CHAPTER 1

Introduction to Aquatic Ecosystems

The organisms that scientists consider fishes represent the most diverse groups of all vertebrates as there are more species of fishes than of all other vertebrates combined. Fishes occupy diverse habitats such as normal surface waters, great ocean depths exceeding 8,000 m, heated desert pools and caverns that may exceed 40 °C, caves deep in the Earth, under the ice in the Arctic and Antarctic seas, and a variety of other extreme habitats. Adaptation to these habitats has resulted in extreme diversity in fish physiology and anatomy, coupled with differences in foraging patterns and other behaviors. This variability makes it hard to generalize the responses of fishes to local conditions but makes their adaptation to environments very interesting.

There has been much recent debate about what exactly is a fish. Historically, fishes have been considered to include five classes of vertebrates, although the taxonomic status of fossil groups is unsure. Currently existing fishes represent three classes: Agnatha – hagfish and lamprey; Chondrichthyes – cartilaginous fishes including sharks and rays; and Osteichthyes – bony fishes including the most current species. A recent novel by Miller (2021) has examined not only the history of fish biology and systematics but also the evidence that fishes do not represent a single evolutionary line, which means they have not evolved from a single common ancestor. Genetic evidence has recently shown closer relationships between some of the groups of fishes and reptiles, amphibians, and mammals, questioning whether what we call fishes actually are an evolved group or are just an animal life form. Ecologists have included all aquatic living vertebrates with gills, scales, and fins as fishes (although some species have secondarily lost some of these traits), and we will follow that pattern in this book. Certainly cladists (evolutionary biologists that study species relationships) can better explain the evolution of different classes of vertebrates, which may change this higher level of taxonomy. For the purpose of this book, we will continue to consider the three classes of vertebrates listed above as fishes as they share similarities in their life form.

Freshwater organisms are among the most endangered of all species in the world. Analysis by The Nature Conservancy shows that 70% of all freshwater mussels, 50% of crayfishes, and 40% of freshwater fishes are at risk of extinction in the United States (Master et al. 1998). In comparison, approximately 18% of reptiles, 15% of mammals, and 14% of birds are in a similar status. This is particularly daunting when we realize that the highest diversity of vertebrates is found in the classes known as fishes, where there exist at least 32,000 species. This is more than all the species of birds, mammals, reptiles, and amphibians, combined. Such a high fraction of the fauna being endangered among freshwater fishes is due to the various challenges we

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place on freshwater ecosystems, including the use of water for irrigation, industry, and human consumption, as well as the discharge of chemicals into water for disposal. In addition to direct use of water, humans alter habitat by building dams, channelizing streams for ship passage, and building canals. All of these changes in aquatic ecosystems have resulted in major reductions in the fish fauna. There have been a number of evaluations of factors causing animal extinction in various ecosystems. All of these divide the causes of extinction into three main groups of approximately the same magnitude: introduction of exotic species, overexploitation, and habitat disruption. Since fishes are the only major group of organisms remaining that are hunted as food on a global scale, much damage is due to overexploitation, as well as habitat disruption and exotic species. It is no wonder why freshwater organisms, in particular freshwater fishes, are under such threat.

Ecology has a variety of popular, or lay, definitions, but the science of ecology has been well defined and accepted by most scientists. The definition has evolved over time, depending largely on the level of our understanding of ecological interactions. Krebs (2009) provided the best definition: ecology is the study of the interactions that determine the distribution and abundance of organisms. These can be categorized as interactions with physical, chemical, or biological factors in the environment. The purpose of this textbook is to overview the means by which fish distributions and abundances are influenced by physical, chemical, and biological factors.

This book is divided into six main topics that focus on the three major disciplines of ecology: physiological, behavioral, and community ecology. These three disciplinary areas of ecology have boundaries that are intentionally unclear, so some concepts will be presented several times throughout the book.

