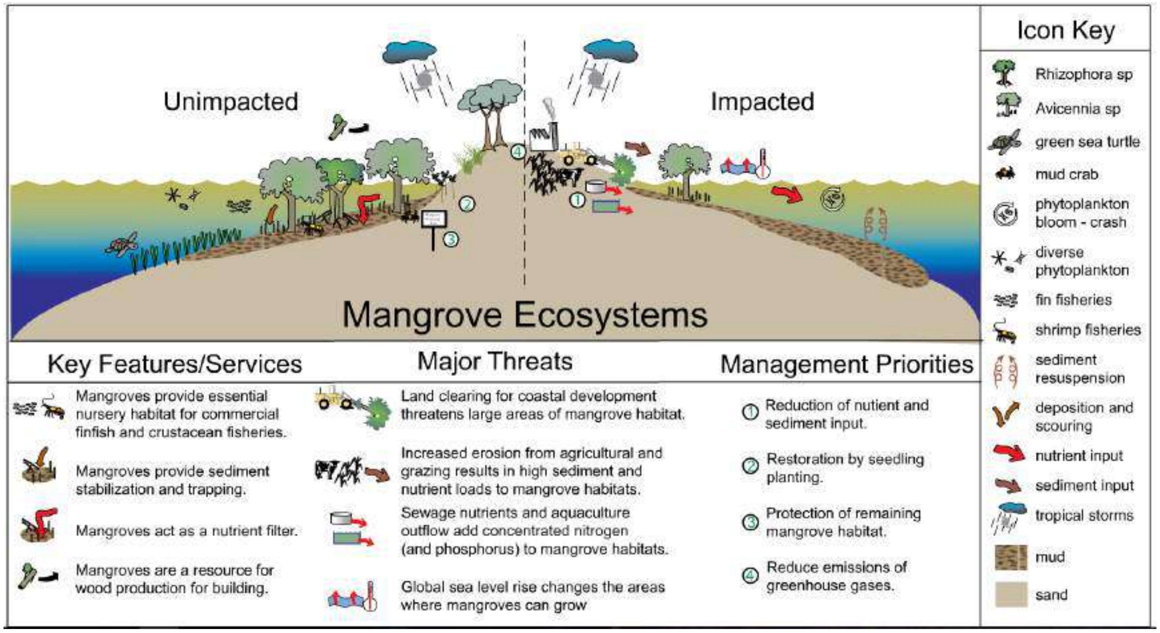


Figure 22.3. Some key characteristics and ecosystems services of mangrove ecosystems, and how they change in mangroves heavily impacted by human activities. Source: Land Ocean Interactions in the Coastal Zone (LOICZ).

22.1.3. Seagrasses

Seagrass communities provide habitat for many tropical marine fish, including many that are an important source of food in SIDS. Seagrasses also reduce erosion as the system of rhizomes of seagrass beds consolidates sediment. Finally, seagrasses are an important source of food for manatees, dugongs, and green sea turtles.

22.2. Changes in tropical marine ecosystems

22.2.1. Coral reefs

Coral reefs around the world have declined severely over the past several decades. This deterioration has been particularly severe in the Caribbean where live coral cover declined from about 50% of reefs in the 1970s to less than 10% by the early 2000s (Figure 22.5). This decline in coral has been accompanied by an increase in the prevalence of seaweeds, and in some cases a large increase in filamentous cyanobacteria. Many factors are responsible for this shift, including climate change, coastal development and overfishing. Increased sea surface temperatures associated with climate change have led to an increased frequency of bleaching events—during which coral lose their symbiotic algae. Prolonged bleaching episodes such as those seen in 1998, 2005 and 2015 have led to extensive coral mortality. Sub-lethal stress caused by bleaching is also linked to more widespread coral disease outbreaks. Agriculture and coastal development has led to erosion and increased sedimentation on downstream reefs; corals thrive in clear waters, and excess sediment reduces light available for photosynthesis, requires energy to remove, reduces the amount of substrate available for coral larvae to settle, and can smother coral. Agriculture and coastal development has also led to increased nutrients on many reefs, which favor macroalgae, sponges and cyanobacteria while being detrimental to coral. Unsustainable fishing practices have led to a large decline in reef fish biomass in many SIDS around the world (e.g. Figure 22.6). This decline of course affects human populations that depend on these reef fish for subsistence, but it also affects the entire ecosystem, as decreases in the abundance of herbivorous fish allow for greater growth of seaweeds which compete with coral for space on the reef.