To appreciate the ecology of fishes, it is important to first understand the habitat in which fish exist – the aquatic system. This chapter reviews living in the water, the characteristics of fish, and aquatic ecosystems, emphasizing several systems that are more familiar. A key theme throughout this book (highlighted in this chapter) is that the environments in which fish exist differ in two important dimensions: the distribution of temperature in time and space, and the distribution of food in time and space.

Properties of Water

Water has a number of physical properties that are challenging to organisms living in the water and yet promote life within the water because of the long-term stability of water conditions. Water is one of the few compounds that is liquid at ambient temperatures and has high viscosity and surface tension. This means that movement through the water is difficult, and diffusion across the water surface level is limiting. Animals moving within the water must overcome this high viscosity in order to shoulder their way through this dense and difficult medium. The maximum density of water occurs at 3.9 °C, which is unusual for liquids because the freezing point of water is 0 °C. The fact that water does not freeze at its maximum density allows water to exist under the ice in winter conditions and is key to sustaining life in many aquatic ecosystems. Water also has an extremely high heat capacity. It requires 1 kcal of energy to increase 1 kg of water by 1 °C. In fact, this demonstrates the importance of water to humans because many of our characteristics in physics are based on water, such as the Celsius scale of temperature and the caloric scale of energy. Because of this high specific heat, water does not change temperature very easily and remains relatively consistent over time. As a result, living in the water is actually living in a moderate thermal condition, where it is neither extremely cold nor extremely hot. In fact, fishes utilize this thermal characteristic to specialize within even narrower ranges within the typical temperatures of surface waters.

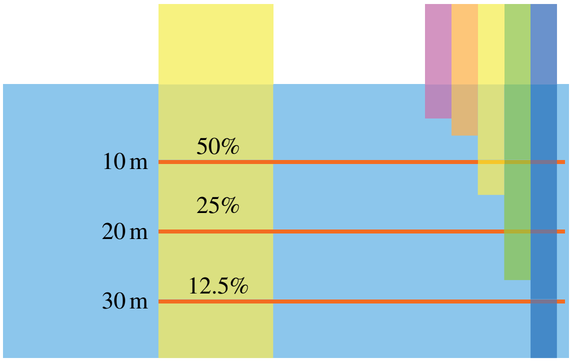

FIGURE 1-1 Schematic of penetration by different wavelengths of light into freshwater.

In addition to the characteristics above, water has several other characteristics that are important to life in the water. There is very low gas concentration in water. The atmosphere contains 21% oxygen and is relatively light and reasonable to ventilate. In contrast, water at saturation contains maximum level of 14.6 mg of oxygen for every liter of water. If we equate the two, 1 kg of air would contain 0.23 kg of oxygen, while 1 kg of water contains only 0.0000146 kg of oxygen, over 5 orders of magnitude less than the same mass of air. Clearly, this low oxygen concentration results in difficulties passing enough water across respiratory surfaces to allow animals living in water to attain high metabolic rates. This is one of the major specializations in fish – that of extracting oxygen from water at low oxygen concentration.

Water is known as the universal solvent, which means almost all materials can dissolve in water. This is both a benefit and a difficulty for aquatic life as many materials from the land and industrial processes dissolve in the water and influence physiology of fish breathing water containing that material. This universal solvent property is important in the discharge of waste as assimilation by natural ecosystems is one of the ways humans dispose of sewage. At the same time, waste dissolved in water can cause significant damage to aquatic species living in the region receiving wastes.

Finally, light is absorbed rapidly with depth in water and differentially depending on the wavelength of the light. Maximum light transmission in distilled water is approximately 100 m, and only the blue wavelengths of light penetrate to this depth. In contrast, infrared wavelengths, which include heat, only penetrate to a very shallow depth – usually less than 1 m – and there is differential distribution of wavelengths between those two extremes (Figure 1-1). These penetration depths are achieved only in very clear water; once water contains dissolved materials, there is considerably less light penetration as well as different penetration for various wavelengths. Given the oceans have a mean depth of 4,000 m, most of the ocean is below the level of light penetration, and organisms living there have difficulty using eyesight as a means of orientation.

What is a Fish?

Given the constraints placed upon fish by living in aquatic habitats, the characteristics of fish vary dramatically to allow locomotion, respiration, and feeding in this medium. A fish is an aquatic vertebrate, that is, fish spend most of their life cycle in water and belong to the phylum Chordata (chordates), subphylum Vertebrata. There are fishes that can remain out of water for considerable periods of time, utilizing modified lungs to breathe from air under moist conditions. All chordates have a notochord, which is a flexible nerve cord that extends the length of the body. In most fishes, this notochord is surrounded by bony or calcified tissue to protect it from damage and allow for more vigorous muscle action. Fishes have 5–7 gill arches, which vary in complexity and range, from each gill arch having a separate opening to existence of one opening under the operculum for more advanced fishes. There are many fishes that have lungs, which evolved into swim bladders in more advanced fishes. Some of the more advanced fishes have secondarily developed lungs as a means of living in poorly oxygenated environments or for respiration while transporting themselves across land. Fishes have fins to help propel themselves through the water, including medial fins along the middle of the body, a caudal fin at the posterior extreme, and paired pectoral and pelvic fins. Most fishes also have scales to protect their bodies; these have evolved over time from being absent in early fishes, to very stout scales, to more flexible and lightweight scales in advanced fishes. Finally, fishes have a two-chambered heart, from which the blood is circulated through the gills to the body and then returns to the heart. All of these characteristics vary among groups of fishes but are common characteristics of the three classes of vertebrates considered to be fishes.

The details above indicate that there are many challenges to being a fish. Water is a dense and viscous medium; thus, swimming through the water utilizes much muscle power and fin activity. The low concentration of dissolved gases means the gill structure and function must be efficient in order to allow for high rates of metabolism. The high thermal capacity of water means that most fishes are ectothermic and poikilothermic, or what we refer to as cold blooded. Their body temperature will vary with the temperature of water, and there is generally no difference between their body temperature and water temperature. In addition, the conditions are generally dark and difficult to see in aquatic systems. Some advantages of being a fish include buoyancy that can be maintained by simple changes in swimming motion, inflation of swim bladder, retention of lipids in the body, and other such characteristics. Since fishes live in the water, it is never too hot or cold, and few fishes have developed a system of insulating their body from extremely cold external conditions. Water transmits chemicals and sound from long distances, and thus, senses of smell, hearing, and taste are acute and can occur over long distances, allowing fish to utilize these senses very efficiently. In addition, fishes can sense movement in the water and water currents and are capable of adjusting to these through the lateral line sense. These senses are also effective in some species of fish for finding prey or escaping predation.

Lentic Systems

Much of our knowledge of aquatic ecology comes from work in temperate freshwater ecosystems. This is not due to any special importance of these ecosystems, but more to their proximity to scientists and institutions interested in aquatic ecology. This section on fish habitats will begin with details on temperate lakes. The emphasis on aquatic systems has broadened to include tropical and Arctic freshwaters, as well as marine ecosystems, but the preponderance of ecological studies still deals with organisms living in freshwaters of the temperate zone.

Most people are familiar with standing water ecosystems, that is, lakes and ponds. They are termed lentic because the movement of water is relatively unimportant in the ecology of the system. The kinds of habitats available in lentic systems are related to lake types, which are determined by the internal processes in lakes and in watersheds where lakes are located. The largest differences within temperate lakes occur during midsummer when productivity and thermal processes vary most dramatically in regions of a lake.

Vertical Stratification of Temperature

One interesting seasonal process in temperate lakes occurs because of the physical relationship between temperature and density of water. Water that is colder or warmer than 4 °C floats on top of this cool and heavy water. As water warms, the warmer water floats on the surface of colder water. This process of vertical segregation of water by temperature is termed vertical stratification. The classic stratification pattern of an inland lake varies with season (Figure 1-2). During winter, ice covers the lake, and immediately below the ice, temperatures between 0 and 4 °C occur. Water at 4 °C is at the bottom of the lake because of its density, and the amount of water between 0 and 4 °C depends on the rate of cooling that occurred in the lake prior to freezing.