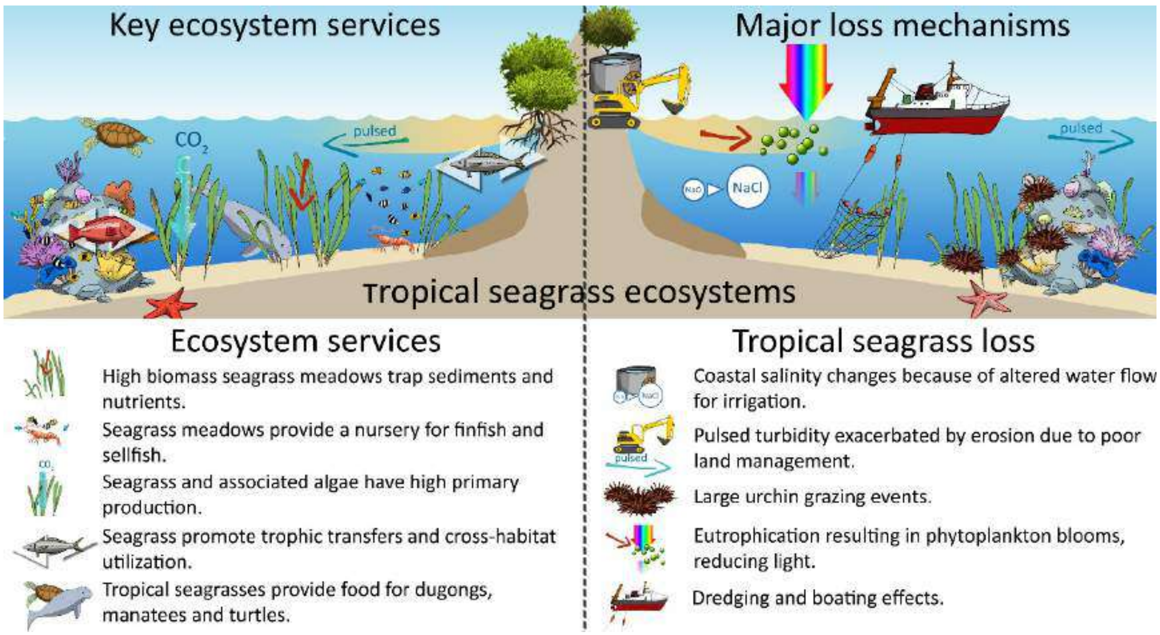


Figure 22.4. Some key characteristics and ecosystems services of seagrass ecosystems, and how they change in seagrass meadows heavily impacted by human activities. Source: Land Ocean Interactions in the Coastal Zone (LOICZ).

22.2.2. Mangroves

Mangrove forests have also seen significant declines in recent decades, from direct exploitation, clearing of mangroves for aquaculture ponds, and loss of mangrove habitat due to climate change. For example, the nation of Antigua and Barbuda (eastern Caribbean) is currently losing its mangrove ecosystems at an annual average rate of about 1.5–2%, with a sea-level rise of 3–4 mm a year. Based on this, it is estimated that there will be few, if any, mangroves left in this nation by 2075. If the sea level rises at a rate of 10 mm a year, mangroves could disappear from Antigua and Barbuda by as early as 2030 or 2035.

22.2.3. Seagrasses

Seagrasses have been disappearing at a rate comparable to that of mangroves and coral reef, and it is estimated that that 29% of the known areal extent has disappeared since seagrass areas were initially recorded in 1879. Furthermore, rates of decline have accelerated from a median of 0.9% per year before 1940 to 7% per year since 1990.