In spring, warming by the Sun allows the ice to melt on the lake, and wind blowing across the surface of the lake mixes water from top to bottom in most lakes. During this time, lakes are isothermal, having the same temperature from top to bottom. Also during this time, oxygen is mixed throughout lakes, and nutrients and other chemicals that might be tied up in bottom sediments or in deep water are redistributed to the surface.

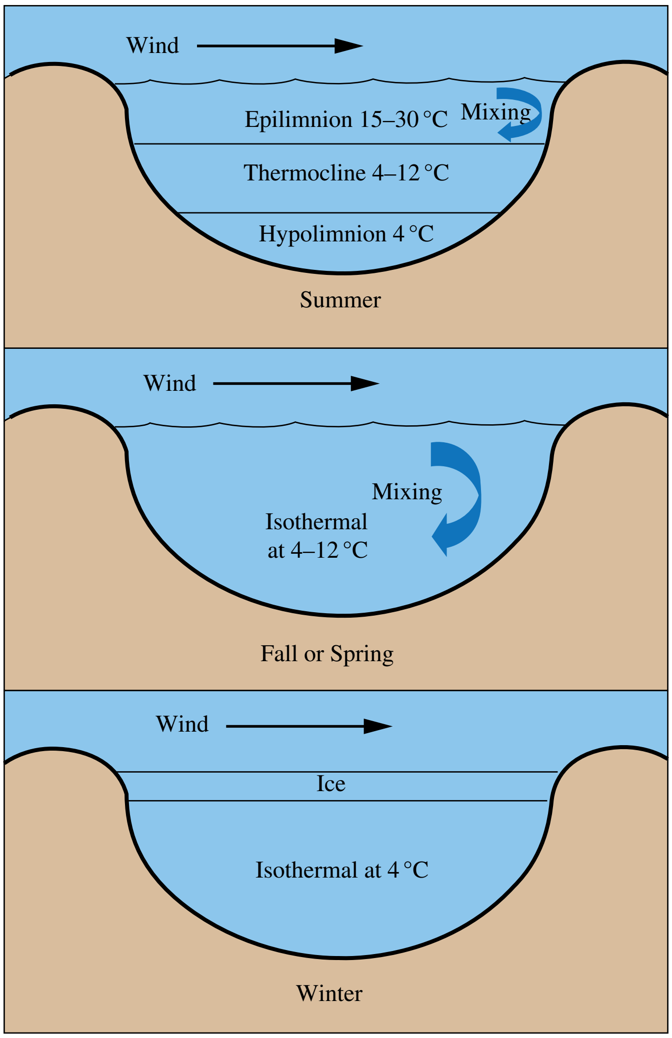

FIGURE 1-2 Diagram of a lake and its zonation by depth during climatic seasons.

Two other processes affect temperature stratification of lakes: the absorption of light within a lake and circulation of lakes by wind. Wind mixing occurs as wind blows across the surface of lakes and causes turbulence. The amount of wind mixing depends on the length (fetch) of lake exposed to wind, the wind intensity, and whether the nearby topography is hilly or flat. Wind mixing dramatically varies among lakes due to local and regional geographic effects. During warming in spring, all heat is absorbed at the surface and is spread throughout the lake by wind mixing. During spring, this mixing often occurs top to bottom and causes isothermal conditions. However, as warming at the surface continues into summer, surface water becomes much warmer and lighter than deep water, and the lake stratifies into three zones. The epilimnion, which is the surface area that is mixed completely by winds, has the warmest temperature in the lake. The metalimnion, or thermocline, has temperatures that dramatically plunge from near surface conditions at the top of the thermocline to near 4 °C at the bottom. In fact, the thermocline is defined as the region in which temperature declines 1 °C for every meter in depth. The hypolimnion, or deep water, has a constant temperature of 4 °C. As stratification proceeds, wind cannot continue mixing between the density layers in a lake; therefore, all wind mixing occurs only at the surface. The epilimnion remains completely mixed, the metalimnion partly mixed, and the hypolimnion receives no mixing throughout the course of a stratified summer.

As the year progresses to fall and air temperature drops, the temperature of surface waters declines until another isothermal condition occurs, when wind can blow on the lake and cause it to mix again. This period is called fall turnover; the lake is entirely mixed at this time, and water conditions are isothermal from top to bottom.

Obviously, the extent and significance of the seasonal cycle for any lake largely depends on climate and geography. Winter conditions may not exist in semitropical lakes, and summer stratification may not occur in Arctic lakes. Additionally, whether the zonation of lakes into three habitats occurs may depend on the depth and surface area of the lake. Relatively shallow lakes may not completely stratify. However, this classic stratification pattern occurs in many lake systems, modified by local conditions.

Lake Productivity

In addition to temperature, primary productivity dramatically varies among lakes, from an extreme of an oligotrophic or lowly productive lake to a eutrophic or highly productive lake. Primary production is the elaboration of new plant material due to photosynthesis, and it can be measured by carbon fixation or oxygen evolution in the water column.

Productivity cycles in oligotrophic lakes are partly limited by morphological characteristics of the lake and partly by internal nutrient processes. Oligotrophic lakes are generally deep and V-shaped. There is limited littoral (nearshore) habitat, and volume of the hypolimnion is most commonly much greater than volume of the epilimnion. Most oligotrophic lakes occur in areas in which nutrient runoff from the watershed is relatively low and sediments in the lake are minimal, so there is low nutrient availability. The main nutrients necessary for primary production – phosphorous and nitrogen – are in very limited supply. There is a very low rate of primary production in oligotrophic lakes, and similarly low fish production because of the limited nutrient availability. Since respiration by plants and animals is relatively low, oxygen is usually available at all depths, even during summer stratification. Oligotrophic lakes comprise the deep blue mountain lakes many people consider classic lakes, yet in reality, they have limited primary and secondary productivity. Secondary productivity is the elaboration of new animal tissue due to consumption of food.

The other extreme in lake productivity is a eutrophic lake. Eutrophic lakes have much larger littoral areas than oligotrophic lakes. These lakes are usually shallow, bowl-shaped basins. The epilimnions of eutrophic lakes are much larger than the hypolimnions; in fact, many eutrophic lakes do not have hypolimnions. Lake sediments are muddy and occasionally have covered lake bottoms that were formerly deep hypolimnetic waters. These sediments are high in nutrients. Eutrophic lakes have much higher primary production, particularly in phytoplankton, because they have higher nutrient concentrations than do oligotrophic lakes. High nutrient availability and abundance of organisms lead to larger oxygen demand, and oxygen may become limiting in the hypolimnion of a eutrophic lake during summer or winter stratification. Oxygen becomes limiting because these lakes have low light penetration into the hypolimnion, where much decomposition and respiration occurs.

The identification of lakes as either eutrophic or oligotrophic is rather arbitrary. Obviously, there is a continuum of lakes across these two extremes, and many systems of classification are used to distinguish different categories of lakes. For example, the trophic state index (Carlson 1977) evaluates the lake's relative status on a scale of 1–100, where 1 would be highly eutrophic and 100 highly oligotrophic. This index uses phosphorus concentration, chlorophyll *a* content, or Secchi disk depth as indicators of productivity. Phosphorus is commonly the most limiting nutrient in a lake, while chlorophyll *a* is a measure of phytoplankton biomass, and Secchi disk depth is related to water transparency, and therefore inversely related to chlorophyll *a* content.