22.2.4. Marine habitat degradation and impacts on Small Island Developing States

The cumulative effect of the reported losses in seagrass, mangrove, and coral reef ecosystems signals a serious deterioration of coastal environments around the world. This is leading to serious concerns about food security in SIDS, and means the loss of many ecosystem services.

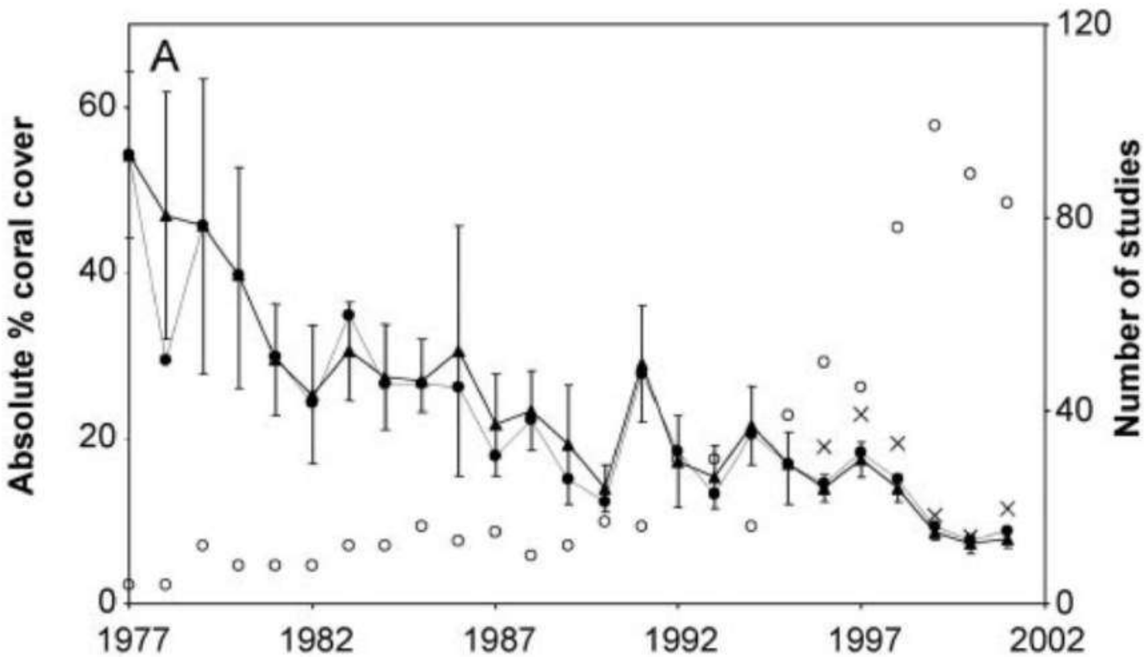


Figure 22.5. Changes in live coral cover in the Caribbean from 1977 to 2002. From Gardner et al 2003 Science.