The characteristic of most importance to ecology is that the interaction between temperature stratification and oxygen availability allows for much habitat segregation with depth in a lake system. For example, an oligotrophic lake may have warmwater fishes, such as bass and bluegill, in the epilimnion, coolwater fishes, such as perch and pike, in the thermocline, and coldwater fishes, such as trout, in the hypolimnion. These fishes can survive through summer near their optimal temperatures for growth by vertically segregating because oxygen is available at all depths in the lake. This segregation is very common in the Laurentian Great Lakes. The stratification of habitat vertically allows coexistence of different thermal guilds of fishes in the same water body. It may be limited in smaller inland lakes by low productivity and food availability of oligotrophic systems.

In comparison, a eutrophic lake might not produce this "two-story" or "three-story" type of fish community. A eutrophic lake with an anoxic hypolimnion will contain no trout because trout cannot survive high summer temperatures at the surface or low oxygen levels at depth. Similarly, eutrophic lakes with anoxic or poorly oxygenated thermoclines may not have coolwater fishes. Due to the high productivity of eutrophic lakes, energy is available for a much higher standing crop of fish if there are adequate physical conditions.

The combination of summer stratification and oxygenated conditions allows for a more diverse fish fauna in a given lake. At any time, lakes can be categorized on the basis of their oligotrophic or eutrophic conditions, but a lake proceeds from an oligotrophic to a eutrophic state over time. An oligotrophic, or relatively new lake, has low nutrient availability, low primary production, low decomposition, and low sedimentation, and remains in that state for some time. Eventually, erosion from the watershed and internal processes in the lake increase sedimentation and nutrient concentrations, which boost primary production and further sedimentation, and eventually result in filling in of the lake. Over time, oligotrophic lakes become eutrophic lakes by these erosion and internal processes.

This book emphasizes the relationship of fishes with temperature and food, key factors driving metabolism of fishes. Brown et al. (2004) have formalized the interactions between metabolism and size into the metabolic theory of ecology, where these defining characteristics of organisms set the stage on which animals perform, and can reflect processes in populations and communities as well. The primary production and trophic (food web) relationships of various habitats within a lake vary significantly. In the epilimnion, the basis for most productivity is phytoplankton. Phytoplankton, or small floating algae, dominate the plant community of most lakes and are limited by sunlight, temperature, and nutrient availability. Phytoplankton produce tissue through photosynthesis, and they are utilized by bacteria or herbivorous zooplankton and fishes. The production of herbivores must be lower than the productivity of phytoplankton because of the inefficiency of biological processes. Carnivores, feeding on herbivorous animals, are even lower in productivity, and this sort of a trophic pyramid follows the typical pattern of declining productivity with increasing trophic level.

Phytoplankton have very rapid birth and death rates and very high individual rates of productivity per unit biomass; therefore, the biomass of phytoplankton in a lake at any given time is relatively low. Similarly, bacteria with rapid life cycles also have relatively low biomass per unit of production. Herbivores and carnivores, on the other hand, have higher amounts of biomass maintained per unit of productivity. The trophic pyramid of a lake epilimnion based on biomass may be inverted, indicating a lower biomass of phytoplankton compared to the biomass of herbivores and carnivores. This sort of inverted pyramid indicates that food availability at the lower trophic levels is very much related to primary production within the phytoplankton rather than to the standing crop of phytoplankton present.

In the hypolimnion of a stratified lake, photosynthesis becomes unimportant because light does not penetrate with sufficient intensity into the depths to allow much primary productivity. The basis for nutrient availability is detritus in the hypolimnion, and the primary consumers are the detritivores. Detritus is dead and decaying animal and plant tissue, and detritivores are animals that feed upon such material. Within a hypolimnion, there is a much higher base in detritus than there are detritivores or carnivores, whether measured on a productivity or biomass basis.

In comparison with the epilimnion of an oligotrophic lake, a highly eutrophic lake has much macrophyte production within the littoral zone as well as phytoplankton production in the pelagic zone (the open water zone not influenced by the lake bottom). Macrophytes are rooted vascular plants. Compared to phytoplankton, macrophytes are relatively poor food sources for most herbivores. In fact, many herbivorous invertebrates that live on macrophytes actually feed upon periphyton or algae attached to the surface of these macrophytes.

In summary, combinations of physical processes, nutrient availability, and oxygen availability influence the vertical profile of the lake and the distribution of plants and animals within the lake. This distribution affects the source and sink of energy within a lake and therefore the rate of productivity as well.

Lotic Systems

In comparison with freshwater lakes, flowing freshwater systems generally show very limited, if any, stratification. Lotic, or flowing water systems, commonly have longitudinal zonation rather than vertical zonation. Physical and chemical conditions within streams are constant with depth because of the movement and mixing of water. The longitudinal zonation of streams occurs along a continuum from a headwater area to a very mature area near the mouth of most rivers.

Stream Types

Water inputs to headwater streams include runoff from snow melt or precipitation as well as ground water. Runoff may vary dramatically with season due to the snow melt or irregularity of rain. Often these water sources, through snow melt or ground water, are relatively cold, and water may warm during day due to insolation and cool during night due to additional runoff. This may produce large diel (24-hour) fluctuations in temperature at a given site within a headwater stream. Since the runoff for headwater streams occurs over a limited catchment area, there are few nutrients within the stream, and most of these nutrients are from external sources, such as erosion. Headwater streams tend to segregate longitudinally into riffles and pools. Riffles are quick-running areas with rapid currents and usually rocky substrates. Pools are deeper, slower-moving waters with more sedimentation of smaller particle sizes. Riffles and pools may be separated by runs, which are geomorphic units sharing some of the characteristics of both riffles and pools – deep with quick flow but not as turbulent as riffles.

In contrast with headwater areas, a more mature stream receives most of its water from other tributary streams rather than direct runoff from the nearby watershed. These tributary streams contain water that has been exposed to terrestrial conditions for some period of time and are often warmer and more stable in temperature on a diel basis, although they can fluctuate seasonally with air temperature. As water continues to flow into the river systems, more of the nutrients spiral or cycle internally, rather than being added from external sources, and many nutrients are retained in sediments. Mature streams, rather than having clearly defined riffles and pools, tend to have meandering zones, with slower water on the inside bend of a meander and faster water on the outside. This causes segregation of substrate types and flows across the stream rather than in a longitudinal pattern. This meandering pattern of a more mature stream is typical of most flood plains.

Most streams have oxygen conditions near saturation as oxygen is continually diffused into the moving water and mixed by physical motion. Since motion is important, plankton communities (which drift in water) are also uncommon in streams and rivers. Primary production for a youthful stream is mainly based on periphyton and is combined with detritus from external sources as the primary inputs of energy to the trophic pyramid. Many temperate streams rely on detritus from annual leaf fall as the major input of energy and have large communities of shredding insects that feed upon leaves that accumulate in the steams from deciduous trees, as well as on periphyton or attached algae that grow on the leaf substrate. External detritus and periphyton form the basis of the food chain, which usually flows through benthic (bottom dwelling) insects, or other benthic invertebrates, and ultimately to carnivores. A more mature stream has periphyton or detritus, produced by internal processes rather than external loadings, forming the basis of primary production.

Fish Communities in Streams

Much as stream types zone longitudinally in physical and biological conditions from headwater to mouth, fish communities in streams also change longitudinally. The zonation of streams has been illustrated by data from European and North American fish communities. Headwater areas of streams are the trout zones, where coldwater fishes such as trout predominate. Mid-elevations of streams, where stream velocity has slowed and temperatures are warmer and more constant on a diel basis, include fishes such as the grayling and minnows. The lower reaches of streams, which are more lake-like, are considered the bream zones, where species such as sunfishes and catfishes predominate. Thus, stream fish communities and ecosystems vary with elevation from headwater to mouth. Obviously, there are areas of overlap among these different communities at the edges of the zones, but these categories are often fairly distinct.