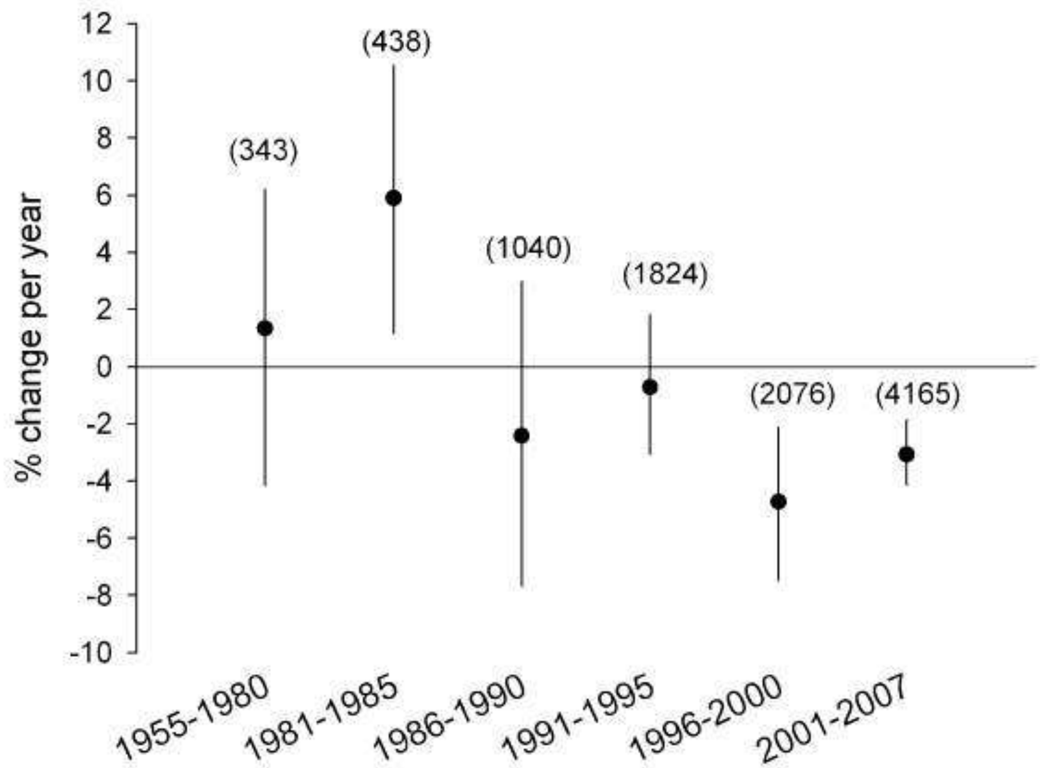


Figure 22.6. Change in reef fish biomass in the Caribbean from 1955 to 2007. From Paddack et al 2009 Current Biology. Note that from 1996-2007, reef fish biomass is declining at a rate of 3-5% annually.

22.3. Climate change and small island nations

The United Nations has identified climate change to be the most pressing environmental threat to SIDS. The United Nation's Environment Programme's (UNEP's) Small Island Developing States Foresight Report estimates that the 52 island nations, home to over 62 million people, emit less than one per cent of global greenhouse gases, yet they suffer disproportionately from climate change. Besides warming-associated coral bleaching, climate change-induced sea level rise is having a strong impact on island nations, in particular low-lying ones. This can impact coastal ecosystems (e.g. section 22.2), and human populations. Several such island nations have plans to facilitate the relocation of their citizens to neighboring countries, should the islands become uninhabitable. For example, the government of Kiribati has purchased land in Fiji as part of a plan to help the migration of Kiribati citizens when necessary. Tuvalu and the Maldives have both approached the Australian government with similar plans.

Climate change is also likely to lead to an increased frequency and increased strength of tropical storms for small island nations. At the United Nation's climate chance conference in Doha, the envoy from the Philippines made an emotional plea for all countries to act in order to limit climate change. The Philippines had just been struck by a typhoon that killed over 300 people.

22.4. Complexities of conservation in Small Developing Island States

Conservation efforts often represent a trade-off, e.g. between short-term economic growth and long-term sustainability, and it is important to realize that these trade-offs are often perceived and understood differently from different perspectives (e.g. fishermen, industry leaders, dive operators, hotel owner, etc…). These complexities are perhaps most acute in developing countries that are highly depending on their natural resources, such as SIDS. In SIDS, the reduction in fishing grounds (e.g. from the establishment of a marine reserve) may cause the loss of employment in an economy where other jobs are extremely scarce. In many cases, limits to fishing directly impact access to enough protein and calories for coastal communities. In this context, it is easy to understand why poaching often occurs when fishing limitations are established in SIDS.

SIDS also exhibit governance complexities that are inherent to their small size. Small nations tend to have a bigger relative size of government, yet small economies mean limited funds for public services including appropriate management of environmental resources. SIDS also have capacity constraints due to a limited pool of talent, exodus of many highly trained/specialized individuals, and the limited ability for specialized positions on the island—meaning that talented individuals often must remain in more general positions even if they would be better suited for a more specialized task.