Marine Systems

The marine environment is extremely diverse compared to the freshwater environment because oceans continuously span a variety of climatic as well as physical areas. Over 70% of the world's surface is covered by oceans, so obviously the largest available habitat for animals and the largest area for fish habitation is the ocean. The open pelagic zone of the ocean has some characteristics similar to a freshwater lake. It commonly stratifies with temperature although the stratification may be seasonal; it has oxygen and primary production limited by light penetration, and it has primary production due to phytoplankton. The pelagic zone differs from a freshwater lake in other ways, mostly in depth. The average depth of the ocean is about 4,000 m, so most of the ocean water is at a depth exceeding the penetration of light. The epipelagic zone, or the shallow area of the ocean, is a limited habitat in terms of area (at least among oceanic habitats) but is the source of virtually all primary production, as well as much of the fish production in the oceans.

In addition to the pelagic zone of the oceans, the nearshore environment also differs significantly from that of lakes. The largest difference in the nearshore environment is in the importance of tides and intertidal zones to the production and distribution of plants and animals. Tides are caused by the force of gravity from the moon and occur differently in various regions of the world but result in diurnal changes in water level. As the water level changes, some attached plants and animals are exposed to air during a portion of the day and to water during another portion of the day. Tidal heights also vary at different times of the month, so within extreme zones there may be exposure to air or water for only a short period each month. Many attached algae grow in the intertidal zone and are the basis for much food production for the native fishes and invertebrates.

Two other marine ecosystems addressed several times in this book that receive specific emphasis are coral reefs and upwelling areas because they differ from typical lake systems in important ecological processes. A brief overview of each is important at this point because fishes occupying these conditions are mentioned sporadically throughout this text.

Coral Reefs

Coral reefs are ecosystems limited geographically to a zone of 30° north or south of the equator. They occur in tropical, relatively low productivity areas and can grow to a depth of 50 m. The physical basis for coral reefs is the coral organism itself, which secretes a hard calcareous skeleton that becomes the structure of the reef after coral polyps themselves die. The calcareous material is secreted in relationship to growth of the coral polyps, so there is much structural complexity. A wide variety of fishes occurs on coral reefs, and there are more fish species per unit area associated with coral reefs than with any other ecosystem. These fishes also have developed a wide range of feeding specializations.

The coral reef ecosystems, while existing in waters low in nutrient availability, actually have a high degree of primary production because symbiotic zooxanthellae coexist with the corals. The symbiotic algae can fix nitrogen for photosynthesis, and surplus energy produced by them is available for coral nutrition. These symbionts, plus the attraction of wider-ranging animals to the reef, result in high productivity and biomass of organisms occurring on coral reefs. Coral reefs are rather isolated habitats spatially and usually do not cover large geographic areas.

Upwelling in the Ocean

Upwelling systems occur when the cold bottom waters of the ocean move upward and mix with surface waters. This generally occurs where currents move offshore, taking surface waters offshore as well. Upwelling areas bring up cold, nutrient-rich waters and are characterized by high primary productivity due to nutrient enrichment and high fish yield due to food availability. Deep oceanic waters are nutrient rich due to decomposition in that zone but generally do not return these nutrients to shallow waters during mixing. High pelagic fish production occurs due to upwelling of nutrients. Many of the major fisheries of the world occur in these upwelling zones, including the coasts of Peru and California. Upwelling zones are also important features of large lakes but are transient in location due to the general lack of consistent current patterns.

Summary

Ecology is the study of the interactions that determine the distribution and abundance of organisms. Several major factors in aquatic environments vary, including temperature, oxygen, and food. These factors vary with habitat type and may affect fish distribution and abundance. Some habitats in lakes, streams, or coral reefs may have large fluctuations in conditions daily or seasonally, while others experience relative consistency. The absolute level of primary productivity, as well as seasonal timing of production, strongly affects the distribution and abundance of animals. The remainder of this book addresses some of the physiological effects of these factors on fish distribution and abundance as well as the means by which fishes adjust, both behaviorally and in terms of population changes. It is important to keep the physical nature of the habitats in mind throughout the following chapters.

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