For example, the Tree Bays national park was recently established along the northern coast of Haiti—with the main goal of increasing fish stocks which are heavily depleted. There is currently little funding for enforcement and therefore fishing is still occurring in the national park. Non-profit organizations are working with the government to raise funds for enforcement of the no-take zones, and to provide alternate livelihoods for fishermen (including honey production, and seaweed and oyster aquaculture). There are also concurrent efforts to help Haitians fabricate charcoal briquettes from sugarcane wood—to relieve the pressure on mangroves that are harvested for wood fuel, and to limit the impacts of industrial development and coral mining. Each SIDS is different and the particular conservation measures that can be successful are likely to vary; yet these types of multi-faceted approaches are likely to lead to the best results.

22.5. Sustainable tourism

Tourism is a major economic sector in many small island states. In many SIDS, the numbers of annual visitors substantially exceed the number of inhabitants (Figure 22.7). In many countries, tourism also makes a significant contribution to employment. For example, the tourism industry provides jobs for 70% of the labor force in the Bahamas, 40% in Malta, and 20% in the Seychelles.

A shift from an economy dominated by fishing to one dominated by tourism can represent a possible avenue to reduce fishing pressure on fragile reef fish stocks and can lead to greater sustainability. However, tourism itself can lead to environmental degradation in some cases, for example via boat grounding, anchor damage and impact of high numbers of scuba divers in fragile environments (see section 20.1.3). Therefore, efforts should be made to limit any negative impacts of tourism, especially as it grows in importance. In some cases, managers set a limit to the number of divers that can visit a given dive site every year. Simply requiring the purchase of a dive permit often reduces the number of divers that dive at a given location, and can help generate revenue for monitoring and enforcement. The installation of mooring balls can greatly reduce potential damage from boat anchors, and requiring the use of holding tanks by vessels visiting the area can limit eutrophication. For example, the Dry Tortugas National Park in Florida prohibits the discharge of sewage by boats, even it is has been treated.

Country	Number of Tourists (000s)[a]	Tourists as % of Population[a]	Tourist Receipts[b]	
			as % of GNP	as % of Exports
Antigua and Barbuda	232	364.2	63.4	73.5
Bahamas	1618	586.4	42.0	75.6
Barbados	472	182.4	39.2	56.2
Cape Verde	45	11.4	11.5	37.3
Comoros	26	4.9	10.6	47.8
Cuba	1153	10.5	8.8	n/a
Cyprus	2088	280.7	24.0	49.1
Dominica	65	97.6	15.9	32.5
Dominican Republic	2211	28.1	13.6	30.2
Fiji	359	45.3	19.2	29.1
Grenada	111	116.2	27.0	60.6
Haiti	149	2.2	3.9	50.5
Jamaica	1192	45.6	31.6	39.8
Maldives	366	130.7	95.0	68.4
Malta	1111	294.7	22.9	28.7
Mauritius	536	46.4	15.7	26.8
Papua New Guinea	66	1.5	2.1	3.0
St. Kitts and Nevis	88	210.5	30.6	63.6
St. Lucia	248	164.7	41.1	66.6
St. Vincent	65	54.6	23.8	45.9
Samoa	68	31.1	19.6	48.8
Seychelles	130	166.7	34.6	52.2
Singapore	7198	209.2	6.2	4.1
Solomon Islands	16	3.7	2.8	4.2
Trinidad and Tobago	324	28.7	4.2	8.3
Vanuatu	49	27.1	19.3	40.9

Figure 22.7. Importance of tourism in Small Island Developing States, in relation to population size, gross national product and exports.

22.6. Final thoughts on conservation in Small Island Developing States

Small island developing states face unique challenges in the conservation of their natural resources. Yet given that they have a very high dependence on natural resources, it is especially critical that they manage their environment sustainably. Effective planning by local governments, partnerships between various organization, and involvement of all stakeholders is likely to lead to the greatest successes. It is also critical that governments around the world agree to take action to limit climate change, which is having a disproportionally high impact on SIDS.